Ruth Nielsen, Steffen Lundsteen and Juliet Brodie

Seaweeds of Denmark

Red algae (*Rhodophyta*)

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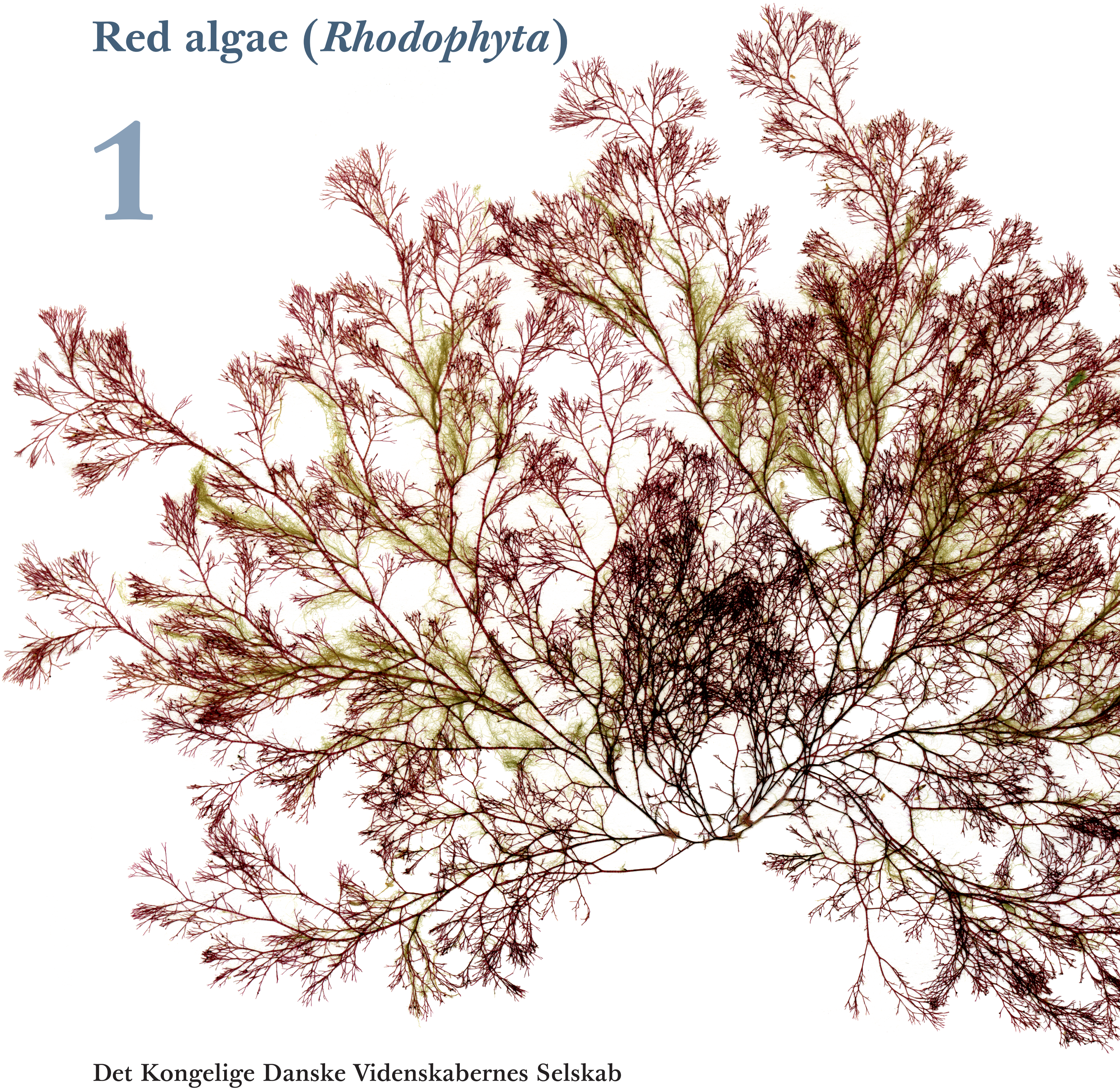

Det Kongelige Danske Videnskabernes Selskab
The Royal Danish Academy of Sciences and Letters

Seaweeds of Denmark Volume 1

Red algae (Rhodophyta)

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 1
Red algae (Rhodophyta)

By
Ruth Nielsen, Steffen Lundsteen and Juliet Brodie
Bangiophyceae: Agnes Mols-Mortensen
Corallinophycidae: Susse Wegeberg
Map of collection localities: Karl Gunnarsson
English translation: Ruth Nielsen and Juliet Brodie

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Illustration on front cover: *Ceramium* sp.
Illustration on back cover: *Callithamnion corymbosum*

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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

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Volume 2

Introduction

The first impression many people will get of Danish seaweeds is piles of drift seaweed on sandy beaches or maybe an unpleasant raft of drifting algae to wade through at shallow water before reaching clear seawater for a swim further out. Maybe it is the algae growing on a harbour jetty, or perhaps individual species of drift seaweed on a sandy beach, where it is possible to realize how beautiful these organisms really are.

A closer look reveals the diverse range of colours and symmetrical branching patterns. This may create a desire to take the seaweeds home to find out more about them, how to tell them apart and what they are named. This book will answer these questions and will hopefully be of use and a pleasure for interested naturalists as well as for trained phycologists.

All the marine red, brown and green algae recorded in Danish waters are mentioned in this book and can be identified from the text, identification keys and illustrations. It is possible to recognise some species with the naked eye by comparing them with the illustrations, but for others it is necessary to look more carefully and use a microscope for a reliable identification. For some species, it is only possible to identify them when they are well developed and bear reproductive structures.

The content of the book is based on the collections maintained in the algal herbarium, Natural History Museum of Denmark, University of Copenhagen.

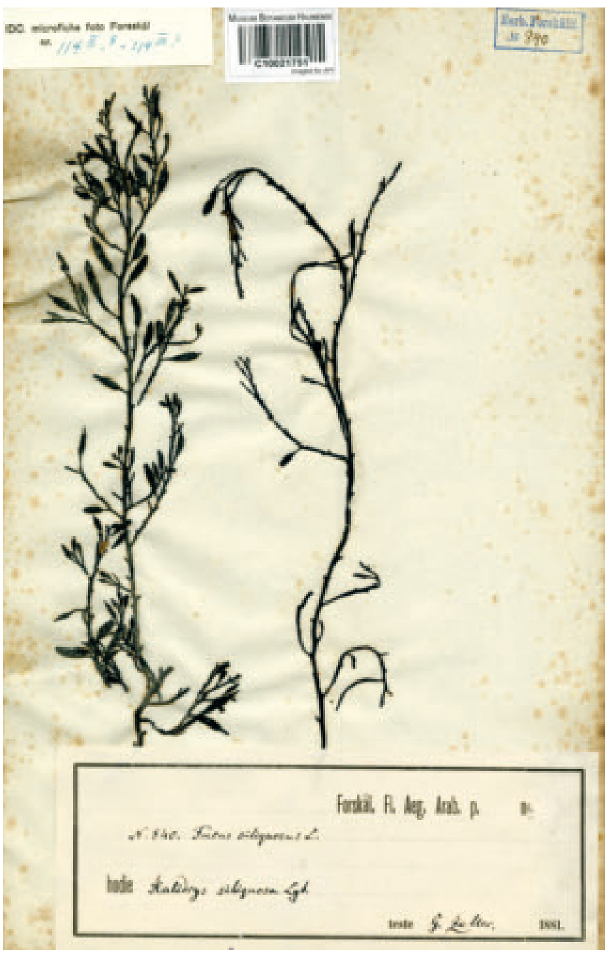
Furcellaria lumbricalis with different red algae. Lysegrund, 10.5 m, 19.1.1997. Scale 2 cm.

The Herbarium

Interest in the Danish marine algae dates back many years as documented by herbarium specimens in the algal herbarium, Natural History Museum of Denmark. The oldest algae in the herbarium are a pair of charophytes collected in 1656.

An early collector, Peter Forsskål (1732-1762), is best known for his participation in the expedition to the Arabian countries (1761-1767). He collected Danish seaweeds at the beginning of the expedition when a big storm forced the ship to stay in Elsinore. These algae from January and February 1761 are maintained in the algal herbarium.

There are big collections from North Funen, starting when Niels Hofman Bang (1776-1855) was the owner of the Hofmansgave estate. He was very interested in natural history and especially in the algae. He employed Hans Christian Lyngbye (1782-1837) as a private tutor for his children in 1812. Lyngbye was educated as priest and, like Hofman Bang, was interested in botany. He was also a skilful illustrator and made many drawings of the algae they found and gained a great deal of knowledge about them. The subject for the prize essay of the University of Copenhagen in 1816 was a systematic survey of all the algae known in Denmark up to that time. It was answered so well by Lyngbye that he was awarded the prize and encouraged to get the essay published. The monumental work about the Danish algae, '*Tentamen*



Forsskål's herbarium sheet of Brown Sea Oak (*Halidrys siliquosa*). Elsinore, January 1761.

Lyngbye's herbarium sheet of Delicate Bush Weed (*Callithamnion corymbosum*) with small capsules for the algae, pressed on paper or mica (arrow), and a drawing.

Niels Hofman Bang (1776-1855), owner of the Hofmansgave estate. From the archive, Natural History Museum of Denmark.

Hydrophytologiae Danicae', was published in 1819, with support from the king. It includes algae from the Faroe Island, Greenland, Iceland and Norway, countries which were included in Denmark at that time. The original detailed and very beautiful colour drawings are maintained in the Natural History Museum of Denmark and Lyngbye's algal herbarium is one of the treasures at the museum. Lyngbye described many new species and genera, which are documented with specimens in the collection. These original specimens (types) are of great value. Scientists all over the world use them to ensure a precise understanding of a species and for comparison with modern collections. The red algal genus *Bangia* was created by Lyngbye and named in honour of Hofman Bang. Lyngbye himself is honoured by the name of a genus of blue-green algae, of which *Lyngbya aestuarii* Liebman ex Gomont is a common species, and very frequent in saltmarshes.

Caroline Rosenberg (1810-1902) also came to Hofmansgave and became interested in the algae. She grew up in Altona in Germany and went to Hofmansgave as a foster daughter a few years after the death of her parents. There are innumerable sheets of herbarium paper with Caroline Rosenberg's pressed algae in the algal herbarium, Natural History Museum of Denmark. They are all very skilfully and aestheti-

Caroline Rosenberg (1810-1902). From the archive, the Natural History Museum of Denmark.

Herbarium sheet of Purple Siphon Weed (*Leptosiphonia fibrillosa*) carefully arranged by Caroline Rosenberg.

cally prepared and carefully labelled with her beautiful handwriting. She must have been very diligent. Caroline Rosenberg had an extensive correspondence with Danish and Scandinavian botanists and phycologists and sent pressed algae to them. Notes and labels on some of the herbarium sheets show that these specimens had belonged to various botanists and were later donated to the museum. Some of Caroline Rosenberg's herbarium specimens are recognizable in floras, for example, the charophyte *Lamprothamnium papulosum* in *Florae Danicae* 1867 fasc. 46, Tavle 2745 (as *Chara alopecuroides*) is a copy of Caroline Rosenberg's pressed algae, which is in the algal herbarium, Natural History Museum of Denmark.

The person who has contributed most to the knowledge of the Danish seaweeds was Janus Lauritz Andreas Kolderup Rosenvinge (1858-1939). He undertook extensive collections in Danish waters both at shallow water from the shore and at greater depth with tools such as seine and triangular dredge, which were towed by boat. The triangular dredge consists of an iron-frame with coarse teeth which scratch algae off the substrata. The loose algae are collected in a net bag that is attached to the frame. Rosenvinge made most of his collections from deep water in the years 1891-1895, where he had public support, but he continued collecting for many years. He gave the collected algae consecutive collecting numbers, and the last number in his protocol is 11324 from the summer of 1934. These collections are kept in the algal herbarium, most of them dried on herbarium sheets. The collection numbers are on the sheets, often supplemented with a code of two letters indicating the place of collection. The letter codes are also present on his maps and in his protocols. Rosenvinge probably had the ambition to write about all Danish seaweeds. He

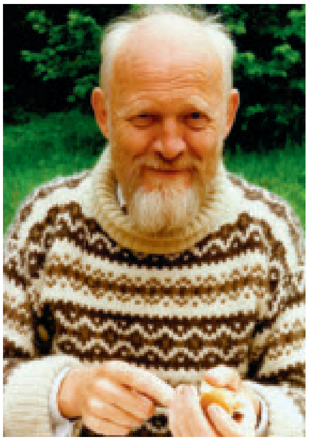
Janus Lauritz Andreas Kolderup Rosenvinge (1858-1939), photo 1908. From the archive, Natural History Museum of Denmark.

Søren Lund (1905-1974). Studied Danish brown algae. From the archive, Natural History Museum of Denmark.

Henning E. Petersen (1877-1946). Studied Danish Pincer Weeds (*Ceramium*) and Gut Weeds (*Ulva*, formerly *Enteromorpha*). From the archive, Natural History Museum of Denmark.

Lisbeth Mathiesen (1928-2009) on board the boat 'Sømusen' 1980. Photo by R. Nielsen.

Tyge A. Christensen (1918-1996). On a picnic, 1995. Photo by U. Søchting.



finished the study of the red algae and published a paper on selected brown algae. He studied the algae with care, and his descriptions and illustrations are so careful that it is still surprising how many details he noticed and described. The Danish red algae were described in 'The marine algæ of Denmark, Rhodophyceæ', published in four parts in 1909-1931. Additions and an account of the geographical distribution in Danish waters were published in 1935. His paper on brown algae was published in 1935, with contributions by Søren Lund (1905-1974). A grant from the Carlsberg Foundation made it possible to employ Søren Lund as an assistant and he continued the work on the brown algae even after the death of Rosenvinge. 'The marine algæ of Denmark, Phæophyceæ' was published in four parts in 1941-1950. This work includes many of the Danish brown algae, but unfortunately not all of them and only a few of Rosenvinge's collections of green algae have been studied in detail.

Henning E. Petersen (1877-1946) dealt with the distinctive and difficult genera Banded Pincer Weeds (*Ceramium*) and Gut Weeds (*Ulva* (*Enteromorpha*)). He published papers on Banded Pincer Weeds (*Ceramium*) in 1908, 1911, 1929, and also contributed to Rosenvinge's 'The marine algae of Denmark' (1923-24). A paper about Gut Weeds (*Ulva* as *Enteromorpha*) was published in 1939. Henning E. Petersen tended to split the genera, particularly Banded Pincer Weeds (*Ceramium*), into many species, subspecies and forms. A lot of his new species were considered identical with other species for many years, but Cimbri Pincer Weed (*Ceramium cimbricum*) was confirmed to be a distinct species in later studies (Rueness, 1992).

Later floristic studies in selected areas have contributed to algal knowledge, including their seasonal variation and distribution on the shore. These studies include those of Ebeltoft Vig (Andersen, 1983); Tuborg Havn (Kristiansen, 1972); Saltholm (Kristiansen, 1978a); Stege Nor (Lund, 1934); Vorupør (Lund, with collections in 1934, but still not worked on in detail), the Limfjord, Mariager Fjord, Randers Fjord, Åbenrå Fjord and Aarhus Bugt (Lisbeth Mathiesen with students in 1957-1997), Nordre Rønner, Læsø, (Nielsen, 2005b). The algae from all these studies are documented with herbarium specimens maintained in the algal herbarium, Natural History Museum of Denmark.

The algal herbarium also maintains algae of particular groups, such as the extensive collections of *Vaucheria*, a genus of Tribophyceae studied by Tyge A. Christensen.

The University of Copenhagen has held summer field courses in marine biology since 1890. The field courses took place in different localities to begin with but from 1926 onwards, it was held in Frederikshavn in collaboration with the local technical school (Tendal, 2011). The teaching took place in a few of the classrooms whereas others were made into dormitories for the students. A small laboratory and storage room in the basement were available for the biologists all year. There was also collaboration with the Danish Navy in several years in the late 1950s, who assisted

The marine biological laboratory, Frederikshavn. Most of the algal teaching took place in the white house. The tall building behind was the former technical school which became the zoological house.

with collections from the Northern stone reef Herthas Flak which was difficult to locate. This is reported in an exchange of letters between the assistant professor J.B. Hansen and officers in the Navy in 1956 and 1957. Copies of the letters are at the Natural History Museum of Denmark. The marine biological laboratory was thriving in the middle of the 1970s, with several courses over the summer month. All biology students from the universities in Copenhagen and Aarhus attended a three week-long obligatory course in marine biology. At that time, the University of Copenhagen had taken over the buildings in Kirkegade 8 and Kirkegade 6, Frederikshavn, which previously were the technical school and the rectory. In addition, a new build house was in Tordenskjoldsgade 13, where most of the teaching in algae took place. At that time, there were sleeping facilities for about 50 people and four well-appointed classrooms. The collections took place using local fishing boats for many years. The fishermen were extremely knowledgeable about the sea bed and were able to find the localities where each day's collections were planned to take place using echolocation and sight lines to land. It could be difficult to find the places in misty weather, especially the distant Herthas Flak. Gradually it became difficult to find interested fishermen with boats of a suitable size and the marine biological laboratory obtained its own boat, 'Sømusen', in 1980.

The students obtained knowledge about organisms and learnt how to undertake fieldwork. In addition, considerable knowledge was obtained of interesting localities and the marine environment in general for the Northern Kattegat. Changes in species composition over the summer and through the years were followed very carefully, and this is documented by many herbarium specimens that were collected and prepared by the students, the teachers and visitors. Many of the herbarium sheets have been given to the algal herbarium, Natural History Museum of Denmark over the years. Unfortunately, the marine biological laboratory in Frederikshavn is now closed due to changes in student schedules and a lack of funds at the University of Copenhagen.

Between 1988-2010, there was a large increase in specimens of Danish marine algae deposited in the algal herbarium. These collections were made by scuba divers and obtained as a result of a collaboration with state, country and regional biologists who undertook national surveys of the marine environment.

Frequent collections over several years supple-

Shore with boulders. Upper part covered by green species of Gut Weeds and Sea Lettuces (*Ulva* spp.), the water's edge covered by a dense population of brown species of Wracks (*Fucus* spp.). Nordre Rønner, Læsø, 2005.

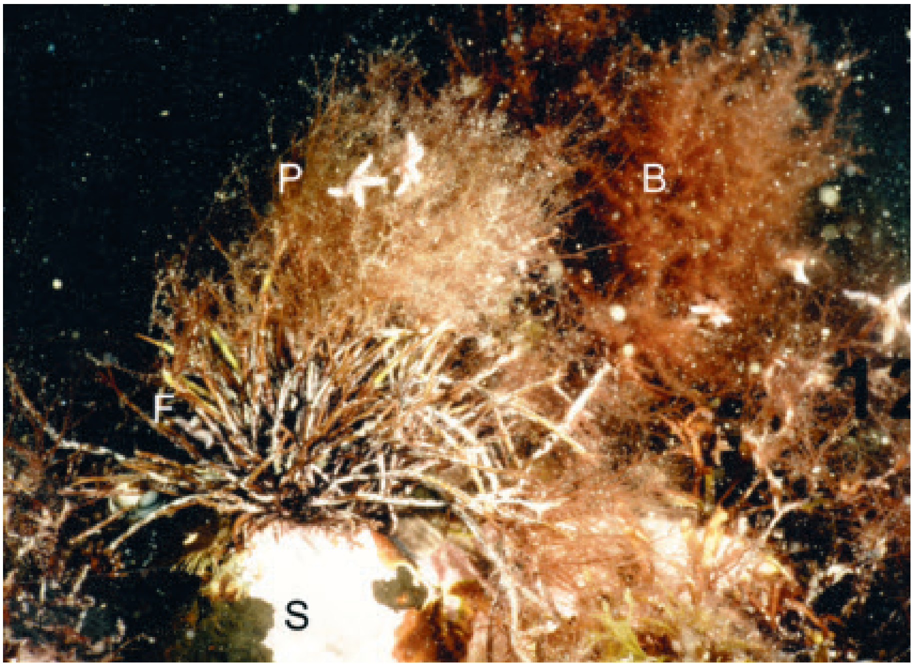
mented by culture studies have revealed the seasonal variation and life history for a few selected species, as well as their preferences for day length, temperature and salinity (Kristiansen 1984, Kristiansen and Pedersen 1979, Kristiansen et al. 1991). Documentation for these studies is also kept at the algal herbarium, Natural History Museum of Denmark.

In this book, the general appearance of the algae is, in most cases, shown by photographs of herbarium sheets.

Conditions for growth of algae

The algae all contain the green pigment chlorophyll a and gain their energy from photosynthesis and dissolved nutrients. The most important condition for a rich algal flora is therefore sufficient light for photosynthesis and furthermore hard substrata on which the algae can attach.

In Danish waters, there is rock at Bornholm, but otherwise suitable substrata consist of boulders, stones of different size, gravel, and pebbles, materials which came from mountains in other areas before, during and after the last ice age and were later rearranged. The same substrata are found on the shores in Denmark and particularly visible on small islands such as Hirsholmene and Nordre Rønner, Læsø in the Northern part of Kattegat, Omø in the Great Belt and Rågø in the archipelago Småslandfarvandet between Sealand and Lolland. Stone reefs, i.e. large collections of blocks with stones, pebbles and gravel between them in the sublittoral, are a distinctive feature in Danish waters. They are typically stable substrata for algal vegetation and covered by a perennial and vigorous growth of seaweeds. These stone reefs occur in all the Danish districts and at different water depths to approximately 30 m depth. The sea bottom around the stone reefs consists of sand and gravel and at greater depths of silt and clay. When sand is moved around large boulders, it may cause partial burial of these rocks and minimize the available stable substrata. Another consequence is sand scouring of boulders, making them only available for algal growth during calm periods. Boulders, therefore, in such areas are unstable substrata. Gravel beds are good substrata for algae, but water movements may roll the gravel around and as a result the vegetation is torn off. Therefore, the vegetation on such unstable bottoms consists of resistant algal crusts and small, fast-growing species. Such species can take advantage



Stone reef boulder covered by a rich algal vegetation of several layer. Basal are bright calcified crusts (S) and darker red and brown algal crusts. Clawed Fork Weed (*Furcellaria lumbricalis*) (F) is in the lowest level of perennial upright algae covered by delicate, branched epiphytic annual species, Purple Siphon Weed (*Leptosiphonia fibrillosa*) (P), and Brongniart's Thread Weed (*Vertebrata byssoides*) (B). Briseis Flak, 9 m, 10.8.1992.

of the bare gravel and colonize the unstable substrata but do less well in competition with perennial species on the stable substrata.

When light penetrates the water column it diminishes with depth. How much light is lost depends on the quantity of particles in the water, amongst other things. Nutrient-rich water causes large plankton production, which reduces the light and thus prevents it from penetrating the water column to any great depth.

Different species do not have the same demand for light intensity so the composition of the algal vegetation changes with the decreasing light downwards through the water column. It is typical to find a vigorous growth of several algal layers on the big boulders at 5-10 m depth. The crust-forming algae are at the bottom of the vegetation directly attached to the boulders. Above the crusts, coarse perennial species occur which support delicate bushy epiphytic annual species. Only crustose and very small upright species are found in the deepest waters for the algae in general, which is at 25-30 m depth in Danish waters. At this depth, the light is dim and not sufficient for the survival of larger algae, and the bottom consists of sand and mud and therefore lacking hard substrata on which the algae can attach.

The salinity is another factor with great influence on the algal vegetation, and interesting to study in Danish waters. The salinity is highest (30-34) in the North Sea and Skagerrak, but the available hard substrata are sparse in these districts. The algal vegetation is therefore scattered and there are fewer species than in the Northern Kattegat where the salinity of the surface water is relatively high at c. 28, and there are many stone reefs at different depths. The Northern Kattegat is therefore, the most species rich district in Danish waters. The salinity decreases to c. 15 at the North coast of Sealand and is only c. 8 at Bornholm, so although there are solid rocks there, the number of species is very reduced compared to the number in the Northern Kattegat.

Some species require a relatively high salinity for survival, and some of them become slender and delicate when they grow in brackish water compared to the morphology at higher salinities. Other species change their life history strategy to only asexual reproduction in localities where they survive at the low salinity.

The salinity also changes downwards through the

Species rich and vigorous vegetation at 9.5 m. Store Middelgrund, 14.6.1990. Scale 6 cm.

Low and scattered species-poor vegetation at 23 m. Store Middelgrund, 14.6.1990. Scale 6 cm.

water column and becomes more saline towards the bottom. The difference in salinity is mainly caused by the relatively large influx of freshwater into the Baltic Sea and consequently an outflow of brackish water from the Baltic Sea through the Danish straits towards the North Sea. Simultaneously there is an influx of more saline water from the North Sea. The saltier water has a higher specific gravity than the brackish water. Generally, therefore, the brackish water from the Baltic Sea flows out on top of the saltier North Sea water which flows in along the bottom. The two water masses mix slightly with time. The layering of the water column causes some algae to grow at greater depth further into the Danish districts

Southern harbour jetty Hirsholm with well-developed algal vegetation seen from the head of the jetty towards land. Velvet Thread Weed (*Bangia fuscopurpurea*) (left arrow), Tough Laver (*Porphyra umbilicalis*) (right arrow), and green Gut Weeds (*Ulva* spp.) above the water's edge at low water. The blue-green alga *Calothrix scopulorum* makes the boulders black.

than in the Northern Kattegat. Among them are Oar Weed (*Laminaria digitata*) and Sugar Kelp (*Saccharina latissima*), which can both be picked by hand in the Northern Kattegat at c. 1 m depth, whereas they only grow attached below 6 m depth south of Elsinore. The number of species declines from the Northern Kattegat towards the Baltic Sea, particularly the red and brown algae and to a lesser extent the green algae.

The decreasing salinity is often used as the explanation for the fall in species number towards the Baltic Sea, although there are also other important factors. One is the distance to the source area (the species-rich Northern Kattegat) and transition area without much hard substrata which functions as a barrier for a rapid immigration (Middelboe et al. 1997, 1998).

Waves have great influences on the algal vegetation indirectly by acting on the substratum, but also directly because different species do not tolerate the wave action equally well. Some species are very tolerant whereas other are easily torn apart or become detached by the waves. Another effect is the action of waves on the water movements, particularly the changing water levels along the shores, which is visible as a zonation of the algal vegetation.

The reasons for changes of the water levels in the inner Danish waters are mainly the direction of wind and the air pressure. High air pressure forces the water away from an area and results in low water, whereas low air pressure causes high water. The wind may cause water storage resulting in high water levels or blow the water away from the shore causing low water levels. It is noteworthy that strong westerly winds cause high water along east coasts in Kattegat because the winds act on large water masses and push water from the North Sea into the Kattegat, creating a generally high water level even on east facing shores. There is often a wind from the East in the spring which causes low water because the water is blown out of the inner Danish districts. Tides are of minor influence in inner Danish waters and are less than 30 cm amplitude inside Skagen.

The sublittoral zone is the part of the sea permanently covered by water. Above this is the littoral zone sometimes covered by water and sometimes uncovered. Higher up, the shore is influenced by the waves: there is a wave beaten zone, a splash zone, and above these the influence of the sea is restricted to spray (spray zone) and a dusting of salt (salt-dust zone) see Kristiansen (1968).

The vegetation reflects the zones with different species dominating the various levels. The waves are stronger and reach higher up at exposed localities

Sea Beech (*Delesseria sanguinea*) completely overgrown by bryozoans. Briseis Flak, 9 m, 10.8.1992. Scale 2 cm.

Clean blades of Sea Beech (*Delesseria sanguinea*). Briseis Flak, 11 m, 8.6.1989. Scale 2 cm.

than at sheltered localities, therefore, the zones reach a higher level on the shore with increasing exposure. Furthermore, the water changes become more frequent in the littoral, reducing desiccation of the algae. A similar pattern occurs on steep coasts compared to those with a gentle slope. The transition between the zones is gradual or uneven on most shores because of the inter-play between the different factors. The microclimate around a boulder varies according to the different conditions on the exposed and sheltered sides in respect to light/shadow, exposure to sun and drying. The vertical distribution of a species therefore differs on various sides of a boulder.

Harbour jetties provide hard surfaces for algal growth in addition to the natural hard substrata in Danish waters. They commonly have a sheltered side and a side exposed to waves. Relatively long jetties often have a sheltered inner part and an increasingly exposed part towards the outer end. Harbour jetties therefore give excellent opportunities to study how algal vegetation develops according to different conditions over a short distance. It is interesting to compare how the wave-exposure on the exposed and the sheltered sides clearly influence the composition and vertical distribution of the algal vegetation. It is also possible to study the consequences of the direction and slope of the individual parts of a jetty in respect to the main wind direction, the drying effect on stones exposed to the sun or in shade, and how the substratum and vegetation dry out after a period of extreme low water.

The presence of a species is not only dependent on the physical factors, but also influenced by other species. There can be competition for light or for space on the boulders, or considerable pressure from grazing animals. Snails and small crustacea are typical grazers, particularly in shallow water localities, and grazing leads to holes in the algae or to be totally eaten.

In the sublittoral, other species also have an impact on the algae. Surveys of some of the Danish stone reefs are undertaken each year by governmental institutes and document such relationships. One of the stone reefs was completely covered by Blue Mussels (*Mytilus edulis*) one year, with no room for the algae except in small holes and cracks. The following year, the Blue Mussels were attacked and eaten by Sea Stars (*Asterias rubens*), leaving space for the vegetation to recover, which happened the following year. Sea Urchins (*Strongylocentrotus droebachiensis*) may also invade a stone reef and eat all the vegetation, after which they disappear. The sea urchins either die or move to another locality and the vegetation recovers either from basal systems that have survived or from spores.

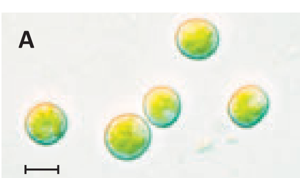
In nutrient rich areas, fast growing species and many diatoms develop and overgrow the perennial vegetation or develop into masses at the surface. The perennial species grow poorly in the shade and may disappear under extreme conditions. Bryozoans cause a similar effect on algae at the stone reefs as they can cover the perennial algae completely. Bryozoans live on plankton and probably benefit from rich plankton production in nutrient rich (eutrophic) conditions.

Seasonal variation

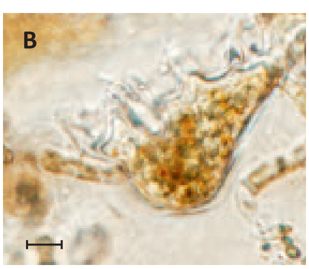
When you start to look at the algae, you soon realize that some species are only present in the winter, whereas others only appear in the summer. Some species grow fast in a single season and perennial species have reproductive structures only during one season. Winter algae in Danish waters generally occur as summer algae in colder North Atlantic areas such as Iceland and the Faroe Islands. The Danish algae that occur in summer are frequent in warmer areas such as the Channel Islands or the Mediterranean Sea.

Some species are only recorded in a single season, and they probably survive as an inconspicuous generation or as spores during unfavourable seasons.

Day length and light intensity in combination with temperature are the most important factors for the change of seasons for the algae and that trigger the change from one life history phase to another but this differs from one species to another. Knowledge is



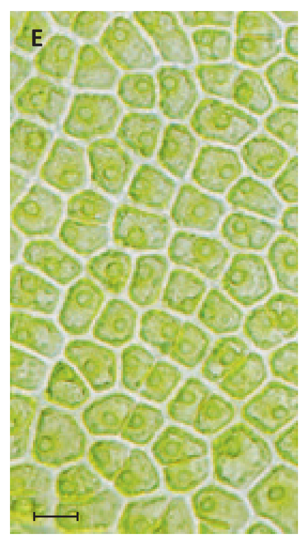
A: Unicellular spherical cysts. Stalked Green Guano Weed (*Prasiola stipitata*). Hirsholm, salt-dust zone, 14.4.2015. Scale 10 µm.



B: Unicellular alga with irregular attenuations. *Gomontia polyrhiza*. Decalcified bivalve shell, Mariager, Mariager Fjord, 0.5 m, 22.3.2014. Scale 10 µm.

C: Filamentous alga with opposite branches, the main axis terete with a few longitudinal and transverse walls (arrows) Winged Thread Weed (*Tilopteris mertensii*). Læsø Trindel, 2 m, 8.6.1991. Scale 20 µm.

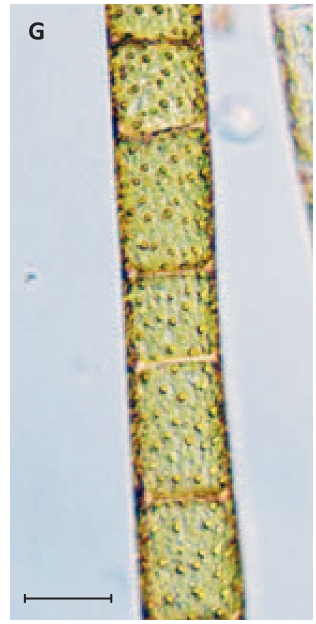
D: Unbranched uniseriate filament. Slender Glossy Fringe Weed (*Urospora penicilliformis*). Boulders at Mariager, Mariager Fjord, 0 m, 22.3.2014. Scale 10 µm.



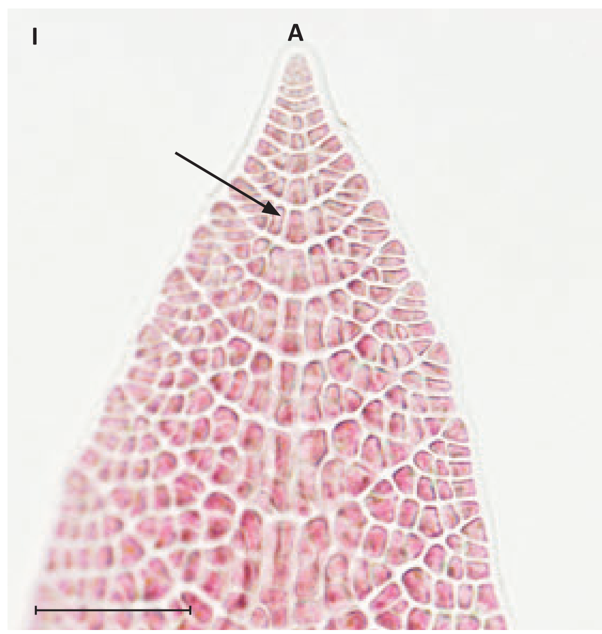
E: Flat parenchyma. Proliferous Gut Weed (*Ulva prolifera*). Beach north of Vesterø Havn, Læsø, 20 cm, 9.5.2014. Scale 10 µm.

F: Apical growth, a small cell cut off from the apical cell (arrow), Bonnemaison's Fern Weed, (*Bonnemaisonia asparagoides*). Kims Top, 14.5 m, 4.2.1996. Scale 10 µm.

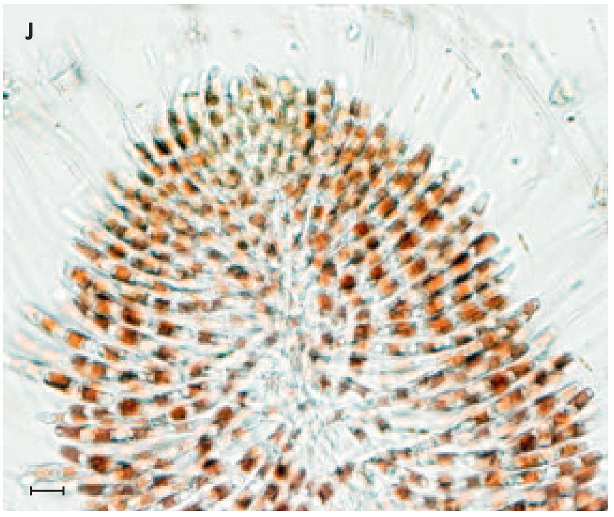
G: Diffuse growth in a uniseriate filament, alternation between short (young) and long (old) cells. Tarantula Weed (*Acrosiphonia centralis*). Hirsholm, 0.2 m, 14.4.2015. Scale 50 µm.



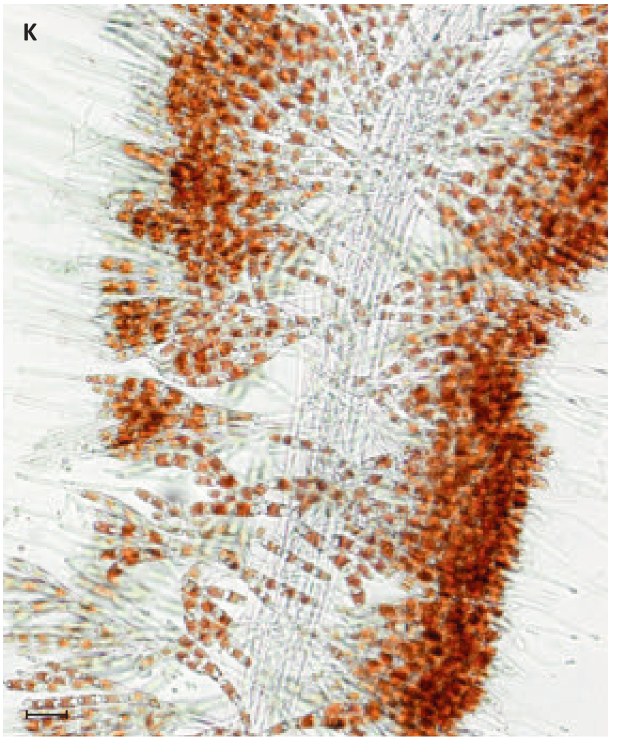
H: Terete uniaxial syntagma, apical cell (A), central axial cell (arrow) with cortex band. Diaphanous Banded Pincer Weed (*Ceramium diaphanum*). Lysegrund, 6 m, 23.8.1996. Scale 20 µm.



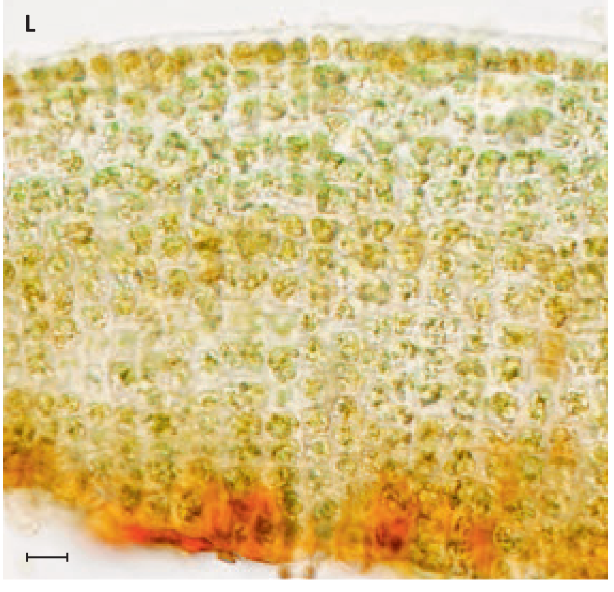
I: Flat uniaxial syntagma, apical cell (A), central axial cell (arrow). Central axis with branches of uniseriate filaments in one plane forming the blade. Winged Weed (*Membranoptera alata*). Møns Klint, 17 m, 2.9.2004. Scale 50 µm.



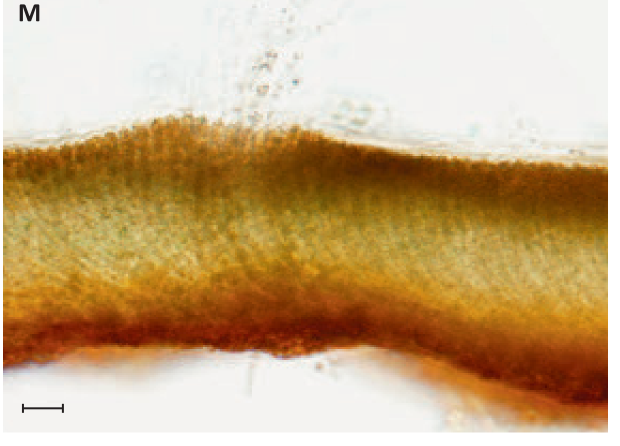
J: Multiaxial syntagma; apex with several apical cells and many red algal hairs. Sea Noodle Worm Weed (*Nemalion multifidum*). Scale 20 µm. J, K: Beach north of Vesterø Havn, Læsø, drift, 23.6.2013.



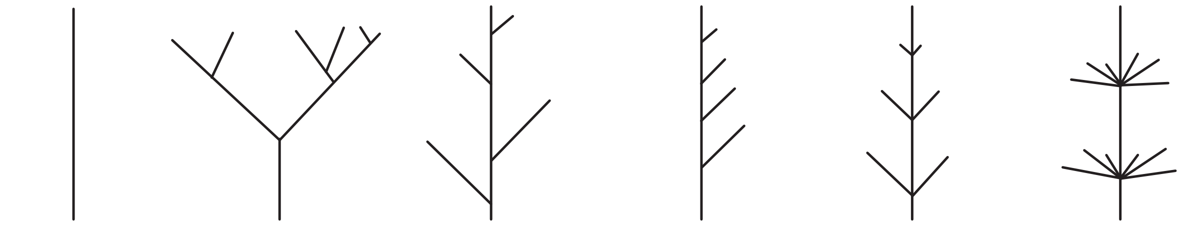
K: Multiaxial syntagma, just below the apex, medulla of thin colourless filaments, and cortex of lateral assimilating filaments, optical longitudinal section, slightly pressed. Sea Noodle Worm Weed (*Nemalion multifidum*). Scale 20 µm.



L: Crust of densely packed upright filaments, longitudinal section of Spreading Brown Rock Crust (*Pseudolithoderma extensum*). Herthas Flak, 20 m, 2.2.1996. Scale 10 µm.



M: Crust of densely packed ascending filaments, longitudinal section of Brown Limpet Paint (*Pseudoralfsia verrucosa*). Saltholm, 0.5 m, 17.7.1997. Scale 20 µm.



obtained about these aspects by detailed culture studies under different physical conditions in the laboratory.

Structure and growth of algae

Unicellular algae are the simplest form. They are often spherical, occasionally with one or more extensions. Uniseriate filaments form when the cells divide in only one direction and remain connected. Filaments may be unbranched or branched. Parenchymatous fronds develop when the cells divide in more than one direction and remain connected. The simplest parenchymatous construction is a uniseriate filament with longitudinally divided single cells. Parenchymatous fronds may be filamentous or flat (blades) with several cells both in longitudinal and transverse direction and consist of one or several cell layers.

Growth is apical when it takes place by divisions of the upper apical cell. Diffuse growth takes place by division of scattered intercalary cells. When the dividing cells occur in a particular area, there is a growth zone. Some of the brown algae have intercalary growth near the apex, with a growth zone which contributes both to the thallus below and to a hair or a hair-like shoot at the apex (trichothallic growth). Growth by stretching is frequent and happens when cells elongate without division.

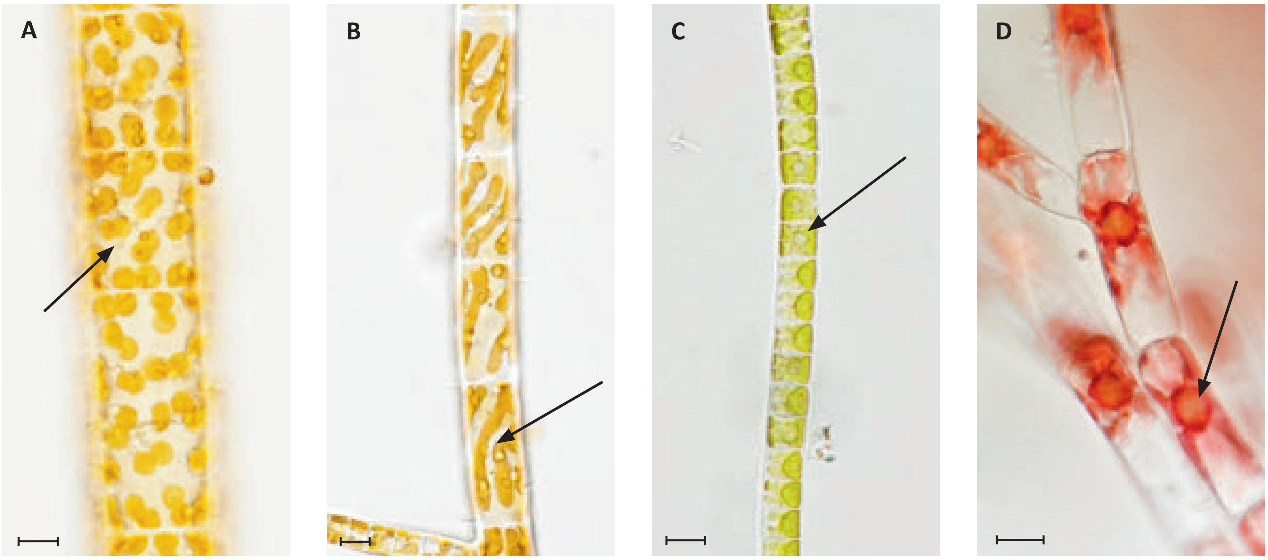
A syntagma consists of several filaments which are coherent and kept together in a common outer wall. A uniaxial syntagma has a central uniseriate filament with branches and has a single apical cell. It may be terete (round in cross-section), and the central filament has branches on all sides, or it may be flat in which case the central filament has long branches in one plane and short branches in other directions. A multiaxial syntagma has several parallel filaments in the middle (medulla) with lateral branches forming the surface (cortex). It may be terete or flat and has several apical cells.

Crusts of algae are more or less extended patches on the substratum. They consist of densely packed filaments, which arise perpendicularly to the substratum (upright) or bend upwards (ascending). They typically have a basal layer of prostrate filaments from which other filaments arise.

Siphonous fronds occur among the green algae. They lack internal cell walls and appear as tubular constructions, with a big vacuole in the middle and nuclei, plastids and other cellular organelles in a layer just below the outer wall.

Branching

Regardless of whether the thallus is filamentous, parenchymatous or has a syntagmatic construction, it can be with or without branches. The branches are scattered when they occur individually. They are unilateral when all branches are scattered and grow on one side in a single series, and alternate when the branches alternately turn to the right or left side. Distichous branches occur in two series. Branches on all sides turn in all directions and may spiral around the branch. Branches are opposite when two branches arise from the same point, opposite to each other. Alternate or opposite branches may form four or more rows. Branches are whorled when three or more branches arise from the same point in different directions.

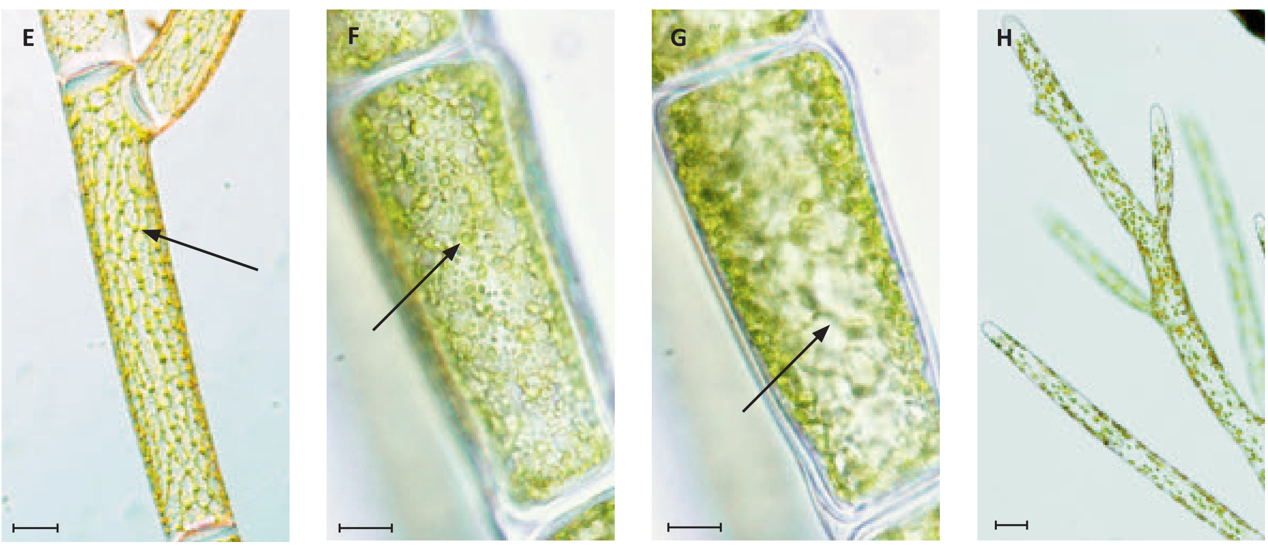


A: Many disc-shaped plastids with drop-shaped pyrenoids (arrow). Pylaie's Brown Filaments (*Pylaiella littoralis*). Margretheholms Havn, Copenhagen, 0.5 m, 27.11.2007. Scale 10 µm.

B: Ribbon-shaped plastids with drop-shaped pyrenoids (arrow). Artist's Brush Cotton Wool Weed (*Ectocarpus penicillatus*). Margretheholms Havn, Copenhagen, 0.5 m, 19.2.2008. Scale 10 µm.

C: Plate-shaped plastids each with one pyrenoid (arrow). Shaggy Hair Weed (*Ulothrix* sp.) Margretheholms Havn, Copenhagen, 0.5 m, 23.2.2009. Scale 10 µm.

D: Star-shaped plastids, each with one pyrenoid in the middle (arrow). Branched Star Hair (*Acrochaetium secundatum*). Sheltered side of Margretheholms Havn, Copenhagen, 0.5 m, 17.9.2008. Scale 10 µm.



E: Reticulate plastid with many pyrenoids (arrow). Tarantula Weeds (*Acrosiphonia centralis*). Hirsholm, 0.5 m, 15.4.2015. Scale 50 µm.

F: Spongy plastid, several angular plates touching each other and form a filamentous mass with many pyrenoids. (arrow). Viewed just below the cell wall. Clustered Green Branched Weed (*Cladophora glomerata*). Gilleleje, 0.5 m, 16.7.2006. Scale 10 µm.

G: Spongy plastid, a filament in the middle (arrow), optical longitudinal section. Clustered Green Branched Weed (*C. glomerata*), same cell as in figure F. Scale 10 µm.

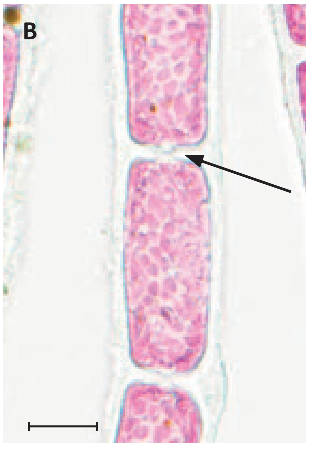
H: Siphonous algae without internal cell walls. Many spindle-shaped plastids. Mossy Feather Weed (*Bryopsis hypnoides*). Flakfortet, Copenhagen, 6 m, 22.6.2016. Scale 50 µm.

Branching is dichotomous or forked when two equal-looking branches continue growth from the apex of a branch. Genuine dichotomous branching develops after equal longitudinal division of an apical cell and both of the daughter cells continue growth into a new branch. Pseudodichotomous branching occurs after displacement of a lateral branch so it appears similar to the main branch.

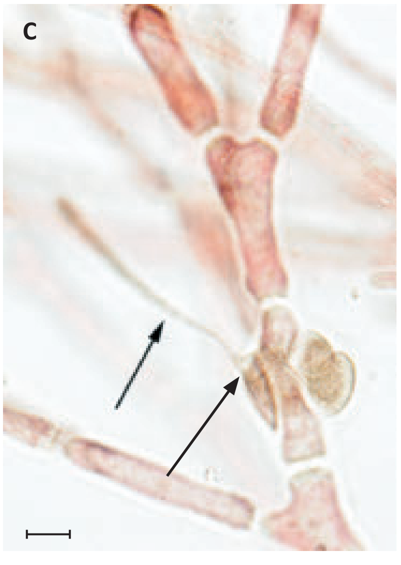
Plastid

Plastids are organelles in the cells, where the colours are located and the light energy taken up. The active green colour is chlorophyll a. The shape of the plastids is an important character for identification of species, and best seen in bright light through the microscope. There can be one or several plastids per cell. They are typically found just below the cell wall, but in some species in the middle of cells. The shape of

A: Unicellular red algal hair with apical cytoplasm. Hooker's Bush Weed (*Gaillona hookeri*). Hirsholm, drift, 25.5.2010. Scale 20 µm.



B: Pit connection (arrow) between cylindrical cells with several disc-shaped plastids. Bonnemaison's Hook Weed, *Trailliella*-phase (*Bonnemaisonia hamifera*). Tønneberg Banke, 10.5 m, 27.8.2013. Scale 20 µm.



C: Female gametophyte, carpogonium (lower arrow) with trichogyne (upper arrow). Slender Beautiful Bush Weed (*Aglaothamnion tenuissimum*). Vejrø, 11 m, 5.6.1991. Scale 10 µm.

D: Gonimocarp, the diploid gonimoblast (lower arrow) surrounded by haploid pericarp (upper arrow). Elongate Siphon Weed (*Carradoriella elongata*). Store Middelgrund, 9 m, 10.6.1991. Scale 50 µm.

E: Antheridia (right arrow) and young red algal hair (left arrow). Sea Noodle Worm Weed (*Nemalion multifidum*). Beach north of Vesterø Havn, Læsø, drift, 23.6.2013. Scale 10 µm.

the plastids are the reasons for naming them as disc-shaped, plate-shaped, ribbon-shaped or star-shaped when they have long or short outgrowths from a central part. Cylindrical plastids also occur, typically with holes so they become reticulate. In some genera, the whole cell is filled by a sponge-like structure. Such spongy plastids consist of several small angular plates touching each other or connected by short narrow filaments, for instance in species of Green Branched Weeds (*Cladophora* spp.).

A small hyaline more or less spherical or drop-shaped structure is connected to the plastids in many species, which is named the pyrenoid and consists of protein. In green algae nutrients are deposited around the pyrenoids.

Red algae (Rhodophyta)

The red algae are primarily characterized by the red colour which varies from rose-pink through shades of violet to reddish brown or very dark bluish red to almost black. The colour may change in some red algae as a response to the intensity of light and become yellow-green in localities which are exposed to high light. The reddish colour in such red algae is typically visible at the base, and in very dark algae it is best seen in light falling through the thallus. The red colour is caused by the water-soluble red pigment (phycoerythrin) which covers the green chlorophyll a, and a blue, water-soluble pigment (phycocyanin). Phycoerythrin is typically dominant, but in a few species, the blue phycocyanin together with the green chlorophyll a, make the red algae appear blue-green. Drifting algae may become very strong violet, purple or orange in colour because some of the original pigments are in part broken down or washed out.

The walls of red algae consist of cellulose and different pectin-like agars, carrageenan, and furcellaran. These products have a thickening effect and are used in industrial processes, particularly in the food industry.

Red algal hairs are special structures that are not present in brown- or green algae. They are long hyaline single cells, with the cytoplasm concentrated in the top as a small greyish substance. The hairs can be seen with a hand lens or microscope. Many hairs are typically present in vigorously growing algae in strong light. The hairs probably provide benefit by the uptake of nutrients and may create some shadow from too strong light.

Pit connections are another special structure present in most red algae. Primary pit connections form during cell divisions between neighbouring cells within the same filament. A new cross wall grows from the side walls towards the centre of a dividing cell leaving a small hole which still connects the two daughter cells. A 'cork' of protein surrounded by several membranes fills the hole. Thus, there is not really a pit between the cells but the term pit connection is generally used, as in this book. The ultrastructure of pit connections differs from one systematic group to another. The microscope reveals the pit connections as small dark points in the cross walls between cells. Secondary pit connections may occur between cells in different filaments running close to each other. These develop when a small cell (the connecting cell) is cut off from one of the filaments while a pit connection is formed, then the cell wall between the connecting cell and a cell of the neighbouring filament is dissolved (cell fusion) and the pit connection becomes secondary.

The storage product in red algae is a particular kind of starch (floridian starch) deposited in the cytoplasm and not connected with the plastids. Floridian starch may become a brownish colour with the addition of iodine, but not the dark blue colour of starch found in green algae or, for example, in potatoes.

The life histories of red algae typically encompass sexual reproduction in gametophytes, which are often haploid (n) and a diploid sporophyte (2n) with asexual reproduction. The reproductive cells and different kinds of spores do not have flagella in the red algae, but young spores without cell wall may have amoeboid movements.

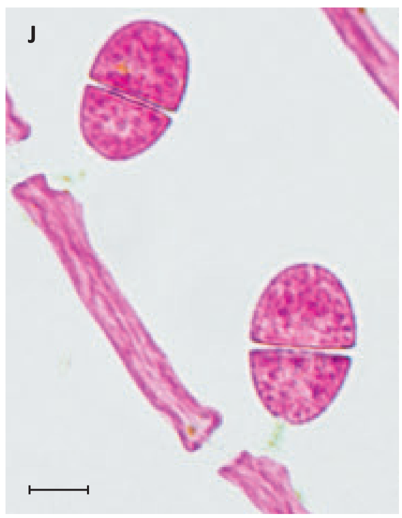
Gametophytes have male and female reproductive structures on different individuals (dioecious) in many species but occur in a single individual (monoecious) in other species. The reproductive male gam-

F: Cruciate tetrasporangium. Purple Felt Weed (*Rhodochorton purpureum*). Herthas Flak, 10 m, 2.2.1996. Scale 10 µm.

G: Zonate tetrasporangium. Purple Claw Weed (*Cystoclonium purpureum*). Schultz's Grund, 7.5 m, 30.8.2013. Scale 20 µm.

H: Tetrahedrally divided tetrasporangium. Pitcher Siphon Weed (*Polysiphonia stricta*). Schultz's Grund, 7.5 m, 30.8.2013. Scale 50 µm.

I: Monosporangia, one almost mature (arrow) and one empty. Branched Star Hair (*Acrochaetium secundatum*). Hirsholm, 0.5 m, 14.4.2015. Scale 10 µm.



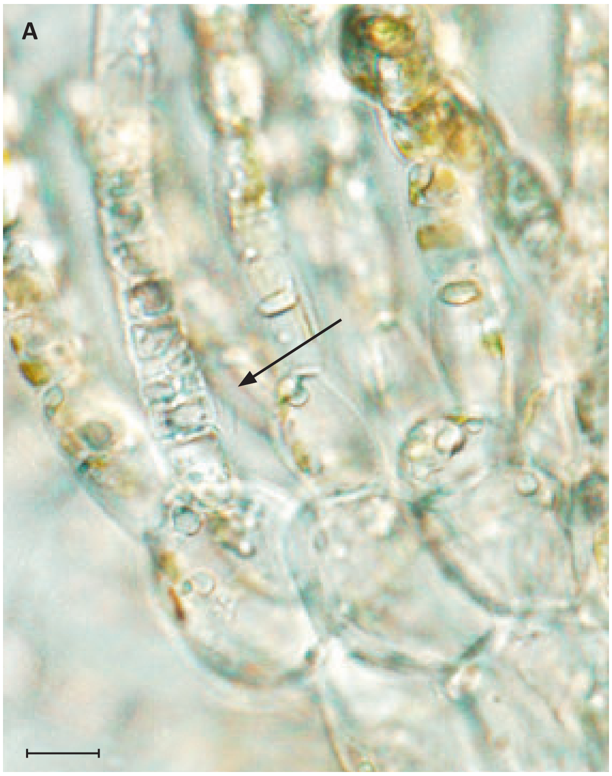
J: Bisporangia. Rose-red Bush Weed (*Gaillona rosea*). Vengeancegrund, 7 m, 28.7.1994. Scale 20 µm.

K: Parasporangium. Hooker's Bush Weed (*Gaillona hookeri*). Læsø Trindel, 8 m, 3.6.1993. Scale 20 µm.

etes (spermatia) are colourless and form in antheridia. These develop from surface cells and occur individually or grouped in antheridial branchlets or in patches on the thallus (sori). The small spherical spermatia are without flagella and drift around in the water.

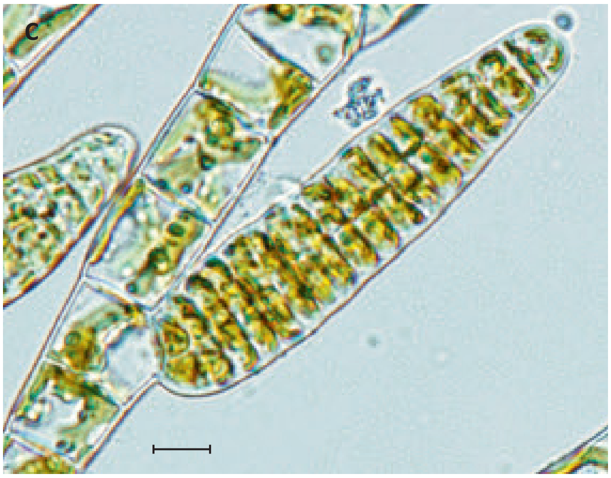
Female gametes (carpogonia) are sessile on the gametophyte. Each carpogonium has a hair-like structure (trichogyne) or a small papilla to catch the spermatia. The fusion between the nuclei takes place in the carpogonium This occurs by a process where a spermatium attaches to the trichogyne, the walls dissolve and the male nucleus moves through the trichogyne to the female nucleus in the carpogonium. The resulting diploid (2n) cell (zygote) divides and a diploid carposporophyte develops, remaining on the female gametophyte. The carposporophyte is often a group of cells (gonimoblast) consisting of short radiating filaments. In some red algae, several gonimoblasts develop from the first one by helping cells (auxiliary cells) that become diploid by cell fusions. It may happen directly from the zygote or from special connecting filaments. Carposporangia develop in the carposporophyte from all cells or from individual cells of the gonimoblast.

The gametophyte may surround the gonimoblast with a protective structure (pericarp). The pericarp with the gonimoblast is named the gonimocarp or by some authors the cystocarp. Unfortunately, this term is not used consistently by various authors and cystocarp is in common use for gonimoblasts both with and without a pericarp. Carpospores (2n) are released into the water. They germinate in contact with a suitable substratum and develop into a diploid phase, the tetrasporophyte. Tetrasporangia develop in the tetrasporophytes and four haploid tetraspores develop after meiotic division in each tetrasporangium. When cell division in the sporangia occurs simultaneously with divisions of the nucleus, the sporangia become divided into cross-shaped (cruciate) or transversely divided (zonate) tetrasporangia. When cell divisions in a sporangium occur after the meiotic divisions of the nucleus, a tetrahedrally divided tetrasporangium develops. The tetraspores germinate after contact with a suitable substratum and develop into new male and female gametophytes. In some species the male, and female gametophyte as well as the tetrasporophyte



A: True brown algal hair with basal growth zone of short cells (arrow). *Chordaria flagelliformis*. Beach north of Vesterø Havn, Læsø, 0.5 m, 23.6.2013. Scale 10 µm.

B: Brown algal hair with a basal sheath (arrow). *Punctaria tenuissima*. Beach north of Vesterø Havn, Læsø, 0.5 m, 23.6.2013. Scale 10 µm.



C: Plurilocular sporangium. *Ectocarpus penicillatus*. Scale 10 µm. C-D: Bovet, Læsø, drift at 10 cm, 28.4.2016.

D: Just emptied plurilocular sporangium. *Ectocarpus penicillatus*. Scale 10 µm.

E: Unilocuilar sporangium. *Ectocarpus penicillatus*. Hirsholm, drift, 14.4.2015. Scale 10 µm.

look alike (isomorphic), whereas in other species they are morphologically very different (heteromorphic).

Asexual reproduction occurs from sporangia which form a single spore (monosporangia) or several spores after division (bi-, tetra-, octo-, para-, or polysporangia) or when the content of vegetative cells are surrounded by a thick wall (akinetes). Vegetative reproduction occurs when fragments, or special branches of the thallus break off and continue growth into new individuals.

Brown algae (Phaeophyceae)

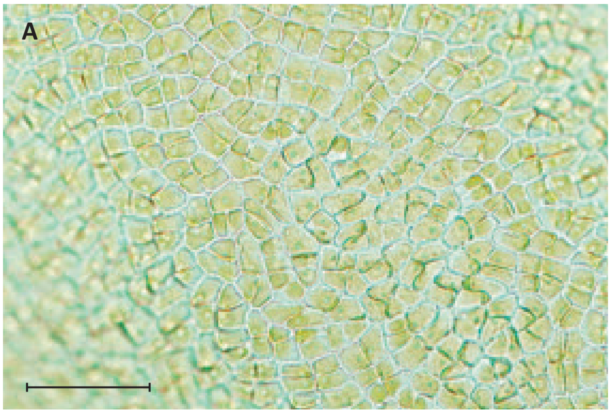
The brown algae may be very dark brown or bright almost yellow to olive green, but never clear green. The colour of the pigment fucoxanthin dominates over the green chlorophyll a, c_1 and c_2.

Cell walls consist of cellulose-fibres, supported by calcium alginate and fucoidan and also contain slimy alginates. Alginic acid is extracted from some of the large brown algae for industrial use. The salts have various useful properties, applied in the food industry as emulsifiers, in textile industry to impregnate cloths and even for production of textile fibres. The storage products in brown algae are various polysaccharides.

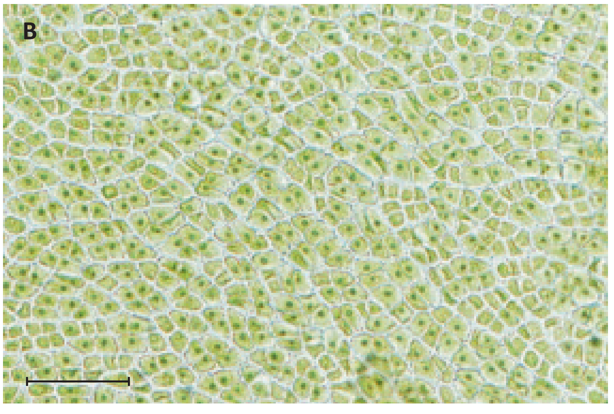
True brown algal hairs are unbranched, colourless, uniseriate structures, of cylindrical cells with a basal growth zone of short cells. In some genera the basal part of the hairs is surrounded by a sheath-like structure which is a remnant of the cell wall from which they arose. In filamentous brown algae, branches often terminate in a series of narrow elongated cells. They contain relatively few plastids so they appear pale and hair-like (false hairs).

Pyrenoids in brown algae are drop-shaped and separate from the plastids, as opposed to the red and green algae, where the pyrenoids are embedded in the plastids.

Life histories in brown algae are very variable with both sexual and asexual reproduction. There is typically a change in the nuclear phase. The generations are alike in some species (isomorphic) whereas they in other species look very different (heteromorphic). Spores with flagella (swarmers) may be vegetative (zoospores) or sexual (gametes or male spermatozoids). The swarmers form in uni- or plurilocular sporangia. The plurilocular sporangia develop from a single cell dividing into several small compartments by mitotic divisions. A single swarmer develops in each compartment and is released separately through a hole in the wall, in some cases into the middle of



A, B: Monostromatic parenchymatous blade, each cell contains a single plastid with one pyrenoid.



B: Iodine has been added which has turned the starch around the pyrenoids dark blue and visible. Greville's Mattress Weed (*Monostroma grevillei*). Beach north of Vesterø Havn, Læsø, 0.2 cm, 14.3.2014.

the sporangium. Meiotic division never takes place in plurilocular sporangia. Unilocular sporangia form after several nuclear divisions within a single cell and contain several swarmers at maturity. A change in the phase of the nucleus may take place in unilocular sporangia in which the process begins with a reduction division (meiosis) followed by mitotic divisions. This does not always happen, and all divisions are mitotic in other cases. Oogamous reproduction occurs in some brown algal species, in which immobile egg cells on female gametophytes are fertilized by swimming male spermatozoids.

Swarmers of brown algae are drop-shaped with a plastid in the rear of the cell, and a lateral red eyespot. They have two flagella in one side of the cell. One of them is smooth pointing backwards and has straight movements (smooth flagellum). The other pointing forwards has very fine appendages and waving movements (hairy flagellum). See Pedersen (2011) for an illustration. The front of a swarmer is the front end during swimming.

Green algae (Chlorophyta)

The green algae are always green and have a bright light or dark green colour. They contain both chlorophyll a and chlorophyll b but no additional colour (pigment) to camouflage the green colour.

The storage product is starch which is typically arranged as granules around the pyrenoids. The number of pyrenoids is an important character for identification of genera and species. Addition of an iodine solution to a slide preparation is useful in revealing the pyrenoids because the starch around them turns a dark blue colour.

Sexual and asexual reproduction occur in the green algae. Many of the marine species have drop-shaped swarmers with two or four flagella in the pointed front end. The individual swarmers have a basal plastid and a lateral red eyespot. The flagella are smooth and of equal length. Swarmers with four flagella are vegetative zoospores. They settle and develop into offspring similar with the parent generation. Swarmers with two flagella may be vegetative and act as zoospores, or sexual gametes. The gametes may be alike (isogametes) or different (anisogametes). Their size may be different, or they behave differently, some settling before others and attracting these so fertilization takes place and the zygote germinates into a new individual.

Phases in the life history may be alike (isomorphic generations) or different looking (heteromorphic generations). In most of the green algae the gametes are haploid (n) and the zygotes diploid (2n). The meiotic division occurs when the zygote germinates in some species. A diploid thallus develops in other species and meiosis takes place later within sporangia. Zoospores are haploid or diploid. The swarmers of many genera are produced in sporangia developing from vegetative cells which keep the same shape and size as in the vegetative condition. In a few genera the sporangia are special structures, which will be dealt with under the respective species.

Classification

The species of the book are arranged in agreement with modern systematic understanding, listed in phyla, classes, subclasses, orders, families, genera and species. Minor entities are occasionally mentioned, classified as subspecies (ssp.), forms (f.), and varieties (var.). The endings of names on the different entities are characteristic, as explained with examples from the red algae in the following. Phylum: Rhodo**phyta**, class: Floride**ophyceae**, subclass: Ahnfelti**ophycidae**, order: Ahnfelti**ales**, family: Ahnfelti**aceae**, genus *Ahnfeltia* and species: *Ahnfeltia plicata*. Subfamilies are mentioned within a few families, for instance Rhodomel**oideae** in which tribes are also mentioned, e.g. Polysiphoni**eae.** In the past, the classification was based on the general appearance of the thalli and traits of reproductive structures also became important. In the red algae, this particularly concerned the female reproductive structures. The tendency in recent years is that the classification must reflect the evolution and relationships as revealed by molecular studies. Phylogenetic studies are still ongoing, therefore it is expected that the future will reveal several new revisions.

The classification of the red algae follows Schneider & Wynne (2007, 2013), Wynne & Schneider (2010), supplemented with Choi et al. (2008) and Le Gall & Saunders (2007).

The classification of the brown algae follows an updated classification by Silberfeld et al. (2014).

Modern molecular studies of the green algae resulted in a new understanding of the evolution and the green algae are split into several classes. The classification of the green algae follows Leliaert et al. (2012). The marine green macroalgae in Danish waters belong in two classes: Trebouxiophyceae, and Ulvophyceae, both in the phylum Chlorophyta.

Naming (Nomenclature)

The description of an individual species or subspecies has not always been recognized or understood by different authors. Therefore, a single species was often described several times and given different names. In such cases, the oldest name must be accepted according to the rule of priority. This is the most important rule in selecting the valid name, and later names applied become synonyms. It has frequently happened that an older name suddenly turns up and according to the rules of priority must replace a name in use.

Homotypic synonyms are names based on the same individual as the holotype. Other names based on different types are heterotypic synonyms.

The many names used for a single species, especially in genera with large morphological variation, makes it difficult to obtain a personal understanding of a species, and makes identification problematic.

A species name in Latin is a combination of the genus name beginning with a capital letter and the species name in lower case. This is followed by the name of the author(s) who is responsible for the description of the species. If the species later moves to another genus, the original author(s) name is surrounded by a bracket and followed by the name of the author(s) being responsible for the transfer to the other genus. If a species moves more times, the original author name remains in the bracket and is followed only by the name of the author(s) being responsible for the last transfer. Usually, the author(s) name(s), referred to as the authority, is only used the first time a species is mentioned in a text.

It may be problematic to give up a name which has been in ordinary use for a long time. To avoid such problems, it is possible to conserve a younger name against an older name. A proposal for this must be presented to the committee of botanical nomenclature with a good argument, and after voting the proposal may be accepted. The Botanical Congress makes rules about naming and has meets every six years. The results are published in 'International Code of Nomenclature for algae, fungi, and plants', which is available at www.iapt-taxon.org/nomen/main.php.

Naming of subspecies, forms, and varieties, must follow the same nomenclatural rules as those for the species.

A database of information on algae is available at www.algaebase.org; it contains information on valid names, synonyms, and information on distribution of the algae, in addition to relevant literature.

The use of synonyms in this book is restricted and mainly presented with references in which the names used are different from those in this book. As a result of recent taxonomic and nomenclatural studies, some names used in this book are different from those in the Danish edition (Nielsen & Lundsteen, 2019a, b). In such cases these older names are noted as 'recent synonyms'.

Types

The individual alga which an author has used to describe a new species, is the type. This is the original material and defines the concept of a species. In other words, there must be a type to define the name and understanding of a species. When the original collection only contains a single specimen, this is the holotype. If the original collection contains more individuals, collected at the same time and locality, these are syntypes. The author of the species, and only that person can select a holotype among the syntypes and when this happens, the remaining individuals become isotypes. When the original description mentions species collected at other localities or dates, they are paratypes. If the author of a new species did not select a holotype, and the original material contains several individuals or none exist, later researchers can select a lectotype as a replacement for the holotype. The lectotype must agree with the original description and preferably selected among the syn- or paratypes, if such exist. When no original material exists, the lectotype can be an illustration.

Palmaria palmata. Paludans Flak, 8 m, 11.9.1993. Scale 2 cm.

Reddish blades of Laver (*Porphyra* sp.) and upright green Gut Weeds (*Ulva* sp.), both edible. On small stone at Kobberhage, 25.8.2017. Photo by K.L. Krabbe.

When the holotype or lectotype is an illustration or when the material is not complete, it is possible to select a neotype as a supplement. A supplement could also be an epitype which is a specimen or illustration selected to serve as an interpretative type when the holotype, lectotype, or previously designated neotype, or all original material associated with a validly published name, cannot be identified for the purpose of the precise application of the name to a taxon (Art. 9.9 in 'International Code of Nomenclature for algae, fungi, and plants').

The original place of collection is the type locality.

Handbooks and local floras

'The marine algæ of Denmark, Rhodophyceæ' (Rosenvinge, 1909-1931) and 'The marine algæ of Denmark, Phæophyceæ' (Lund, 1950, Rosenvinge & Lund, 1941, 1943, 1947) are important handbooks for the study of Danish seaweeds. The series 'Seaweeds of the British Isles' encompasses several volumes written by specialists (Brodie & Irvine, 2003, , Burrows, 1991, Dixon & Irvine, 1977, Fletcher, 1987, Irvine, 1983, Irvine & Chamberlain, 1994, Maggs & Hommersand, 1993) and related texts (Brodie et al. 2007, Bunker et al. 2020) are also valuable for the study of Danish seaweeds. The first part of the series was published in 1977 and Fletcher (in press) is the final volume. The British seaweed flora is more diverse (656 species) than the Danish (373 species) so the books include species that are absent in Denmark, but also contain a lot of information about species which occur in Danish waters. The book on the algae of Helgoland by Kornmann & Sahling (1977) with additions (1983, 1994) is a beautiful photoflora with information about life histories obtained by culture studies. Norsk algeflora (Rueness, 1977) represents a summary of seaweeds of Norway with identification keys. It was the handbook used during the field courses in Frederikshavn in the late 20th century, supplemented by Kylin's books about red, brown and green algae along the Swedish West coast (Kylin, 1944, 1947, 1949). It is probably beneficial for beginners to start identifying species by looking in more popular floras from Denmark and the neighbouring countries. The booklet 'Tang' (Larsen et al. 1986, Larsen & Hansen

2020) has very good illustrations by T.H. Bredsdorff particularly of the algae in the Northern Kattegat. 'Havets dyr og planter' [Animals and plants of the sea] includes a section about algae by Kristiansen (2014), which is a comprehensive survey of the larger algae. Tolstoy & Österlund (2003) gives a survey of algae along the Swedish coast of the Baltic Sea, Rueness (1998) is a field guide for macroalgae along the Norwegian coasts and Bunker et al. (2020) is a guide to seaweeds of Britain and Ireland with photographic illustration, valuable information, distribution maps and many common names.

In this book, references to special literature are given for each individual species while references to handbooks are limited.

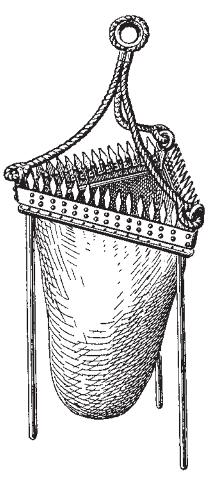
A little about algae in food

There is no tradition for using the algae for food in Denmark, but in recent years it has become popular to introduce seaweeds into the Danish kitchen. Inspiration has probably come from Japan, where there is an ancient tradition for using various algae in the cuisine. Well known dishes include sushi where rice, fish and shellfish are served neatly wrapped in nori which is processed sheets of the blades of species of Laver (*Neoporphyra* J.Brodie & L.-E.Yang, and *Neopyropia* J.Brodie & L.-E.Yang).

There is also a tradition for supplementing the diet with algae in some areas of the North Atlantic. In poor areas next to the sea, seaweeds were an important part of everyday eating and they were easily collected at low tide both in summer and winter. In Wales the people made 'laver bread' prepared using Laver (*Porphyra* spp.). The Laver is washed and boiled for several hours until it resembles a mash. It is traditionally eaten by frying in bacon fat and served for breakfast but it is used now in a variety of dishes as chefs have become more creative. The algae contain valuable proteins, vitamins, minerals, and fibre in addition to healthy unsaturated fatty substances. They have undoubtedly contributed to a healthy diet in poorer coastal communities and were a valuable food in times of famine.

The story of Egil Skallagrimsson in the Icelandic sagas mentions Dulse (*Palmaria palmata*) and bears witness to the use of this seaweed as food in the North Atlantic at the time of the sagas. Today dried Dulse (*P. palmata*) is for sale in supermarkets in Iceland and special shops with vegetarian food in Denmark.

In Denmark, the use of seaweeds may become more frequent, as it is probably a matter of getting used to them and learning how to use them. It is possible to eat most of the Danish seaweeds without being worried that they are poisonous, although it is important to collect them only in areas with clean water. A survey of these matters is presented in the report, 'Forekomst af mikroorganismer på tang – specielt på



Triangular dredge. After Reinke in Oltmanns (1905).

A herbarium cabinet in the algal herbarium, Natural History Museum of Denmark, June 2016. The herbarium sheets are in covers, red for type specimens, otherwise grey. Photo by J. Wynns.

spiseligt tang, der forekommer i de danske farvande' [The presence of microorganisms on seaweeds – particularly on edible seaweeds in Danish waters] by Hendriksen & Lundsteen (2014). The book 'Tang – Grøntsager fra havet' [Seaweeds – vegetables from the sea] (Mouritsen, 2009) provides information on the content of seaweeds in an easily understood text and writes of how the algae are used in different areas around the world. The book also includes recipes for the use of algae in different dishes in everyday meals and for parties. The interest of Mouritsen for the beauty of the algae, their taste and use, is also documented in later publications with more references to the subject (Cornish et al. 2015, 2017, Mouritsen, 2013, 2017, Mouritsen et al. 2018a, b, c).

'Irish Seaweed Kitchen' by Rhatigan (2009) is a beautifully illustrated cookbook. It is based on Prannie Rhatigan's own experiences from childhood on collecting and preparing seaweeds in the Northwest of Ireland. Danish cooking books with use of algae have been published in recent years (Dietz & Andersen, 2017, Krabbe, 2017) as well as a book of how to collect the algae and edible plants at the shore (Krabbe & Swane, 2019). A more technical survey about the contents of the algae is published by Holdt & Kraan (2011). The report 'Dyrkning og anvendelse af alger i Danmark' ['Growth and use of algae in Denmark'] (Hansen, 2013) is a survey of the potential for growing algae as a beneficial large-scale production in Danish waters. Seaweed aquaculture is also a benefit or tool for the maintenance and restoration of the marine environment. The algae will release oxygen during photosynthesis and take up nutrients, which may be in excess and therefore removed from the environment by the harvest.

Practical information
Collecting seaweeds

The algae, whilst highly adapted to their environment, are easily damaged or decay, especially in high temperatures, high light and low or no oxygen and they can die by evaporation. When you want to take the algae home and keep them in good condition, it is important to take care of them. Collect them in a bucket with plenty of seawater from the collection locality, and if they have to be transported for a longer time, transfer them into a plastic bag without water, and make sure that the bag also contains some air before being closed, then place the collections in a cool box. The closed bag prevents evaporation even without water and air which slows down the rate of decay, especially when kept cool. A small container with a lid is an excellent replacement for the plastic bag for tiny species. Place the algae in a refrigerator, or in another cool place when you arrive home, and deal with them within a few days. Bring some seawater from the collection locality so that you can lay the seaweeds out in a tray in the water when they are going to be examined or pressed. Tap water should not be used as this will affect the seaweeds, especially the reds whose pigments are water-soluble.

The algae from shallow water are easily collected by hand. A hand dredge is a net with a small iron frame with a sharp edge mounted on a long stick. The use of such a net makes it possible to reach down to about 2 m depth. To obtain seaweeds from greater depth, a scuba diver or tools used from a boat is necessary. The triangular dredge was previously the preferred tool for collecting algae at greater depth. As mentioned above, it consists of a triangular iron frame with coarse teeth to scrape the algae off the substrata, and a net with a fine mesh attached to the frame to collect the algae. When the dredge moves over the bottom several time, it is possible to get a relatively good impression of the algal vegetation, the number of species and their condition. The dredge may unfortunately also collect drifting algae, which can occur at a various depth and may be in a healthy condition, so it is impossible to tell if such individuals were attached or drift specimens. Another disadvantage of using a dredge is to know the exact depth of collection because the dredge may operate at a depth different from the one where the boat is located, and the difference could be particularly marked at localities with a steep seabed.

Herbaria

To make herbarium sheets, seaweeds are pressed in a plant press between sheets of absorbent paper such as newspaper. An ideal seaweed press is made of wooden slats where the air can circulate and tied with straps, but layers of newspaper are also fine and can be pressed with a weight. To press the seaweeds, they will need to be laid out in seawater. The seaweeds unfold when they are put in the water, especially the tiny, much-branched, bushy specimens, and this is taken advantage of when pressing them. The alga to be pressed is placed on a sheet of paper (ideally acid free paper) and laid down in a shallow tray with seawater and a plate of plexiglass (or similar) on the bottom. The alga is spread on the paper, which is then lifted out of the water by ease of the plate, is then peeled off the plate ready to dry in a plant press on the paper. Many algae stick to the paper by themselves, particularly the tiny ones. To avoid the seaweeds sticking to the material which is placed on top of them in the press, a thin cloth must be used to cover them before they are put in the plant press. The paper in the plant press or the newspaper will drain the water. It should be changed initially within 12 hours and then changed regularly (usually daily) until the seaweeds are dry. When dry, the cloth is carefully drawn away. Thin cloth of synthetic material is excellent, but gauze or thin cotton cloth were in common use in earlier times.

When the dried algae are to be kept as herbarium specimens, the paper on which they are pressed must be mounted on a heavier herbarium sheet and labelled with the name of the alga (if known), collection locality, including the grid reference if possible, date, depth collected and preferably how the collection took place. It is also important to record who made the collection (legit (leg.)), and who made the identification (determinavit (det.)). Detailed information and illustrations of how to press algae are presented by Kristiansen (1978b).

Slide preparations

Slide preparations are easily made permanent by use of Karo® (corn syrup) in a 60-75 % solution in seawater, perhaps with the addition of a few drops of formaldehyde to prevent development of mold in the storage bottle. A piece of the alga, to be studied is placed on the slide in a drop of seawater, and when finished make the slide preparation permanent by adding a drop of Karo® to one side of the coverslip to replace the water little by little, or by drainage with filter paper. After some time when the water has evaporated and the slide preparation is stable it can be sealed using clear nail varnish at the edges of the coverslip. It may be necessary to add slightly more Karo® during the drying process. Corn syrup is obtainable at supermarkets in Britain and the USA and in a few special shops with vegetarian food in Denmark.

Another and more involved method for making permanent slide preparations is mounting in glycerol. The alga is left in glycerol for at least a few hours, then a fragment is moved to a clean slide, but only such a tiny part that the glycerol does not run to the edges of the coverslip, which is placed on top of the alga supported by 3-4 splits of a coverslip. The glycerol is then surrounded by melted petroleum jelly, which flows under the coverslip. The day after when all is cool, it is possible to seal the edges of the coverslip with nail varnish.

For examination of some algae, it is necessary to study thin sections of them. These can be made by hand using a sharp razor blade but requires experience and care, or by using a freezing microtome.

Algal cultures

In some cases, it is desirable to study the algae in culture, or even necessary to obtain a reliable identification of an alga. Initiation of cultures from clean reproductive cells (spores), is preferable but not always possible. A fragment, preferably a tip of a branch is often sufficient to establish a crude culture for small algae with a simple construction, but additional species are often present and develop as weeds. A clean culture is obtained by removal of the unwanted species or alternatively the apex can be cut off growing branches without epiphytes and these tips transferred through a series of clean culture dishes containing sterile seawater, and finally leaving them to continue growth.

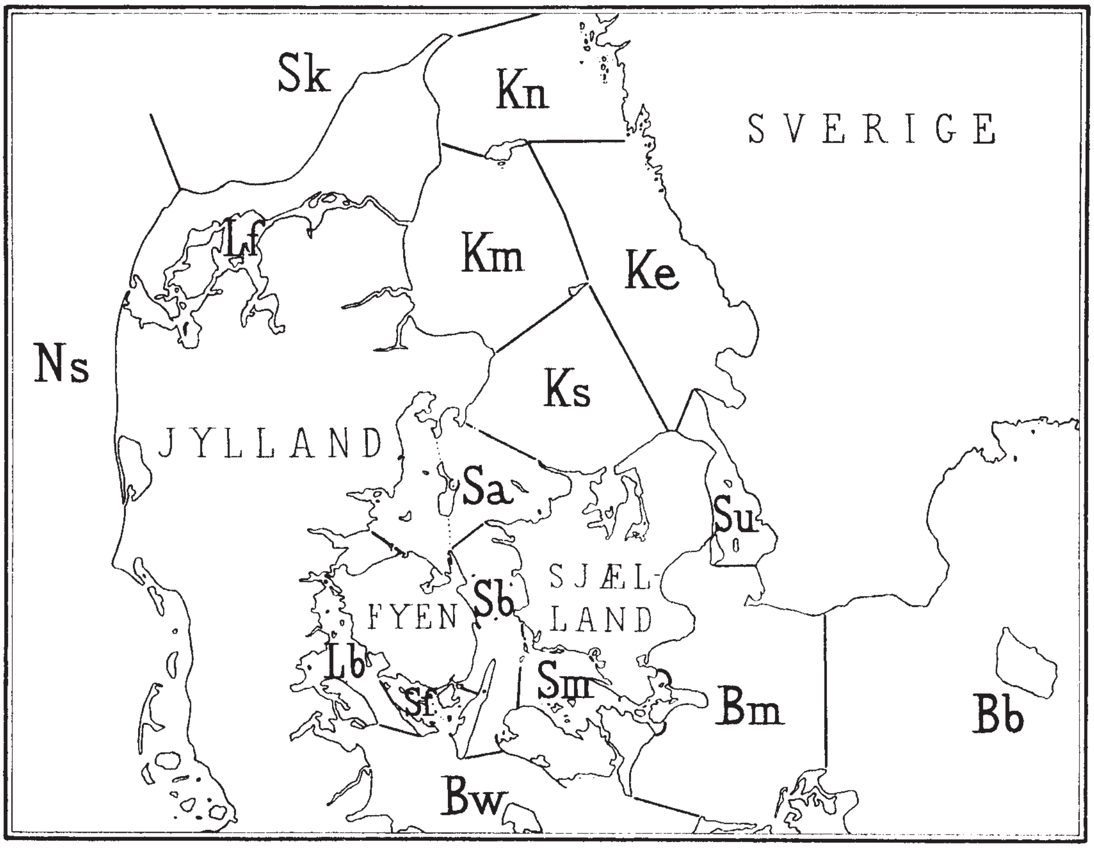
Seawater enriched with minerals and nutrients is in common use for culture studies. Different recipes are available, see for instance R. A. Andersen (2005) and T. Christensen (1988a). The cultures are kept at suitable temperatures, light intensities and day length.

References

Andersen, J. (1983), Andersen, R.A. (2005), Brodie & Irvine (2003), Brodie et al. (2007), Bunker et al. (2020), Burrows (1991), Choi et al. (2008), Christensen, C. (1924-26), Christensen, T. (1980, 1987, 1988a, 1994), Cornish et al. (2015, 2017), Dahl, K. et al. (2001, 2003), Dahl, S. (1941), Dietz & Andersen (2017), Dixon & Irvine (1977), Fletcher (1987), Hansen (2013), Hendriksen & Lundsteen (2014), Holdt & Kraan (2011), Irvine (1983), Irvine & Champerlain (1994), Kornmann & Sahling (1977, 1983, 1994), Krabbe (2017), Krabbe & Swane (2019), Kristiansen (1968, 1972, 1978a, b, 1984, 2014), Kristiansen & Pedersen (1979), Kristiansen et al. (1991), Kylin (1944, 1947, 1949), Larsen et al. (1986), Larsen & Hansen (2020) Le Gall & Saunders (2007), Leliaert et al. (2012), Lund (1934, 1950), Lyngbye (1819), Maggs & Hommersand (1993), Middelboe et al. (1997, 1998), Mouritsen (2009, 2013, 2017), Mouritsen et al. (2018a, b, c), Newton (1931), Nielsen (2005a, b), Nielsen & Lundsteen (2019a, b), Oltmanns (1905). Pedersen (2011), Petersen (1908, 1911, 1929, 1939), Rhatigan (2009), Rosenvinge (1909, 1917, 1923-24, 1931, 1935a, b), Rosenvinge & Lund (1941, 1943, 1947), Rueness (1977, 1992, 1998), Schneider & Wynne (2007, 2013), Silberfeld et al. (2014), Tendal (2011), Tolstoy & Österlund (2003), Wynne & Schneider (2010).

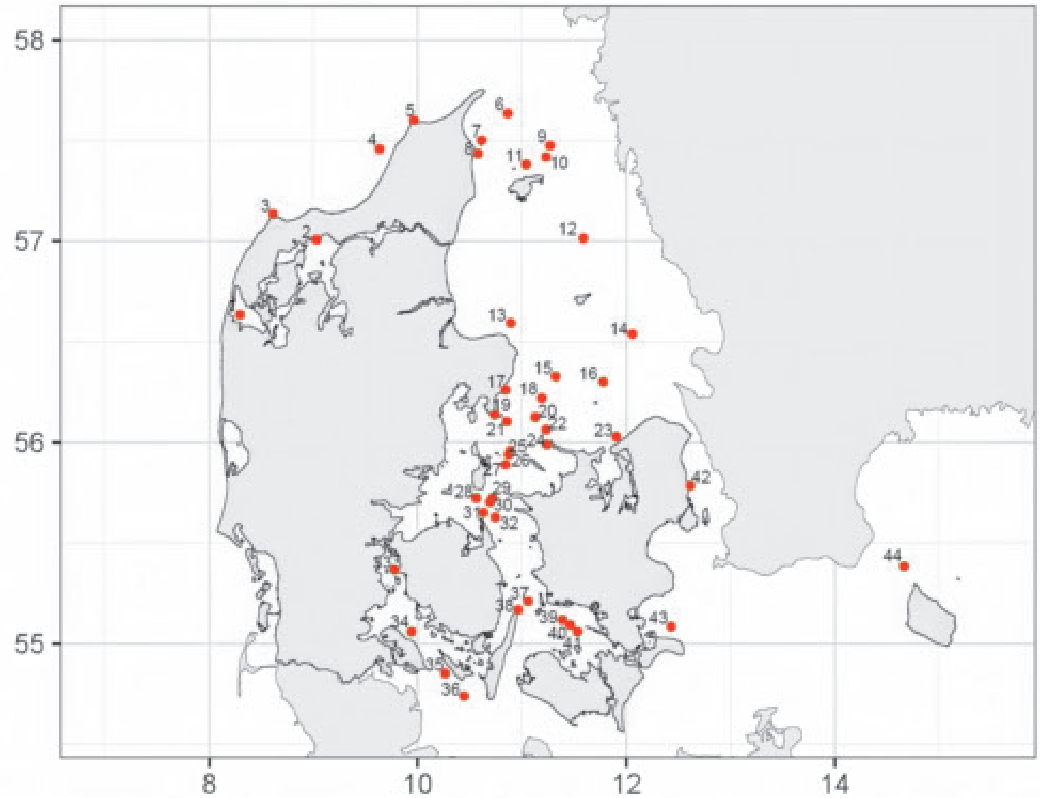
Districts and localities of stone reefs in Danish waters

The distribution of the algae in Danish waters is often referred to 16 districts e.g. in the checklists of Christensen et al. (1985) and Nielsen (2005a). These districts were introduced by Rosenvinge (1909) with exact information of their border. Information for each of the species mentioned by Rosenvinge includes localities of collection and reference to districts (Rosenvinge 1909, 1917, 1923-24, 1931, 1935a, b and also Rosenvinge & Lund 1941, 1943, 1947). Detailed description of the individual localities is presented by Rosenvinge (1909, 1923-24 and 1931).



The Danish districts. After Rosenvinge (1909)

Ns – North Sea
Sk – Skagerrak
Lf – The Limfjord
Kn – Kattegat, northern part
Ke – Kattegat, eastern part
Km – Kattegat, middle part
Ks – Kattegat, southern part
Sa – The waters around the island of Samsø
Lb – Little Belt
Sf – The archipelago south of Funen [Fyn]
Sb – Great Belt
Sm – The archipelago of Smålandshavet, between Sealand and Lolland
Su – The Sound [Øresund]
Bw – The Baltic, western part
Bm – The Baltic, the part around the island of Møn
Bb – The Baltic, the part around the island of Bornholm



Stone reefs mentioned in the book

Stone reef	Number	District
Albatros	24	Sa
Bolsaks	30	Sa
Bornholm, Davids Banke	44	Bb
Briseis Flak	15	Ks
Broen	38	Sb
Falske Bolsaks	29	Sa
Frederikshavn, Trestensrev	8	Kn
Fyns Hoved, Lillegrund	31	Sa
Gyldenløves Flak	43	Bm
Hanstholm, Roshage	3	Sk
Hastens Grund	18	Ks
Hatter Barn	27	Sa
Herthas Flak	6	Kn
Hirsholmene, Hvidstens Rev	7	Kn
Hirtshals, Møllegrund	5	Sk
Holmtange Hage	2	Lf
Jessens Grund	17	Ks
Kims Top	12	Ke
Kirkegrund	39	Sm
Klokkegrund	19	Ks
Læsø Trindel	10	Kn
Lønstrup, Rødgrund	4	Sk
Lysegrund	16	Ks
Middelflak	26	Sa
Moselgrund Nord	21	Sa
Munkegrunde	25	Sa
Nissum Bredning, Vageren	1	Lf
Øresund, Tårbæk Rev	42	Su
Paludans Flak	28	Sa
Per Nilen	11	Kn
Ryggen	32	Sb
Schultz's Grund	20	Ks
Sjællands Rev	22	Ks
Søndre Stenrøn	34	Lb
Store Middelgrund	14	Ke
Tangen	13	Km
Tønneberg Banke	9	Kn
Torup Flak	23	Ks
Vejsnæs Flak	36	Bw
Venegrund	40	Sm
Vengeancegrund	37	Sb
Vodrup Flak	35	Lb
Wedelsborg	33	Lb
Ydergrund	41	Sm

Phylum: Rhodophyta - Red algae

Class: Stylonematophyceae · Order: Stylonematales · Family: Stylonemataceae

Chroodactylon ornatum

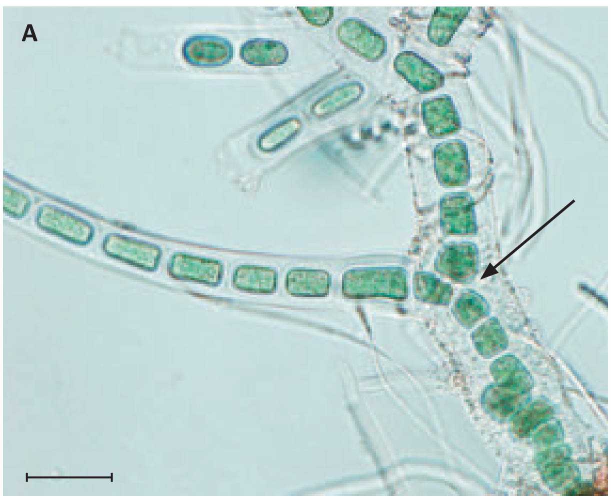
(C.Agardh) Basson

Blue-green Bead Weed

Appearance: Upright, thin, branched, blue-green filaments, usually first observed by microscopic examination.

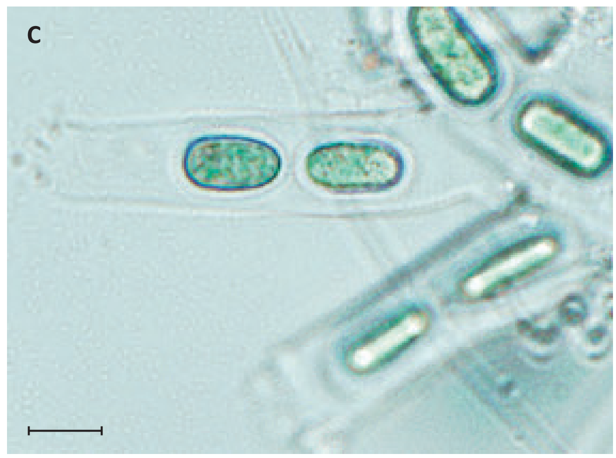
Structure: Upright filaments are uniseriate with sparse branching. The filaments are 9-17 µm in width, but up to 32 µm in older parts. Cells are cylindrical, often with rounded ends, and embedded in a thick, gelatinous outer wall. Cells are (3-) 7-10 µm in width and 1-2 times as long as wide. Growth is diffuse. Each cell contains a stellate blue-green plastid with one pyrenoid. Branching is false, occurring where the cell row separates into two. The part of the filament, that is below the separation point grows out of the thick outer wall and growth continues, looking like a branch. The part of the filament above the break continues to grow in the same direction as before.

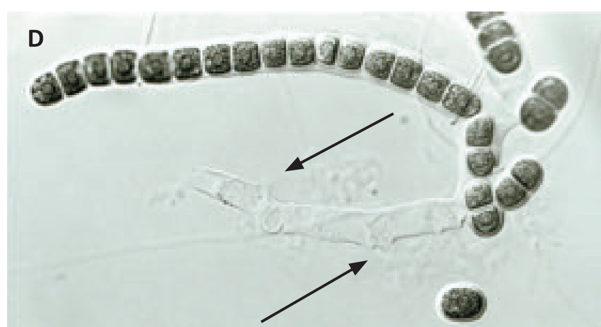
Reproduction: Asexual reproduction is by akinetes. They develop from vegetative cells and have a thick



A: *Chroodactylon ornatum*. False branching of filament with a thick outer wall (arrow). On *Leptosiphonia fibrillosa*. A, C: Beach south of Vesterø Havn, Læsø, drift, 12.9.2014. Scale 25 µm.

B: *Chroodactylon ornatum*. Stellate blue-green plastid, one pyrenoid. Sheltered side of Margretheholms Havn, Copenhagen, 0.5 m, 18.7.2013. Scale 10 µm.





C: *Chroodactylon ornatum*. Akinetes released through the apex of the outer wall. Scale 10 µm.

D: *Chroodactylon ornatum*. Akinetes released through pores in the outer wall (arrows). Alga in culture, initiated from material collected from the sheltered side of Margretheholms Havn, Copenhagen, 0.5 m, 9.9.2004.

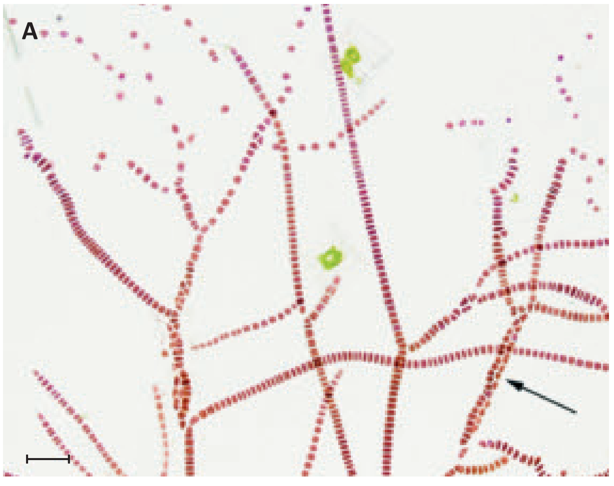
wall. Akinetes are released through pores in the outer wall that resemble small papillae, or they slide out through the apical part of the outer wall.
Seasonal variation: Collected in July-September.
Habitat: Epiphytic on other algae, particularly in brackish water in sheltered localities, 0.5-3 m depth.
Resembles: Red Threads (*Stylonema alsidii*) looks similar but this species has red plastids and many cells that are wider than long.
References: Brodie & Irvine (2003), Christensen (1980, *Asterocytis ramosa*), Rosenvinge (1909, *A. ramosa*).

Stylonema alsidii

(Zanardini) K.M.Drew
Red Threads

Appearance: Thin, reddish purple to bright brownish red upright filaments up to 5 mm in length. Usually first observed by microscopic examination.
Construction: Upright, repeatedly branched filaments of cylindrical cells in a thick, gelatinous outer wall. The filaments are usually uniseriate, but bi- or multiseriate cell rows may occur at irregular intervals. The thickness of the outer wall increases gradually

B: *Stylonema alsidii*. Cells with a stellate plastid per cell. Scale 25 µm.



A: *Stylonema alsidii*. Uniseriate alga of short cells and false branches. Short, biseriate parts (arrow) and released akinetes by disintegration of outer wall. Scale 50 µm. A, B: Thisted Bredning, 1 m, 18.8.2008.

C: *Stylonema alsidii*. Basal cell and thick, gelatinous outer wall. Store Middelgrund, 11 m, 25.8.1993. Scale 50 µm.

towards the base where filaments may be more than 50 µm in diameter, but only 15-20 µm near the apex of the filament. The filaments have a rounded basal cell that, with material of the wall, attaches the alga and the substratum together.

Cells within the thick outer wall are approximately equal in width from the base to top, 7.5-13 µm in width and 0.25-3 times as long as wide. Each cell contains a stellate plastid with one pyrenoid. There is diffuse growth with all cells able to divide. The branching is false as in *C. ornatum*.

Reproduction: Asexual reproduction is by akinetes that are released from the apex or by disintegration of the outer wall.

Seasonal variation: Collected in April-September.

Habitat: On pebbles and epiphytic on other algae, 0.5-18 m depth.

Resembles: Blue-green Bead Weed (*Chroodactylon ornatum*) is similar but blue-green and has longer cells with rounded ends as opposed to more angular cells in *S. alsidii*.

References: Brodie & Irvine (2003), Christensen (1980, *Goniotrichum alsidii*), Kim & Kim (2011), Rosenvinge (1909, *G. elegans*).

Stylonema cornu-cervi

Reinsch

Deer Horn Weed

Appearance: Irregularly multiseriate in most of the filaments and thereby differing from *S. alsidii*.

Habitat: Only collected once in Danish waters, drift with Scinà's Weed (*Scinaia furcellata*) at Lyngså Strand, 27.8.1975. Leg. & det.: Aa. Kristiansen.

References: Brodie & Irvine (2003).

Class: Compsopogonophyceae · Order: Erythropeltales · Family: Erythrotrichiaceae

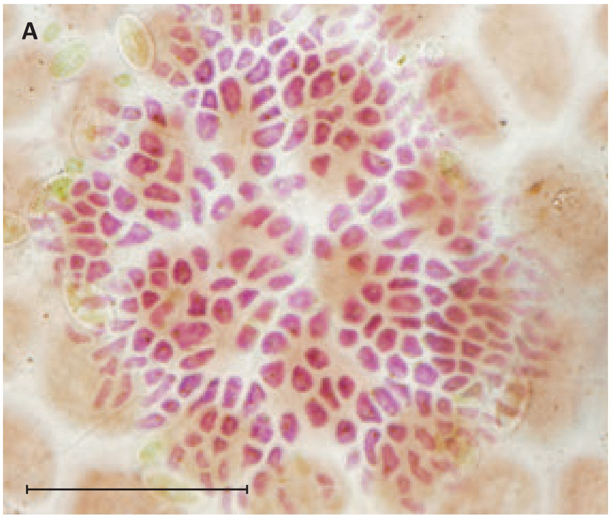
Erythrocladia irregularis

Rosenvinge

Irregular Patch Weed

Appearance: Irregular epiphytic patches up to 100 µm in diameter, with filaments free at the margin.

Construction: The patches consist of closely united branched filaments radiating from the middle. They form a single layer in the middle (pseudoparenchyma) and have mutually free filaments at the margin. Most of the cells are irregularly cylindrical, 3.5-5 µm in width and 7-11 µm in length. A single plate-shaped plastid, with one pyrenoid per cell.



A: *Erythrocladia irregularis*. Pseudoparenchyma with mutually free filaments at the margin. On *Phycodrys rubens*, Tønneberg Banke, 14.5 m, 16.1.1997. Scale 50 µm.

B: *Erythrocladia irregularis* with almost mature monospores (arrow). On the Knotted Thread Hydroid (*Obelia geniculata*), Store Middelgrund, 23 m, 22.8.1991. Scale 25 µm.

Reproduction: Asexual reproduction takes place by monospores formed as one of two cells after equal division of a vegetative cell in the middle of the alga. Monospores are spherical, about 4 µm in diameter, and look like small eyes before they are extruded through a pore in the wall. Sexual reproduction not known.

Seasonal variation: Collected in January-February and May-September, with monospores whenever recorded.

Habitat: Epiphytic on Sea Beech (*Delesseria sanguinea*), Sea Oak (*Phycodrys rubens*), and Pitcher Siphon Weed (*Polysiphonia stricta*), 6.5-20 m depth.

Resembles: Regular Patch Weed (*Sahlingia subintegra*) but this species has forked marginal cells, without mutually free filaments at the margin. Irregular Patch Weed (*Erythrocladia irregularis*) may also resemble young basal discs of Rosy Dew Drops (*Porphyropsis coccinea*), but this has no pyrenoids.

References: Brodie & Irvine (2003), Rosenvinge (1909).

Erythrotrichia

Red Hair Weeds

Appearance: Slender epiphytic filaments, 0.2-3 cm in length.

Construction: Upright filaments of cylindrical cells with diffuse growth. The plastid is stellate with a single distinct pyrenoid in each cell.

Reproduction: Only asexual reproduction, which takes place by monospores. Monosporangia form as the upper cell after oblique divisions of intercalary vegetative cells. When mature, monospores are extruded through a small exit tube. The process is repeated several times from the same vegetative cells, that grow out to fill the empty space after the monospores, have been extruded. Another monospore occurs and extrudes through the same exit tube as the former. The exit tubes gain several old wall layers over time, and the cell wall of the filament bulges with time. The monospores become lens-shaped and darker coloured than other cells at maturity. **References:** Brodie & Irvine (2003), Kornmann & Sahling (1977, 1985), Rosenvinge (1909, 1931).

Erythrotrichia carnea

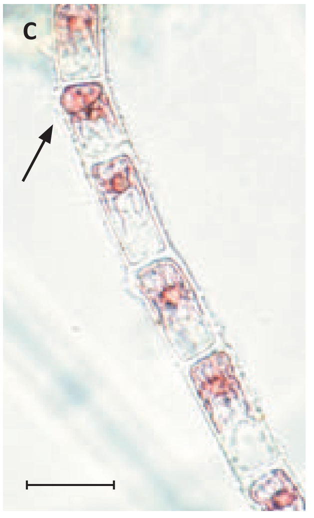
(Dillwyn) J.Agardh

Common Red Hair Weed

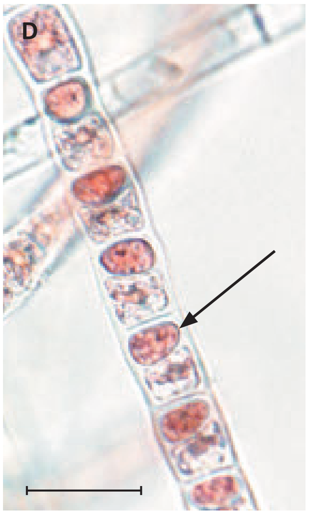
Appearance: Slender epiphytic unbranched filaments, up to 0.5-3 cm in length. The host species seems red-haired when many individuals of Common Red Hair Weed (*E. carnea*) are present.

A: *Erythrotrichia carnea*. On *Ceramium* sp., "red haired" by the presence of the epiphyte. Beach north of Vesterø Havn, Læsø, drift, 23.7.2018. Scale 1 cm.

B: *Erythrotrichia carnea*. Unbranched uniseriate filament. Stellate plastid with one pyrenoid. Margretheholms Havn, Copenhagen, 0.5 m, 21.9.2007. Scale 20 µm.



C: *Erythrotrichia carnea*. Cylindrical cells with stellate plastid. Monosporangia (arrow) in filament with bulging outline. Scale 10 µm. C-D: On *Zostera marina*, beach north of Vesterø Havn, Læsø, drift, 1.9.2014.



D: *Erythrotrichia carnea*. Monosporangia in several consecutive cells (arrow). Scale 10 µm.

E: *Erythrotrichia carnea*. A single basal cell (arrow). On *Ceramium* sp., beach north of Vesterø Havn, Læsø, 0.2 m, 2.9.2017. Scale 10 µm.

Construction: Uniseriate unbranched filaments of cylindrical cells. The filaments attached to the substratum with a single basal cell having a few short radiating extensions. The filaments are 6-24 µm wide and the cells 0.5-3 (-4) times as long as wide. The cell wall is relatively thick.
Seasonal variation: Collected all year with monosporangia recorded in July-September.
Habitat: Epiphytic on various red, brown, and green algae, on Eelgrass (*Zostera marina*) and epizoic on hydroids and bryozoans, 0.5-21 m depth.

Erythrotrichia reflexa

(P.Crouan & H.Crouan) Thuret ex De Toni
Recurved Red Hair Weed

Appearance: Dark red epiphytic filaments up to 2-5 mm in length. Seldom branched in Danish waters.
Construction: Young filaments uniseriate. In the middle part of older filaments longitudinal divisions occur and the filaments become bi- to multiseriate with two to four rows of cells and 32-63 µm wide. The filaments remain uniseriate in the upper and lower parts, 17-35 µm wide at the basal end. The filaments are often bent or curved and may have small branches near

B: *Erythrotrichia reflexa*. Multicellular basal part of filament. On Creeping Bush Weed (*Spermothamnion repens*), Stålhage, Hirsholm, 8 m, 3.2.1996. Scale 25 µm.

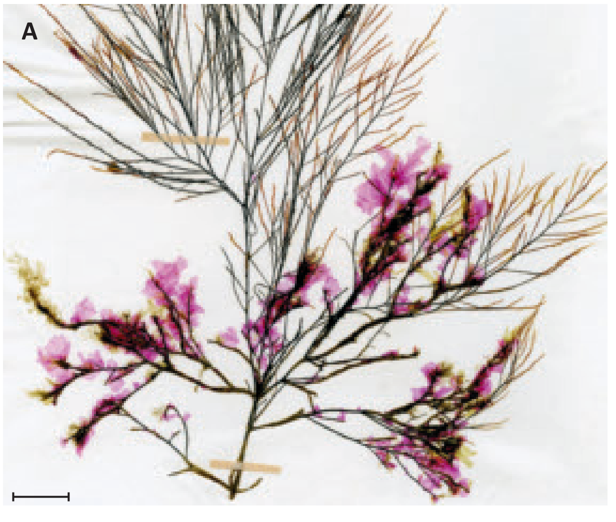
A: *Erythrotrichia reflexa*. Upright filament, multiseriate in the middle (lower arrow). Monospores and a bulging outline (upper arrow). On *Sphacelaria cirrosa*, Læsø Trindel, 11 m, 21.8.1991. Scale 25 µm.

the base. They have a multicellular basal attachment, which may be slightly conical in older filaments.
Seasonal variation: Collected in February, May-August.
Habitat: Epiphytic on various red and brown algae, 1-19 m depth.

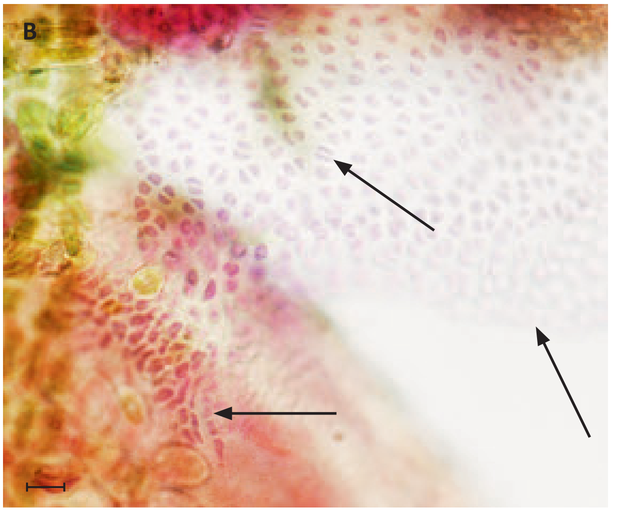
Porphyropsis coccinea

(J.Agardh ex Areschoug) Rosenvinge
Rosy Dew Drops

Appearance: Thin rounded blades, membranous, bright violet rose, up to 4 cm in height without a stipe, and without veins in the blade.
Construction: Specimens are initially disc-shaped consisting of closely united radiating filaments to form a single layer, although mutually free at the margin. Growth is diffuse. In time, the central part expands vertically to form a small sac (bladder) that splits to form a blade of one cell layer. Initially, the blade is shaped like a bowl, but later becomes a flat. The edge of the blade may be wavy, like a frill, due to many cell divisions near the margin. Cells are rounded to slightly angular towards neighbouring cells, and measure 3-8 µm in diameter. Cell walls are relatively thick. There is a single lobed plastid without pyrenoid in each cell.
Reproduction: Sexual reproduction unknown. Asexual reproduction by monospores, produced by scattered vegetative cells or cells near the margin of the blades.
Seasonal variation: Collected in April-October, monosporangia recorded in July.
Habitat: Epiphytic on various larger algae, frequent on Desmarest's Prickly Weed (*Desmarestia aculeata*), 2-24 m depth.
Resembles: The young disc resembles Irregular Patch Weed (*Erythrocladia irregularis*), but this has cylindrical cells, and plastids with a pyrenoid. Rosy Dew Drops (*Porphyropsis coccinea*) differs from species of *Neopyropia*, *Porphyra*, *Pyropia*, and *Wildemania* by having small cells.
Comment: Studied in culture by Kornmann & Sahling (1985).
References: Brodie & Irvine (2003), Kornmann & Sahling (1985), Rosenvinge (1909).



A: *Porphyropsis coccinea*. On lower part of *Desmarestia aculeata*. Stone reef outside Frederikshavn, 3-4 m, 20.6.1975. Scale 2 cm.



B: *Porphyropsis coccinea*. Part of basal disc (left arrow) with a young blade (right lower arrow). Diffuse growth (right upper arrow). Tønneberg Banke, 15 m, 8.6.1991. Scale 10 µm.

Sahlingia subintegra

(Rosenvinge) Kornmann

Regular Patch Weed

Appearance: Epiphytic, microscopic, almost circular discs up to 1 mm in diameter.

Construction: The discs consist of closely united radiating filaments forming a monostromatic pseudoparenchyma. The cells in central part are often oval, those at the margins approximately cylindrical, about two times as long as wide. The cells are 3-5 µm in width and 8-10.5 µm in length, occasionally forked. There is a parietal plastid with a single pyrenoid in each cell.

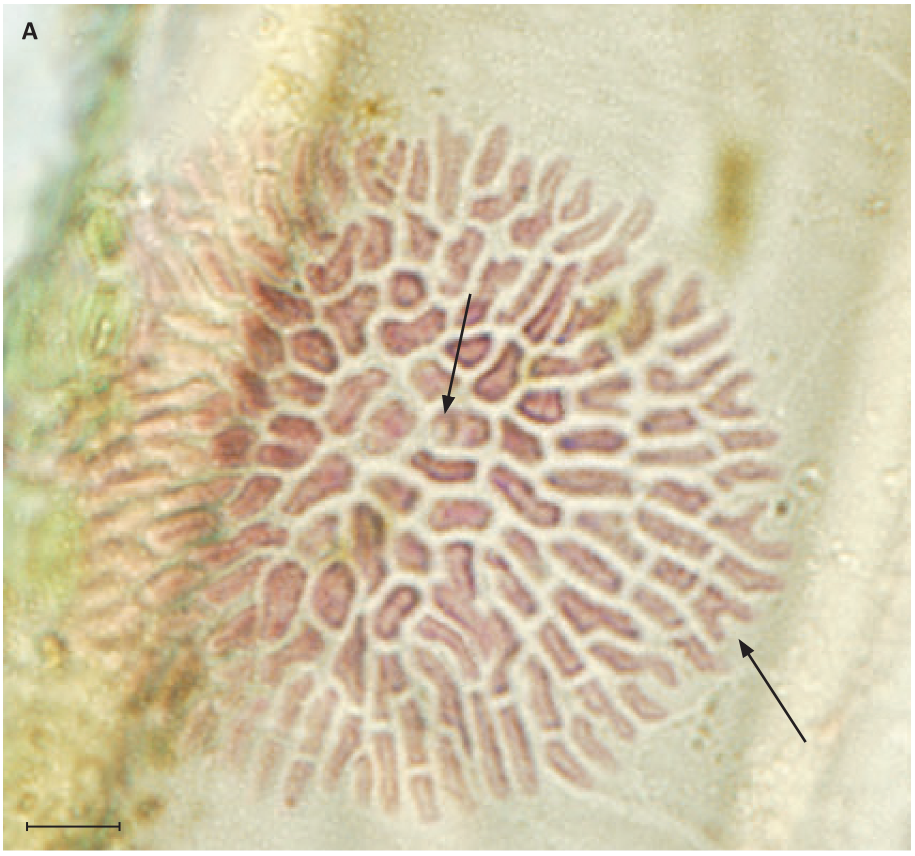
Reproduction: Asexual reproduction takes place by monospores from vegetative cells in the middle of the disc. The monospores are rounded and 4 (-5) µm in diameter. Sexual reproduction unknown.

Seasonal variation: Collected in June-October.

Habitat: Epiphytic on Pitcher Siphon Weed (*Polysiphonia stricta*), epizoic on hydroids and bryozoans, 7-20 m depth.

Resembles: Irregular Patch Weed (*Erythrocladia irregularis*) may look similar but has mutually free filaments at the margin.

References: Brodie & Irvine (2003), Kornmann (1989), Kornmann & Sahling (1985, *Erythropeltis*), Rosenvinge (1909, *Erythrocladia*).

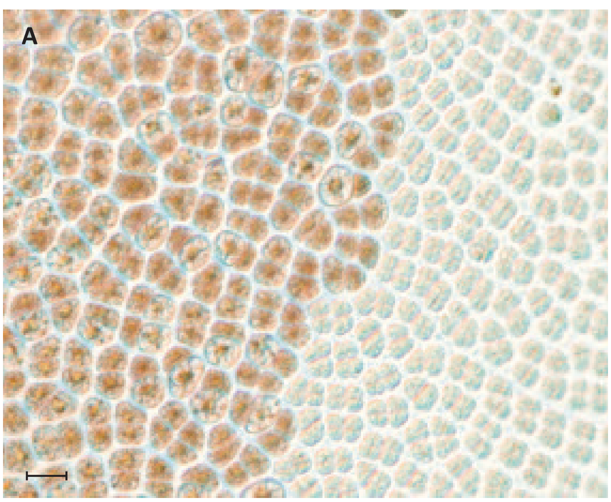


A: *Sahlingia subintegra*. Disc with forked marginal cells (arrow) and monosporangia from the middle cells (arrow). On the edge of a hydroid. Herthas Flak, 15 m, 28.8.1993. Scale 10 µm.

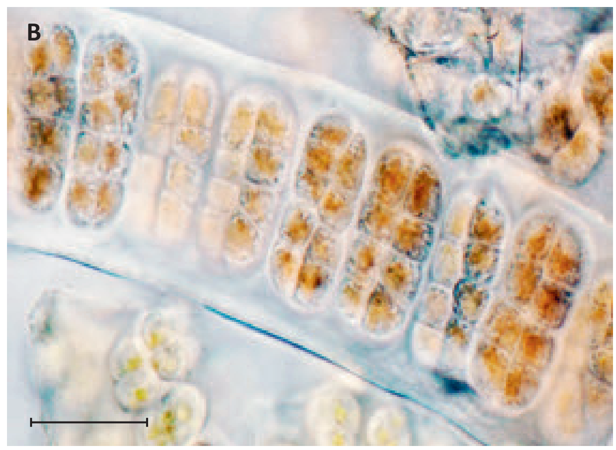
Class: Bangiophyceae · Order: Bangiales · Family: Bangiaceae

The species of Bangiales are blades or filamentous parenchyma. The bladed species were previously referred to *Porphyra* and the filamentous species to *Bangia*. There is considerable variation within individual species in shape as well as in colour, which makes it difficult to delimit and identify species. In recent years, the application of molecular techniques has led to a better understanding of the taxonomy and as a consequence, both *Bangia* and *Porphyra* have been split into more genera. In addition, species concepts have been revised due to the recognition of cryptic species previously considered variation of a single species. In Danish waters, four genera of bladed Bangiales occur: *Neopyropia*, *Porphyra*, *Pyropia* and *Wildemania*, all identified with the 298 base pairs in the 3' end of the plastid *rbc*L gene. The filamentous Danish species of *Bangia* have not been examined genetically and are retained here as *Bangia fuscopurpurea*, and the English name "Laver" is maintained for all species of *Neopyropia*, *Porphyra*, *Pyropia* and *Wildemania*.

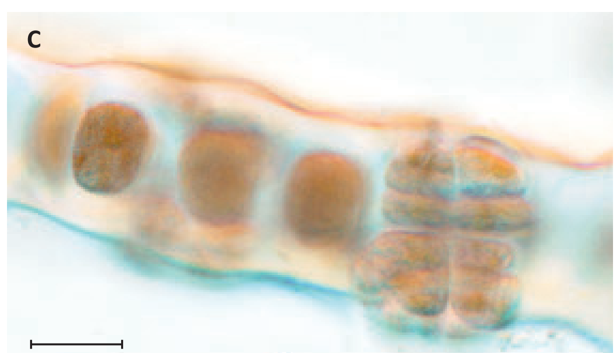
Reproduction: Life history heteromorphic, with blade or filamentous gametophytes, and a shell-boring, filamentous sporophyte (conchocelis). Gametophytes may be monoecious or dioecious. Male reproductive cells (spermatia) are produced by mitotic divisions in spermatangia. Special areas of the thalli with spermatangia (male sori) are pale cream in colour. Female gametes have a trichogyne (sometimes referred to as a prototrichogyne) to which spermatia attach as in trichogynes of other red algae. After fertilization, the zygote remains on the gametophyte and divides mitotically into zygotospores in zygotosporangia that are bright red in colour. The zygotospores are released by degradation of the wall of the zygotosporangium and germinate into the conchocelis. There are various vegetative reproductive cells. Archeospores form after differentiation of a vegetative cell. They are released



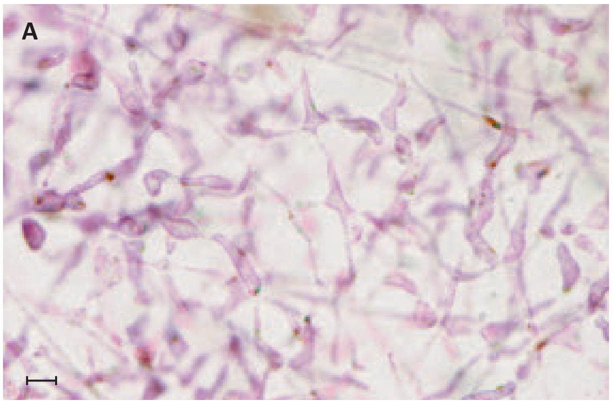
A: *Porphyra purpurea*. Light male part and dark female part of thallus. Scale 25 µm. A-C: Exposed side, Margretheholms Havn, Copenhagen, 18.7.2006.



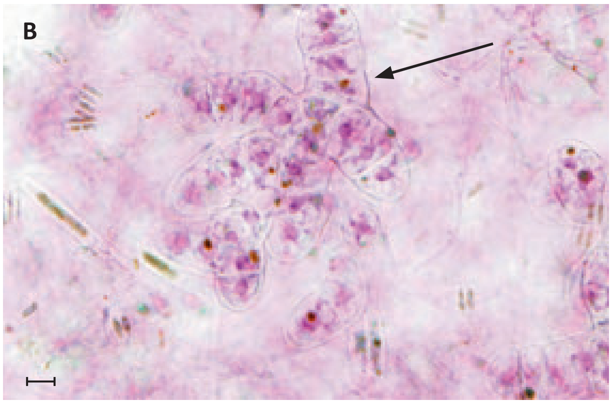
B: *Porphyra purpurea*. Male sori in transverse section. Scale 25 µm.



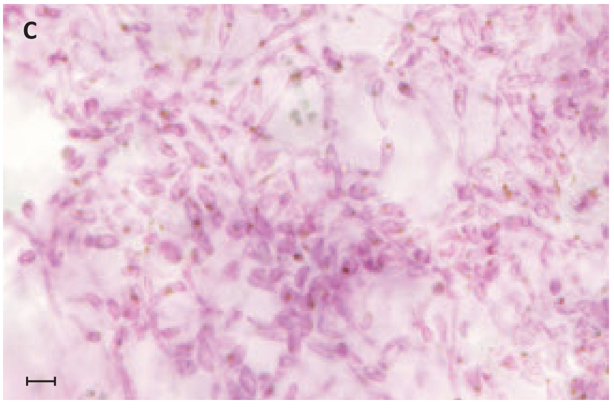
C: *Porphyra purpurea*. Young zygotosporangia in section, female part of thallus. Scale 25 µm.



A: Conchocelis. Filaments with scattered and opposite branches in a calcified shell. Vodrup Flak, 10 m, 31.7.1994. Scale 10 µm. A-C: Decalcified in 2 % acetic acid.



B: Conchocelis. Upright conchospore filaments, short cells with a central stellate plastid (arrow). Section of the alga in figure C, above the calcified shell. Scale 10 µm. B-C: Gyldenløves Flak, 10 m, 4.7.1997.



C: Conchocelis. Entangled filaments in the calcified shell. Scale 10 µm.

and germinate into a new upright thallus. Phyllospores is a collective term for zygotospores, agamospores and neutral spores which all form in packets of mitotically divided vegetative cells. Agamospores and neutral spores form after mitotic divisions of a vegetative cell. Unless these spores are germinated, it is not possible to know which sort they are. Agamospores germinate into conchocelis and neutral spores germinate into upright thalli.

The **conchocelis** is a system of filaments growing into calcified material such as shells of animals which become pink in colour. The conchocelis consists of uniseriate prostrate filaments with scattered and opposite branches. The cells are relatively long and narrow, c. 2 µm in diameter, interspersed at irregular intervals with inflated cells. These cells have a parietal plastid. Upright filaments may grow out of the calcified material from the prostrate filaments. The upright filaments have scattered branches consisting of relatively short cells, 14-16 or 9-11 µm in diameter. These cells have a central stellate plastid. They have a pit connection between cells of the same filament, a character in the Bangiales which is only known in the conchocelis. In the upright conchospore filaments, conchosporangial branches form conchospores which when released germinate into upright thalli. The conchocelis can also form neutral conchospores which when released develop either haploid or diploid conchocelis. Archeospores can also form which when released develop into the conchocelis.

Habitat: In Danish waters, the conchocelis occurs in shallow water in Acorn Barnacles (*Semibalanus balanoides*) and is frequent in Toothpaste Worm (*Spirorbis spirorbis*) on Wrack (*Fucus*). In deep water localities it is common in empty mollusc shells, and other calcified material such as worm tubes. Collected by dredge to 32 m depth. The conchocelis is known from culture studies of various species, but so far, has not been characterised for individual species in nature. Collections of conchocelis from Danish waters therefore have not been referred to species.

Comment: The conchocelis was originally described as a separate species (*Conchocelis rosea* Batters). In 1949 the British phycologist Kathleen Drew published it as

part of the life history for Tough Laver (*Porphyra umbilicalis*). Later culture studies showed that the conchocelis was part of the life history for species of Bangiales.
References: Brodie & Irvine (2003), Drew (1949), Mols-Mortensen (2007, 2014), Nelson et al. (1999), Rosenvinge (1909, 1931, *Conchocelis rosea*), Rueness (1977), Sánchez et al. (2014, 2015), Sutherland et al. (2011).

Identification key to species of Bangiaceae

1a.	Filament	*Bangia fuscopurpurea*
1b.	Blade	2
2a.	Uniformly coloured light brown, pink to mauve blades	3
2b.	Colour varies across the blade	4
3a.	Margins wavy, central part of blade may be partially distromatic, 14-40 µm in cross-section	*Wildemania amplissima*
3b.	Margins flat, blade monostromatic, 18-27 µm in cross-section	*Pyropia collinsii*
4a.	Blade broadly oval, circular or heart-shaped	5
4b.	Blade lanceolate or elongated oval	8
5a.	Blades like plastic and undulate, often forming a rosette to give an umbilicate appearance. Blades 58-70 µm in cross-section	*Porphyra umbilicalis*
5b.	Blade flat with holdfast at base	6
6a.	Blades longer than broad; fertile individuals solitary with a pale male sorus separate from the dark red female sorus. Blades 40-72 µm in cross-section	*Porphyra purpurea*
6b.	Blades circular or short tongue-shaped; fertile individuals with cream streaks or patches of male sori	7
7a.	Male sori oblong in more or less parallel streaks in upper part of blade. Blades 20-30 µm in cross-section	*Pyropia novae-angliae*
7b.	Male sori rounded or angular patches irregularly located in the upper part of the blade. Blade 34-50 µm in cross-section	*Neopyropia leucosticta*
8a.	Pink, elongate ribbon-shaped blades with parallel sides. Blade often folded in half longitudinally. Blades 48-69 µm in cross-section	*Pyropia peggicovensis*
8b.	Brownish lanceolate blades tapering to top	9
9a.	Blade 23-74 µm in cross-section. Small but distinctive robust stipe	*Porphyra linearis*
9b.	Blade 23-35 µm in cross-section	*Pyropia njordii*

Bangia fuscopurpurea

(Dillwyn) Lyngbye

Velvet Thread Weed

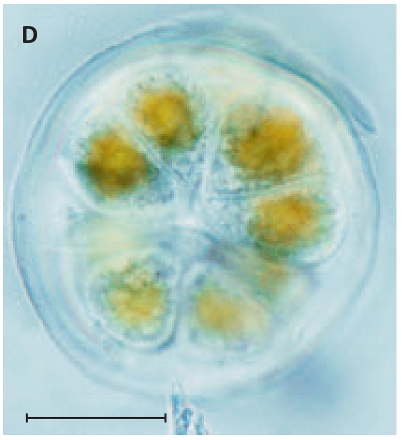
Appearance: Narrow unbranched filaments, up to 20 cm long and 20-50 µm wide. They have a bluish red or red-brown colour. They occur typically in dense stands and form a cover or belt on the substratum.

Structure: Young filaments are uniseriate with diffuse growth with cells as long as wide. Later the cells become relatively short and divided longitudinally by radiating walls, so the filaments become parenchymatous. The cells contain a stellate plastid with a big central pyrenoid. Rhizoids grow downwards from the basal cells and attach the filaments to the substratum.

A: *Bangia fuscopurpurea*. Cover of narrow filaments on a boulder. Margretheholms Havn, Copenhagen, 0 m, 20.7.2004.

B: *Bangia fuscopurpurea*. Uniseriate and parenchymatous filaments, both with short cells each of which contains a stellate plastid. Sheltered side of the jetty, Margretheholms Havn, Copenhagen, 19.2.2008. Scale 25 µm.

C: *Bangia fuscopurpurea*. Basal cells of uniseriate filament. Vesterø Havn, Læsø, 12.8.2015. Scale 25 µm.



D: *Bangia fuscopurpurea*. Parenchyma with radiating cell walls, transverse section. Vesterø Havn, Læsø, 1.3.2016. Scale 25 µm.

E: *Bangia fuscopurpurea*. Male filament with sori. Scale 10 µm. E-F: Wave-exposed jetty Margretheholms Havn, Copenhagen, 15.4.2004.

F: *Bangia fuscopurpurea*. Female filament with spores, a bulging outline and attached spermatia (arrow). Scale 25 µm.

Reproduction: Isomorphic dioecious gametophytes. Reproductive cells form from the vegetative cells in the upper part of the filaments after repeated divisions within the original vegetative cells. Filaments with mature rounded sporangia have a bulging outline. Spores are released by degradation of the sporangia walls.

Seasonal variation: Present all year, well-developed in winter and reduced to small patches in cracks on the shady side of boulders in dry calm summers. Individuals with gametangia recorded in February-April and July and mature zygotospores recorded in February-May. Vegetative spores almost always present.

Habitat: In the wave beaten and splash zone on rocks and boulders at exposed localities.

Comment: The genus name was published by the Danish phycologist H.C. Lyngbye in honour of Niels Hofman Bang (1776-1855), who was a pioneer in studies of Danish algae.

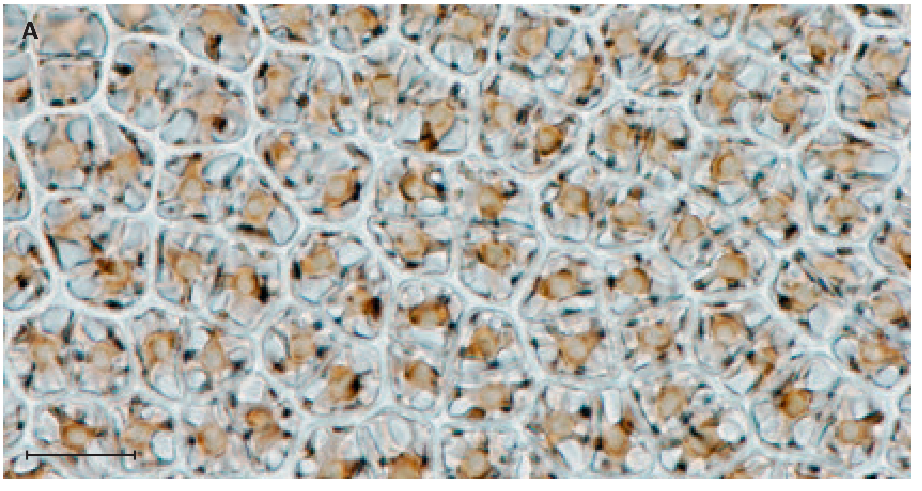
References: Brodie & Irvine (2003, *B. atropurpurea*), Nielsen (2005a), Rosenvinge (1909), Sutherland et al. (2011).

Neopyropia, Porphyra, Pyropia and *Wildemania*

Laver

The blade is membranous and flexible often brown to reddish brown, but the colour may have shades of rose, purple, greyish or greenish when fresh. In herbarium specimens, the colour often changes into bright rose, purple, or dark violet. The thalli are mono- or distromatic parenchymatous blades arising from a minute basal disc and may have a short stipe. Special rhizoidal cells with a club-shaped head and an elongate tail occur in the basal part of the blades and the discs. Cells occur individually just above the rhizoidal cells whereas cells in the upper part of the blades are dividing and occur in pairs. Each of the cells has a central stellate plastid with one pyrenoid.

Comment: The bladed Bangiales are economically important. They are used as an ingredient in various cuisines, particularly in Asia, and named "nori". They are used in sushi where sheets of nori are used as a wrap for small balls of boiled rice often with fish and shellfish. The cultivation of nori in Japan, China and Korea in particular, is economically highly valuable. The blades are grown on nets which cover large areas of the sea.



A, B: *Porphyra purpurea*. Monostromatic parenchyma, cells in pairs in the upper part of blade. Vegetative cells, each with a central stellate plastid with one pyrenoid. A, in surface view. B, transverse section. Exposed side of the jetty, Margretheholms Havn, Copenhagen, 18.7.2006. Scale 25 µm.

Neopyropia leucosticta

(Thuret) Yang & J.Brodie
Recent synonym: ***Pyropia* sp. *'leucosticta'***
Pale Patch Laver

Appearance: The blade is narrow to tongue-shaped, oblong or almost circular, 4-11.5 cm long and 1-9 cm wide. The base is typically heart-shaped with an inconspicuous stipe and a small basal disc. The blade is light red-brown when fresh, whereas the colour becomes light or dark rose when dried as herbarium individuals.

Structure: The blade is monostromatic, 34-50 µm thick.

Reproduction: Monoecious gametophytes. The male sori appear as pale cream oval to quadrangular patches in the upper part of the blades, mixed with female gametes and zygotosporangia. Asexual reproduction not described.

Seasonal variation: Collected in March-August.

Habitat: On Wrack (*Fucus*) and hard substrata in the littoral, and drift fronds collected at Hirtshals and Skiveren, Skagerrak.

Comment: The identity of the drift fronds at Skiveren was confirmed by DNA-sequences.

References: Rosenvinge (1909), Brodie & Irvine (2003), Mols-Mortensen (2014), Yang et al. (2020).

A

A: *Neopyropia leucosticta*. Rose blade with pale patches of male sori (arrow). The identity confirmed with DNA-sequence. Skiveren, drift, 14.6.1981. Scale 2 cm.

B

B: *Neopyropia leucosticta*. Dark rose blade with pale angular male patches. Same individual as illustrated by Rosenvinge (1909, Pl. II figure 4.). Harbour of Skagen, April 1905. Scale 2 cm.

Porphyra linearis

Greville

Winter Laver

Appearance: The blade is typically ribbon-shaped but may be broad and tongue-shaped, 2-37 cm long and 0.4-5 cm wide. It has a short robust stipe and a basal disc. The colour is typically brown to reddish brown with pink shades. Herbarium specimens on drying turn bright purple, wine-red or dark rose, often with a glossy surface.

Structure: The blade is monostromatic, 23-74 µm thick.

Reproduction: Typically dioecious gametophytes with pale male and red female sori at the margin of the blades. Monoecious thalli occasionally occur and have male and female areas in different parts of the frond. The pale male area may be in the upper or the lower part of the blade, in the middle part or to one side. Asexual reproduction is not described.

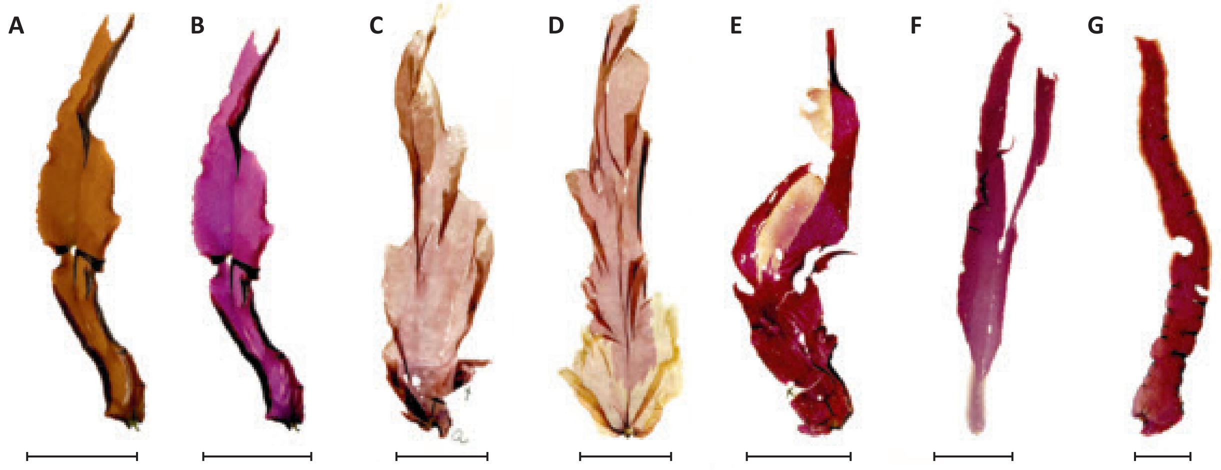
Seasonal variation: A winter species, collected in October-May.

Habitat: On stone at wave-exposed localities in the wave beaten and splash-zone and the littoral.

Resembles: *Porphyra umbilicalis* is reminiscent of *P. linearis* as the morphology in both species is very variable with overlap in appearance and habitat. Furthermore, they are closely related genetically and the mitochondrial COI marker does not separate them.

Comment: The occurrence in Denmark is confirmed with DNA-sequences of thalli from Frederikshavn, Hirsholm and Læsø.

References: Brodie & Irvine (2003), Mols-Mortensen (2007, 2014), Mols-Mortensen et al. (2012), Rosenvinge (1909, *P. umbilicalis* f. *linearis*).



A: *Porphyra linearis*. Brownish individual with robust short stipe, Photographed immediately after collection. Vesterø Havn, Læsø, 19.3.2015. Scale 2 cm.

B: *Porphyra linearis*. Same individual as in fig. A with change in colour to dark purple. Photographed a year after collection. Scale 2 cm.

C: *Porphyra linearis*. Dark rose broad blade. Identification confirmed by DNA-sequence. Scale 2 cm. C-D: Eastern harbour jetty, exposed side, Østerby Havn, Læsø, 29.3.2005.

D: *Porphyra linearis*. Broad blade with pale male sori in lower part of frond. Scale 2 cm.

E: *Porphyra linearis*. Pale male sector as a longitudinal middle part of the frond. Southern harbour jetty, Hirsholm, 13.2.1981. Scale 2 cm.

F: *Porphyra linearis*. Ribbon-shaped blade with pale male sori in lower part of blade and zygotosporangia in the upper part. Gilleleje, 11.1.1975. Scale 2 cm. Leg.: Aa. Kristiansen.

G: *Porphyra linearis*. Dark reddish brown blade with pale margin. Identification confirmed by DNA-sequence. Frederikshavn, 28.11.2008. Scale 2 cm.

Porphyra purpurea

(Roth) C.Agardh

Purple Laver

Appearance: The blade is broad oval to approximately circular or heart-shaped with a slightly curved apex and often a slightly undulate margin. The blade may be up to 100 cm long, but records of Danish individuals were only up to 31 cm long and 20 cm wide. There is a small basal disc and an inconspicuous stipe. The frond is red-brown to brown but may have pink or greyish shades. Herbarium specimens become dark to pale pink with purple shades. Herbarium specimens stick very well to the paper.

Structure: The blade is monostromatic, 40-72 µm thick.

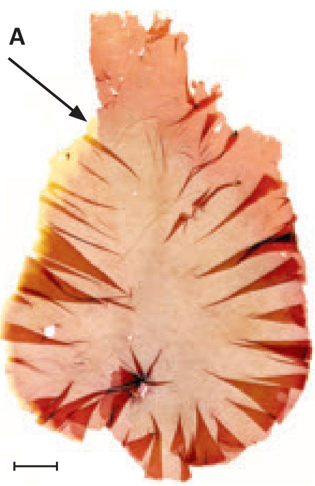
Reproduction: Monoecious gametophytes with male and female sori in clearly separated sectors of the blade and there is a distinct line between the pale male and the clear red female side of the blade. Asexual reproduction not described.

Seasonal variation: The species is best developed in summer and late summer but collected all year with a few and small individuals collected in winter.

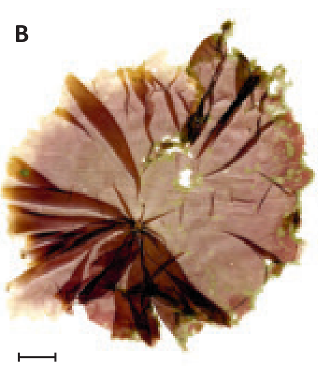
Habitat: On stones, bivalve shells, and on other algae, 0-1 m depth, mainly at sheltered localities.

Comment: The occurrence in Denmark was confirmed by DNA-sequences of thalli from Bønnerup Strand, Ebeltoft Vig, Havnsø, Hirsholm, Nordre Rønner, Læsø, Frederikshavn and Aarhus Bay.

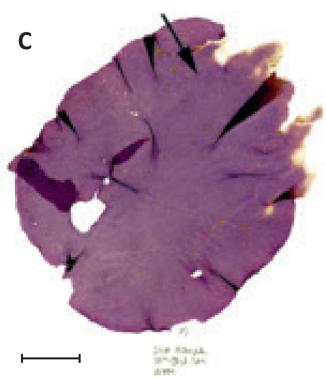
References: Brodie & Irvine (2003), Mols-Mortensen (2014).



A: *Porphyra purpurea*. Typical heart-shaped blade with undulate margin. Distinct line between the pale male and the red female sectors of the blade (arrow). Deget, Frederikshavn, 17.7.1977. Scale 2 cm.



B: *Porphyra purpurea*. Approximately circular blade with a pale male side and dark patches of zygotospores in the opposite side. The identification is confirmed by DNA-sequence. Moesgaard Strand, Aarhus Bay, 11.6.1979. Leg: L. Mathiesen. Scale 2 cm.



C: *Porphyra purpurea*. Dark purple blade, a short separating line between male and female sectors (arrow). The identification is confirmed by DNA-sequence. Southeastern part of Spirholm, Nordre Rønner, Læsø, 19.8.2005. Scale 2 cm.

D: *Porphyra purpurea*. Dark red blade with undulate margin, young individual without reproductive cells. The identification confirmed by DNA-sequence. Harbour jetty, Bønnerup Strand, 9.7.1990. Scale 2 cm.

Porphyra umbilicalis

Kützing

Tough Laver

Appearance: The blade is slightly coarse with the consistency of a plastic bag, slightly elongate, irregularly circular or with oblong lobes. The blade is often curly, occasionally growing like a rosette and it appears as if the base is in the centre surrounded by the blade, resembling a navel, without a recognizable stipe. The blade is up to 18 cm long and 15 cm wide, pale or dark brown or red-brown with bluish grey or greenish shades, and often with a greenish colour at the base. Reddish coloured individuals become darker in colour when dried as herbarium specimens, while the pale blades barely change colour. Herbarium specimens stick poorly to the paper and become very fragile so tear easily.
Structure: The blade is monostromatic, 58-70 µm thick.
Reproduction: Dioecious gametophytes are typical, but monoecious individuals occasionally occur. Both the pale male sori and the red zygotosporangia develop in the margin of the blades. Asexual reproduction is observed in Tough Laver (*P. umbilicalis*) from the Faroe Islands, neutral spores developed in the blade and grow into new blades. It is also very likely that agamospores occurred, and germinated and developed into conchocelis (personal observation, A. Mols-Mortensen).
Seasonal variation: Present all year.
Habitat: On stone and barnacles in the littoral, on wave exposed shores the splash-zone. The typical rosette-shape occurs in the upper zones at wave-exposed localities. Pale individuals occur at localities exposed to strong sun. Thalli with darker colours occur in shaded localities, although these colours may also be caused by nutrient rich conditions.
Comment: The occurrence in Denmark is confirmed by DNA-sequences of thalli from Copenhagen, Ebeltoft, Frederikshavn, Hirsholm, Kalø Vig, Korsør, Skagen, Skovshoved, Svendborg, Thyborøn and Aarhus.
References: Brodie & Irvine (2003), Kakinuma et al. (2008), Mols-Mortensen (2007, 2014), Mols-Mortensen et al. (2012).

A

A: *Porphyra umbilicalis*. Light greenish grey male gametophyte with pale sori at margin. Northern harbour jetty, Frederikshavn, 17.6.2000. Scale 2 cm.

B

B: *Porphyra umbilicalis*. Dark reddish female gametophyte; note the greenish shades around the centre. Dark red zygotosporangia at margin. Northern harbour jetty, Frederikshavn, 6.6.2002. Scale 2 cm.

Pyropia collinsii

C.Neefus, T.Bray & A.C.Mathieson

Dot Patch Laver

Appearance: The frond is an elongate oval or ovoid blade. Occasionally, the basal part is heart-shaped. The blade, 4-17 cm long and 1.5-9.5 cm wide, has a basal disc but no stipe. It is light brown to pink when fresh whereas herbarium specimens are pink with greyish shades at the base.

Structure: The blade is monostromatic, 18-27 µm thick.

Reproduction: Monoecious gametophytes, with male gametangia visible as small dots mixed with female gametes and zygotosporangia along the margin of the blade. Asexual reproduction not described.

Seasonal variation: Collected in February and May.

Habitat: On stone and other algae in the upper littoral to 0.5 m depth.

Resembles: Pale Patch Laver (*Neopyropia leucosticta*) also has patches of pale male sori, but these are larger than the small dots in Dot Patch Laver (*P. collinsii*).

Comment: The occurrence in Danish waters is confirmed by DNA-sequences of thalli from Gilleleje and Lynæs.

References: Bray (2006), Mathieson & Dawes (2017), Mols-Mortensen (2014).

A

A: *Pyropia collinsii*. Elongate oval blade, rounded base without stipe. The identity confirmed with DNA-sequence. Scale 2 cm. A-B: Eastern harbour jetty, sheltered side near the outer end, Gilleleje, 3.5.2008.

B

B: *Pyropia collinsii*. Blade with heart-shaped base. The identity confirmed with DNA-sequence. Scale 2 cm.

Pyropia njordii

Mols-Mortensen, J.Brodie & Neefus

Njords Laver

Appearance: The frond is a narrow, ribbon-shaped blade, occasionally broad oval, up to 13 cm long and 4.5 cm wide. Individuals in the few Danish collections were up to 11 cm long and 1.5 cm wide. Bases typically heart-shaped with an inconspicuous stipe and a small basal disc. The blade is light brown to pink when fresh, whereas herbarium individuals become dark purple.

Structure: The blade is monostromatic, 22.5-35 µm thick.

Reproduction: Monoecious gametophytes. The pale male area in one sector of the blade is distinctly separated from the red female gametes and zygotosporangia in the other side. The individuals collected in Danish waters did not have separate sectors and were considered to be young thalli. Asexual reproduction not described.

Seasonal variation: The few Danish collections were obtained in February, May and June.

Habitat: On stones in the wave beaten zone.

Comment: The occurrence in Danish waters was confirmed by DNA-sequences of thalli from Gilleleje and Hirsholm.

References: Mols-Mortensen et al. (2012), Pedersen (2011).

A

A: *Pyropia njordii.* Ribbon-shaped blade with heart-shaped base and inconspicuous stipe. The identity confirmed with DNA-sequence. Hirsholm, southern harbour jetty, 25.6.1985. Scale 2 cm.

B

B: *Pyropia njordii.* Ribbon-shaped, slightly split blade. The identity confirmed with DNA-sequence. Eastern harbour jetty, Gilleleje, 24.2.1993. Scale 2 cm.

Pyropia novae-angliae

T.Bray, Neefus & A.C.Mathieson

Striped Laver

Appearance: The blade is circular, oval or lanceolate, 4-18 cm long and 1-9 cm wide. Young blades have a small stipe which becomes inconspicuous in older individuals. The blade is light brown to olive green when fresh whereas herbarium specimens become light to dark rose with greyish shades in the middle and at the base, typically with a glossy surface.

Structure: The blade is monostromatic, 20-30 µm thick.

Reproduction: Monoecious gametophytes. Male sori are very distinct elongate pale cream streaks so the upper part of the frond appears striped. Male sori occur mixed with female gametes and zygotosporangia. Asexual reproduction not described.

Seasonal variation: Collected in February-December.

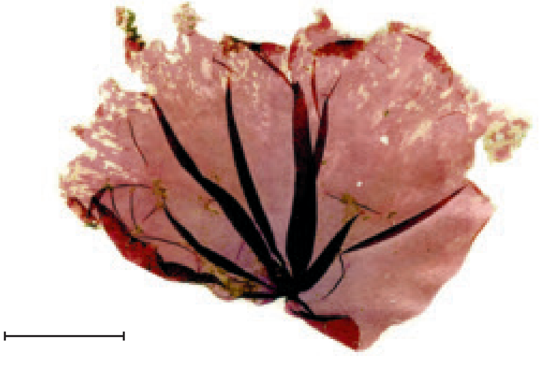
Habitat: On Serrated Wrack (*Fucus serratus*) and boulders in the wave beaten zone and the littoral.

Comment: The occurrence in Danish waters is confirmed by DNA-sequences of thalli from Ebeltoft, Elsinore, Korsør, Copenhagen, Læsø, Strib and Årøsund.

References: Bray (2006), Mathieson & Dawes (2017), Mols-Mortensen (2014).

A

B



C

C: *Pyropia novae-angliae*. Ribbon-shaped individual. The identity confirmed with DNA-sequence. C, E: Korsør Havn, 5.5.1936. Leg.: S. Lund. Scale 2 cm.

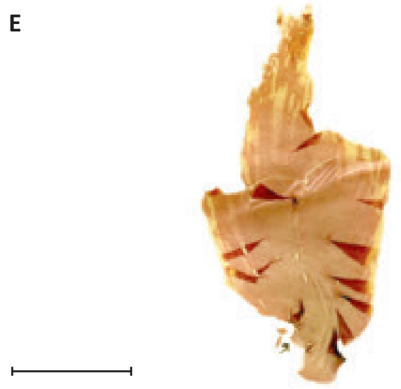
A: *Pyropia novae-angliae*. Brown roughly circular blade with olive green shade near the base. Many streaks of male sori in upper part. Photographed a few days after collection. Sheltered side of eastern harbour jetty, Gilleleje, 3.5.2008. Scale 2 cm.

B: *Pyropia novae-angliae*. Colour change to dark rose. Same individual as in fig. A, photograph obtained c. 9 months after collection. Scale 2 cm.

D

D: *Pyropia novae-angliae*. Circular blade. The identity confirmed with DNA-sequence. Southern harbour jetty, Tuborg Havn, The Sound, 7.10.1957. Leg.: Aa. Kristiansen. Scale 2 cm.

E

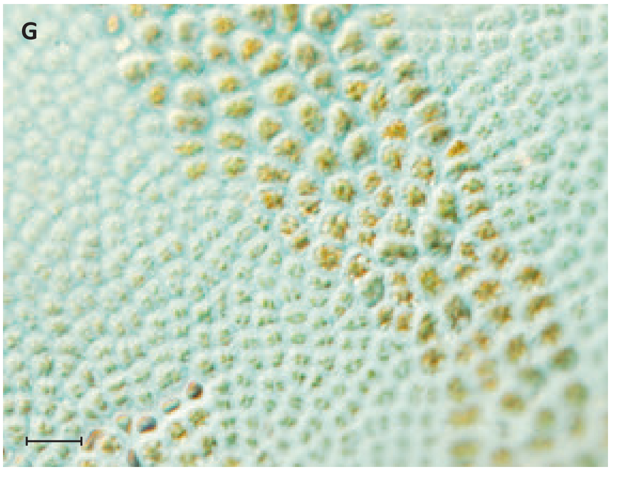


E: *Pyropia novae-angliae*. Lanceolate blade, stripes of male sori. The identity confirmed with DNA-sequence. Scale 2 cm.

F

F: *Pyropia novae-angliae*. The largest blade in Danish collections. The identity confirmed with DNA-sequence. Strib Marina, 26.4.1989. Leg.: L. Mathiesen. Scale 2 cm.

G



G: *Pyropia novae-angliae*. Male sori form pale patches among darker female gametes and zygotosporangia. Exposed side of jetty, Margretheholms Havn, Copenhagen, 28.5.2015. Scale 25 µm.

Pyropia peggicovensis

H.Kucera & G.W.Saunders

Ribbon Laver

Appearance: The blade is linear or ribbon-shaped, occasionally with a wavy margin, 5.5-22 cm long and 0.35-1.5 cm wide. Narrow individuals are often folded in half longitudinally and may be difficult to unfold. The base is rounded, typically with a distinct stipe and a small basal disc. The blade is light red with greyish shades towards the apex.

Structure: The blade is monostromatic, 48-69 µm thick.

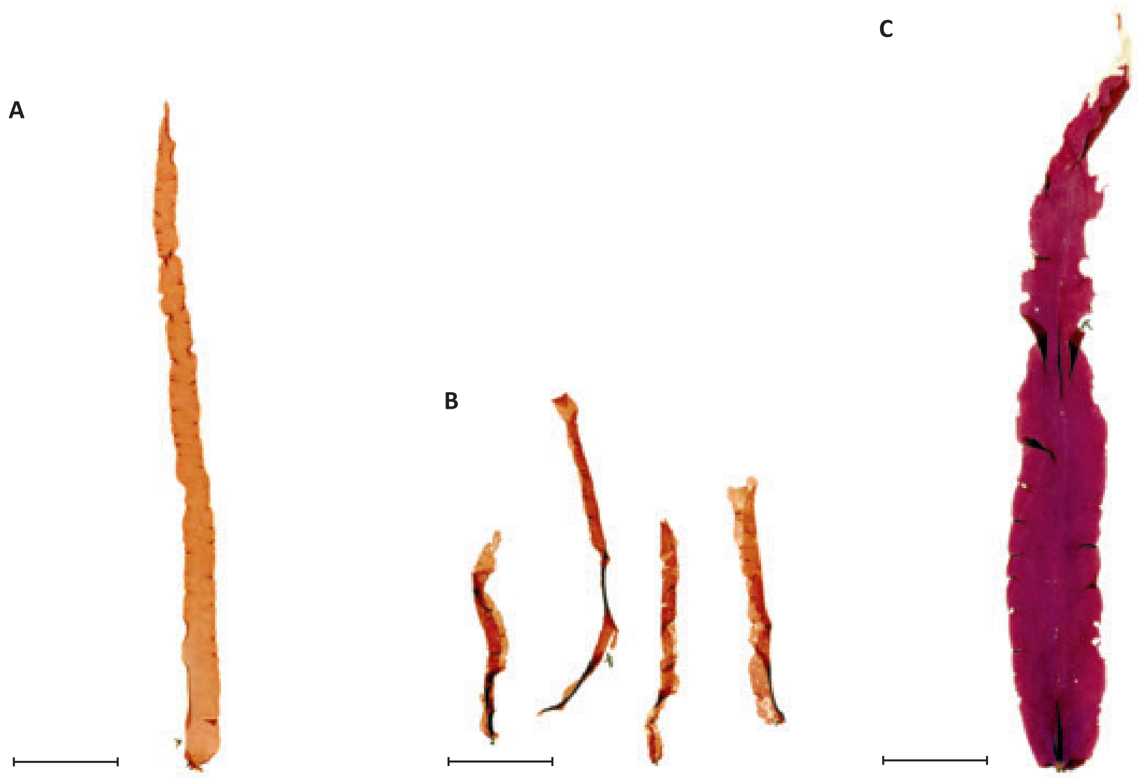
Reproduction: Observed phyllospores at the margin arranged in groups of four cells. So far, it is not known if they represent sexual or asexual reproduction. Male gametes not observed. Reproductive cells not observed in Danish collections.

Seasonal variation: Occur all year, collected in January-November.

Habitat: On boulders in the splash zone and the upper part of the littoral.

Comment: The occurrence in Danish waters was confirmed by DNA-sequences of thalli from Ebeltoft Vig, Frederikshavn, Hirsholm, Læsø, Skagen and Aarhus Bay.

References: Kucera & Saunders (2012).



A: *Pyropia peggicovensis*. Linear light red blade with narrow wavy edges. The identity confirmed with DNA-sequence. Northern harbour jetty, Hirsholm, 21.7.1978. Scale 2 cm.

B: *Pyropia peggicovensis*. Tiny linear light red blades, in part folded in half longitudinally. The identity confirmed with DNA-sequence. Risskov Søbad, Aarhus Bay, 8.4.1992. Leg: L. Mathiesen. Scale 2 cm.

C: *Pyropia peggicovensis*. Dark red ribbon-shaped blade. The identity confirmed with DNA-sequence. The windmill park, Ebeltoft Vig, 22.2.1989. Leg: L. Mathiesen. Scale 2 cm.

Wildemania amplissima

(Kjellman) Foslie

Northern Pink Laver

Appearance: The blade is broad oval, c. circular or oblong, typically with wavy margin, up to 100 cm long and 23 cm wide, but does not attain this size in Danish waters where the largest individuals collected were up to 33 cm long and 16 cm wide. Individuals collected attached at the stone reefs were 1.5-5 cm long and 1-2 cm wide. The base is triangular, or in older specimens, heart-shaped. There is a small distinct stipe and a basal disc. The blade is rose pink to purple with a glossy surface.

Structure: The blade is monostromatic apart from the middle part, which is partly distromatic, 14-40 µm thick.

Reproduction: Monoecious gametophytes. There are inconspicuous male sori mixed with female gametes and zygotosporangia along the margin of the blade. Asexual reproduction not described.

Seasonal variation: Annual, collected in spring and summer.

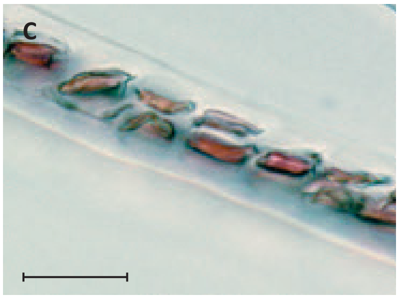
Habitat: Epiphytic on other algae and on shells and stone, 2-15 m depth.

Comment: The occurrence in Danish waters confirmed by DNA-sequences of thalli from Hirsholm.

References: Brodie & Irvine (2003).

A: *Wildemania amplissima*. Rose pink blade with a wavy margin. Male and female sori mixed in the upper eroded margin. On Forest Kelp (*Laminaria hyperborea*), Hirsholm, the bay northeast of the island, 3 m, 3.7.1987. Scale 2 cm.

B: *Wildemania amplissima*. Small blade from stone reef. Læsø Trindel, 8 m, 3.6.1993. Scale 2 cm.



C: In part distromatic, transverse section of the middle part of blade. Same individual as in fig. A. Scale 25 µm.

Class: Florideophyceae · Subclass: Ahnfeltiophycidae · Order: Ahnfeltiales · Family: Ahnfeltiaceae

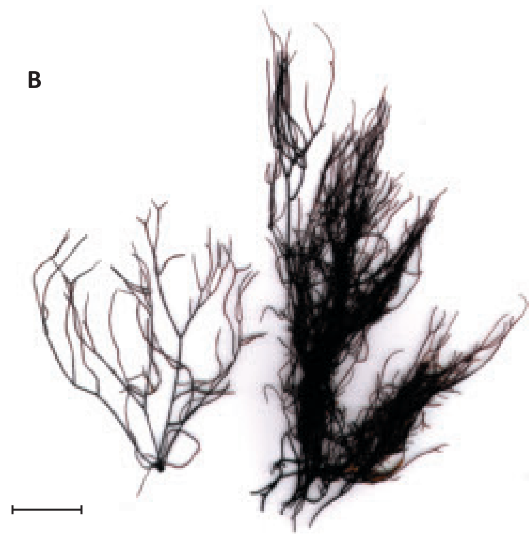
Ahnfeltia plicata

(Hudson) E.M.Fries

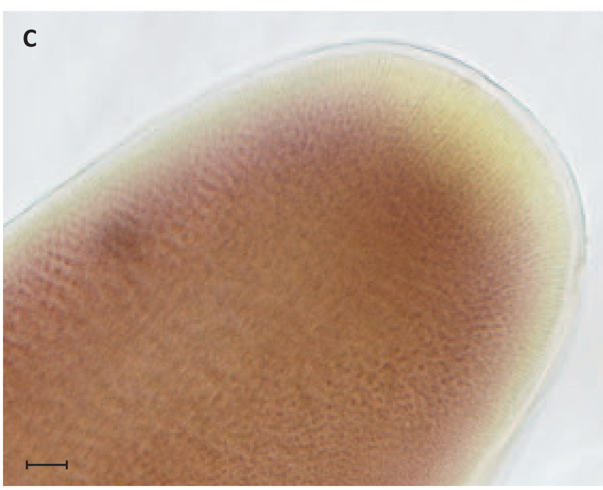
Black Scour Weed

Appearance: Upright wiry stiff bush-like thallus with branches of equal thickness, 500-900 µm diameter. Branching pattern variable, sometimes dichotomous, or in rows or scattered irregularly on all sides. In Danish waters the species is typically 5-10 cm but may reach 16 cm in length. It is very dark red-brown to almost black, but the colour varies to yellow-green in shallow

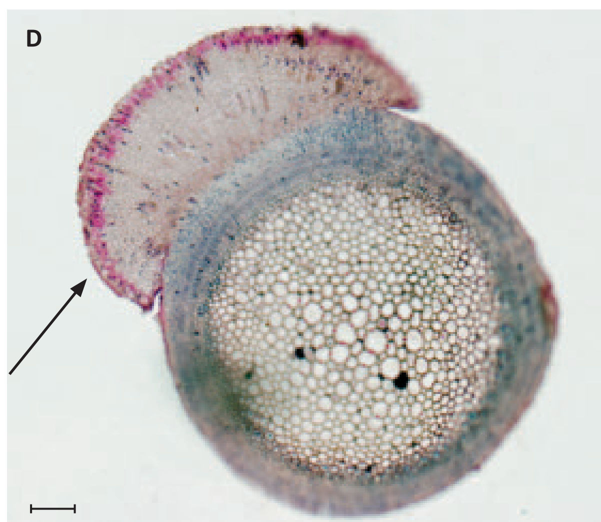
A: *Ahnfeltia plicata* Repeated dichotomous branching. Fiskerhagen, Aarhus Bay, 0.5 m, 4.3.1969. Scale 2 cm. Leg.: L. Mathiesen.



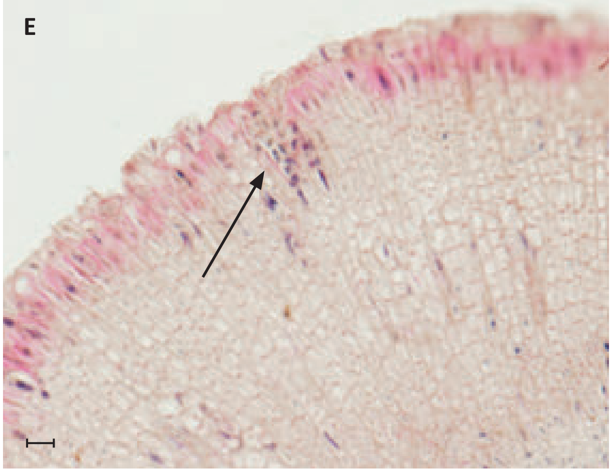
B: *Ahnfeltia plicata*. Terete, entangled branches. Briseis Flak, 6 m, 18.1.1997. Scale 2 cm.



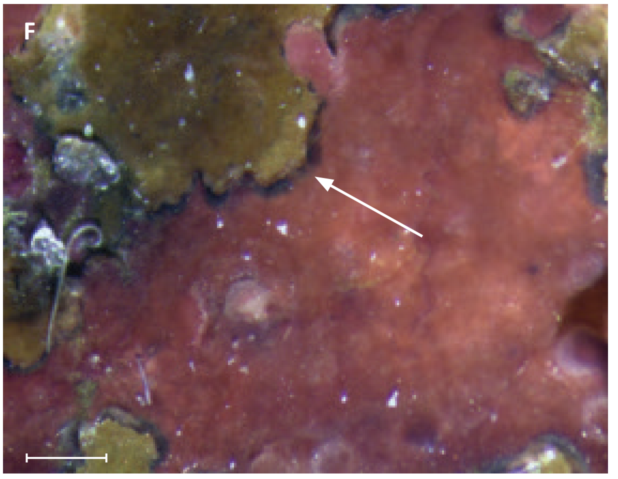
C: *Ahnfeltia plicata*. Apex of the multiaxial arrangement, longitudinal optical section. Briseis Flak, 5 m, 7.6.1990. Scale 20 µm.



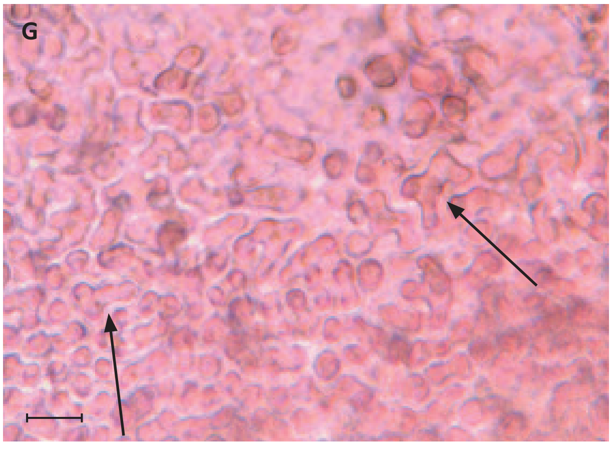
D: *Ahnfeltia plicata*. Female gametophyte with nemathecium (arrow) in cross section. Scale 50 µm. D, E: Slide preparation of Rosenvinge. Kerteminde, 29.11.1929.



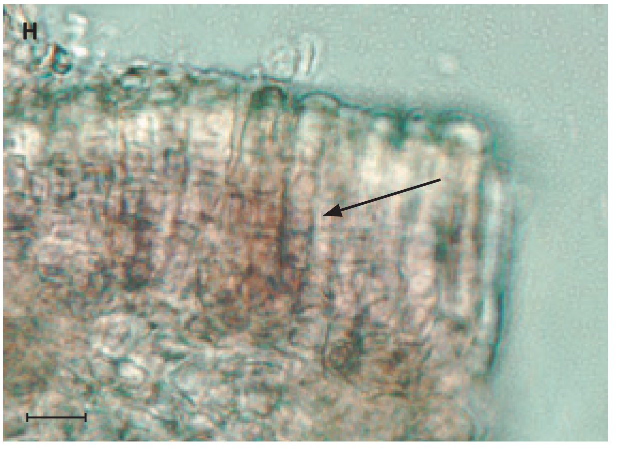
E: *Ahnfeltia plicata*. Gonimoblast (arrow). Part of figure D. Scale 10 µm.



F: *Ahnfeltia plicata*. Crustose phase with dark margin (arrow). Schultz's Grund, 7.4 m, 30.8.2013. Scale 500 µm. Photo by S. Lundsteen.



G: *Ahnfeltia plicata*. Basal layer of crustose phase with cell fusions (arrows). Schultz's Grund, 4.5 m, 30.8.2013. Scale 20 µm.



H: *Ahnfeltia plicata*. Crustose phase dense upright filaments (arrow), longitudinal section. Vejrø, 5 m, 8.4.1989. Scale 10 µm.

water exposed to in strong light. Drift specimens on the beach keep their shape even when completely bleached. The uprights arise from a crustose base, up to 1 cm in diameter.

Tetrasporophytes form extensive, thin, compact crusts on stones and boulders. They often have a characteristic dark margin when observed with a dissecting microscope.

Structure: The uprights are very compact and multiaxial in construction; filaments are composed of small cells with thick walls. The basal crusts and the tetrasporophytes have a characteristic blue-violet colour when seen in transparent light under the microscope. They have upright filaments of thick-walled cells 2.5-4 µm in width and twice as long as wide. There are many cell fusions in the basal layer, but no secondary pit connections.

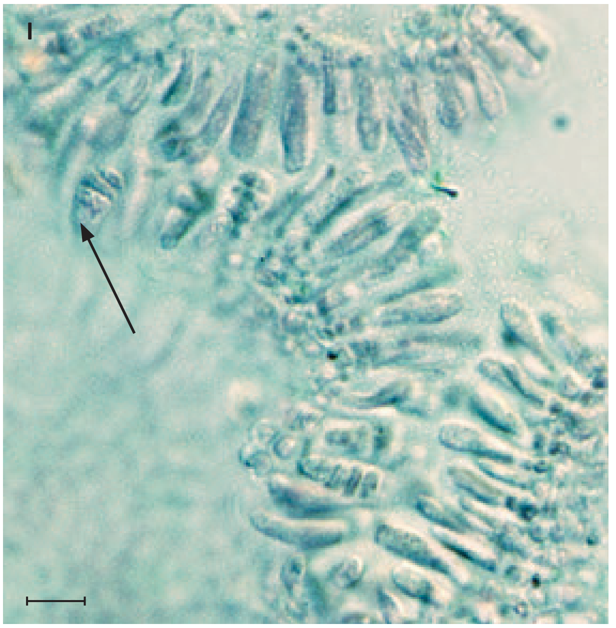
Reproduction: The life history is heteromorphic with upright male and female gametophytes and a crustose tetrasporophyte, previously considered to be a separate species, *Porphyrodiscus simulans* Batters. The gametophytes are monoecious and isomorphic. The reproductive structures develop in wart-like structures (nemathecia) approximately the size of a pinhead and confluent with the branches. These structures were previously considered a separate species, *Stereocolax decipiens* F.Schmitz. The antheridia form from surface cells and are colourless. The gonimoblasts develop between the radiating filaments forming the nemathecium. Tetrasporangia occur in small rounded sori on the crusts. They develop from surface cells and are zonate without sterile cells in between them. The fertile area protrudes slightly and is slightly slimy.

Seasonal variation: Perennial, growth of the upright thalli stops in winter, resuming again in early spring. Nemathecia observed in April-June, September-November and January, tetrasporangia in January.

Habitat: On stones and boulders, 0.5-18 m depth.

Resembles: Species of Hildenbrand's Red Weeds (*Hildenbrandia*) are similar to the crusts but bright red and without cell fusions.

References: Dixon & Irvine (1977, *A. plicata* and *Porphyrodiscus simulans*), Maggs & Pueschel (1989), Maggs et al. (1989), Rosenvinge (1931).



I: *Ahnfeltia plicata*. Crustose phase sorus of almost mature, zonate tetrasporangia (arrow). Schultz's Grund, 7 m, 18.1.1997. Scale 10 µm.

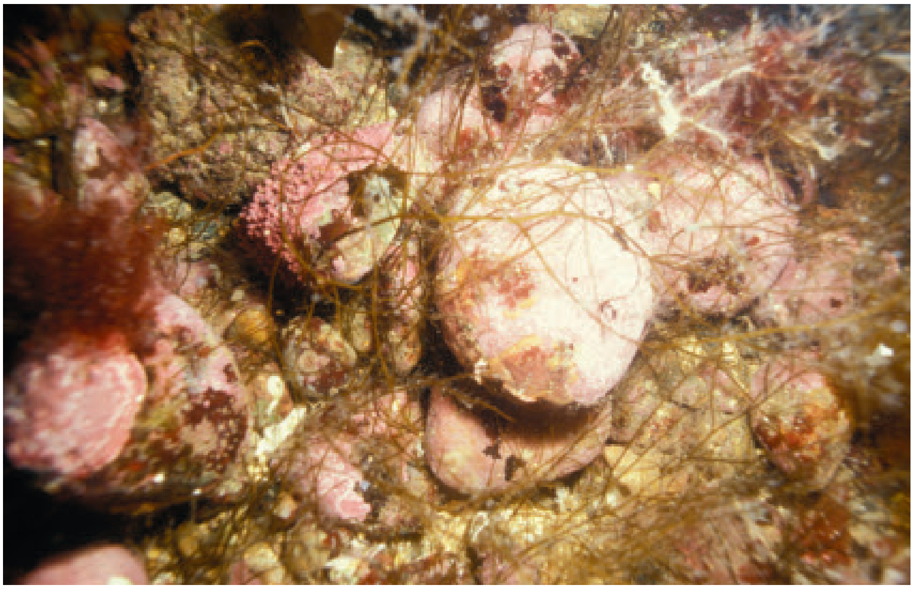
Subclass: Corallinophycidae · Order: Corallinales

Calcified red algae are perennial and have calcite in the cell walls which gives the thallus a chalky hue to the range of colours from pale pink through red to mauve/purple.

These coralline algae are extensive in Danish waters, particularly on the stone reefs with solid substrata and relatively high salinity. The number of calcified red algae decreases, when moving through the Danish waters towards the Baltic Sea and only one species, Common Shore Paint Weed (*Phymatolithon lenormandii*) occurs at Bornholm.

In the Danish waters there are 21 species of which 8 are crust-forming on stone (epilithic). One species, Northern Maerl (*Lithothamnion glaciale*), occasionally has branches (protuberances), which may break off and continue to grow unattached. Such free-living forms are called rhodoliths or maerl and occur for instance in the Limfjord. Southern Maerl (*Lithothamnion corallioides*) and Celtic Maerl (*Phymatolithon calcareum*) are species which only occur as rhodoliths in Danish waters. They are often the main components of maerl. There are no large areas of maerl beds in Danish waters but they are well-known for instance north of Brittany in France and in Iceland where maerl is used to improve farmland.

Two species are geniculate (articulated) and bush-like with branches consisting of calcified segments separated by successive uncalcified joints. Only Common Coral Weed (*Corallina officinalis*) is common in Danish waters whereas Slender-beaded Coral Weed



Crustose calcified red algae: Northern Maerl (*Lithothamnion glaciale*) has protuberances and the smooth species might be *Phymatolithon laevigatum*. Tønneberg Banke, 10 m, 10.6.1990. Photo by K. Dahl.

(*Jania rubens*) has recently been observed at a few localities in Danish waters (Nielsen, 1998). There are 9 epiphytic species on various algae such as Clawed Fork Weed (*Furcellaria lumbricalis*) and the haptera of Kelp (*Laminaria* spp.) or on leaves of Eelgrass (*Zostera marina*). These are small reasonably inconspicuous species, but well characterized.

The thallus of coralline algae is a pseudoparenchymatous multiaxial syntagma, distinguished as monomerous thallus or dimerous thallus. A monomerous thallus has filaments along the substratum which curve upwards and become perpendicular to the substratum. A dimerous thallus has creeping filaments along the substratum from which upright filaments arise and become perpendicular to the substratum. The filaments in both monomerous thalli and dimerous thalli are occasionally connected by cell fusions or secondary pit connections which are important characters for the systematics of families.

In some species, the monomerous thallus is coaxial. The cells here are uniform in length and the end-cell walls form curving rows in a transverse direction to the filaments.

Epithallial cells form the dorsal surface of the thallus and are therefore the apical cells in the filaments which form the thallus. The epithallial cell in *Phymatolithon* is released from the calcite before it is extruded which means that the cell increases and appears balloon-shaped, while the similar cell in *Lithothamnion* is boat-shaped. For further details on this subject and the shape of the meristem-cells see Wegeberg & Pueschel (2002). The growth of a filament occurs in a meristem cell which in some species is just below the epithallial cell(s). The meristem cell may be relatively long below the epithallial cell, as in *Lithothamnion*, or smaller as in *Phymatolithon*, in which new cells elongate gradually and become larger downwards in the filament below the epithallial cell.

The life history of the calcified red algae comprises antheridia, gonimoblasts and sporangia as in other red algae, although with the difference that most of the reproductive structures occur in cavities (conceptacles), which are elevated or submerged in the surface of the thallus. The conceptacles have a 'roof', and spores are released through pores in the conceptacle roof. Uniporate conceptacles have one pore whilst multiporate conceptacles each have several pores in the roofs. Gonimoblasts and antheridia always develop in uniporate conceptacles. Sporangia develop in multiporate conceptacles in the Hapalidaceae and in other families in uniporate conceptacles. The sporangia are zonate tetrasporangia with 4 spores or bisporangia with two spores.

When the spore attaches to the substratum and the first cell divisions take place without increase in thickness, a germination disc develops in some genera (Chamberlain, 1994). In *Hydrolithon* (Hydrolithaceae) species, the germination disc consists of 4-cells, whilst the germination disc in species of *Pneophyllum* (Corallinaceae) has 8 cells (Chamberlain, 1994, Wegeberg, 2001). It is possible to observe the germination disc with the light microscope when *Pneophyllum fragile* is epiphytic on leaves of Eelgrass (*Zostera marina*).

Characters to distinguish between the families of Corallinales in Danish waters appear in Table 1. For more details see Brodie et al. (2016), Kato et al. (2011) and Woelkerling (1988).

The identification key includes species collected in Danish waters and identified to species within the last 40 years, and the key is exclusively developed for these species. If the key is used for a flora with more species, for instance the British flora, it may not be exact. Irvine & Chamberlain (1994) contains more details and is also of help for identification of Danish species.

A magnifying glass or dissection microscope is necessary in some cases and the individuals must be well-developed and possess the characters that are necessary for identification, for instance conceptacles. Some genera are difficult to distinguish without sections for light-microscopy because the genus characters rely on morphology of, for example, epithallial cells as described above. Calcified red algae can be sectioned with a glass knife in a microtome, where the necessary sections 5-8 µm thick can be obtained. The best sections with the most details are obtained after the material is decalcified and embedded in resin in a gradual process after which the sections can be made. A less demanding procedure for sectioning is obtained by use of a freezing-microtome, which is sufficient for slightly thicker sections for identification of e.g. *Pneophyllum* species. These epiphytic species are identified based on filaments around the pore of the conceptacle and must be sectioned for light-microscopy for a reliable identification.

References: Brodie et al. (2016), Chamberlain (1994), Irvine & Chamberlain (1994), Kato et al. (2011), Le Gall & Saunders (2007), Nielsen (1998), Wegeberg (2001), Wegeberg & Pueschel (2002), Woelkerling (1988).

Table 1. Families in Corallinales based on the characters which separate the species representing families in Danish waters.

Corallinaceae		**Hydrolithaceae**	**Lithophyllaceae**	**Hapalidaceae**
Geniculate; bushy and geniculate	Crusts; diminutive <0.5 cm in diameter	Crusts; diminutive <0.5 cm in diameter	Crusts; often epiphytic	Crusts; some species form rhodoliths
	Germination disc 8-celled	Germination disc 4-celled		
	Cell fusions	Cell fusions	Secondary pit connections	Cell fusions
	All types of conceptacles uniporate	All types of conceptacles uniporate	All types of conceptacles uniporate	Sporangia conceptacles multiporate

Identification key to species of Corallinales

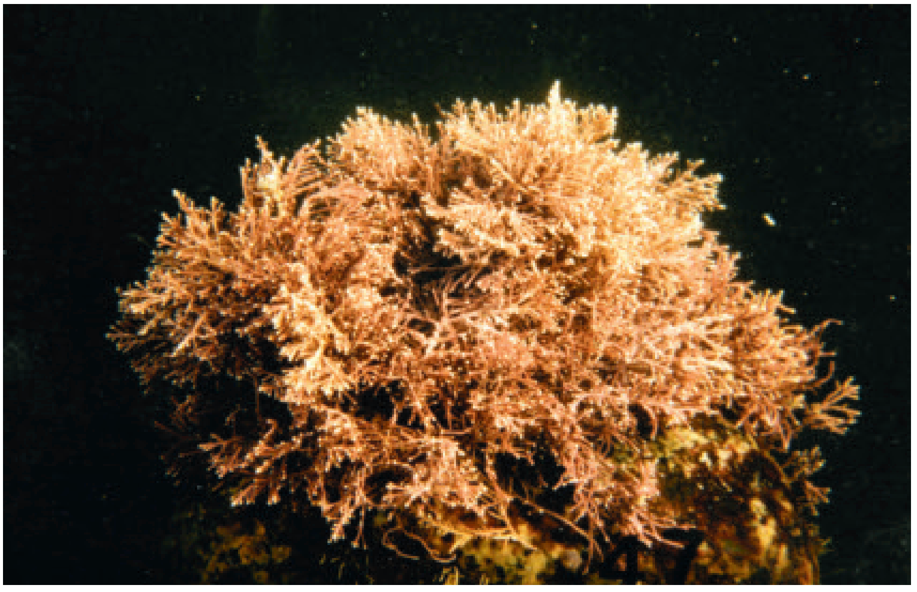
This field key is a help to identify Danish specimens of coralline red algae. A magnifying glass can be helpful and in some cases, it is necessary to observe specific characters. Some of the epiphytes can only be identified with sectioning and need to possess the characteristic features (e.g. conceptacles).

For further help, the Corallinales and Hildenbrandiales volume of Seaweeds of the British Isles (Irvine & Chamberlain, 1994) is recommended.

1a.	Loose-lying (rhodolith)	2
1b.	Attached to substratum (epiphytic, epizoic or epilithic)	3
2a.	Small fragile rhodolith with attenuating, spreading branches	*Lithothamnion corallioides* or *Lithothamnion glaciale*
2b.	Perpendicular branch angles, flat branch tips	*Phymatolithon calcareum*
3a.	Epilithic (on stone) or epizoic (e.g. shells)	4
3b.	Epiphytic	14
4a.	Geniculate bushy thallus	5
4b.	Non-geniculate. Crust-forming thallus	6
5a.	Branching pinnate	*Corallina officinalis*
5b.	Branching dichotomous	*Jania rubens*
6a.	Diminutive thallus, < 0.5 mm in diameter, a keen eye possibly helped by a magnifying glass necessary for observation of imbricate thallus or thallus not covering the substratum completely	7
6b.	Larger thallus, observable with the naked eye	8
7a.	Conceptacles with a characteristic white top	*Pneophyllum lobescens*
7b.	Conceptacles of same colour as thallus	*Hydrolithon boreale*
8a.	Relatively thin crust, often < 1 mm thick	9
8b.	Relatively thick crust > 1-2 mm thick	12
9a.	Granulated crust. Conceptacles elevated, often numerous and slightly trapezoid in profile. Old, emptied conceptacles are often broken, leaving cup-shaped scars	*Phymatolithon lenormandii*
9b.	Relatively thin and smooth crust	10
10a.	Conceptacles submersed often with a narrow white ring	*Phymatolithon laevigatum*
10b.	Conceptacles elevated above thallus surface	11
11a.	Conceptacles white and prominent, as if "put on the top" of the thallus surface	*Lithothamnion sonderi*
11b.	Large (c. 1 mm in diameter), multiporate conceptacles of the same colour as the thallus surface	*Phymatolithon tenue*

12a.	Smooth crust. Texture matt, colour grey-bluish. Conceptacles submersed and visible as small pinholes at the surface, often gathered in more whitish areas of the thallus surface	*Lithophyllum crouaniorum*
12b.	Uneven crust with more or less glossy surface	13
13a.	Undulating crust "floating" over the stone. Conceptacles submersed with a thick elevated ring. This species dries to a characteristic grey-greenish colour	*Phymatolithon purpureum*
13b.	Protuberant crust. Conceptacles level with or slightly to completely elevated above thallus surface	*Lithothamnion glaciale*
14a.	Multiporate sporangial conceptacles with dark depression (resembling a volcano) in the middle	*Melobesia membranacea*
14b.	Uniporate sporangial conceptacles	15
15a.	Relatively well-developed thallus (250 µm to several millimetres thick)	16
15b.	Very thin thallus (≤ 100 µm thick)	17
16a.	Conceptacles prominent	*Titanoderma pustulatum*
16b.	Conceptacles in level with thallus surface. Epiphytic on *Corallina officinalis* and *Furcellaria lumbricalis*	*Titanoderma corallinae*
17a.	Conceptacles in level with thallus surface	*Pneophyllum fragile*
17b.	Conceptacles prominent. Microscopic examination of sections needed for further identifications	*Pneophyllum coronatum*, *P. confervicola*, *P. limitatum*, or *P. myriocarpum*

Family: Corallinaceae



Corallina officinalis. Læsø Trindel, 8 m, 3.6.1993. Photo by K. Lundshøj.

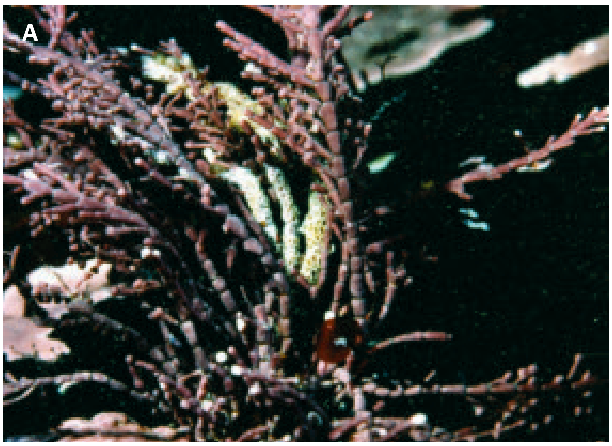
Corallina officinalis

Linnaeus

Common Coral Weed

Appearance: Upright bushy geniculate chalky red alga, up to 8-10 cm high, attached to stones and boulders by a basal-crust. Thallus flattened with feather-like branching, and slightly flexible due to the geniculate construction of calcified segments separated by successive uncalcified joints.
Structure: Monomerous and coaxial thallus.
Resembles: Slender-beaded Coral Weed (*Jania rubens* (Linnaeus) J.V.Lamouroux) is another bushy chalky red alga but has forked branches. Collected at Jegens Odde, Læsø, 10-12 m depth, 23.8.2021. Also recorded at a few other localities in recent years.
Habitat: Appears in shallow water at wave-exposed localities and collected by divers to 15 m depth.
Comment: The Latin species name *C. officinalis* refers to previous medical use as a vermifuge.
References: Chapman & Chapman (1980).

A, B: Common Coral Weed (*Corallina officinalis*). Bushy chalky red seaweeds with segmented branches and feather-like branching.



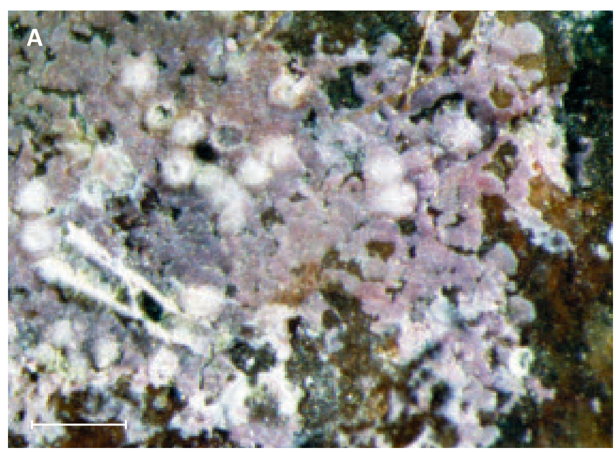
A: Briseis Flak, 7 m, 30.8.1993. Photo by K. Lundshøj.

B: Briseis Flak, 7 m, 29.5.1992. Scale 0.5 cm.

Pneophyllum

Dainty Crust Weeds

Appearance: The genus includes crusts which are typically epiphytic and very thin, < 100 µm thick and diminutive, < 0.5 cm in diameter. Epilithic species, e.g. *P. lobescens*, do not cover the substratum completely. Male, female and sporangial conceptacles are uniporate, some level with the surface of the thallus and other prominent.
Structure: The genus is characterised by an 8-celled germination disc and dimerous thallus. The species



A: Pneophyllum lobescens. Thin epilithic crust, not covering the substratum completely. Small uniporate conceptacles with white tops. Læsø Trindel, 11 m, 8.6.1991.
Scale 0.5 mm. Photo by S. Lundsteen.

are primarily separated on characters of the conceptacle morphology and particularly the filaments around the pore canal (Table 2).

Comment: Six species of this genus are known in Danish waters. Information about the distinguishing characters appears in Table 2. Microscopic examination of thin sections of the thallus is necessary for a reliable species identification, particularly structures around the pore canals of the conceptacles.

Pneophyllum coronatum (Rosanoff) Penrose
Recent synonym: *Pneophyllum caulerpae* (Foslie) P.L.Jones & Woelkerling

B: *Pneophyllum limitatum*. Female conceptacle with filaments around the conceptacle pore canal which may be partially transversely fused. B-C: On Clawed Fork Weed (*Furcellaria lumbricalis*), Kims Top, 19 m, 9.8.1995.

C: *Pneophyllum myriocarpum*. Female conceptacle with a transparent collar at the conceptacle pore canal.

Table 2. *Pneophyllum* spp. in Danish waters with species characters after Chamberlain (1994).

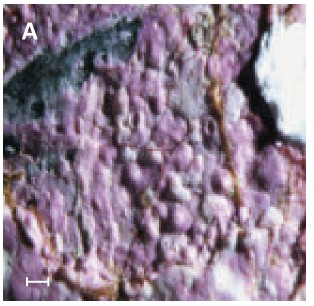
	Conceptacle morphology	**Cells or filaments around the conceptacle pore canal**
Pneophyllum fragile **Kützing**	Level with thallus surface	No specialized cells
Pneophyllum lobescens **Y.M.Chamberlain**	Level with or slightly elevated above the thallus surface and with a characteristic white top	Small cells, forming a calcified dome above the conceptacle pore canal
Pneophyllum coronatum **(Rosanoff) Penrose**	Elevated above the thallus surface	Free filaments
Pneophyllum confervicola **(Kützing) Y.M.Chamberlain**	Elevated above the thallus surface	No special cells around the conceptacle pore canal
Pneophyllum limitatum **(Foslie) Y.M.Chamberlain**	Elevated above the thallus surface	Conceptacle pore canal surrounded by a crown of amalgamated filaments
Pneophyllum myriocarpum **(P.Crouan & H.Crouan) Y.M.Chamberlain**	Elevated above the thallus surface	Conceptacle pore canal surrounded by a transparent collar

Family: Hydrolithaceae

Hydrolithon boreale

(Foslie) Y.M.Chamberlain
Northern Tile Weed

Appearance: Thin crust with imbricating thallus (like overlapping roof tiles) on stone with very small conceptacles, c. 100 µm in diameter. Conceptacles are generally of the same colour as the rest of the crust. Male, female and sporangial conceptacles are all uniporate.
Structure: Thallus is dimerous and has secondary pit connections. The horizontal part of the thallus is monostromatic. The species has a 4-celled germination disc, surrounded by 4 cells.
Resembles: It is possible to confuse this species with *H. cruciatum* or *H. farinosum* (see Chamberlain in Irvine & Chamberlain, 1994), but in these species the germination discs are 4-celled surrounded by 8 cells in *H. cruciatum* or 12 cells in *H. farinosum*.



A: *Hydrolithon boreale*. Thin, crust with imbricating thallus on stone. Very small conceptacles with the same colour as the rest of the crust. Munkegrunde, 13 m, 4.8.1994. Scale 0.5 mm. Photo by S. Lundsteen.

Family: Lithophyllaceae

Lithophyllum crouaniorum

Foslie
Thick Matt Paint Weed

Appearance: Relatively thick white-bluish crust on stone with a matt texture and c. 2 mm thick. All conceptacles are uniporate and submersed and appear like pinholes on the surface. Conceptacles often in densely crowded groups.
Structure: Thallus consists of many cell layers in which the cells form series connected by secondary pit connections. Therefore, the cells may appear extended diamond-shaped by the primary pit connections at the ends and the secondary pit connections in the lateral cell walls.
Resembles: It is possible to confuse it with Common Pale Paint Weed (*Lithophyllum incrustans* Foslie), but this species is not recorded from Danish waters. Both species have submersed conceptacles but *L. crouaniorum* differs from *L. incrustans* by cells forming series transversely to the filaments and from *L. incrustans* where the bottom of sporangial conceptacles is distinctly elevated as opposed to slightly rounded in profile in *L. crouaniorum*.

A: *Lithophyllum crouaniorum*. Relatively thick white-bluish crust with a dull surface, on stone. Submersed conceptacles appear like needlepoints. Store Middelgrund, 23 m, 2.6.1992. Scale 1 mm. Photo by S. Lundsteen.

Titanoderma corallinae

(P.Crouan & H.Crouan) Woelkerling, Y.M.Chamberlain & P.C.Silva

Appearance: A robust epiphytic species on Common Coral Weed *(Corallina officinalis)*. Thallus consists exclusively of uniporate conceptacles that are embedded in the host and relatively small, < 250 µm in diameter. The colour of the crust is yellow-rose.
Structure: Thallus dimerous and has secondary pit connections. The horizontal part of the thallus is monostromatic, with very long cells (palisade cells) in the vertical filaments. Other cells of the filaments may also be characteristically long. Sporangial conceptacles have a floor which is at least 6 cell layers below the surface of the thallus and a roof with a variable number of cell layers.
Resembles: *Titanoderma laminariae* (P. & H. Crouan) Y.M. Chamberlain also has embedded conceptacles, but larger, > 300 µm in diameter, and almost exclusively epiphytic on Kelp (*Laminaria* spp.). *T. laminariae* not recorded in Danish waters.

Titanoderma pustulatum

(J.V.Lamouroux) Nägeli
Little Gem Paint Weed

Appearance: A relatively thin epiphytic crust, < 1 mm thick. It has distinctly projecting conceptacles, all of them uniporate. The colour of the crust is yellow-rose.
Structure: Thallus is dimerous and has secondary pit connections. The horizontal part of the thallus is monostromatic while the vertical part consists of multicellular filaments of very long cells (palisade cells). Other cells in the filaments may also be characteristically long. The prominent sporangial conceptacles have a floor 2-3 cell layers below the surface of the thallus and a roof which is 3 cell layers thick.
Resembles: The species occurs as the variety *T. pustulatum* var. *pustulatum* in Danish waters. This is among other things characterised by the relatively thin conceptacle roof, 3 cell-layers, and the size of the conceptacles, 0.5-1 mm in diameter (Chamberlain & Irvine, 1994). Other varieties are characterised by more cell layers in the conceptacle roof and have large conceptacles (*T. pustulatum* var. *macrocarpum*) or a light red-bluish colour (*T. pustulatum* var. *confine*) respectively.
Comment: Occurs on the haptera of Kelp (*Laminaria* spp.) in Danish waters.

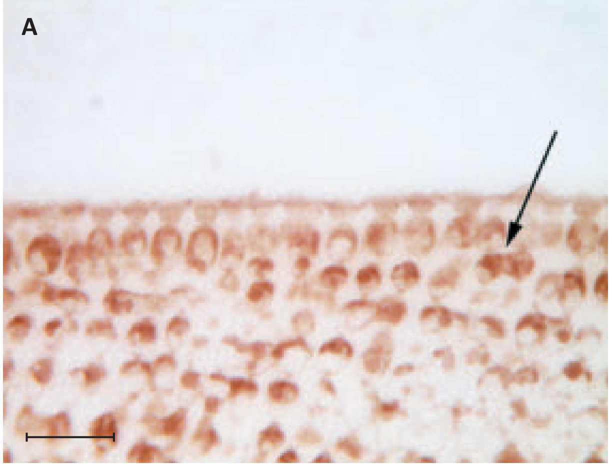
A: *Titanoderma pustulatum*. Robust epiphyte with prominent uniporate conceptacles. On haptera of Kelp (*Laminaria* sp.) or Sugar Kelp (*Saccharina latissima*). Dried material, stipe and blade cut off the host alga and the haptera viewed from above. Vejrø, 15 m, 7.6.1993. Scale 1 cm. Photo by S. Lundsteen.

Family: Hapalidaceae

Lithothamnion

Appearance: Species of *Lithothamnion* are crusts with protuberances or loose lying rhodoliths – Southern Maerl (*L. corallioides*) and Northern Maerl (*L. glaciale*). The species are relatively thin such as Deep Pink Paint Weed (*L. sonderi*) or thick crusts such as North-

ern Maerl (*L. glaciale*). The conceptacles are slightly elevated, sporangial conceptacles are multiporate whereas male and female conceptacles are uniporate.
Structure: Thallus is monomerous with cell fusions. Construction is coaxial in the protuberances. There is a characteristic epithallial cell, which is boat-shaped and has an elongate meristem cell below in the cell filament (Wegeberg & Pueschel, 2002). The old conceptacles are buried within the thallus in some species, e.g. Northern Maerl (*L. glaciale*).
Resembles: The rhodoliths of Southern Maerl (*Lithothamnion corallioides*) and Northern Maerl (*L. glaciale*) may easily be confused with rhodolith-forming species of *Phymatolithon* and *Lithophyllum*. Distinguished from *Phymatolithon* by the morphology of the epithelial cell which is rounded with a relatively flat meristem cell below in *Phymatolithon*, and distinguished from *Lithophyllum* by the occurrence of cell fusions, while *Lithophyllum* has secondary pit connections. However, rhodolith-forming species are not reported from Danish waters.



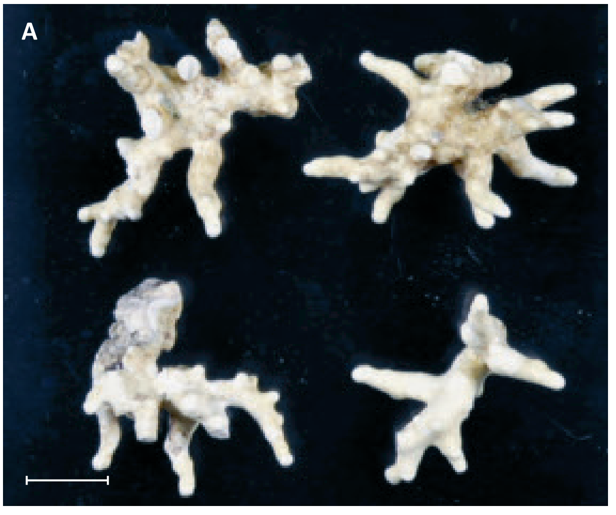
A: Longitudinal section of *Lithothamnion*. The filaments terminate in a boat-shaped epithelial cell with an elongate meristem cell just below. Cell fusions between cells of neighbouring filaments (arrow). Scale 20 µm.

Lithothamnion corallioides

(P.Crouan & H.Crouan) P.Crouan & H.Crouan

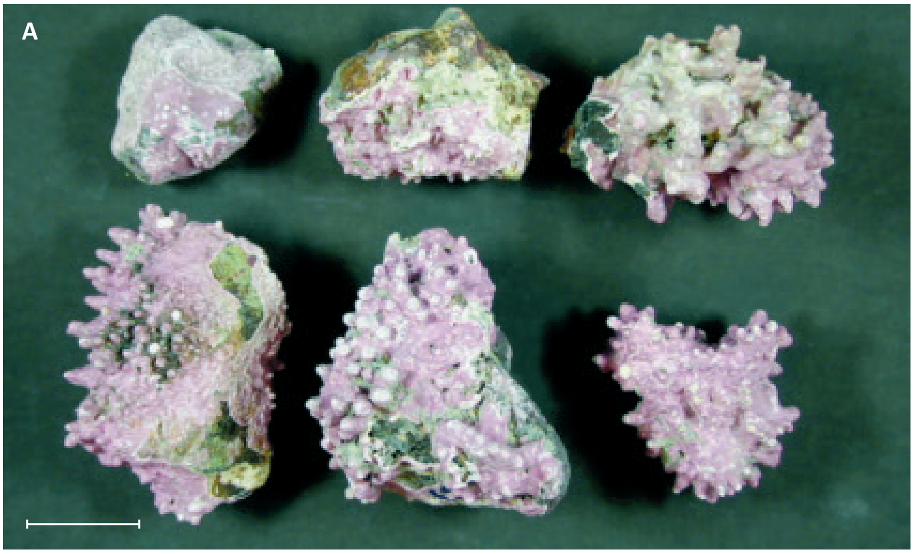
Southern Maerl

Appearance: Loose lying relatively small and fragile rhodoliths with characteristic pointed spreading branches.
Resembles: The two maerl-forming species, Southern Maerl (*L. corallioides*) and Celtic Maerl (*Phymatolithon calcareum*), often occur together and are difficult to distinguish from each other morphologically. The morphology of the epithallial cells is typical for the genera as mentioned above, where in *Lithothamnion* they are boat-shaped and in *Phymatolithon*, rounded in shape. The rhodoliths of Northern Maerl (*L. glaciale*) may also look similar but are more compact and bone-like.
Comment: Relatively rare and does not form large areas of maerl in Danish waters.



A: *Lithothamnion corallioides*. Loose lying small fragile rhodoliths with pointed, spreading branches. Schultz's Grund, 15 m, 27.3.1992. Scale 1 cm. Photo by S. Lundsteen.

A: *Lithothamnion glaciale*. Crusts with protuberances. Rotholme at Mors, 3 m, 9.7.1998. Scale 2 cm. Leg.: L. Knudsen. Photo by S. Lundsteen.



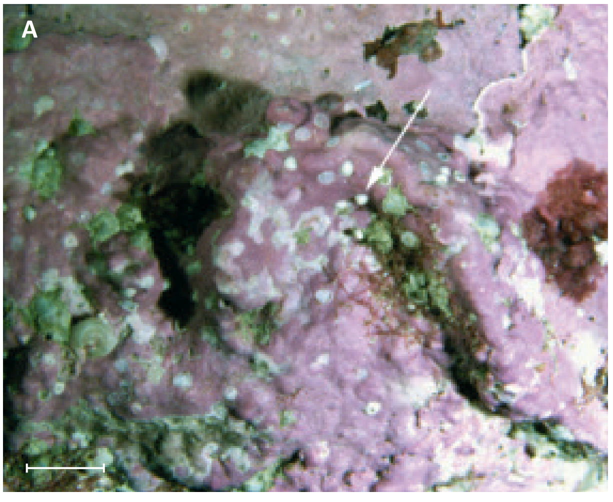
Lithothamnion glaciale

Kjellman

Northern Maerl

Appearance: Crust with characteristic protuberances and also occurs as rhodoliths which are often relatively compact with rounded branched apices.

Resembles: Crusts with protuberances are very characteristic, but the rhodoliths resemble those of Southern Maerl (*L. corallioides*) and Celtic Maerl (*Phymatolithon calcareum*) (see *L. corallioides*).
Comment: Rhodoliths occur particularly in the Limfjord.



A: *Lithothamnion sonderi*. Crust with a clear light red colour. Distinct white conceptacles sharply delimited on the surface of the thallus (arrow). Tønneberg Banke 15 m, 12.8.1990. Scale 2 mm. Photo by S. Lundsteen.

Lithothamnion sonderi

Hauck

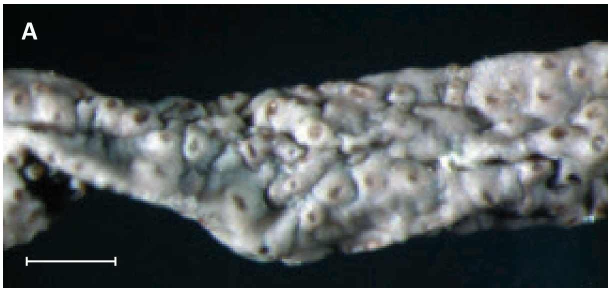
Deep Pink Paint Weed

Appearance: Relatively thin crust, < 1 mm thick with a fairly clear light red colour. The crust is restricted in area, < 5 cm in diameter. Conceptacles are white and appear distinct on the surface of the thallus. Uniporate male and female conceptacles and multiporate sporangial conceptacles typically appear on the same crust.
Resembles: It is possible to confuse this species with *Phymatolithon tenue*, which also is a relatively thin crust of relatively restricted area, < 5 cm in diameter, and with an intense light red colour (see *P. tenue*). It has very large multiporate conceptacles of the same colour as the surface of the thallus contrary to the characteristic white conceptacles of Deep Pink Paint Weed (*L. sonderi*) which makes it possible to distinguish between the two.

Melobesia membranacea

(Esper) J.V.Lamouroux

Black-eyed Volcano Weed

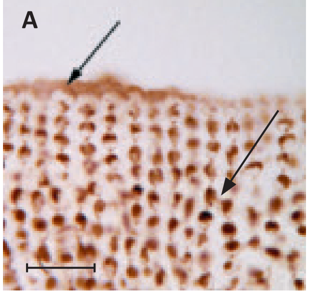


A: *Melobesia membranacea*. Thin epiphytic crust on Clawed Fork Weed (*Furcellaria lumbricalis*). The roofs of the multiporate conceptacles are below the rest of the conceptacle and the centre appears dark. Lysegrund, 10.5 m, 23.8.1996. Scale 0.5 mm. Photo by S. Lundsteen.

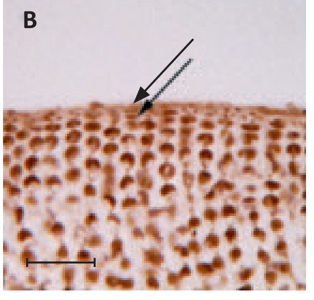
Appearance: Epiphytic thin crust, < 100 µm thick. The conceptacles are elevated above the surface of the thallus. The multiporate sporangial conceptacles each have a roof which appears to have a dark centre because it is below the rest of the conceptacle. The thallus appears dark and may be difficult to see when wet.
Structure: Thallus is dimerous with cell fusions. The horizontal part of the thallus is monostromatic. The thallus may consist of this single cell layer or have filaments up to 7 cells long. Epithallial cells appear ellipsoid or slightly triangular, when viewed in longitudinal section.
Resembles: Not reminiscent of other epiphytic calcified red algae in Danish waters because of the characteristic sporangial conceptacles with lowered multiporate roofs.
Habitat: Often epiphytic on Clawed Fork Weed (*Furcellaria lumbricalis*).

Phymatolithon

Appearance: Species of *Phymatolithon* are more or less smooth crusts without protuberances, or loose branched rhodoliths such as Celtic Maerl (*Phymatolithon calcareum*). The crust may be relatively thin, < 1 mm, such as Common Slippery Paint Weed (*P. laevigatum*) or thick, > 1 mm, such as Common Purple Paint Weed (*P. purpureum*). The conceptacles may be elevated or submerged in the surface of the thallus. Sporangial conceptacles are multiporate, whereas male and female conceptacles are uniporate.
Structure: Thallus is monomerous with cell fusions. The protuberances are without coaxial construction. *Phymatolithon* has flat to almost balloon-shaped epithallial cells and a small meristem cell, after which the new cells produced gradually elongate downwards in the filaments (Wegeberg & Pueschel, 2002). Old conceptacles may become buried in the thallus in some species.
Resembles: As already mentioned for *Lithothamnion*, the rhodolith-forming species may be confused with rhodolith-forming species of the genera *Lithothamnion* and *Lithophyllum*. *Phymatolithon* differs from *Lithothamnion* by the shape of the epithalial cell and from *Lithophyllum* by the occurrence of cell fusions (see *Lithothamnion*).



A: *Phymatolithon* sp. Longitudinal section of thallus. Some of the filaments terminate in swollen epithalial cells which are free of calcification and being released (upper arrow). Cell fusions (lower arrow).



B: *Phymatolithon* sp. Longitudinal section of thallus. The filaments with a narrow ellipsoid epithalial cell (upper arrow) and a narrow meristem cell (lower arrow), after which the cells gradually elongate downwards.

Phymatolithon calcareum

(Pallas) W.H.Adey & D.L.McKibbin ex Woelkerling & L.M.Irvine

Celtic Maerl

Appearance: The species is free-living and has perpendicular branch angles and blunt apices, so it appears slightly bone-shaped.

Resembles: See Southern Maerl (*Lithothamnion corallioides*) and Northern Maerl (*L. glaciale*).

A, B: *Phymatolithon calcareum*. Loose slightly bone-shaped thalli with perpendicular branch angles and blunt apices. Tønneberg Banke, 15 m, 20.8.1991. Scale 0.5 cm. Photo by S. Lundsteen.

Phymatolithon laevigatum

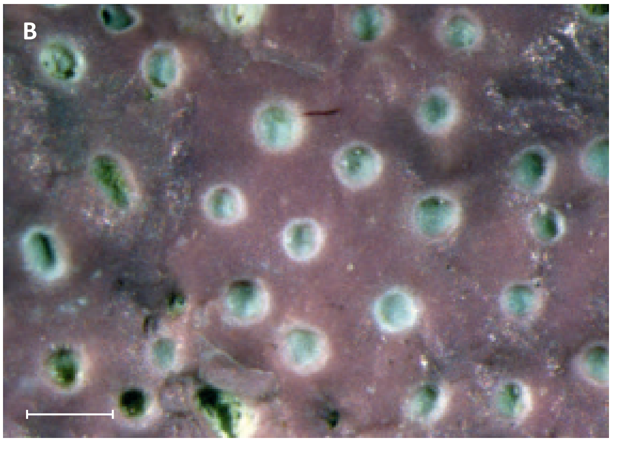
(Foslie) Foslie

Common Slippery Paint Weed

Appearance: Relatively thin and very smooth crust, < 1 mm thick, with slightly glossy surface. The conceptacles are submerged in the thallus surface and typically have a narrow white ring.

Resembles: Common Purple Paint Weed (*P. purpureum*) also has submerged conceptacles but has a thicker ring around the conceptacles of the same colour as the thallus. In addition, Common Purple Paint Weed (*P. purpureum*) is slightly thicker and more uneven than Common Slippery Paint Weed (*P. laevigatum*) and has a greenish shade.

A: *Phymatolithon laevigatum*. Smooth slightly glossy surface. Scale 2 mm. A, B: Pullerterne, northeast of Hjelm, 6.5 m, 7.3.1997. Photo by S. Lundsteen.



B: *Phymatolithon laevigatum*. Conceptacles submerged in thallus surface with a narrow white ring. Scale 0.5 mm.

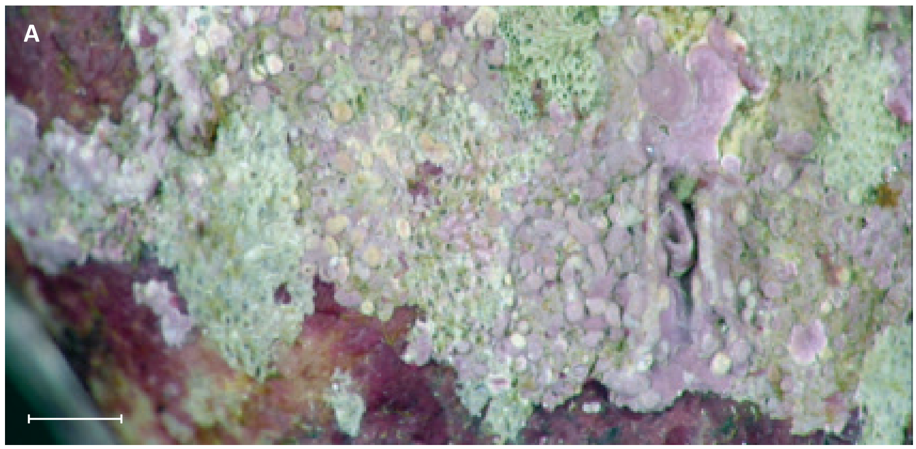
Phymatolithon lenormandii

(Areschoug) W.H.Adey

Common Shore Paint Weed

Appearance: Relatively thin granulated crust slightly brown-purple. Often with densely packed conceptacles and elevated above the thallus surface. They are trapeziform in profile, whereas older emptied conceptacles are often broken, leaving a cup-shaped scar.

A: *Phymatolithon lenormandii*. Relatively thin and granulated brown-purple crust. Many dense conceptacles elevated above the thallus surface. Also with many grey bryozoans. Pullerterne, 8 m, 7.3.1997. Scale 2 mm. Photo by S. Lundsteen.

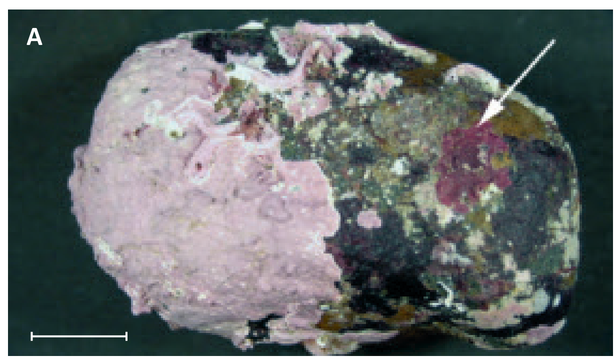


Phymatolithon purpureum

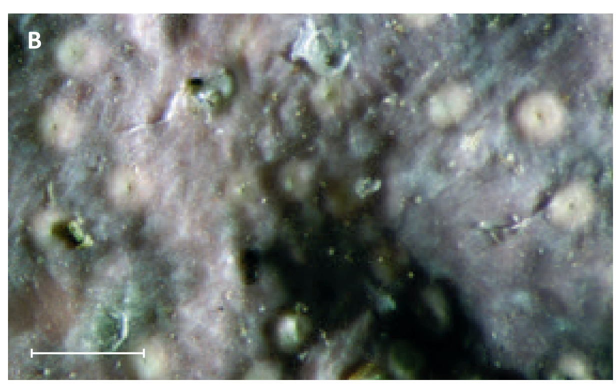
(P.Crouan & H.Crouan) Woelkerling & L.M.Irvine

Common Purple Paint Weed

Appearance: Undulating crust almost floats over the stone with a characteristic light red to grey-greenish colour. The conceptacles are submerged in the thallus surface, although with a relatively thick elevated ring of the same colour as the thallus.
Structure: Old buried conceptacles occur in the thallus.
Resembles: See *P. laevigatum*.



A: *Phymatolithon purpureum*. A wavy crust appearing to float on the stone, with a light red to grey-greenish colour. Also on the stone a Peysonnel's Brick-red Crust (*Peyssonnelia dubyi*) (arrow). Scale 2 cm. A, B: Herthas Flak, 10 m, 12.6.1990. Photo by S. Lundsteen.

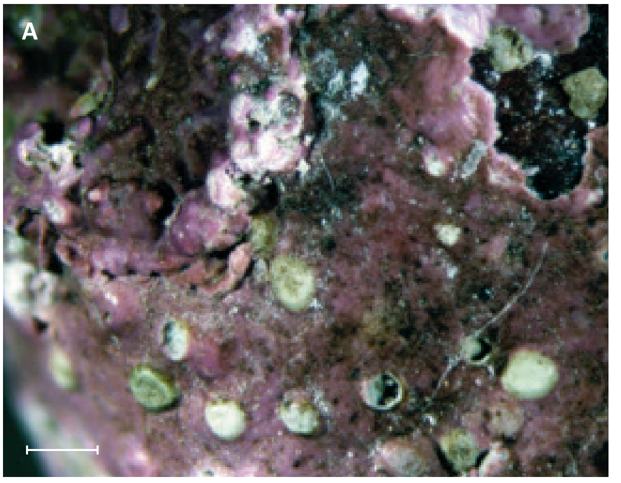


B: *Phymatolithon purpureum*. Conceptacles submerged in thallus surface surrounded by a relatively thick ring. Scale 0.5 mm.

Phymatolithon tenue

(Rosenvinge) Düwel & Wegeberg

Appearance: A smooth crust with a relatively restricted area on the substratum, < 5 cm across. Large elevated multiporate conceptacles c. 1 mm in diameter of same colour as the rest of the thallus. The surface may appear slightly 'dirty'.
Resembles: See Deep Pink Paint Weed (*Lithothamnion sonderi*).
Comment: For details about the name *Leptophytum laeve* see AlgaeBase (Guiry in Guiry & Guiry 2021) and Brodie et al. (2016).
References: Brodie et al. (2016), Düwel & Wegeberg 1996, Guiry in Guiry & Guiry (2021).



A: *Phymatolithon tenue*. Smooth crust with large elevated multiporate conceptacles. Thallus surface appears slightly 'dirty'. Store Middelgrund, 23 m, 22.8.1996. Scale 1 mm. Photo by S. Lundsteen.

Subclass: Hildenbrandiophycidae · Order: Hildenbrandiales · Family: Hildenbrandiaceae

Hildenbrandia

Hildenbrand's Red Weeds

Appearance: Compact crustose thalli forming extended red, to reddish brown patches on the substratum. They are up to 1 mm thick and closely adherent to the substratum.
Structure: Upright filaments of densely packed almost cube-shaped cells, 3-6.5 µm in width. Each cell contains a parietal plate-shaped plastid in the upper part of the cell. There is no special basal layer, or secundary pit connections and no cell fusions. The two Danish species have similar cell measurements and reliable identification is only possible when sporangia are present.
Reproduction: Tetrasporangia are the only known reproductive structures. They form from cells at the base and sides of conceptacles (small cavities) in the crusts. They occur scattered on the crusts from the surface into the thallus. When the tetrasporangia divide, the transverse wall is formed first and is slightly oblique. In Hildenbrand's Zonate Red Weed (*H. crouaniorum*) the walls of the second divisions are parallel to the first formed, resulting in transversely divided zonate sporangia. In Hildenbrand's Oblique Red Weed (*H. rubra*), the walls of the second divisions are approximately perpendicular to the first, resulting in oblique cruciate or irregular sporangia.
Habitat: On pebble, stones, boulders, and rocks.
Resembles: The crustose phase of Black Scour Weed (*Ahnfeltia plicata*), is of a similar construction but blue-violet in colour and with an almost black border when growing against other crustose algae.
References: Irvine & Pueschel (1994), Rosenvinge (1917).

Identification key to species of *Hildenbrandia*

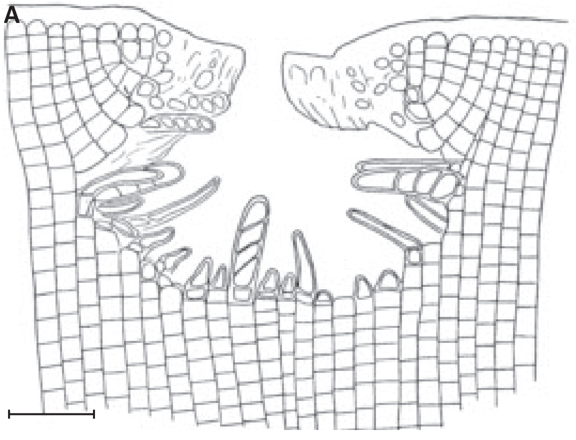
1a.	Tetrasporangia zonate	*H. crouaniorum*
1b.	Tetrasporangia obliquely cruciately divided	*H. rubra*

Hildenbrandia crouaniorum

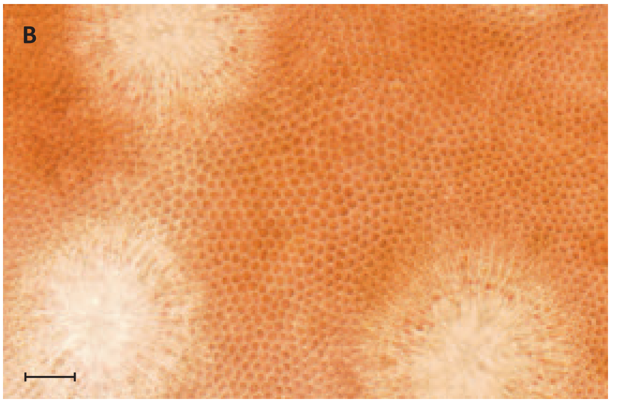
J.Agardh

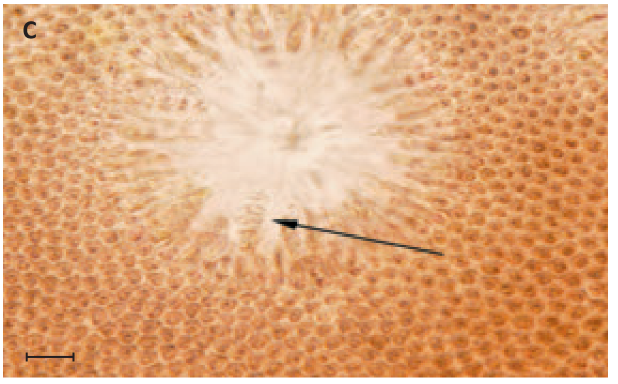
Hildenbrand's Zonate Red Weed

Seasonal variation: Perennial. Collected in January-September with tetrasporangia, but these are probably present all year.
Habitat: On stone reefs, 5.5-28 m depth.



A: *Hildenbrandia crouaniorum*. Conceptacle, longitudinal section. After Rosenvinge (1917) as *H. crouani*.





B: *Hildenbrandia crouaniorum* with many conceptacles, transverse section. Scale 20 µm. B, C: Vejrø, 13 m, 13.6.1990.

C: *Hildenbrandia crouaniorum*. Conceptacle with zonate tetrasporangia (arrow), transverse section. Scale 10 µm.

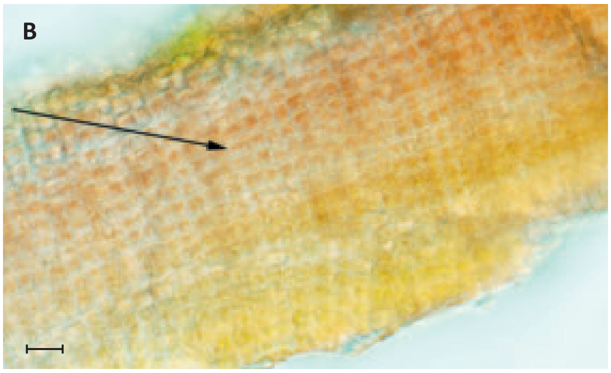
Hildenbrandia rubra

(Sommerfelt) Meneghini

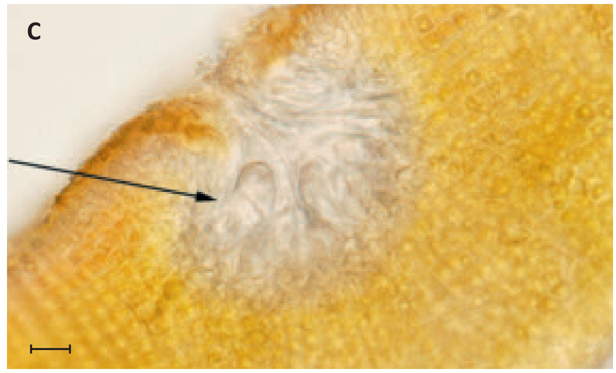
Hildenbrand's Oblique Red Weed

Seasonal variation: Perennial. Conceptacles and tetrasporangia present all year.
Habitat: On hard substratum in the littoral to 27 m depth collected by divers and obtained by dredge at 38 m depth.
Comment: Upper limit of distribution of Hildenbrand's Oblique Red Weed (*H. rubra*) is used to define the upper border of the littoral at sheltered localities in Danish waters. It is probably the most common Danish seaweed known in all the districts and has a large vertical distribution.
References: Rosenvinge (1917, *H. prototypus*).

A: *Hildenbrandia rubra*. Red-brown colour on boulders (arrow) just above the water level caused by a dense cover of *H. rubra*. Deget, Frederikshavn, 13.5.1983.



B: *Hildenbrandia rubra*. Upright filaments densely packed, of isodiametric cells, each with a plate-shaped plastid in the upper end of the cell (arrow). Scale 10 µm. B, C: Beach north of Vesterø Havn, Læsø, 0.5 m, 2.4.2013.



C: *Hildenbrandia rubra*. Obliquely cruciately divided tetrasporangium (arrow) in conceptacle, longitudinal section. Scale 10 µm.

Subclass: Nemaliophycidae · Order: Acrochaetiales · Family: Acrochaetiaceae

Acrochaetium

Star Hairs

Uniseriate branched filaments, microscopic to a few millimetres in height. Vegetative cells contain a stellate plastid often in the middle at the distal end of the cells. Most species have one pyrenoid. It is common for these algae to develop red algal hairs. Sexual reproduction occurs in most species. The life history includes monoecious or dioecious gametophytes with a single basal cell and a tetrasporophyte with a multicellular basal system. Tetrasporangia are cruciate. Asexual reproduction with monospores is frequent. Monosporangia occur on thalli with or without other reproductive structures.

References: Clayden & Saunders (2014), Harper & Saunders (2002), Hwang & Kim (2011), Stegenga & Mulder (1979, *Chromastrum*).

Identification key to species of *Acrochaetium*

1a.	Epiphytic or epizoic	2
1b.	Endophytic or endozoic	17
2a.	Basal system consists of a single cell	3
2b.	Basal system multicellular	8
3a.	Cells almost spherical to barrel-shaped	4
3b.	Cells cylindrical	5
4a.	Lower wall of the basal cell thickened, upright filaments of few cells. On the assimilating filaments of *Chordaria flagelliformis* and *Mesogloia vermiculata*	*A. collopodum*
4b.	Basal cell resembles the other cells. Thallus decumbent or with ascending filaments and may have unilateral upright branches	*A. moniliforme* (gametophyte)
5a.	Upright filaments 9-11 µm in width	*A. secundatum* (gametophyte)

5b.	Upright filaments ≤ 9 µm in width		6
6a.	Cells (5-) 6-7 (-9) µm in width and 4-6 (-7) times as long as wide. 4-6 sparsely branched filaments arise from the basal cell	*A. balticum*	
6b.	Cells shorter		7
7a.	A few (2-4) upright branches (4-) 5-6 µm in width	*A. hallandicum* (gametophyte)	
7b.	More (up to 6) upright branches (5-) 6-7 µm in width	*A. parvulum*	
8a.	Upright branches form the largest part of the alga		9
8b.	Decumbent branches form the largest part of the alga		14
9a.	Basal cells confluent to a disc, the middle cell triangular		10
9b.	Basal system of branched filaments		11
10a.	Upright branches 7-12 (-14) µm in width, with cells 1-2 times as long as wide	*A. secundatum* (tetrasporophyte)	
10b.	Upright branches 10-14 (-16-20) µm in width, with cells 3-5 times as long as wide	*A. luxurians*	
11b.	Upright filaments with few branches or have only short branches		12
11a.	Upright filaments much branched		13
12a.	Upright filaments 7-10 µm in width	*A. hallandicum* (tetrasporophyte)	
12b.	Filaments 3-5 µm in width	*A. leptonema*	
13a.	Upright filaments sparsely branched in the lower half and much branched in the upper half of the alga. Filaments are 5-7 µm in width. Monosporangia in short rows	*A. catenulatum*	
13b.	Prostrate and upright filaments, with short endophytic filaments between the cells of host alga (*Dumontia*). Upright filaments 6.5-9 µm in width	*A. dumontiae*	
14a.	Epiphytic prostrate filaments		15
14b.	Endophytic filaments		17
15a.	Basal system of extended prostrate filaments, monosporangia with or without stalk-cell	*A. reductum*	
15b.	Basal system, a pseudoparenchyma of dense filaments		16
16a.	No or a few short upright filaments, monosporangia with or without stalk-cell	*A. macula*	
16b.	Short upright filaments of a few cells, they arise from each cell in the basal system	*A. moniliforme* (tetrasporophyte)	
17a.	Endophytic filaments in cells of *Porphyra*	*A. cytophagum*	
17b.	Branched filaments in cells and internal cell walls of the host algae, *Leptosiphonia*, *Rhodomela* or *Vertebrata*. Sporangia formed from cells close to the surface of the host and form on the outside of the host	*A. immersum*	

Acrochaetium balticum

(Rosenvinge) Aleem & Schulz

Appearance: A single, almost spherical basal cell, 10.5-14 µm in diameter. From the basal cell 4-6 sparsely branched, upright filaments arise, up to 4 mm in height.

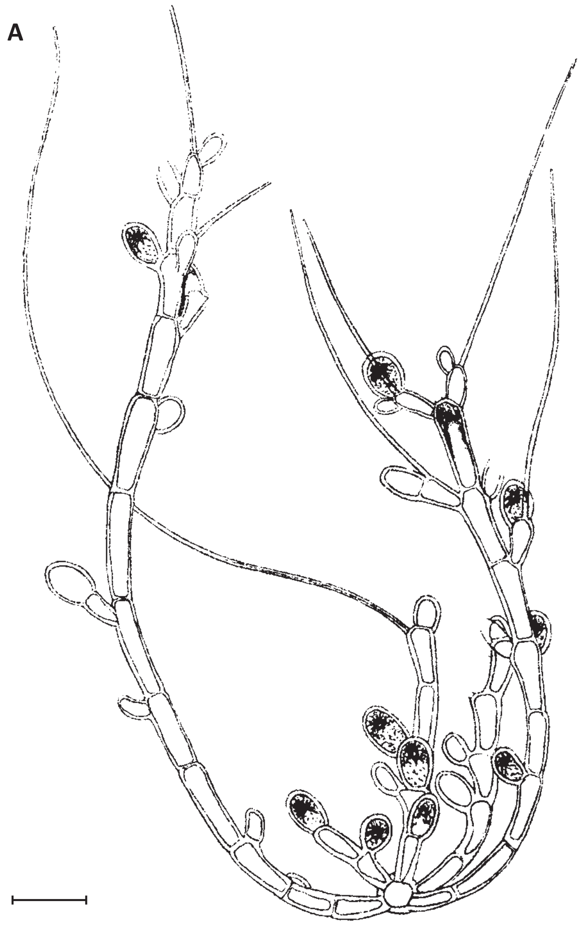
Structure: Cells of the upright filaments are (5-) 6-7 (-9) µm in in width and 4-6 (-7) times as long as wide. There is a single stellate plastid with one pyrenoid in each cell. Red algal hairs develop at the apex but appear lateral as the filament grows.

Reproduction: Asexual reproduction takes place by monospores. The monosporangia are ovoid, and slightly elongate, (8-) 10 µm in width and (12-) 14 (-16) µm in length. They occur scattered on the branches with or without a stalk-cell. Sexual reproduction not known.

Seasonal variation: Recorded in July-August.

Habitat: On Elongate Siphon Weed (*Carradoriella elongata*) and Purple Siphon Weed (*Leptosiphonia fibrillosa*), 7.5-8.5 m depth.

References: Rosenvinge (1909, *Chantransia*), Stegenga (2000).



A: *Acrochaetium balticum*. A single basal cell with 5 upright branches of long cylindrical cells. Scattered monosporangia with or without a stalk-cell. On *Leptosiphonia fibrillosa*. Gyldenløves Flak, 9.5 m. Scale 20 µm. After Rosenvinge (1909).

Acrochaetium catenulatum

M.Howe

Recent synonym: *Acrochaetium densum* **(K.M.Drew) Papenfuss**

Appearance: Epiphytic red bush-like tufts up to 0.2 mm in length.

Structure: Basal system of prostrate filaments with scattered branches of cylindrical cells. The filaments are tightly interconnected or more openly branched and have numerous upright branches.

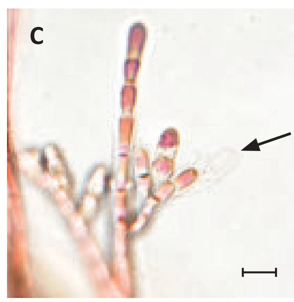
Upright filaments have almost no branches in the lower half, while there are many dense branches in the upper half of the alga. These branches are often unilateral. Cells of the upright filaments are 5-7 µm in width and 1-2 times as long as wide. Cells in prostrate filaments, are 2-4 times as long as wide. There is a stellate plastid with one pyrenoid in the middle of each cell. Red algal hairs may be present.

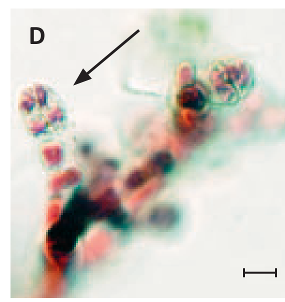
Reproduction: Dioecious gametophytes and tetrasporophyte, known from life history studies in culture by Stegenga & Vroman (1976). Gametophytes had a single basal cell and the tetrasporophyte a basal system of filaments. Asexual reproduction in both generations was by monospores, formed, in long rows at the apex of the branches. In individuals from Danish waters, monospores occurred in short rows of 2-3 (-4) cells and the monosporangia were c. 7 µm in width and slightly longer. When mature, the spores escaped through a pore in the wall of the sporangium. Cruciate tetrasporangia at the apex of short branches were also observed.

Seasonal variation: Collected in October with mono- and tetrasporangia.
Habitat: Epiphytic on Purple Siphon Weed (*Leptosiphonia fibrillosa*), 6 m depth.
Comment: Only a single collection from Danish waters.
References: Stegenga & Vroman (1976).

A: *Acrochaetium catenulatum*. Uprights without branches in the lower part and many unilateral branches in the upper part. Scale 50 µm. A-D: On Purple Siphon Weed (*Leptosiphonia fibrillosa*). Egholm, Agersø, 6 m, 25.10.2013. Leg.: P. Stæhr.

B: *Acrochaetium catenulatum*. Branches with 3 monosporangia in a row (arrow). Stellate plastid. Scale 10 µm.

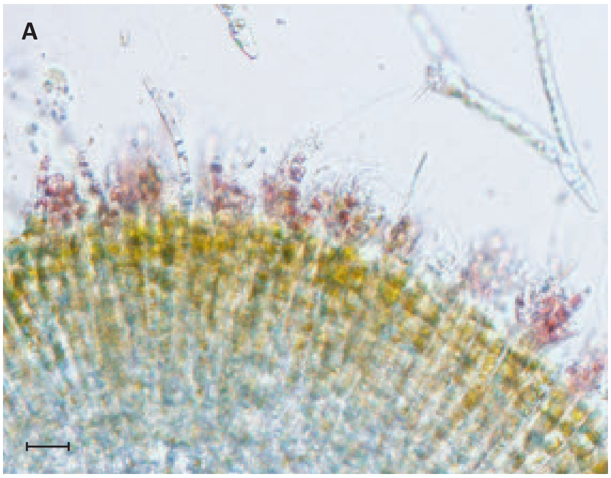


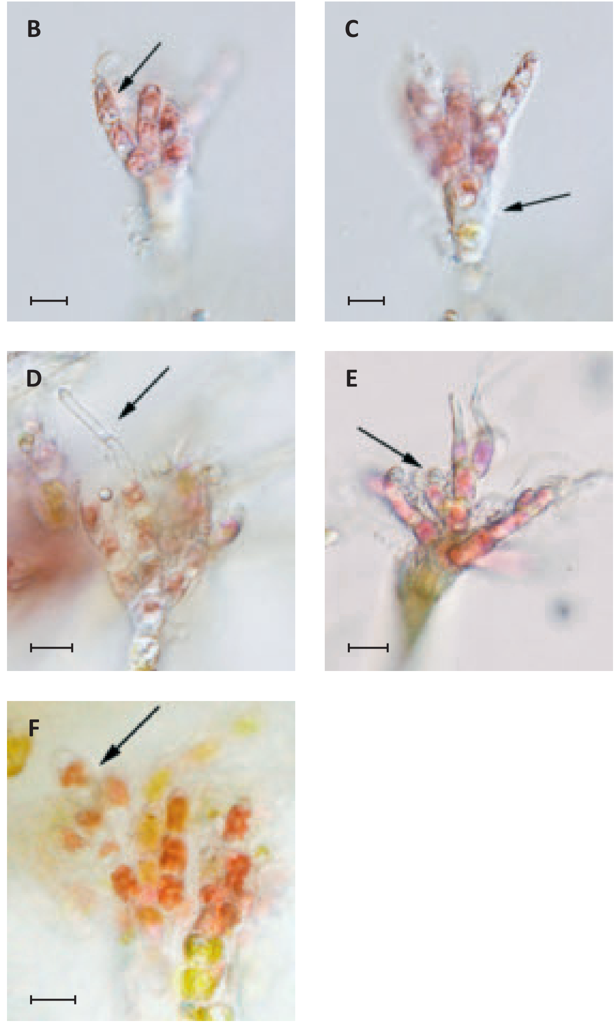


C: *Acrochaetium catenulatum*. Empty monosporangium, exit pore visible (arrow). Scale 10 µm.
D: *Acrochaetium catenulatum*. Cruciate tetrasporangium (arrow). Scale 10 µm

Acrochaetium collopodum
(Rosenvinge) Hamel

Appearance: Microscopic epiphytic alga, less than 100 µm in height.
Structure: A large basal cell up to 15 µm in diameter. It attaches to the substratum with a relatively thick wall material. From the basal cell short upright branched filaments arise, up to 50 (-85) µm in height. Young cells are cylindrical, 5-8 µm in width and 1-2 (-3) times as long as wide; older cells are rounded, 10-13 µm in width and 15 µm in length. There is a stellate plastid with one pyrenoid in the middle of each cell. An apical red algal hair is often present.
Reproduction: There is sexual reproduction with isomorphic, dioecious gametophytes. Antheridia are often in pairs on a unicellular branch. According to culture studies by Stegenga & Mulder (1979) the carpogonial





A: *Acrochaetium collopodum*. Small algae on Slimy Whip Weed (*Chordaria flagelliformis*). Scale 25 µm. A-F: Kobberhage, 0.5 m, 8.9.2016. Leg.: K.L. Krabbe.

B: *Acrochaetium collopodum*. Stellate plastid (arrow). Scale 10 µm.

C: *Acrochaetium collopodum*. Basal cell attached to apical cell of an assimilating filament of Slimy Whip Weed (*C. flagelliformis*) with a thick wall material (arrow). Figures B and C are the same alga in different focus. Scale 10 µm.

D: *Acrochaetium collopodum*. Large specimen, stellate plastid and apical red algal hair (arrow). Scale 10 µm.

E: *Acrochaetium collopodum*. Two antheridia (arrow). Scale 10 µm.

F: *Acrochaetium collopodum*. Ellipsoid monosporangium (arrow). Scale 10 µm.

cell is lateral or at the apex of main branches and has a long trichogyne. Carpogonia not reported on the algae from Danish waters. Asexual reproduction takes place by monospores; monosporangia are ellipsoid to ovoid, 5-8.5 µm in width and (8.5-) 10 (-16) µm in length.
Seasonal variation: Recorded in July-September with antheridia and monosporangia in September.
Habitat: Epiphytic on assimilating filaments of Slimy Whip Weed (*Chordaria flagelliformis*) and Slimy Wormweed (*Mesogloia vermiculata*), 0.5 m depth.
Comment: Described from Greenland by Rosenvinge (1898) as *Chantransia microscopica* var. *collopoda*, but in 1909 (footnote p. 81) he considered it to be an independent species. Culture studies of Swedish material by Stegenga & Mulder (1979) revealed a heteromorphic life history and the authors proposed that the tetrasporophyte could be identical with *A. dumontiae* or *A. cytophagum* (as *Chromastrum*). They also mentioned that the species be considered a subspecies of *A. microscopicum* (Nägeli ex Kützing) Nägeli, as Rosenvinge (1898) had originally proposed. It is possible that the specimens collected on Slimy Wormweed (*Mesogloia vermiculata*) are identical with *A. moniliforme* var. *mesogloiae* C.C. Jao.
References: Jao (1936), Lund (1942, *Chantransia collopoda*), Rosenvinge (1898, 1909, *C. collopoda*), Stegenga & Mulder (1979, *Chromastrum*), Woelkerling (1972 figs 12-14, *Audouinella microscopica*).

Acrochaetium cytophagum

(Rosenvinge) Hamel

Appearance: The alga looks like small tufts up to 0.2 mm in height.

Structure: Prostrate filaments on the surface of the host from where numerous filaments arise, both upright and short endophytic filaments growing into cells of the host alga. Upright filaments are unbranched or have a few short branches. The cells are 7-10 µm in width and approximately twice as long as wide. The stellate plastid does not appear to have a pyrenoid. Terminal red algal hairs occur on the upright filaments and become lateral.

Reproduction: Asexual reproduction with mono- and tetraspores. Monosporangia on the upright branches often occur in clusters of 2-3 from the same cell and without a stalk-cell. They are ovoid or ellipsoid, 7.5-8 µm in width and (11-) 13-17 µm in height; tetrasporangia are c. 10 µm in width and 19 µm in height.

Seasonal variation: Collected in September.

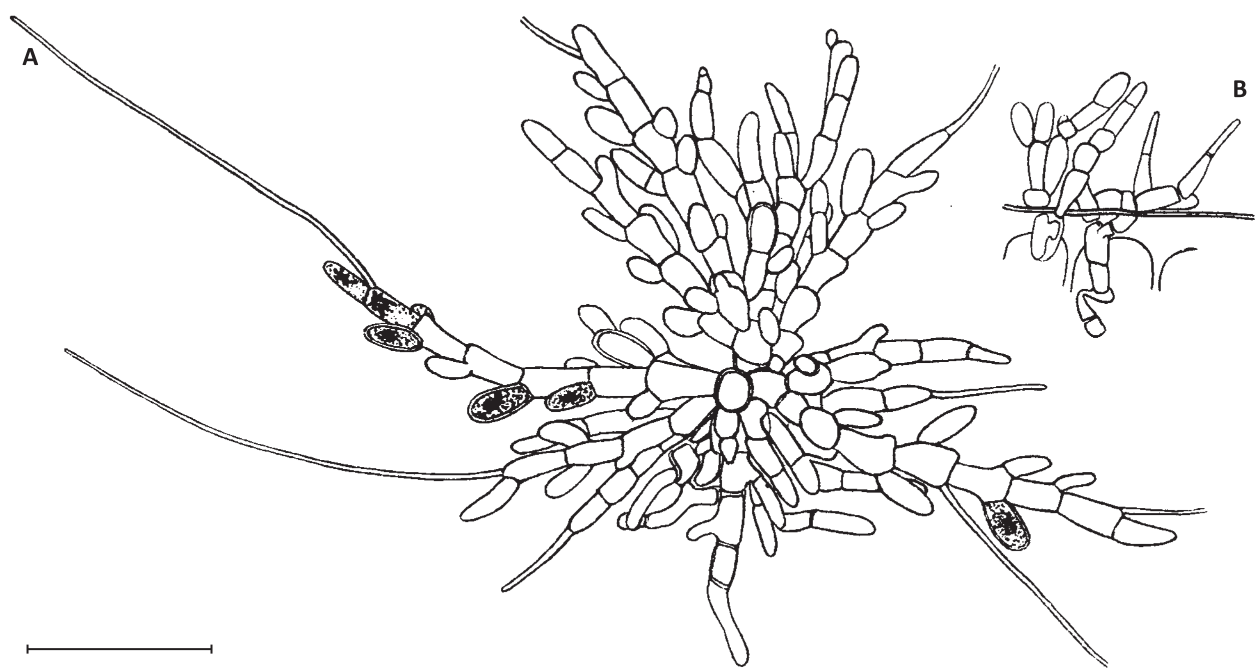
Habitat: On Tough Laver (*Porphyra umbilicalis*) where it grows close to the edge of the blade.

Resembles: Can be distinguished from the tetrasporophytes of *A. moniliforme* and *A. hallandicum,* by the presence of pyrenoids in these algae and they have no endophytic filaments. Resembles *A. dumontiae* but is not as branched as this species and does not have apical sporangia or endophytic filaments in the host cells like *A. dumontiae*.

Comment: It may represent the tetrasporophyte of *A. collopodum*, just like *A. dumontiae*, and may be a subspecies of *A. microscopicum* (as *Chromastrum*) according to Stegenga & Mulder (1979).

Described by Rosenvinge (1909) with type locality at Elsinore.

References: Rosenvinge (1909, *Chantransia*), Stegenga & Mulder (1979, *Chromastrum*).



Acrochaetium cytophagum on Tough Laver (*Porphyra umbilicalis*), A: Alga in surface view. B: Transverse section of the host species with *A. cytophagum*. Elsinore. After Rosenvinge (1909). Scale 20 µm.

Acrochaetium dumontiae

(Rosenvinge) Hamel

Appearance: Dark red tufts or a more confluent cover of narrow filaments, 0.5-1 mm in length.
Structure: Numerous upright, scattered, branched filaments arise from a basal system of creeping epiphytic and partially endophytic filaments. Branches originate from the middle and marginal parts of the basal system. Upright filaments branch from the base and branches can be repeatedly branched. Cells are 6.5-9 µm in width and 3 times as long as wide. Prostrate filaments are irregular with thick short cells. A stellate plastid without a visible pyrenoid is present in each cell. Apical red algal hairs become lateral by the continued growth of branches.
Reproduction: Asexual propagation by tetraspores. Tetrasporangia are ellipsoid, 8-11 µm wide and 15-19 µm in length. They may be lateral or apical on branches, with or without a stalk-cell, scattered or opposite and sometimes in pairs on the same cell. Monosporangia not observed.

A: *Acrochaetium dumontiae* with tetrasporangia and at base descending filaments. Scale 20 µm. After Rosenvinge (1909).

Seasonal variation: Collected in May with tetrasporangia.
Habitat: On Dumont's Tubular Weed (*Dumontia contorta*).
Comment: May represent the tetrasporophyte of *A. collopodum*, just like *A. cytophagum*. According to Stegenga & Mulder (1979), probably a subspecies of *A. microscopicum* (as *Chromastrum*).
References: Rosenvinge (1909, *Chantransia*), Stegenga & Mulder (1979, *Chromastrum*).

Acrochaetium hallandicum

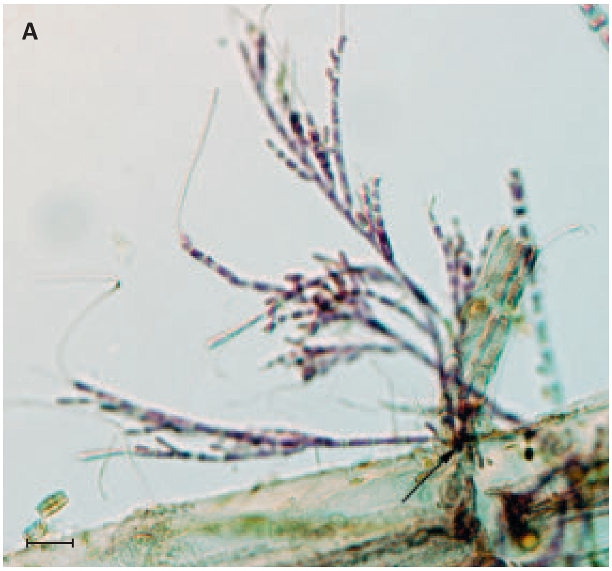
(Kylin) Hamel

Appearance: Microscopic epiphytic bush-like tufts of fine filaments. The life history is heteromorphic with monoecious gametophytes and a tetrasporophyte previously known as *A. polyblastum* (Rosenvinge) Børgesen.
Structure: The gametophyte has a rounded, thick-walled basal cell, (7.5-) 9-11 (-14) µm in diameter. From the basal cell 2 to 4 upright filaments arise with scattered and opposite branches. The cylindrical cells are (4-) 5-6 µm in width and 2-4 (-5) times as long as wide.

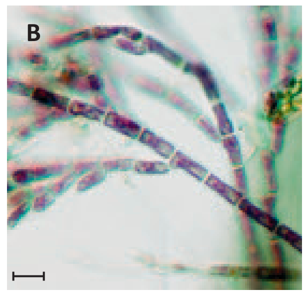
The tetrasporophyte has a basal system of prostrate filaments. The spore from which the tetrasporophyte originated begins the germination process by dividing into two cells, followed by growth of filaments in opposite directions from each of these two cells, both of which are still visible in the mature thallus. Filaments continue to develop resulting in a dense basal system, usually with one upright branch from each of the cells but sometimes two from the same cell, develop from this basal system. Most of the uprights are short, unbranched filaments, a few have dense branches with one or two branches from a single cell, in which case they grow in the same direction, not opposite. The cylindrical cells are 7-10 µm in width and 2-3 (-4) times as long as wide. There is a stellate plastid with one pyrenoid in the middle of each cell. Red algal hairs are apical on many branches but lateral hairs also observed.

Reproduction: Antheridia are apical on small branches, one or 2-3 from the same cell, are rounded 3 µm in length and 2.5 µm wide. Carpogonia are apical on branches that are 1-5 cells long. Asexual reproduction is by mono- or tetraspores. Monosporangia are sessile on the filaments or on a stalk-cell. They are ovoid or ellipsoid (4-) 6-7 (-9) µm in width and (8.5-) 9.5-10.5 (-13) µm in height. Monosporangia occur on separate individuals or on those with other kinds of reproductive structures. Tetrasporangia are lateral or apical on the upright branches and may be sessile on the prostrate filaments. They are cruciate, 10-12 µm in width and (16-) 18-21 µm in height.

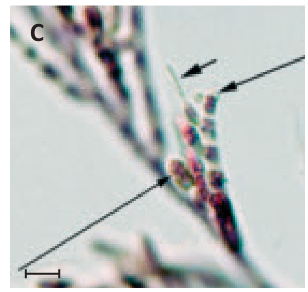
Seasonal variation: Sexual reproductive structures



A: *Acrochaetium hallandicum.* Much branched gametophyte with single basal cell (arrow). Scale 25 µm. A-C: On Purple Siphon Weed (*Leptosiphonia fibrillosa*), Ebbeløkke, 11 m, 26.7.1994.

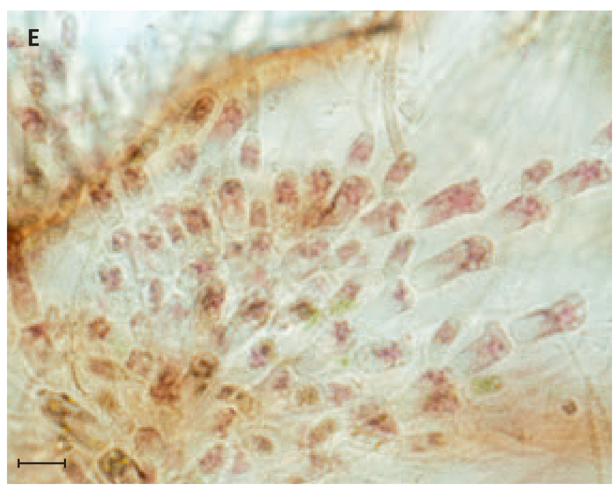


B: *Acrochaetium hallandicum.* Vegetative cell with stellate plastid. B, C: Same alga as shown in figure A. Scale 10 µm.



C: *Acrochaetium hallandicum.* Pair of antheridia (right hand long arrow), carpogonium with trichogyne (short arrow) and monosporangium (left hand arrow). Scale 10 µm.

D: *Acrochaetium hallandicum.* Young tetrasporophyte, the original spore divided transversely (arrows). Cylindrical cells with stellate plastid. Scale 10 µm. D-E: On Purple Siphon Weed (*L. fibrillosa*), Briseis Flak, 5 m, 6.6.1993.



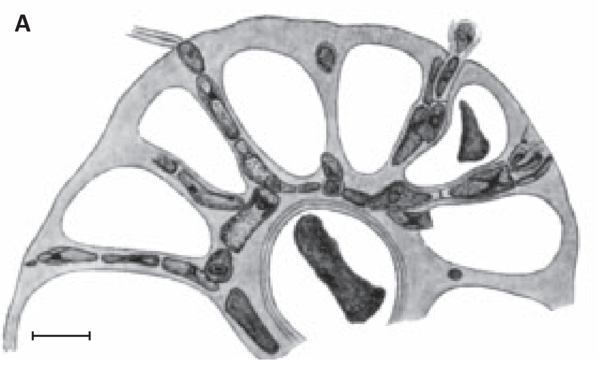
E: *Acrochaetium hallandicum.* Part of tetrasporophyte with short, unbranched, upright filaments a few much branched. Scale 10 µm.

recorded in February and April-September, monosporangia in May-August and tetrasporangia in April-May.
Habitat: Frequent on Purple Claw Weed (*Cystoclonium purpureum*), Purple Siphon Weed (*Leptosiphonia fibrillosa*) and Black Siphon Weed (*Vertebrata fucoides*), 0.5-15 m depth.
Comment: The heteromorphic life history documented by culture studies of algae from the Netherlands by Stegenga & Borsje (1977). Afonso-Carrillo et al. (2007) observed a parietal plastid with one pyrenoid per cell in specimens collected from the Canary Islands and transferred the species to *Colaconema hallandicum* (Kylin) Afonso-Carrillo, Sanson, Sangil & Diaz-Villa, but as the Danish individuals seem to have a stellate plastid, we will keep *Acrochaetium* until further evidence.
References: Afonso-Carrillo et al. (2007), Kylin (1944, *Kylinia hallandica*), Rosenvinge (1909, *Chantransia hallandica* (except f. *parvula*), *C. polyblasta*), Stegenga & Borsje (1977), Stegenga & Mulder (1979, *Chromastrum*).

Acrochaetium immersum

(Rosenvinge) Hamel

Appearance: Microscopic alga with short sparsely branched filaments that grow in the internal cell walls of the host.
Structure: The cells are 8-10 µm in width and 40-53 µm in height, often slightly swollen in the middle. They have a stellate plastid with long rays and one pyrenoid. Filaments in the inner part of the host have cells which are several times longer than wide while filaments closer to the surface of the host have short cells, only a little longer than wide.
Reproduction: Asexual reproduction by monospores. Monosporangia form from cells level with the surface of the host or slightly protruding. They are approximately the same size as the short vegetative cells. When emptied, a new sporangium may form within the walls of the former sporangium.
Seasonal variation: Recorded in September.
Habitat: Rosenvinge (1909) described two forms, one of them as *Chantransia immersa* f. *rhodomelae*, forms tumour-like growths on Straggly Bush Weed (*Rhodomela confervoides*). The other, *Chantransia immersa* f. *polysiphoniae*, is endophytic in Purple Siphon Weed (*Leptosiphonia fibrillosa*) and Black Siphon Weed (*Vertebrata fucoides*).
Comment: The description by Rosenvinge (1909) is based on algae from Frederikshavn, Hirsholm and Læsø Trindel. Not observed in recent collections in the algal herbarium, Natural History Museum of Denmark.
References: Rosenvinge (1909, C*hantransia immersa*).



A: *Acrochaetium immersum*. In cell walls of Black Siphon Weed (*Vertebrata fucoides*). Scale 20 µm. After Rosenvinge (1909).

Acrochaetium leptonema

(Rosenvinge) Børgesen

Appearance: A felty layer of numerous prostrate and upright filaments up to 0.3 mm in length.

Structure: The prostrate filaments are irregularly branched with cells more or less swollen, 3-4 µm in width and 1-3 times as long as wide. A straight filament typically arises from each cell of the prostrate filaments, except for the outer ones. Upright filaments unbranched or sparsely branched. The cells are 3-5 µm in width and 2-5 times as long as wide. There is a stellate plastid with one pyrenoid per cell. Apical red algal hairs frequent but become lateral by continued growth (sympodial growth).

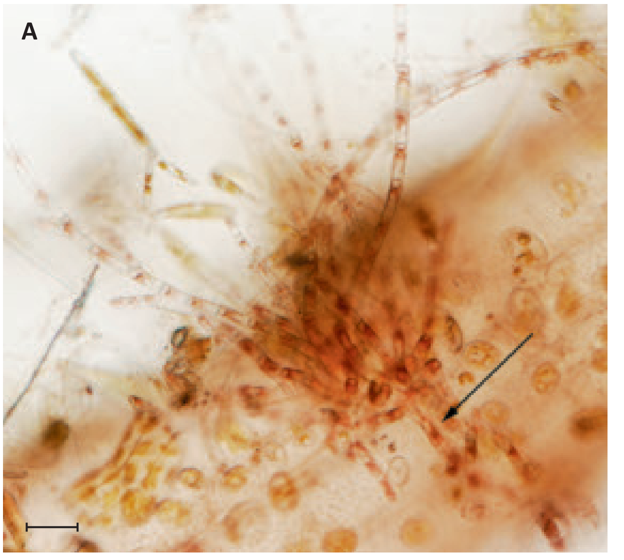
Reproduction: Asexual reproduction by monospores. Monosporangia are lateral or apical on the branches sometimes on a stalk of one or two cells and often in unilateral rows. They are ovoid or ellipsoid 5.5-6.5 µm in width and 10-12.5 µm in height. Branches with sporangia often curved with the sporangia on the upper side.

Seasonal variation: Collected in June-September.

Habitat: On Irish Moss (*Chondrus crispus*), Purple Siphon Weed (*Leptosiphonia fibrillosa*) and Pitcher Siphon Weed (*Polysiphonia stricta*), 2-15 m depth.

Comment: We have retained the name *Acrochaetium leptonema* for Danish individuals pending further investigation, as they have a very pronounced stellate plastid, and therefore do not warrant transfer to *Colaconema*, as proposed by Alongi et al. in Cormaci et al. (2017).

References: Alongi et al. in Cormaci et al. (2017), Rosenvinge (1909, *Chantransia*), Stegenga & Mulder (1979 fig. 41, *Chromastrum*).



A: *Acrochaetium leptonema*. Upright sparsely branched filaments from a basal system of branched filaments (arrow). Scale 25 µm. A-E: On Purple Siphon Weed (*Leptosiphonia fibrillosa*), Tønneberg Banke, 14 m, 27.8.2013.

B: *Acrochaetium leptonema*. A single upright filament arising from each cell in the basal system. Cells with stellate plastid. Scale 10 µm.

C: *Acrochaetium leptonema*. Apical red algal hair. Scale 10 µm.

D: *Acrochaetium leptonema*. Sympodial growth, red algal hair in a lateral position as a result of continued growth. Scale 10 µm.

E: *Acrochaetium leptonema*. Monosporangium on a 2-celled stalk. Scale 10 µm.

Acrochaetium luxurians

(J.Agardh ex Kützing) Nägeli

Luxuriant Star Hair

Appearance: Small bush-like tufts, with straight branches up to 2 mm in height.

Structure: The basal disc is almost circular in young individuals, with a triangular cell in the middle, later the disc become slightly irregular. Upright branches straight with two to three generations of long branches. They consist of cylindrical cells, 10-14 (-16-20) µm in width and 3-5 times as long as wide. There are small branches of 2-3 cells, they are scattered often unilateral or opposite, unbranched or sparsely branched and often have apical red algal hairs.

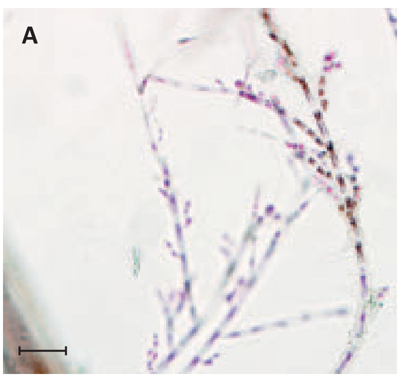
Reproduction: Asexual reproduction by monospores. The monosporangia occur on the small distal branches with a single or two sporangia from the same cell. They are ovoid or broad ellipsoid 13-16 (-19) µm wide and 17-21 (-26) µm in length.

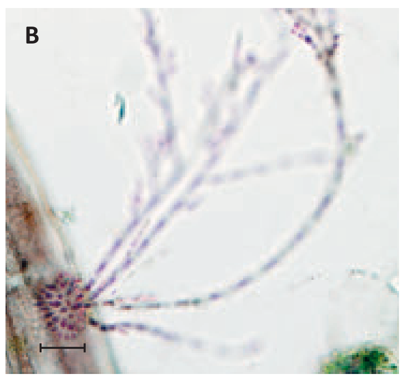
Seasonal variation: Collected in April-November.

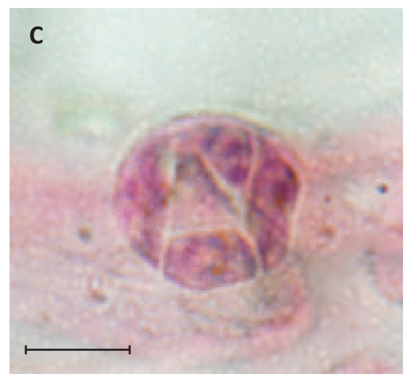
Habitat: On various red algae and on the hydroid *Dynamena pumila*, 0.5-11.5 m depth.

Comment: Recognized as an independent species after studies of type material and molecular studies by Clayden & Saunders (2014). The alga with the basal disc probably represents a vegetative generation while a sexual generation is unknown.

References: Clayden & Saunders (2014), Rosenvinge (1909, *Chantransia virgatula* var. *luxurians*).

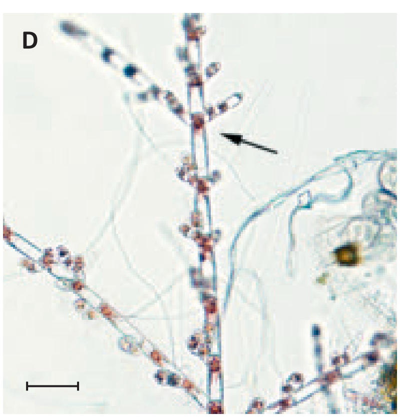


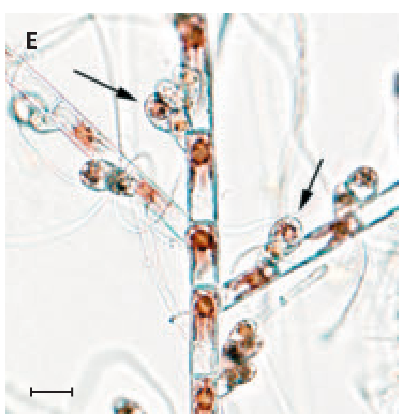




A, B: *Acrochaetium luxurians*. Basal disc and straight upright branches. The two figures are of the same individual in different focus. On Purple Siphon Weed (*Leptosiphonia fibrillosa*), Ebbeløkke, 7 m, 24.7.1994. Scale 50 µm.

C: *Acrochaetium luxurians*. Young basal disc with central triangular cell. On Purple Siphon Weed (*Leptosiphonia fibrillosa*), Sjællands Rev, 5 m, 10.9.1996. Scale 10 µm.





D: *Acrochaetium luxurians*. Straight, upright branch with relatively long cells, scattered and opposite branches (arrow). The beach east of Holtemmen, Læsø, drift, 23.7.2013. Scale 50 µm.

E: *Acrochaetium luxurians*. Vegetative cells with stellate plastid, monosporangia (arrows). Part of the alga in figure D. Scale 20 µm.

Acrochaetium macula

(Rosenvinge) Hamel

Spot Star Hair, Stain Star Hair

Appearance: A small, almost circular epiphytic disc c. 70 µm in diameter.

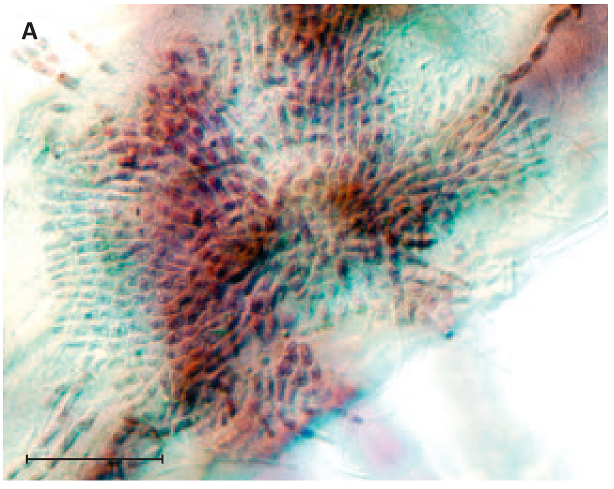
Structure: On germination, the original spore undergoes transverse division followed by tangential divisions, and thus a central area is formed from where, more or less radiating prostrate filaments arise densely to form a pseudoparenchymatous basal layer. The cells are 3.5-5 µm wide and 1-2 times as long as wide. They have a stellate plastid and one pyrenoid per cell. Short upright filaments, a few cells long, may develop from scattered cells of the basal system, sometimes with an apical red algal hair.

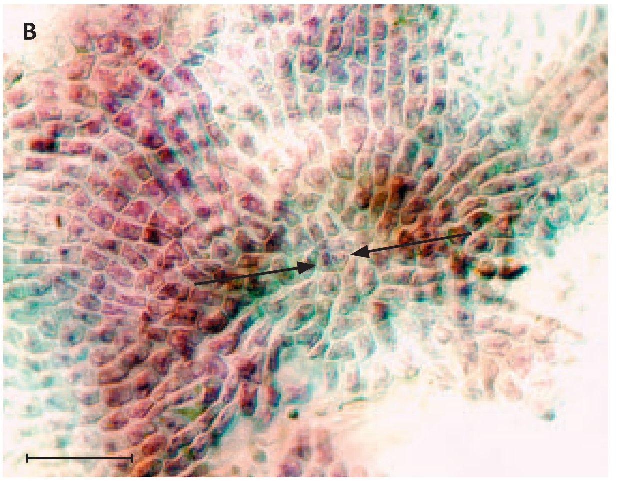
Reproduction: Asexual reproduction by monospores. Monosporangia sessile on the basal layer or apical on short upright filaments. Sporangia are ovoid or ellipsoid 6.5-7 µm wide and 10-11.5 µm in length.

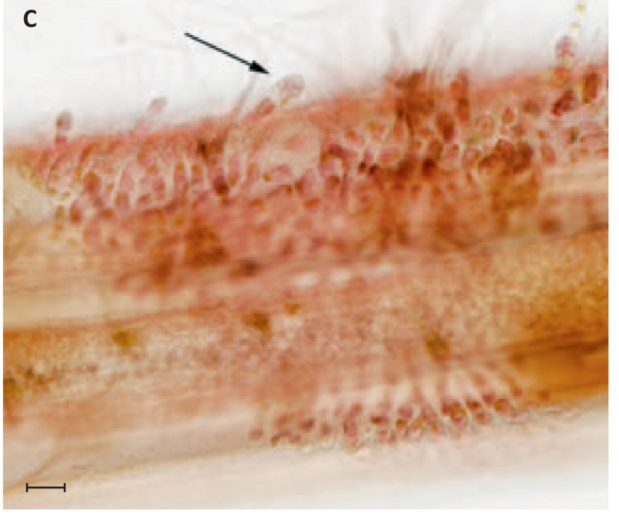
Seasonal variation: Collected in May and August-September.

Habitat: On Purple Siphon Weed (*Leptosiphonia fibrillosa*), and the Knotted Thread Hydroid (*Obelia geniculata*), 7.5-11.5 m depth and on Clustered Green Branched Weed (*Cladophora glomerata*), 0.5 m depth.

References: Rosenvinge (1909, *Chantransia*).







A: *Acrochaetium macula*. Pseudoparenchymatous basal layer of radiating filaments. Scale 50 µm. A-C: On Purple Siphon Weed (*Leptosiphonia fibrillosa*), Schultz's Grund, 4.5 m, 30.8.2013.

B: *Acrochaetium macula*. Basal layer, the original spore transversely divided (arrows). Same alga as in figure A. Scale 25 µm.

C: *Acrochaetium macula*. Short upright filaments with monosporangium (arrow). Scale 10 µm.

Acrochaetium moniliforme

(Rosenvinge) Børgesen

Necklace Star Hair

Appearance: Powder-like microscopic epiphytes, up to c. 60 µm in length. The life history is heteromorphic, the gametophytes have a single basal cell, and the tetrasporophyte has a basal system of prostrate filaments. The tetrasporophyte was previously known as *A. humile* (Rosenvinge) Børgesen.

Structure: The basal cell of the gametophytes attaches to the substratum with a thin wall material. Two to three filaments arise from the basal cell. Cells are rounded to almost spherical in young individuals, becoming barrel-shaped later. They are almost the same size as the basal cell, 7-10 µm in width and 1-2 times as long as wide. In the tetrasporophyte, two equal cells are formed by spore germination. Prostrate filaments arise from these cells. The filaments consist of short cells and are confluent in the middle. Two to three upright filaments arise from each of the prostrate cells. Upright filaments are unbranched and consist of only 2-4 cells. Cells are 5.5-7 µm in width and 2-3 times as long as wide, a stellate plastid with one pyrenoid occur in each cell. Apical red algal hairs are frequent in the upright filaments, seldom lateral.

Reproduction: Sexual reproductive structures are not recorded on the gametophytes in Danish waters, apart from a single individual with antheridia. Asexual reproduction takes place by mono- and tetraspores. Monosporangia are scattered, unilateral, or opposite, seldom on a stalk. They are ovoid or ellipsoid, 7 µm in width and 13.5-15 µm in length. The cruciate tetrasporangia are apical on upright filaments, 8-10 µm in width and 13-18 µm in length. Monosporangia also occur on the tetrasporophytes, where they are apical and oblong ovoid, 7 µm in width and 11-14 µm in height.

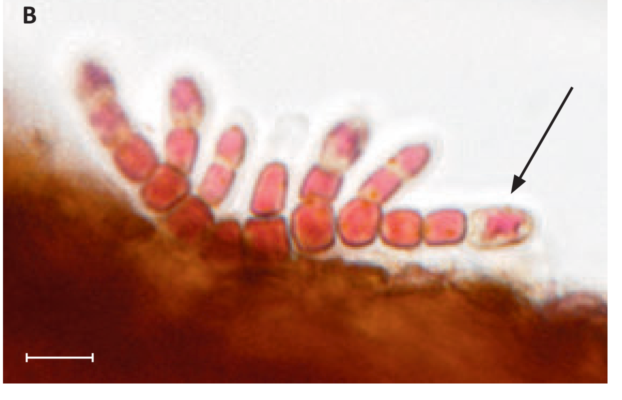
Seasonal variation: Gametophytes recorded in May-September and tetrasporophytes in May-June.

Habitat: Gametophytes occur on Banded Pincer Weed (*Ceramium* sp.), Purple Siphon Weed (*Leptosiphonia fibrillosa*), and Black Siphon Weed (*Vertebrata fucoides*), 1-17 m depth. Tetrasporophytes recorded on Black Siphon Weed (*V. fucoides*), 0.5 m depth.

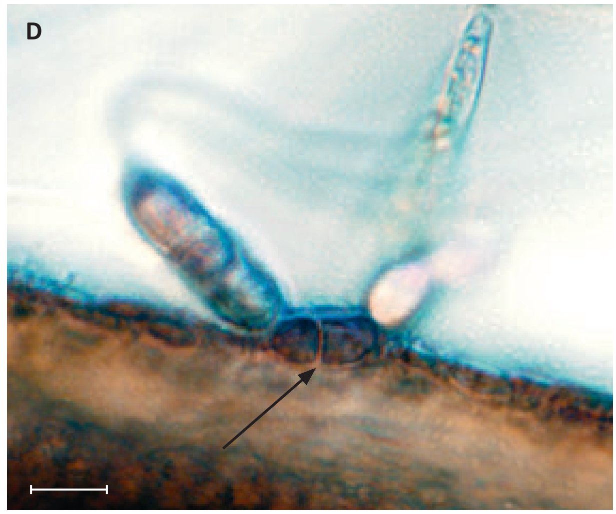
Comment: The tetrasporophyte superficially resembles the tetrasporophyte of *A. hallandicum* but differs by the short upright unbranched filaments and smaller monosporangia. Culture studies of Swedish algae by Stegenga & Mulder (1979) documented the life history.

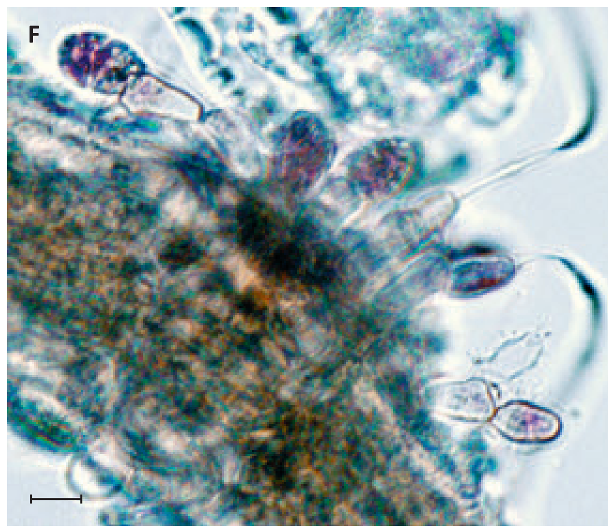
References: Rosenvinge (1909, *Chantransia humilis, C. moniliformis*), Stegenga (1985), Stegenga & Mulder (1979, *Chromastrum*).

A: *Acrochaetium moniliforme*. Gametophyte, rounded basal cell with 2 upright branches. Vegetative cells with stellate plastid. Scale 10 µm. A, B: Store Middelgrund, 9 m, 24.8.1993.



B: *Acrochaetium moniliforme*. Gametophyte with monosporangium (arrow). Scale 10 µm.





C: *Acrochaetium moniliforme*. Gametophyte with 2 antheridia (arrow). Egholm, Agersø, 6 m, 25.10.2013. Leg.: P. Stæhr. Photo by S. Lundsteen. Scale 10 µm.

D: *Acrochaetium moniliforme*. Young tetrasporophyte, the original spore partitioned. Scale 10 µm. D-F: Spodsbjerg, 1 m, 6.6.2016, (type locality).

E: *Acrochaetium moniliforme*. Tetrasporophyte, vegetative cells with stellate plastid. Scale 10 µm.

F: *Acrochaetium moniliforme*. Short upright filaments with monosporangia. Scale 10 µm.

G: *Acrochaetium moniliforme*. Prostrate filaments with uprights of few cells. Apical cruciate tetrasporangium (arrow). Schultz's Grund, 5 m, 6.6.1991. Scale 10 µm.

Acrochaetium parvulum

(Kylin) Hoyt

Tiny Star Hair

Appearance: Epiphytic microscopic bush-like tufts, 100-350 µm in height.

Structure: Up to 6 upright or prostrate branched filaments arise from a single basal cell. The filaments consist of cylindrical cells, (5-) 6-7 µm in width and 2 times as long as wide, with a stellate plastid and one pyrenoid in each cell. Red algal hairs frequent.

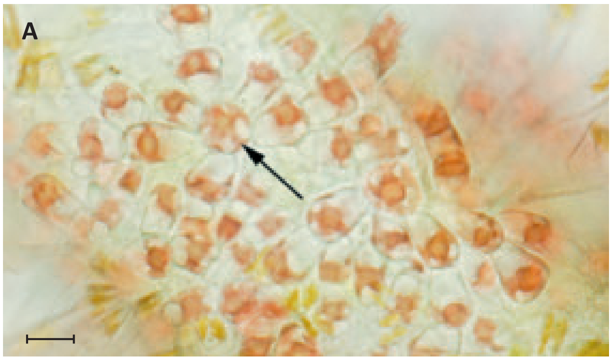
Reproduction: Asexual reproduction by monospores. Monosporangia often opposite, seldom on a stalk.

Seasonal variation: Collected in May-September.

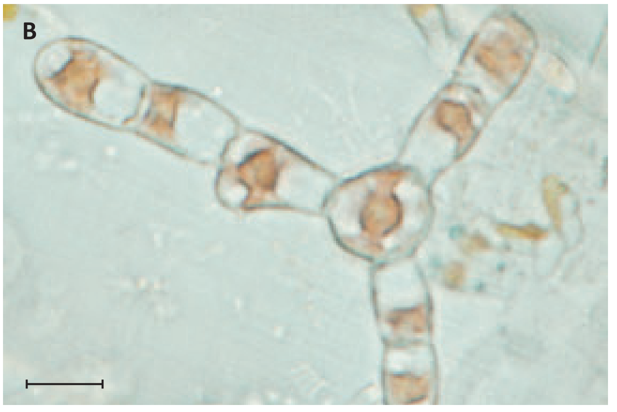
Habitat: Epiphytic on Banded Pincer Weed (*Ceramium* sp.), Purple Siphon Weed (*Leptosiphonia fibrillosa*), Tough Laver (*Porphyra umbilicalis*), Black Siphon Weed (*Vertebrata fucoides*), and Clustered Green Branched Weed (*Cladophora glomerata*), 0.5-9.5 m depth.

Comment: Dioecious gametophytes and a tetrasporophyte observed in culture studies of Tiny Star Hair (*A. parvulum*) from Roscoff by Abdel-Rahman (1984). The cultures initiated from an individual with tetrasporangia.

References: Abdel-Rahman (1984), Kylin (1944, *Kylinia parvula*), Rosenvinge (1909 *Chantransia hallandica* f. *parvula*).

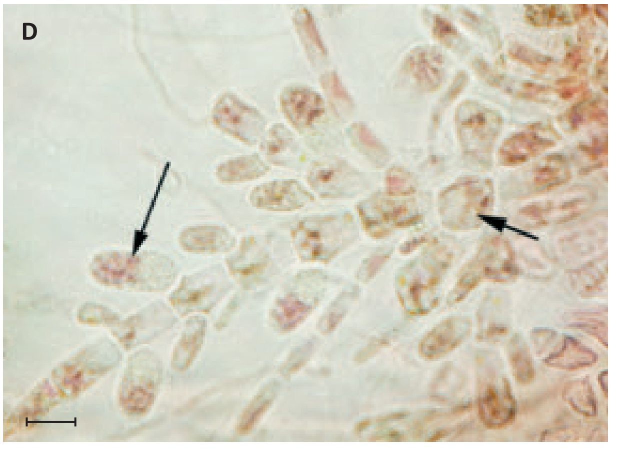


A: *Acrochaetium parvulum*. Rounded basal cells and short vegetative cells with a stellate plastid and one pyrenoid. From one basal cell (arrow) 6 branches arise. Scale 10 µm. A-C: On Clustered Green Branched Weed (*Cladophora glomerata*). The sheltered side of Margretheholms Havn, Copenhagen, 0.5 m, 18.7.2013.



B: *Acrochaetium parvulum*. Young alga, basal cell with 3 branches. Scale 10 µm.

C: *Acrochaetium parvulum*. Empty monosporangium (arrow). Scale 10 µm.



D: *Acrochaetium parvulum*. Opposite branches and monosporangium (left arrow). Basal cell (right arrow). On Banded Pincer Weed (*Ceramium* sp.), Sjællands Rev, 4.5 m, 11.9.1996. Scale 10 µm.

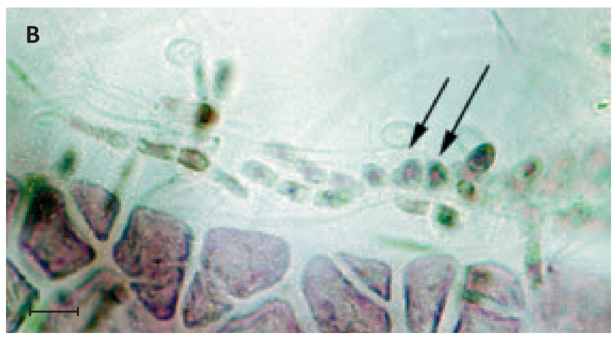
Acrochaetium reductum

(Rosenvinge) Hamel

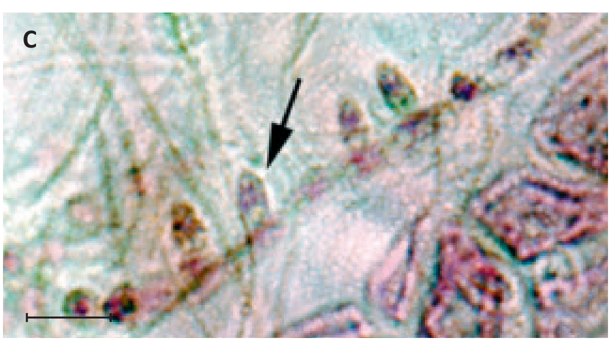
Creeping Star Hair

Appearance: Microscopic prostrate filaments, occasionally with a few upright filaments of 1-3 cells.
Structure: The upright filaments have cylindrical cells, 4.5-6 µm in width and as long as wide. Upright filaments typically consist of only a single cell, which becomes a monosporangium. During germination, the spore divides into two equally large cells, from where prostrate filaments with scattered branches arise. The cells are cylindrical, c. 4 µm in width and 1-2 times as long as wide. They contain a stellate plastid with one pyrenoid. Apical red algal hairs may occur.
Reproduction: Asexual reproduction by monospores. Monosporangia are sessile on the prostrate filaments or apical on upright filaments. They are ovoid or almost spherical, 5.5-7.5 µm in width and 7-9.5 µm in height. Tetrasporangia not recorded on Creeping Star Hair (*A. reductum*) in Danish waters.
Seasonal variation: Recorded in July-September.
Habitat: On Banded Pincer Weed (*Ceramium* sp.), Straggly Bush Weed (*Rhodomela confervoides*) and Black Siphon Weed (*Vertebrata fucoides*), 0.5-4.5 m depth.
Comment: Stegenga & Wissen (1979) found a heteromorphic life history in culture studies of Creeping Star Hair (*A. reductum*) from Kristineberg, Sweden. The gametophyte was identical with *A. kylinoides* Feldmann. This has a single basal cell from where up to 6 short, often prostrate, filaments arise. The length of the filaments rarely exceeds more than 4 cells. The cells are almost isodiametric, 5-7 µm in diameter. The gametophyte not recorded from Danish waters.
References: Rosenvinge (1909 *Chantransia reducta*), Stegenga & Wissen (1979).

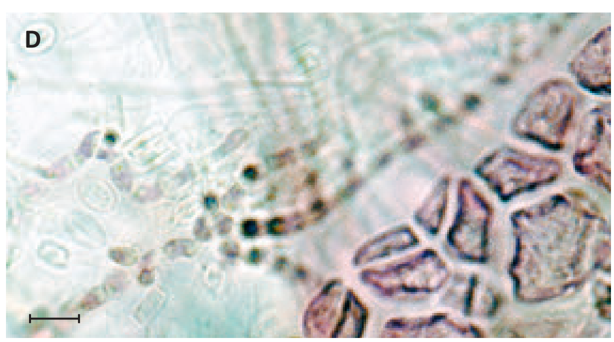
A: *Acrochaetium reductum*. Young alga, the original spore partitioned. Scale 10 µm. A-D: On Banded Pincer Weed (*Ceramium* sp.), Sjællands Rev, 4.5 m, 11.8.1996.



B: *Acrochaetium reductum*. Prostrate filament with short upright branches. The two cells of the original spore still visible (arrows). Scale 10 µm.



C: *Acrochaetium reductum*. Prostrate filament with monosporangia (arrow). Scale 10 µm.



D: *Acrochaetium reductum*. Larger prostrate filament with upright branches. Scale 10 µm.

Acrochaetium secundatum

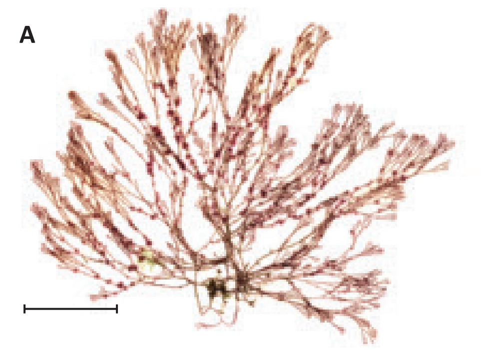
(Lyngbye) Nägeli

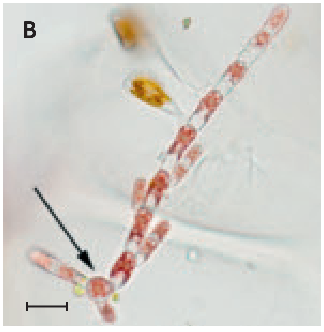
Branched Star Hair

Appearance: Microscopic tufts to a few millimetres in height. The life history is heteromorphic with dioecious gametophytes and a tetrasporophyte. The gametophyte previously known as *A. rhipidandrum* (Rosenvinge) Hamel.

Structure: The gametophytes have an almost spherical basal cell. It is 13-15 µm in diameter and attached to the substratum on the flat underside. From the basal cell, arise 2-3 sparsely branched upright filaments of cylindrical cells, (7.5-) 9-11 µm in width and 2-3 (-4) times as long as wide. The tetrasporophyte has a basal disc with a triangular central cell surrounded by three elongated cells. This structure is visible in old specimens even when the disc has increased in diameter. From the middle of the basal disc, arise one or a few upright filaments. They have scattered, unilateral or opposite branches and appear slightly complanate in some cases. Cylindrical cells are 7-12 (-14) µm in width and 1-2 times as long as wide. Vegetative cells have a stellate plastid with one central pyrenoid. Red algal hairs may occur apically on the branches.

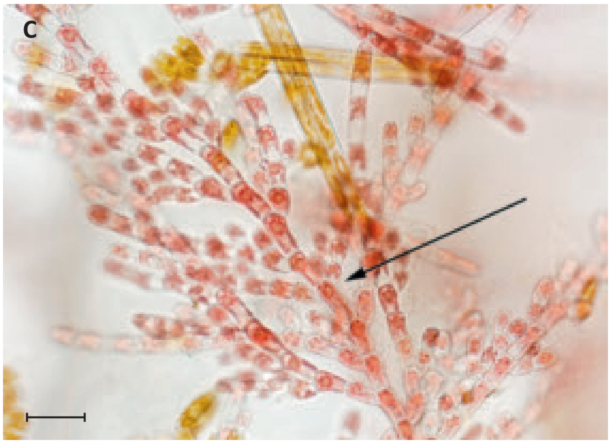
Reproduction: Male gametophytes have apical antheridia on small branches occurring in clusters in the corner of large branches. Female gametophytes have bottle-shaped carpogonia with trichogyne. They are lateral on the upper part of the main axis or on the lower part of branches. The carposporophytes develop directly after fertilization and consist of radiating filaments forming a more or less spherical gonimoblast. Monosporangia may occur lateral on the branches with or without a stalk-cell, scattered





A: *Acrochaetium secundatum*. Red tufts on *Ceramium tenuicorne*. Lynetteløbet, Copenhagen, 0.5 m, 5.4.2004. Scale 2 cm.

B: *Acrochaetium secundatum*. Young gametophyte, a single basal cell (arrow) and upright filaments. Scale 25 µm. B-D: Sheltered side of Margretheholms Havn, Copenhagen, 0.5 m, 17.9.2008.



C: *Acrochaetium secundatum*. Larger gametophyte, scattered and opposite branches (arrow). Several brown diatoms. Scale 25 µm.

D: *Acrochaetium secundatum*. Monosporangium on gametophyte (arrow). Scale 10 µm.

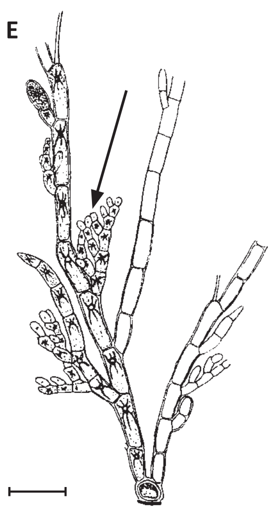
and often unilateral or opposite. They are ovoid or ellipsoid, 9-10 µm in width and 14-18.5 µm in height. Tetrasporangia are lateral on the axis, apical on branches or opposite or unilateral on the adaxial side of branches. They are 13-17 µm in width and 19-22 µm in height. Monosporangia are frequent on tetrasporophytes, they are unilateral on the adaxial side of small branches or they are apical. Monosporangia are ovoid or broad ellipsoid to more or less spherical, (9-) 10-14 (-15) µm in width and (13-) 15-20 (-21) µm in height.

Seasonal variation: Gametophytes collected in August with reproductive structures. Tetrasporophytes collected all year.

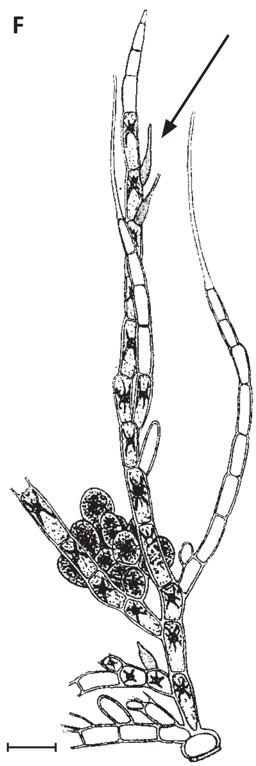
Habitat: Gametophytes recorded on *Ceramium tenuicorne* and Tough Laver (*Porphyra umbilicalis*) and only noticed in shallow water, harbour of Frederikshavn. Tetrasporophytes are frequent on various algae such as Tough Laver (*Porphyra umbilicalis*), Black Siphon Weed (*Vertebrata fucoides*), Glaucous Brick Weed (*Chaetomorpha melagonium*), and on other organisms including the hydroid *Dynamena pumila* and the Knotted Thread Hydroid (*Obelia geniculata*), 0.5-18 m depth.

Comment: Stegenga & Mulder (1979) found by culture studies that the gametophyte is identical to *Chantransia rhipidandra* Rosenvinge. They also found that *Acrochaetium virgatulum* (Harvey) Batters is a synonym of *A. secundatum*, which Clayden & Saunders (2014) confirmed by comparing type material and undertaking genetic investigations. Rosenvinge (1909) described specimens with many tetrasporangia as *Chantransia virgatula* f. *tetrica* Rosenvinge.

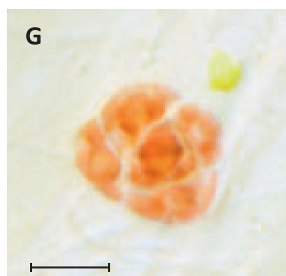
References: Clayden & Saunders (2014), Lee & Lee (1988), Rosenvinge (1909, *Chantransia rhipidandra, C. virgatula*), Stegenga (1985), Stegenga & Mol (1983), Stegenga & Mulder (1979).

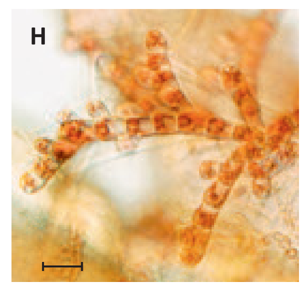


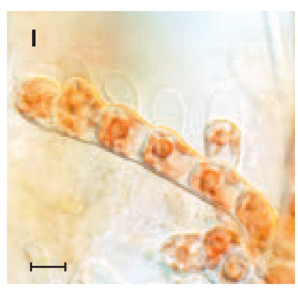
E: *Acrochaetium secundatum.* Male gametophyte with antheridia (arrow). Scale 20 µm. E-F: Frederikshavn. After Rosenvinge (1909).

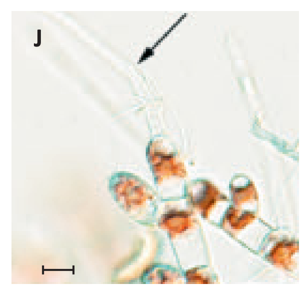


F: *Acrochaetium secundatum.* Female gametophyte with carpogonia (arrow) and gonimoblast. Scale 20 µm.









G: *Acrochaetium secundatum.* Young basal disc of tetrasporophyte with a central triangular cell. Scale 10 µm. G, J: Southern harbour jetty, Hirsholm, 0.5 m, 14.4.2015.

H: *Acrochaetium secundatum.* Tetrasporophyte, short cells with stellate plastid. Scale 25 µm. H, I: Herthas Flak, 10 m, 17.8.2015

I: *Acrochaetium secundatum.* Branch with unilateral empty monosporangia. Scale 10 µm.

J: *Acrochaetium secundatum.* Branch with monosporangia and apical red algal hair (arrow). Scale 10 µm.

Grania

Spiral Thread Weed

Uniseriate branched filaments, microscopic to a few millimetres in height. Upright filaments arise from prostrate filaments which are epiphytic, or endophytic, epizoic or endozoic. Vegetative cells contain one or two parietal, ribbon-shaped slightly spiral twisted plastids without pyrenoids.

References: Athanasiadis (2016), Clayden & Saunders (2008), Harper & Saunders (2002), Hwang & Kim (2011), Stegenga & Mulder (1979, *Chromastrum*).

Key to species of *Grania*

1a.	Cells of upright filaments, 4-7.5 µm wide and 6-16 times as long as wide	*G. efflorescens*
1b.	Cells of upright filaments, 6-9 (-10.5) µm wide at the base and 3.5-4 µm at the apex and 4-6 (-7) times as long as wide	*G. pectinata*

Grania efflorescens

(J.Agardh) Kylin

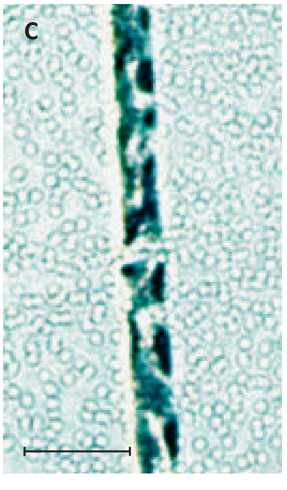
Appearance: Tiny branched bright red-violet tufts, 5-6 mm in height. Epiphytic on larger algae and on hydroids occasionally as a felty cover to 2 mm in height.

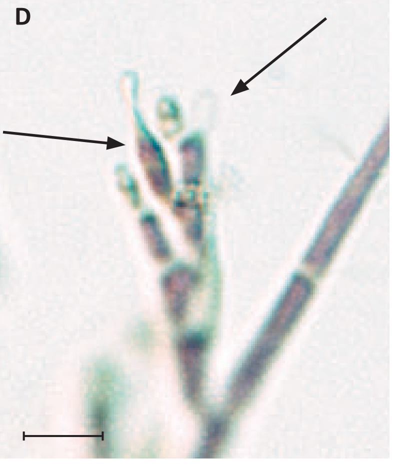
Structure: Upright, uniseriate, branched filaments arise from a basal system, which also consists of branched filaments. The branches are mainly scattered, but thalli with tetrasporangia or monosporangia have few-celled opposite branches. Cells of the upright filaments are 4-7.5 µm in width and 6-16 times as long as wide. Downward-growing filaments are sometimes present in the lower part of upright filaments. Each cell has one or two parietal, ribbon-shaped and spirally twisted plastids without pyrenoids. The spiral shape of the plastid is best developed in the young cells while older cells may have irregularly and fragmented plastids.

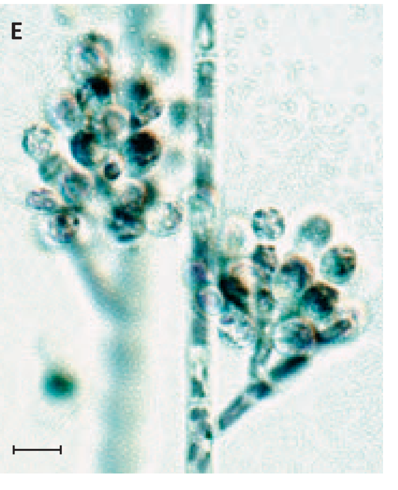
Reproduction: Tufts of monoecious gametophytes and tetrasporophytes forming a velvet-like cover up to 2 mm in height. Gametophytes have male and female reproductive structures typically close to each other on the same few-celled branch. Antheridia are apical, often in pairs. Carpogonia are lateral just below the antheridia or may be intercalary, they have a relatively long trichogyne at the upper end. Following fertilization, the carposporophyte develops into an approximately spherical gonimoblast, each branch a row of carposporangia. The tetrasporangia are individual or in pairs and may be apical on short branches or opposite. The cruciate tetrasporangia are elongate ellipsoid, 8-12.5 µm in width and 15-28 µm in

A: *Grania efflorescens*. Bright red-violet tufts on Purple Claw Weed (*Cystoclonium purpureum*). Grenå Kalkgrund, 9 m, 14.7.1968. Scale 2 cm. Leg.: L. Mathiesen.

B: *Grania efflorescens*. Young gametophyte, narrow branched filaments. Store Middelgrund, 20.5 m, 9.6.1993. Scale 100 µm.



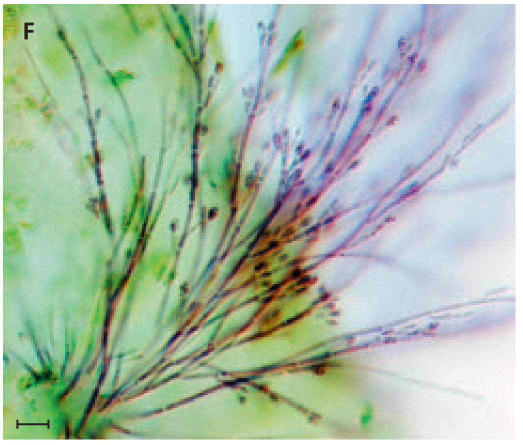




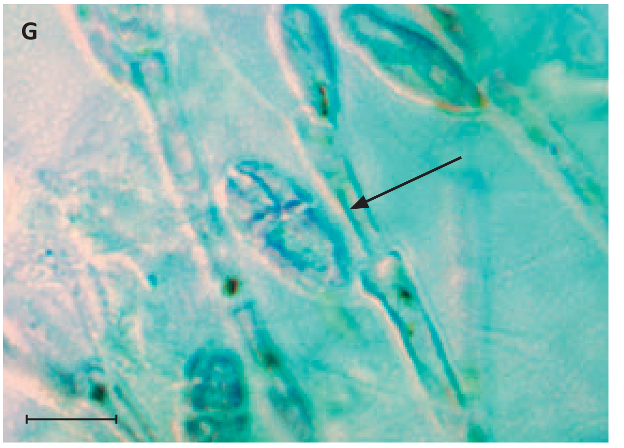
C: *Grania efflorescens*. Cells with spiral-shaped plastid without pyrenoids. Vejrø, 15 m, 5.6.1991. Scale 10 µm.

D: *Grania efflorescens*. Antheridia (right arrow), one empty, and carpogonium with trichogyne (left arrow). Ebbeløkke, 11 m, 26.7.1994. Scale 10 µm.

E: *Grania efflorescens*. Gonimoblasts, with rows of carposporangia. Kims Top, 14.5 m, 5.6.1993. Scale 10 µm.



F: *Grania efflorescens*. Monosporangia. Endozoic basal filaments, not visible. Store Middelgrund, 15 m, 9.6.1993. Scale 25 µm.



G: *Grania efflorescens*. Filament with tetrasporangium (arrow). On a hydroid, Lysegrund, 10.5 m, 19.1.1997. Scale 10 µm.

height. Monosporangia occur in the same way as the tetrasporangia and are similar, but smaller, 5-7 (-8) µm in width and (10-) 11-18 µm in height.

Seasonal variation: Recorded in April-August with sexual reproductive structures. Mature carposporangia collected in January, June-August and tetrasporangia in April-June.

Habitat: On other algae including Purple Claw Weed (*Cystoclonium purpureum*), Sea Beech (*Delesseria sanguinea*), and Desmarest's Prickly Weed (*Desmarestia aculeata*), and on hydroids and fungi. Collected by divers at 4-29 m depth and in older collections by dredging to 38 m depth.

Resembles: Particularly characteristic are the spherical gonimoblasts of carposporangia in rows.

Comment: Clayden & Saunders (2008) accepted the genus *Grania* based on culture and molecular studies of algae from Danish waters.

References: Clayden & Saunders (2008), Dixon & Irvine (1977, *Audouinella efflorescens*), Kylin (1944), Pedersen (2011), Rosenvinge (1909, *Chantransia efflorescens*).

Grania pectinata

(Kylin) Athanasiadis

Recent synonym: *Colaconema pectinatum* (Kylin) J.T.Harper & G.W.Saunders

Appearance: Tiny bushy tufts, 1-3 mm in height, of narrow filaments with scattered branches.

Structure: Basal system of prostrate, branched filaments, which are epi- or endophytic or occasionally grow in the wall (the tough, chitinous perisarc) of hydroids. The upright filaments have scattered branches on all sides, most branches are small with sporangia. Upright filaments are 6-9 (-10.5) µm wide near the base and become gradually narrower towards the apex where they are 3.5-4 µm wide. The cells are 4-5 (-7) times as long as wide. Plastids, without pyrenoids, are parietal, irregular band-shaped to slightly spirally twisted in young cells and irregular plate-shaped in old cells.

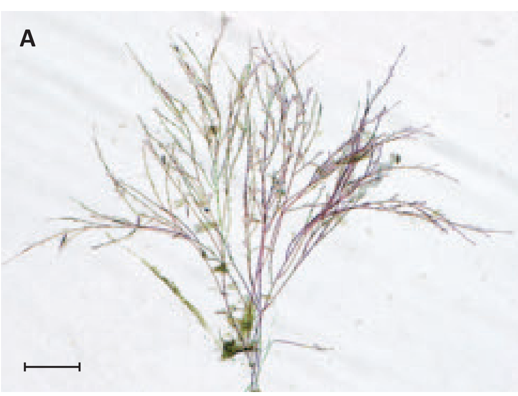
Reproduction: Asexual reproduction by monospores and tetraspores. Monosporangia are unilateral on the adaxial side of small branches or opposite. They might be sessile on the branches but frequently in pairs on a stalk-cell. Sporangia are ellipsoid 5.5-7.5 µm in width and 10-14 µm in height. Tetrasporangia occur in the same way as the monosporangia and on individuals with monosporangia. The tetrasporangia are c. 10 µm in width and 16 µm in height, but rarely recorded on epiphytic algae from Danish waters.

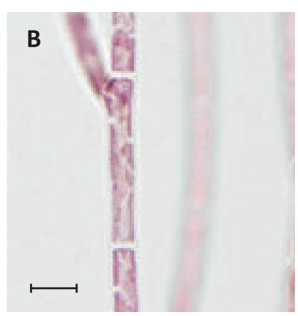
Seasonal variation: Collected in April-September, monosporangia recorded in May-September and tetrasporangia in May-June.

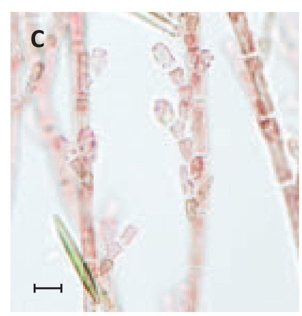
Habitat: Epiphytic on various algae like Banded Pincer Weed (*Ceramium* sp.), Lobed Leaf Bearer (*Coccotylus brodiei*), Short Leaf Bearer (*C. truncatus*), Sea Oak (*Phycodrys rubens*), Desmarest's Prickly Weed (*Desmarestia aculeata*), on stipe and haptera of Kelp (*Laminaria* sp.), and epizoic on Common Whelk (*Buccinum undatum*), the bryozoan Horn Wrack (*Flustra foliacea*) and hydroids, 13-24.5 m depth.

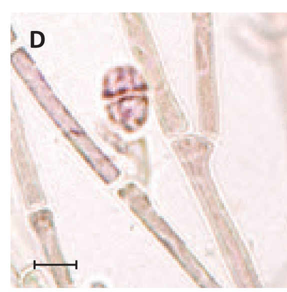
Comment: May grow endozoic in Pink-mouthed Hydroids (*Tubularia* sp.) and have upright filaments with tetrasporangia according to Rosenvinge (1935a).

References: Harper & Saunders (2002), Rosenvinge (1909, *Chantransia*, 1935a, *Rhodochorton*), Stegenga (1985, *Audouinella*).









A: *Grania pectinata*. Bushy tuft of upright filaments, short branches with monosporangia. Scale 200 µm. A-C: Vengeancegrund, 10 m, 12.9.1991.

B: *Grania pectinata*. Vegetative cells with irregular parietal plastid without pyrenoids. Scale 10 µm.

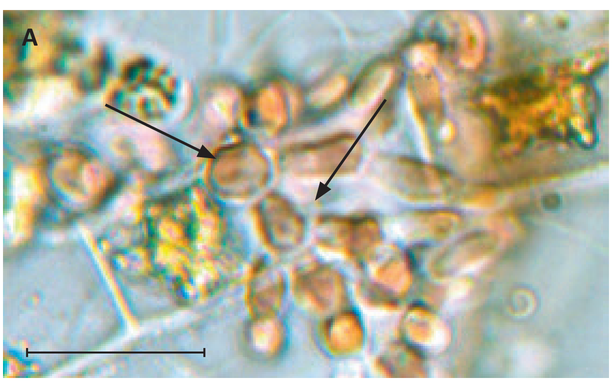
C: *Grania pectinata*. Short branches with unilateral monosporangia. Scale 10 µm.

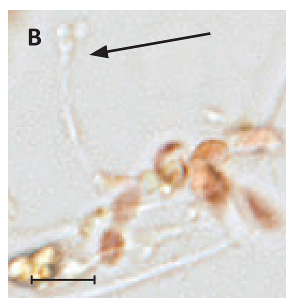
D: *Grania pectinata*. Tetrasporangium. Herthas Flak, 13 m, 4.6.1993. Scale 10 µm

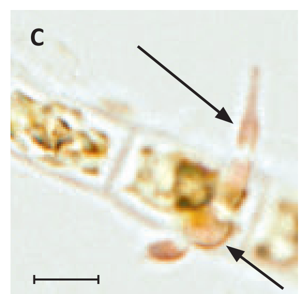
Kylinia rosulata

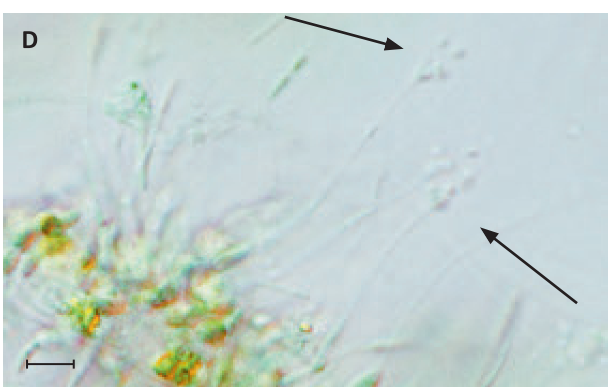
Rosenvinge

Appearance: Microscopic epiphytes with branches along the surface of the host.
Structure: From a hemispherical basal cell, arise radiating uniseriate branches, of which there may be up to seven. They are up to five cells long and may have short opposite branches. Cells are 4.5-6.5 µm in width and 1.5-2 times as long as wide. They have a parietal plastid without pyrenoid. Red algal hairs are frequent and may arise from the basal cell.
Reproduction: Sexual reproduction in monoecious or dioecious gametophytes and asexual reproduction by monospores, the sporangia usually form on separate thalli. Male gametophytes have a specialised long cell (androphor) with a wide apex where the 2-6 antheridia form. Female gametophytes have apical carpogonia on short branches or direct on the basal cell, and long trichogyne. Small clumps of cells observed by Rosenvinge (1909) probably represent gonimoblasts. Monosporangia are ellipsoid and often apical on short branches.
Seasonal variation: Collected in July-September with antheridia, carpogonia, and monosporangia.
Habitat: Recorded only a few times in Danish waters, epiphytic on Cotton Wool Weed (*Ectocarpus* sp.) that grows on drifting Bootlace Weed (*Chorda filum*), on Artist's Brush Cotton Wool Weed (*E. penicillatus*), and on Woolly Seed Weed (*Sporochnus pedunculatus*), 4-16 m depth.
Comment: *Kylinia* differs from other Acrochaetiales by the long androphor, and also by lacking a stellate plastid. Material referred to *K. rosulata* by Kylin (1944) are instead *A. kylinoides* Feldmann (1958). Thalli with a heteromorphic life history, studied in culture as *Kylinia rosulata-Acrochaetium strictum* by Stegenga & Wissen (1979), are misidentified according to Stegenga (1985 p. 292).
References: Feldmann (1958), Kylin (1944), Nicolaisen in Moestrup et al. (1975), Rosenvinge (1909), Stegenga (1985), Stegenga & Wissen (1979).









A: *Kylinia rosulata*. Large basal cell (left arrow), with several branches some with opposite branches (right arrow). Scale 10 µm. A-D: On Cotton Wool Weed (*Ectocarpus* sp.) Schultz's Grund, 4.5 m, 30.8.2013.

B: *Kylinia rosulata*. Male gametophyte, basal cell with radiating short branches and apical androphor (arrow). Scale 10 µm.

C: *Kylinia rosulata*. Female gametophyte with basal cell (lower arrow) and an upright branch with apical carpogonium (upper arrow). Scale 10 µm.

D: *Kylinia rosulata*. Several individual almost cover the host. Many upright androphores with antheridia (arrows). Scale 10 µm.

Family: Rhodochortonaceae

Rhodochorton purpureum

(Lightfoot) Rosenvinge

Purple Felt Weed

Appearance: Often form dense velvet-like covers of red brown filaments. Thalli are typically c. 5 mm in height but may be up to 15 mm.

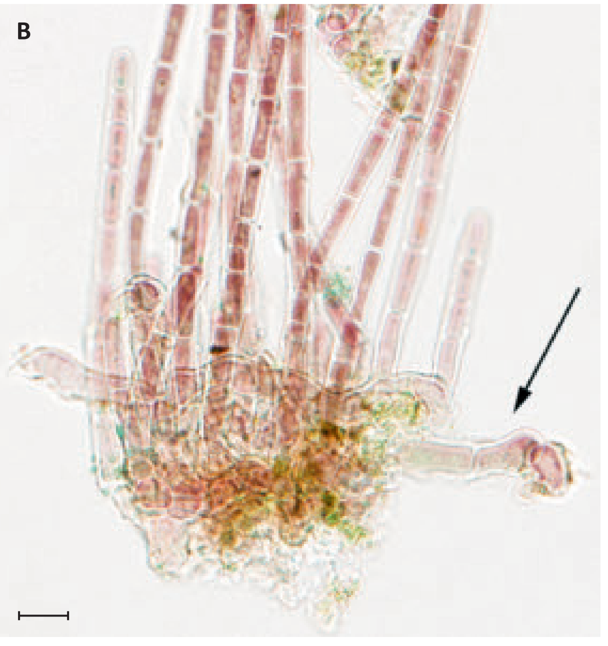
Structure: Upright uniseriate filaments from a basal layer of prostrate filaments. Upright filaments are uniformly thick and consist of cylindrical cells, 10-15 µm in width and 2-3 times as long as wide. Branching is sparse and scattered. Lateral branches occur particularly in the upper part of the thallus and often in connection with formation of sporangia which have short stalks. Growth may continue from the stalk-cells through emptied sporangia. Downward-growing filaments may occur in the lower part of uprights. Prostrate filaments have scattered branches often matted to form irregular crusts. Their cells are cylindrical or slightly irregular in shape, 10-16 µm wide. Vegetative cells contain several disc-shaped plastids without pyrenoids.

Reproduction: Tetrasporangia are the only reproductive structures recorded in Danish waters. They are apical on small branches at the apex of the thalli. They are ellipsoid and cruciately divided.

Seasonal variation: Occur all year, mature tetrasporangia in winter month recorded in January-May.

Habitat: Very frequent on boulders but also epiphytic on coarse algae such as Lobed Leaf Bearer (*Coccotylus brodiei),* Short Leaf Bearer (*C. truncatus*), Stalked Leaf Bearer (*Phyllophora pseudoceranoides*), stipe and haptera of Forest Kelp (*Laminaria hyperborea*), and Glaucous Brick Weed (*Chaetomorpha melagonium*). Purple Felt Weed (*Rhodochorton purpureum*) occurs in shaded places in the littoral such as between big boulders or under the cover of larger algae, for instance *Fucus* species.

A: *Rhodochorton purpureum.* Upright branches from matted basal filaments, a few mutually free (arrow). At the apex, small branches with tetrasporangia. Læsø Trindel, 7.5 m, 1.2.1996. Scale 100 µm.



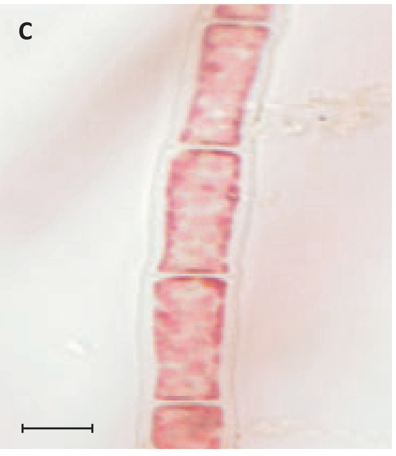
B: *Rhodochorton purpureum*. Prostrate filaments (arrow) and basal part of upright filaments. Søndre Stenrøn, 6.5 m, 6.9.1993. Scale 20 µm.

Collected to 27 m depth by divers and in older collections with dredge to 36 m depth.

Resembles: Reminiscent of *Meiodiscus spetspergensis*, but this has a pseudoparenchymatous basal disc of radiating filaments and almost spherical tetrasporangia with a characteristic thickened top of the cell wall. The tetrasporangia are apical on main branches not in bundles of small branches.

Comment: Sexual reproduction only known from culture studies. In these, tetrasporophytes grow directly from cells cut off from the fertilized carpogonium without formation of free carpospores (Stegenga, 1978). Gametophytes not reported from nature except a single observation of antheridia (Breeman et al., 1984).

References: Breeman et al. (1984), Dixon & Irvine (1977, *Audouinella purpurea*), Harper & Saunders (2002), Rosenvinge (1923-24, *R. rothii*), Stegenga (1978).



C: *Rhodochorton purpureum*. Cells with many disc-shaped plastids without pyrenoids. Vodrup Flak, 9.5 m, 31.7.1994. Scale 10 µm.

D: *Rhodochorton purpureum*. Cruciate tetrasporangia (arrow). Tønneberg Banke, 11.5 m, 1.2.1996. Scale 20 µm.

Order: Colaconematales · Family: Colaconemataceae

Colaconema

Plate Threads

Branched uniseriate filaments, microscopic to a few millimetres in height. Epiphytic or epizoic, occasionally with endophytic or endozoic filaments. Cells contain a parietal plate-shaped plastid or several more or less spiral-shaped plastids per cell. Sexual reproduction known in some species with monoecious or dioecious gametophytes. A diploid carposporophyte develops after fertilization. Tetrasporophytes have cruciate tetrasporangia.

References: Harper & Saunders (2002), Hwang & Kim (2011).

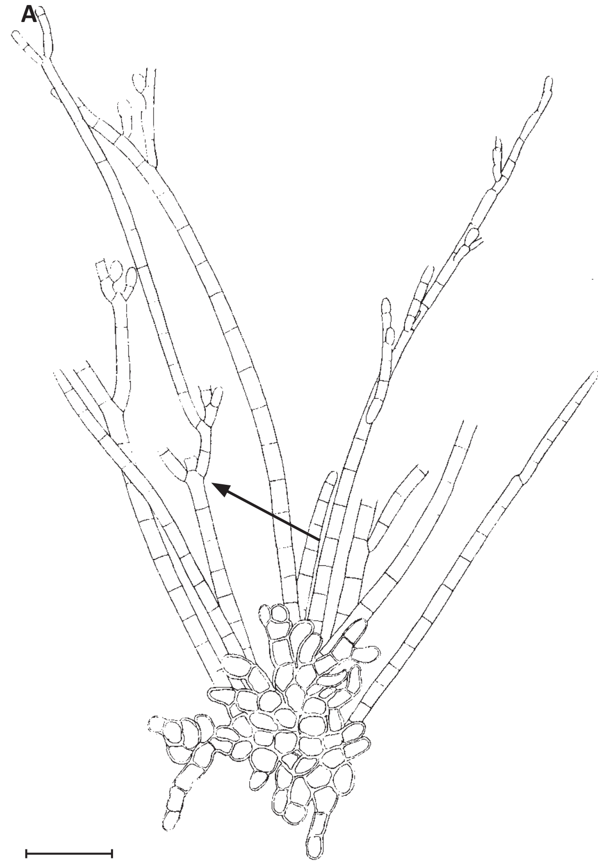
Identification key to species of *Colaconema*

1a.	Epiphytic or epizoic; endophytic or endozoic basal filaments may occur	2
1b.	Endophytic or endozoic filaments	7
2a.	A single basal cell, upright sexual filaments, on *Ectocarpus* sp.	*C. gynandrum*
2b.	Multicellular basal system	3
3a.	Opposite branches present, basal system well developed, consisting of confluent filaments of short cells. Cells in upright filaments, 5-7 µm in width and 3-4 times as long as wide	*C. attenuatum*
3b.	No opposite branches	4
4a.	Upright filaments sparsely branched. They arise from basal filaments, which are confluent or extended. Cells are 4-7 µm in width and 3-4.5 times as long as wide	*C. strictum*
4b.	Upright filaments have many branches	5
5a.	Cells < 10 µm in width and 5-8 times as long as wide. Monosporangia > 14 µm in height	6
5b.	Cells short, 7-10 µm in width and 2-4 times as long as wide, with thick walls. Monosporangia < 14 µm in height with beaker-shaped stalk-cells, apical on short branches in clusters in axils of larger branches	*C. daviesii*
6a.	Monosporangia, (17.5-) 19-22 (-25) µm in height, often unilateral on the adaxial side of branches, sessile or on a stalk-cell and may occur in pairs	*C. savianum*
6b.	Monosporangia, 14.2-19 µm in height, they have a cylindrical stalk-cell, adaxial or apical on short branches in clusters in axils of larger branches	*C. nemalii*
7a.	Endophytic with opposite branches. Only structures outside the surface of the host are monosporangia on stalk-cells	*C. emergens*
7b.	Endozoic branched filaments in the outer covering (perisarc) of the Knotted Thread Hydroid (*Obelia geniculata*). Opposite branches occur. Monosporangia sessile on the creeping filaments, in part outside the surface of the host	*Colaconema* sp. '*obeliae*'

Colaconema attenuatum

(Rosenvinge) R.Nielsen

Appearance: Tufts of sparsely branched filaments, up to 0.5 mm in length.
Structure: Basal layer well developed and consists of confluent filaments of isodiametric cells. Numerous upright filaments up to 550 µm in height arise from the basal layer. Upright filaments have sparse branches which are scattered or opposite and attenuate towards the apex. Filaments are 6.5-7 µm in width at the base with cells twice as long as wide, cells just below the apex are c. 5 µm in width and 3-4 times as long as wide. Apical red algal hair often present. Opposite branches occur, particularly below an apical cell with a hair. Each cell contains a parietal plastid with one pyrenoid.
Reproduction: Asexual reproduction by monospores. Monosporangia are 4.5-6 µm in width and 7.5-9 µm in height. They occur individually or two together on a stalk-cell, seldom sessile on the filaments.
Seasonal variation: Collected in August with monosporangia.
Habitat: On Desmarest's Prickly Weed (*Desmarestia aculeata*), 5 m depth.
Resembles: *Colaconema savianum* and *C. nemalii* also have a well-developed basal layer, *C. attenuatum* is distinguished by the presence of frequent hairs and opposite branches. *Colaconema strictum* and *C. gynandrum* also have hairs but no long branches.
Comment: A rare species seldom reported and not observed in recent Danish collections. Described by Rosenvinge (1909) with the type locality in Nissum Bredning, the western part of the Limfjord.
References: Rosenvinge (1909, *Chantransia attenuata*).



A: Colaconema attenuatum. Basal layer of isodiametric cells. Upright filaments with opposite branches (arrow). Nissum Bredning, 5 m, Scale 20 µm. After Rosenvinge (1909).

Colaconema daviesii

(Dillwyn) Stegenga

Appearance: Tufts of narrow filaments typically less than 1 mm in height. The short thick-walled cells and bundles of small branches with monosporangia, make it recognizable when observed with a magnifying glass.
Structure: Base of prostrate filaments are sometimes entangled. The filaments may grow on top of each other on an uneven substratum, and the basal system becomes multi-layered. Numerous upright filaments arise from the basal system and have scattered branches on all sides. The filaments consist of thick-walled cells, 7-10 µm in width and 1.5-4 times as long as wide. Each cell contains a parietal plate-shaped plastid with one pyrenoid.
Reproduction: The only reproductive structure reported are monospores. The monosporangia occur on fan-shaped clusters of small branches in the axils

of larger branches. The sporangia are apical, typically on a beaker-shaped stalk-cell. The sporangia are 5-8 µm in width and 10-14 µm in height.

Habitat: Epiphytic on various algae, epizoic on the bryozoan Horn Wrack (*Flustra foliacea*), and Edible Periwinkle (*Littorina littorea*), 1-23 m depth.

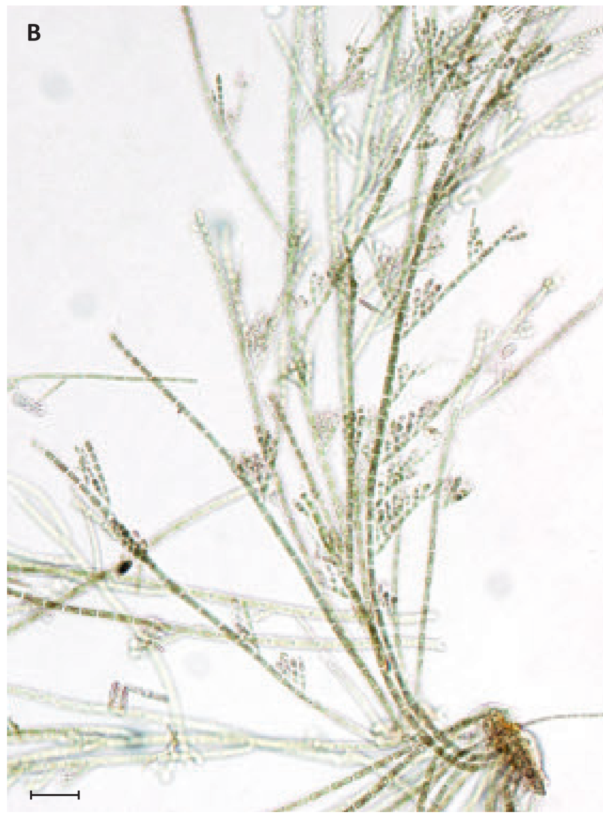
Seasonal variation: Occurs all year, collected with monosporangia in May-December.

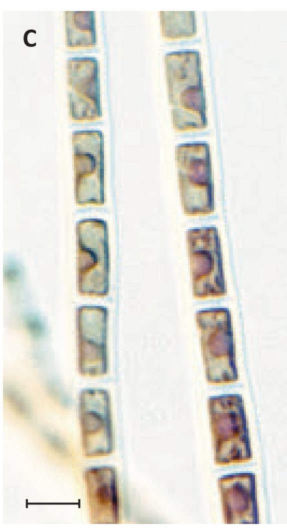
Resembles: Can be distinguished from *C. nemalii* and *C. savianum* by the height of monosporangia, which are more than 14 µm in length in these two species and without a beaker-shaped stalk-cell which is unique for *C. daviesii*. The stalk-cell is cylindrical in the two other species and often carries pairs of monosporangia, not seen in *C. daviesii*.

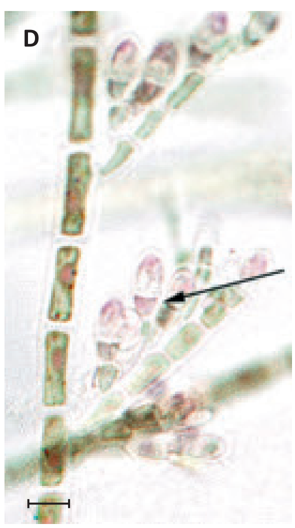
Comment: The mention of *C. daviesii* (as C*hantransia*) by Rosenvinge (1909) includes various algae and only the smallest with sporangia < 14 µm in height are *C. daviesii* according to Stegenga & Erp (1979 p. 443). The specimens with longer sporangia are probably identical with *C. nemalii* (Stegenga & Erp 1979).

References: Harper & Saunders (2002), Stegenga (1985), Stegenga & Erp (1979, *Acrochaetium*), Stegenga & Mol (1983), Rosenvinge (1909, *Chantransia*).

A: *Colaconema daviesii.* Bushy tuft of upright filaments from a dense base. Scale 100 µm. A-B, D: Schultz's Grund, 13 m, 10.8.1992.







B: *Colaconema daviesii.* Upright filaments with monosporangia on clusters of small branches. Scale 25 µm.

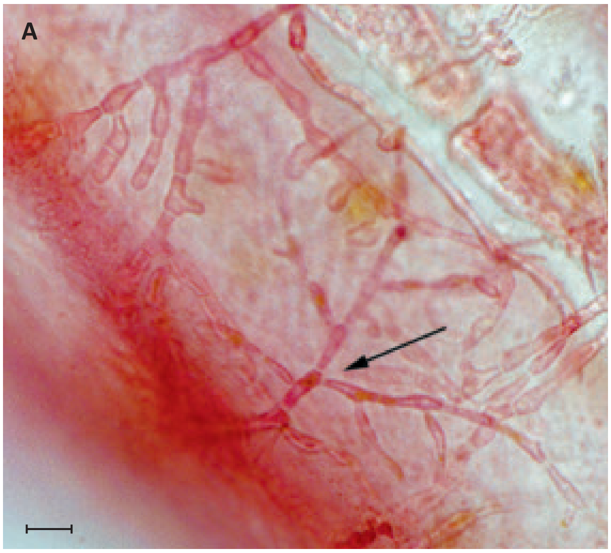
C: *Colaconema daviesii.* Vegetative cells with thick walls, a parietal plastid and one large pyrenoid per cell. Tønneberg Banke, 15 m, 27.8.1993. Scale 10 µm.

D: *Colaconema daviesii.* Monosporangia, each sporangium on a beaker-shaped stalk-cell (arrow). Scale 10 µm.

Colaconema emergens

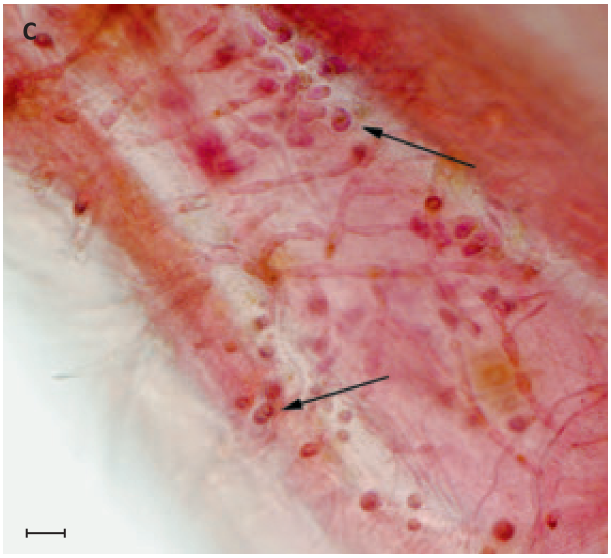
(Rosenvinge) R.Nielsen

Appearance: Microscopic endophytic filaments within the outer wall of the host alga.
Structure: Prostrate filaments with scattered or opposite branches and many branch angles almost perpendicular. Cells are slightly swollen 2-3.5 µm in width and 6-10.5 µm in height, typically 3-5 times as long as wide. Each cell contains a parietal plastid with one pyrenoid.
Reproduction: Asexual reproduction by monospores. Monosporangia are above the surface of the host on a stalk-cell, seldom sessile on the filaments. They are ovoid 3-4 µm in width and 5-6.5 µm in height.
Seasonal variation: Collected in August with monosporangia.
Habitat: Endophytic in the outer cell wall of Purple Siphon Weed (*Leptosiphonia fibrillosa*) and Pitcher Siphon Weed (*Polysiphonia stricta*).
Comment: Described by Rosenvinge (1909) with type locality at Møllegrund outside Hirtshals.
References: Rosenvinge (1909, *Chantransia emergens*).



A: *Colaconema emergens*. Vegetative filaments with sparse, opposite branches (arrow). Scale 10 µm. A-C: In the cell wall of Purple Siphon Weed (*Leptosiphonia fibrillosa*), Tønneberg Banke, 10.5 m, 27.8.2013.

B: *Colaconema emergens*. Monosporangium on stalk-cell (arrow) outside the cell wall of the host. Scale 10 µm.



C: *Colaconema emergens*. Monosporangia visible as dark rounded cells (arrows). Scale 10 µm.

Colaconema gynandrum

(Rosenvinge) R.Nielsen

Appearance: Microscopic filaments about 200 µm in length on Artist's Brush Cotton Wool Weed (*Ectocarpus penicillatus*).

Structure: The single basal cell is almost spherical or slightly flattened, 7.5-9 µm in diameter. Two to four upright filaments arise from the basal cell, one of them often relatively long. Filaments are unbranched or with a few short branches of one or two cells. The cells are cylindrical or slightly barrel-shaped, 5-7 µm in width and 2 to 4 times as long as wide. Each cell contains a parietal plastid and one pyrenoid. Red algal hairs are frequent. They are apical when young but become lateral by continued growth. In the upper end of the cells there is often a small slope with red algal hairs, also visible when the hair is shed. In a few cases, the hairs are produced laterally.

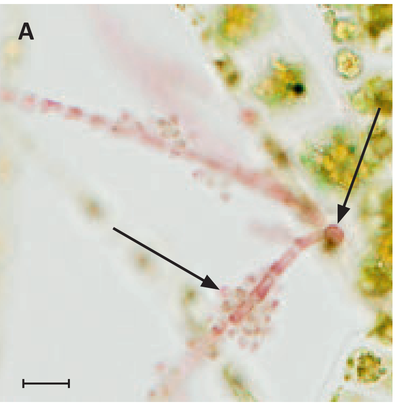
Reproduction: Sexual reproduction by monoecious gametophytes, with antheridia, carpogonia and monosporangia on the same alga. Antheridia are apical on short branches, often two or more together or they occur individually on the carpogonial branches. Carpogonia are lateral on the filaments or apical on short branches. The gonimoblasts form irregular clusters of radiating filaments with apical carposporangia. Monosporangia are ovoid 5-6 µm in width and 9.5-10 µm in height. They occur individually or sometimes two together sessile on the branches or apical on short branches.

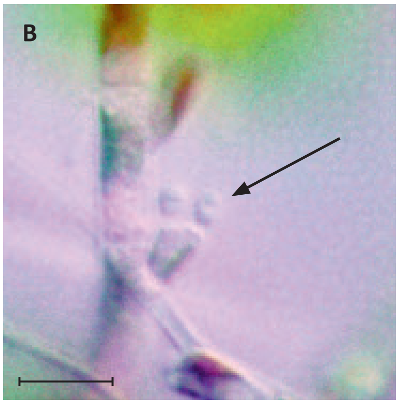
Seasonal variation: Collected in July-September.

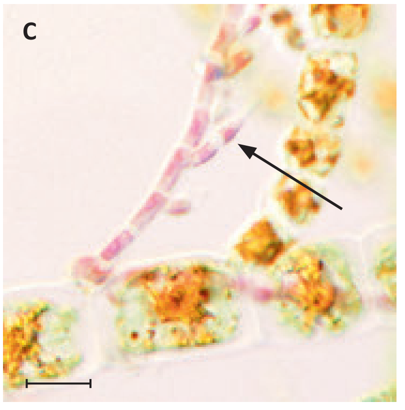
Habitat: On Artist's Brush Cotton Wool Weed (*Ectocarpus penicillatus*), collected by divers, 1-10.5 m depth and by dredging, 12-18 m depth.

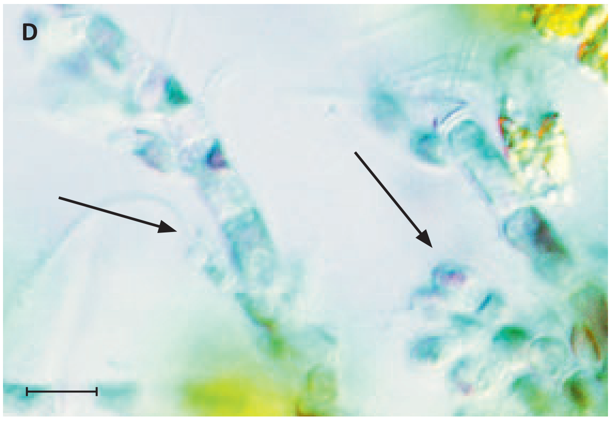
Comment: Described by Rosenvinge (1909) with type locality at Tønneberg Banke. It is an atypical feature to have a single basal cell and parietal plastids. This feature also occurs in *Kylinia*.

References: Rosenvinge (1909, *Chantransia gynandra*).









A: *Colaconema gynandrum*. Two upright branches from the single basal cell (right arrow). Gonimoblast of radiating filaments of small cells (left arrow). Scale 20 µm. A-D: On Artist's Brush Cotton Wool Weed (*Ectocarpus penicillatus*). Læsø Trindel, 8 m, 20.8.1991.

B: *Colaconema gynandrum*. Antheridia (arrow). Scale 10 µm.

C: *Colaconema gynandrum*. Carpogonium (arrow), vegetative cells with a parietal plastid and one pyrenoid. Scale 20 µm.

D: *Colaconema gynandrum*. Antheridia (left arrow) and gonimoblast (right arrow). Scale 10 µm.

Colaconema nemalii

(De Notaris ex Dufour) Stegenga

Appearance: Small bush-like alga with narrow branches, up to 2-3 mm in height.

Structure: Basal system of prostrate filaments occasionally endophytic. From the basal system several straight upright filaments arise with scattered branches on all sides. The branches become slender towards the apex and the cells become longer and pale. The cylindrical cells, 7-11 (-13) µm in width and 2-5 times as long as wide, have relatively thick walls. Each cell contains a parietal plate-shaped plastid with one pyrenoid.

Reproduction: Sexual reproduction in monoecious gametophytes. The reproductive structures occur on few-celled branches, typically with the antheridia and the carpogonia close together. Antheridia are often in pairs on the upper cells of a branch and a carpogonium with trichogyne, often sessile on the cell immediately below. Gonimoblasts develop into more or less spherical structures of short branches, the apical cells being carpospoprangia. Monosporangia develop on separate individuals, they might be apical on clusters of small branches or 2-3 closely after each other on the adaxial side of branches. They occur singly or two together on a cylindrical stalk-cell. Monosporangia are elongate ellipsoid, 6.5-10 µm in width and 14.2-19 µm in height. Within the emptied sporangia wall, new sporangia might form and the sporangium wall becomes multilayered.

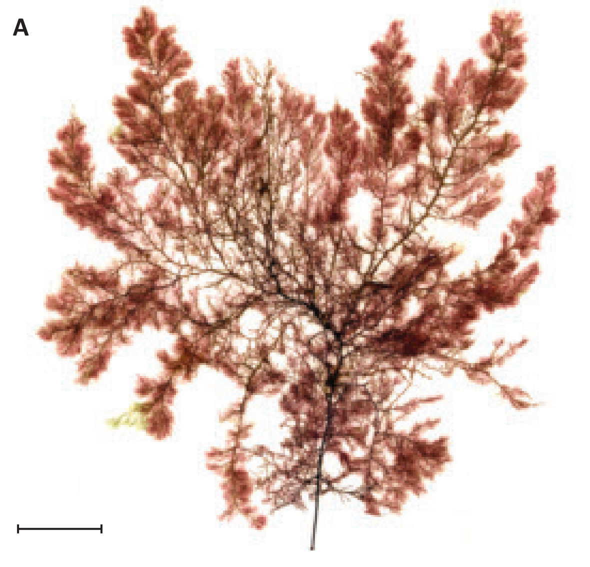
Seasonal variation: Collected in April-September. Monosporangia recorded in June-September and gametophytes with gonimoblasts in July-September.

Habitat: On various algae, 0.5-16 m depth.

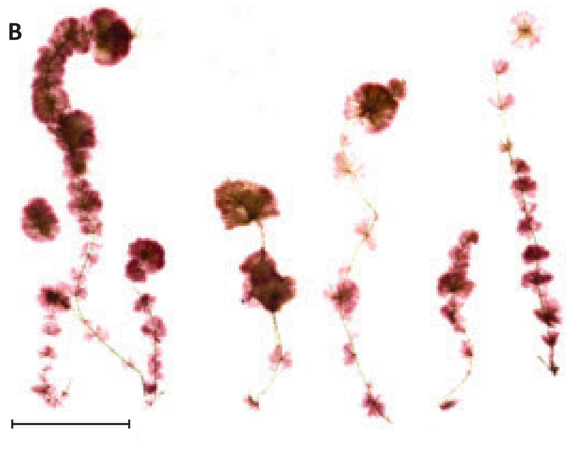
Resembles: The gametophyte is reminiscent of *Grania efflorescens*, but it has narrower filaments, the plastid is spirally twisted without pyrenoid, and the carposporophytes consist of carposporangia in short rows.

Comment: The alga Rosenvinge (1909 as *Chantransia daviesii*) referred to *C. daviesii*, had monosporangia either, 8-10 µm in width and 10-14 µm in height or 9-10 µm in width and 15-19 µm in height, althouhgh according to Stegenga & Erp (1979) only the first belong in *C. daviesii,* and the other in *C. nemalii*. The alga with monosporangia on cylindrical stalk-cells, illustrated by Rosenvinge (1909, fig. 34) also belongs in *C. daviesii* according to Stegenga & Erp (1979) who also stated that the concept of *C. nemalii* by Rosenvinge (1909) represents *C. savianum*.

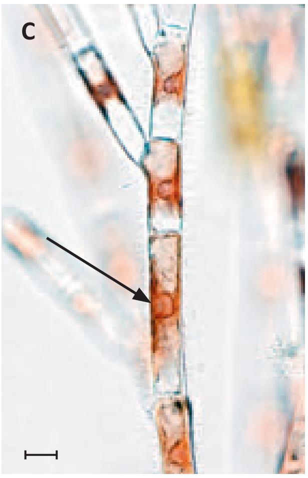
References: Rosenvinge (1909, *Chantransia thuretii* var. *amphicarpa* and in part *C. daviesii*), Stegenga 1985 (*C. nemalionis*), Stegenga & Erp (1979, *Acrochaetium*).

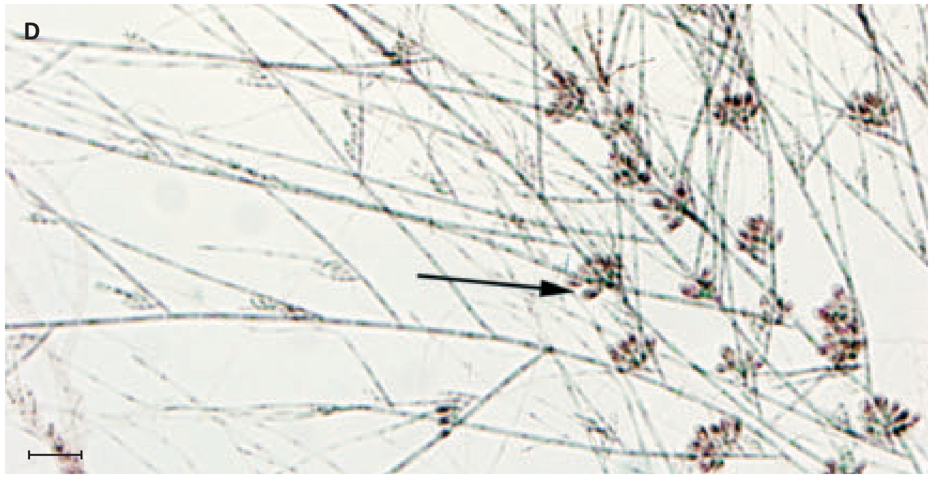


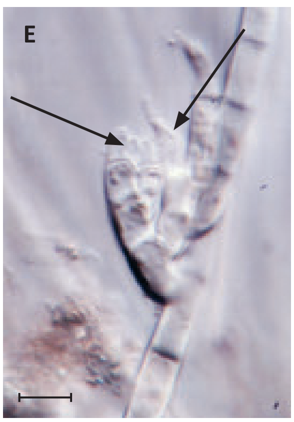
A: *Colaconema nemalii*. On Straggly Bush Weed (*Rhodomela confervoides*), shaggy by the small epiphyte. Munkegrunde, 6 m, 18.9.1991. Scale 2 cm.

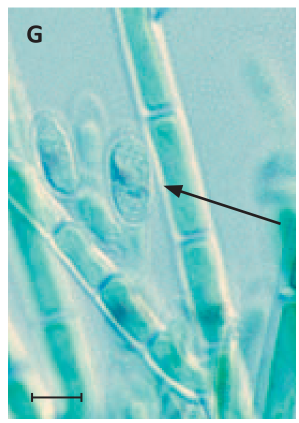


B: *Colaconema nemalii*. Small bushes on Flax Brick Weed (*Chaetomorpha linum*). Margretheholms Havn, Copenhagen, 0.5 m, 29.8.2002. Scale 2 cm.









C: *Colaconema nemalii*. Vegetative cells, parietal plate-shaped plastid with one pyrenoid (arrow). Scale 10 µm. C, I: Margretheholms Havn, Copenhagen, 0.5 m, 17.9.2008.

D: *Colaconema nemalii*. Gametophyte with many gonimoblasts (arrow). Sjællands Rev, 8.5 m, 10.9.1996. Scale 50 µm.

E: *Colaconema nemalii*. Gametophyte, pair of antheridia (left arrow) and carpogonium (right arrow). Per Nilen, 6 m, 12.8.2015. Scale 10 µm. Photo by S. Lundsteen.

F: *Colaconema nemalii*. Gonimoblast with apical carposporangium (arrow). Torup Flak, 9 m, 25.7.1994. Scale 10 µm.

G: *Colaconema nemalii*. Cluster of monosporangia (arrow). Læsø Trindel, 11.5 m, 11.6.1990. Scale 10 µm. Photo by S. Lundsteen.

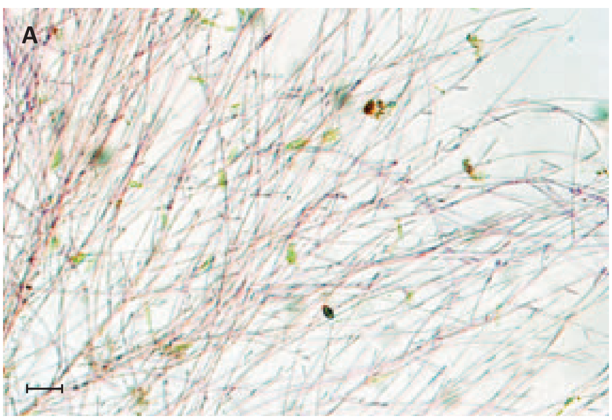
H: *Colaconema nemalii*. Monosporangia, some emptied with a multilayered wall (arrow). Kirkegrund, 8 m, 26.8.2010. Scale 10 µm. Photo by S. Lundsteen.

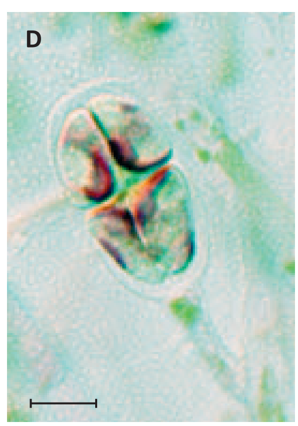
I: *Colaconema nemalii*. Branch with unilateral monosporangia in pairs on a stalk-cell. Scale 20 µm.

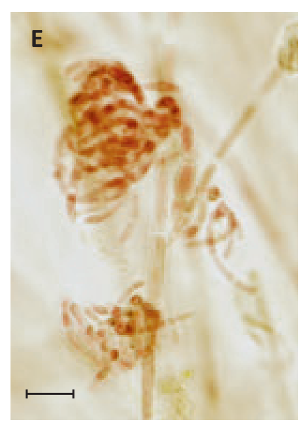
Colaconema savianum

(Meneghini) R.Nielsen

Appearance: Bushy much branched narrow filaments, up to 2-5 mm in height.
Structure: Basal system of prostrate filaments with several uprights. These have scattered branches on all sides. Branches become slender towards the apex and hair-like in some individuals. Cells are cylindrical (7-) 8-11 (-12) µm in width and 3.5-8 times as long as wide. Each cell contains a parietal plastid with one pyrenoid.
Reproduction: Asexual reproduction with mono- and tetraspores. Monosporangia are scattered and might be unilateral on the adaxial side of the branches, occasionally in pairs. They are sessile on the branches or on a cylindrical stalk-cell or the stalk consists of 2-3 cells. Monosporangia are elongated ellipsoid, (7-) 8.5-12 (-13) µm in width and (17.5-) 19-22 (-25) µm in height. Small, few-celled curved filaments sometimes surround the monosporangia and make irregular tufts on the branches. Cruciate tetrasporangia are wide ellipsoid or more or less spherical, 18.5-22 µm in width and 25-26 µm in height. Tetrasporangia are observed on individuals with monosporangia but rarely found in Danish waters. Sexual reproductive structures are not observed on the alga from Danish waters.
Seasonal variation: Recorded in January, April-December with monosporangia, tetrasporangia recorded in June and August.
Habitat: Epiphytic on Banded Pincer Weed (*Ceramium* sp.), Purple Claw Weed (*Cystoclonium purpureum*), Purple Siphon Weed (*Leptosiphonia fibrillosa*), Tubular Net Weed (*Dictyosiphon foeniculaceus*), Eelgrass (*Zostera marina*), and epizoic on hydroids and bryozoans, 11-13 m depth.
References: Kylin (1944, *Acrochaetium thuretii*), Rosenvinge (1909, C*hantransia thuretii* var. *agama*; *Chantransia nemalionis*), Stegenga & Borsje (1976, *Acrochaetium dasyae*), Stegenga & Erp (1979, *Acrochaetium*).







A: *Colaconema savianum*. Bushy narrow filaments, with scattered monosporangia. Scale 50 µm. A, D: Fjellerup Strand, 5 m, 21.6.1994.

B: *Colaconema savianum*. Elongate ellipsoid monosporangia, unilateral on the adaxial side of branches (arrow). Thisted Bredning, 1.5 m, 18.8.2008. Scale 20 µm.

C: *Colaconema savianum*. Monosporangia on stalk-cells. Kirkegrund, 8 m, 26.8.2010. Scale 10 µm. Photo by S. Lundsteen.

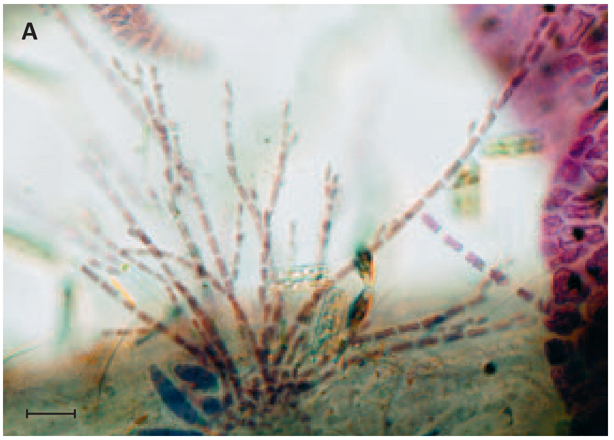
D: *Colaconema savianum*. Tetrasporangium. Scale 10 µm.

E: *Colaconema savianum*. Tufts of curved filaments surrounding monosporangia. Læsø Trindel, 5 m, 20.8.1991. Scale 10 µm.

Colaconema strictum

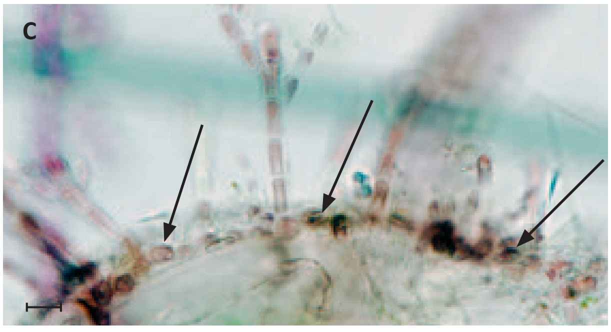
(Rosenvinge) R.Nielsen

Appearance: Tufts of sparsely branched filaments, microscopic and up to 1 mm in height.
Structure: Basal system of extended prostrate filaments or forming a monostromatic disc with a few upright filaments arising from the middle part. Upright filaments are straight, 4-7 µm in width and consist of cylindrical cells, 3-4.5 times as long as wide. Filaments are unbranched or have very few branches, mainly few-celled branches with monosporangia. Each cell contains a parietal plastid with one pyrenoid. Red algal hairs are frequent on the small branches.
Reproduction: Asexual reproduction by monospores. Monosporangia are sessile or apical on small branches and often slightly bent towards the branch. Sporangia are narrow ovoid, (5-) 6-7 µm in width and (12-) 13-14 µm in height.
Seasonal variation: Collected in January and July-September.
Habitat: Epiphytic on various red algae, as Banded Pincer Weed (*Ceramium* sp.), Purple Siphon Weed (*Leptosiphonia fibrillosa*.), and Creeping Bush Weed (*Spermothamnion repens*), 5-16 m depth.
Comment: Described by Rosenvinge (1909) based on specimens collected at Gjerrild Klint, Issefjord and Fyns Hoved. Tetrasporangia noticed in culture studies by Stegenga & Wissen (1979).
References: Rosenvinge (1909, *Chantransia*), Stegenga & Wissen (1979).

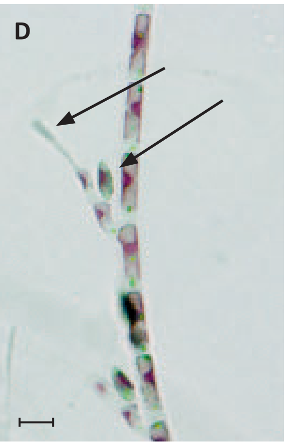


A: *Colaconema strictum*. Several upright filaments from an almost disc-shaped base. Vejrø, 9 m, 2.9.1993. Scale 25 µm.

B: *Colaconema strictum*. Dense basal filaments, few upright branches. Scale 10 µm. B, D: On Purple Siphon Weed (*Leptosiphonia fibrillosa*), Ebbeløkke, 7 m, 26.7.1994.



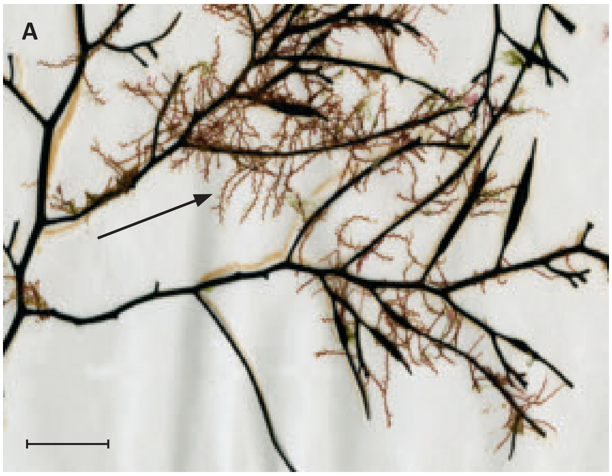
C: *Colaconema strictum*. Extended basal filaments (arrows) with uprights. Sjællands Rev, 8.5 m, 10.9.1996. Scale 10 µm.



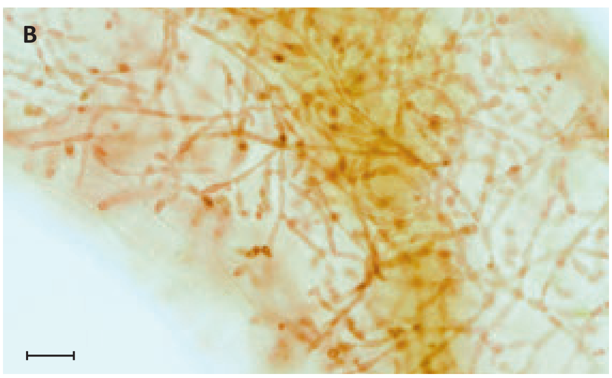
D: *Colaconema strictum*. Upright filament, vegetative cells, each with a parietal plastid and one pyrenoid. Small branches with monosporangia (lower arrow). Apical red algal hair (upper arrow). Scale 10 µm.

Colaconema sp. *'obeliae'*

Appearance: Microscopic filaments creeping within the outer covering (perisarc) of the Knotted Thread Hydroid (*Obelia geniculata*), which turns rose red.
Structure: Open branched with scattered and sometimes opposite branches. Cells more or less cylindrical, but often slightly swollen in the middle. Cells, 2.5-4.5 µm in width at the cross walls and 19-24 µm in length. Cells in older part of the alga are relatively short and wide, and the filaments almost confluent. Plastids are irregularly twisted. Pyrenoids absent.
Reproduction: Monosporangia, 5-6.5 µm in width, are apical on short branches, obovate with the broad end slightly above the surface of the host. No upright filaments with sporangia.
Seasonal variation: Collected in January-September.
Habitat: Frequent in the perisarc of Knotted Thread Hydroid (*Obelia geniculata*), which grows on various coarse algae, 2-20 m depth.
Resembles: Differs from Membranous Red Intrusion Weed (*Rubrointrusa membranacea*) by the narrow filaments, the open branching and monosporangia without stalk, sessile and scattered on the creeping filaments.
Comment: Rosenvinge (1924) referred all the small endozoic red algae within the outer covering of hydroids in Danish waters to Membranous Red Intrusion Weed (*Rubrointrusa membranacea*) (as *Rhodochorton membranaceum*) but indicated that red algae within various hydroids might be various species. Culture studies and molecular investigations are necessary to document the identity of *Colaconema* sp. *'obeliae'*.
References: Rosenvinge (1923-24, in part *Rhodochorton membranaceum*).



A: *Colaconema* sp. '*obeliae*'. Knotted Thread Hydroid (*Obelia geniculata*) (arrow) red by the presence of *Colaconema* sp. '*obeliae*' and other small red algae. On Brown Sea Oak (*Halidrys siliquosa*). Læsø Trindel, 11 m, 4.6.1989. Scale 2 cm.



B: *Colaconema* sp. '*obeliae*'. Creeping filaments. Scale 25 µm.
B-D: In outer covering of the hydroid (*O. geniculata*), Kims Top, 18.5 m, 15.1.1997.

C: *Colaconema* sp. '*obeliae*'. Creeping filaments with red spots of monosporangia (arrow). Same individual as in fig. B, but different focus. Scale 25 µm.

D: *Colaconema* sp. '*obeliae*'. Opposite branches and obovate monosporangium (arrow). Scale 10 µm.

Order: Nemaliales · Family: Liagoraceae

Helminthocladia calvadosii

(J.V.Lamouroux ex Duby) Setchell

Branched Worm Weed

Appearance: Terete upright thallus with a distinct main axis 2-5 mm in width and scattered branches on all sides. The thallus is dark red in colour and up to 57 cm in length.

Structure: The thallus is a multiaxial syntagma. Apical cells of the filaments much larger than the rest of the cells. The surface therefore consists of relatively large club-shaped cells with a stellate plastid.

Seasonal variation: Collected in July-September.

Comment: The species was found as drift at the Skagerrak shore by Caroline Rosenberg in 1859. Rosenvinge collected attached specimens at shallow water on stone reefs just east of Hirtshals harbour in 1914. We have no later collections from Danish waters in the algal herbarium, Natural History Museum of Denmark.

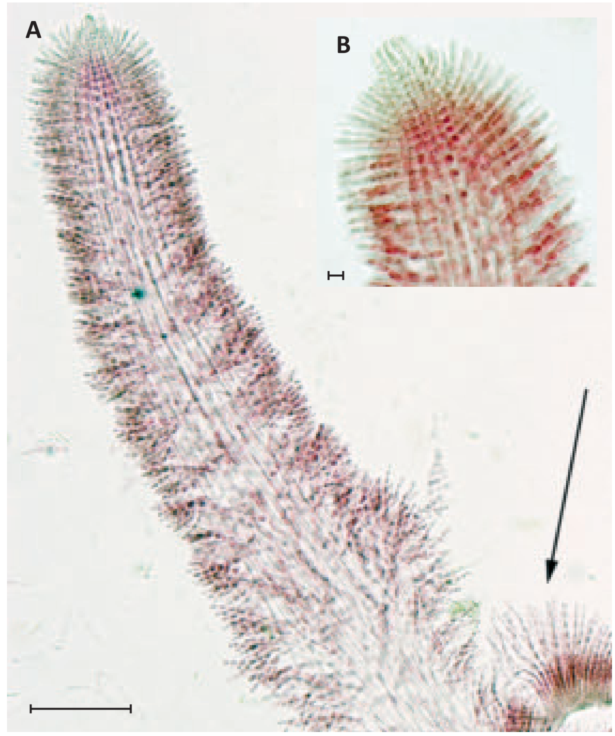
References: O'Dwyer & Afonso-Carrillo (2001), Rosenvinge (1909, *Helminthocladia purpurea*).

A: *Helminthocladia calvadosii*. Herbarium specimen of Rosenvinge. Hirtshals, 13.7.1914. Scale 2 cm.

Helminthora divaricata

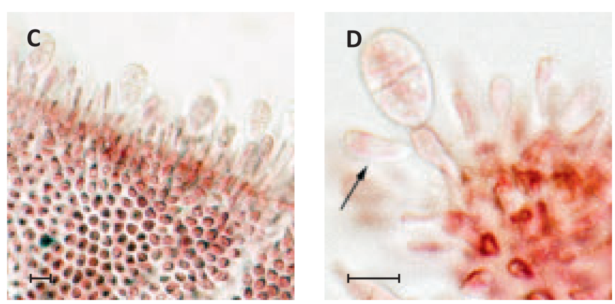
(C.Agardh) J.Agardh

Spreading Worm Weed



A: *Helminthora divaricata*. Upright multiaxial thallus and a crustose alga (arrow). Medulla of parallel filaments with dichotomous branches forming the cortex. Scale 100 µm. A-D: Tønneberg Banke, 15 m, 8.6.1991.

B: *Helminthora divaricata*. Apex of multiaxial thallus, several apical cells, cortex of narrow filaments. Scale 10 µm.



C: *Helminthora divaricata*. Surface of crust with tetrasporangia on stalk-cells, (seen in an oblique angle). Scale 10 µm.

D: *Helminthora divaricata*. Crust, a stalk-cell with tetrasporangium and initiation of a new sporangium (arrow). Scale 10 µm.

Appearance: Terete soft, red-brown thalli, only collections of small individuals, 1-5 cm in length in Danish waters. They are much branched and up to 25 cm in length in the British Isles.

Structure: A multiaxial syntagma with a medulla of pale, narrow parallel filaments of cylindrical cells, c. 3 times as long as wide. The cortex consists of repeatedly forked assimilating filaments of small, rounded cells, that are c. 3 times as long as wide. The filaments are held together in a relatively thick gelatinous wall material. Apical red algal hairs may occur.

Reproduction: The life history is heteromorphic, with isomorphic upright gametophytes. Antheridia form round spots on the apex of assimilating filaments, and were recorded on the alga collected as an epiphyte from Discoid Fork Weed (*Polyides rotunda*) in Danish waters (Rosenvinge, 1909). The tetrasporophyte is only known from culture studies from the West coast of Ireland (Cunningham et al., 1993), and Brittany (Magne & Abdel-Rahman, 1983), where it formed branched filaments, identified as *Chantransia polyidis* Rosenvinge. According to Dixon & Irvine (1977), germinated carpospores develop a disc or filamentous mass with cruciate tetrasporangia that are apical on upright filaments. Based on Dixon & Irvine's (1977) observations, a crustose alga, observed at the base of upright thalli in June 1991, probably represented the tetrasporophyte in nature. This crust consisted of upright, loosely connected filaments with sori of cruciate tetrasporangia that were present with one- to three-celled mutually free filaments on the crust surface. Sporangia were 10-13 µm in width and 20-24 µm in height and occurred on a stalk-cell from where new sporangia developed.

Seasonal variation: Collected in June and September, antheridia recorded in September.

Habitat: Epiphytic on Discoid Fork Weed (*Polyides rotunda*), 4-5.5 m depth, and on stone the size of a hand, 15 m depth.

References: Cunningham et al. (1993, *Helminthora stackhousei*), Dixon & Irvine (1977), Magne & Abdel-Rahman (1983, *Acrochaetium polyidis*), Rosenvinge (1909, *Chantransia polyidis*).

Family: Nemaliaceae

Nemalion multifidum

(Lyngbye) Chauvin

Sea Noodle Worm Weed

Appearance: The terete brownish red thallus is dichotomously branched. It is very soft and smooth, 0.5-5 mm in width and up to 40 cm in length. The thallus is elastic and after a gentle stretch it returns to the original length.

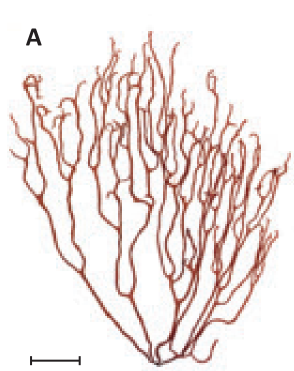
Structure: The thallus is a multiaxial syntagma with a medulla of dense, colourless filaments (Figs J, K page 26). The cells, of these filaments are long and cylindrical, 4-5.5 µm in width. The cortex consists of loosely connected assimilating filaments that are dichotomously branched several times and often terminate in a red algal hair. The vegetative cells are barrel-shaped becoming smaller towards the surface. Each cell contains a stellate plastid with one pyrenoid.

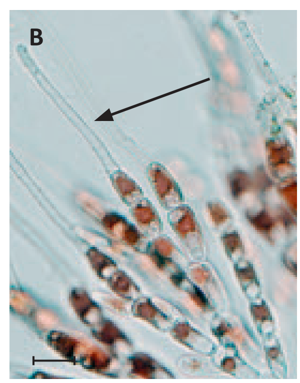
Reproduction: A heteromorphic life history, known from culture studies, comprises upright gametophytes and a tetrasporophyte of prostrate uniaxial filaments (Söderström, 1970). Gametophytes are isomorphic and usually dioecious, but individuals with both male and female branches regularly occur. The colourless antheridia form branchlets of pale cells at the distal end of the assimilating filaments. Carpogonia, each with a trichogyne, are apical on special obconical branches between the assimilating filaments. After fertilization, the zygote divides to develop an approximately spherical gonimoblast of dark red cells with apical carposporangia.

Seasonal variation: Upright specimens collected in June-August with antheridia, carpogonia and gonimoblasts. Tetrasporophytes not observed in nature.

Habitat: On the upper part of the lower shore (*Semibalanus balanoides* zone), on wave-exposed coasts. It is also found on scattered boulders on wind-exposed sandy shores.

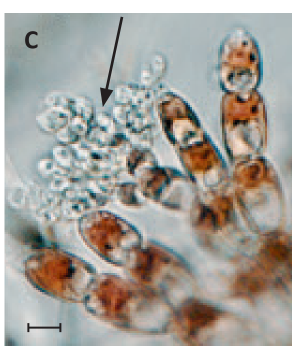
References: Christensen (1966), Le Gall & Saunders (2010a), Lin et al. (2015), Söderström (1970)





A: *Nemalion multifidum*. Terete branches dichotomously divided. On boulder at the sandy beach south of the harbour, Kulhuse, 0.2 m, 21.7.1988. Scale 2 cm.

B: *Nemalion multifidum*. Assimilating, repeatedly dichotomous filaments, barrel-shaped cells each with a stellate plastid and apical red algal hair (arrow). Scale 20 µm.
B-E: Beach north of Vesterø Havn, Læsø, drift, 23.6.2013.



C: *Nemalion multifidum*. Small branchlets of colourless antheridia (arrow). Scale 10 µm.

D: *Nemalion multifidum*. Special branch, apical carpogonium (arrow) with trichogyne. Scale 10 µm.

E: *Nemalion multifidum*. Gonimoblast (arrow). Scale 20 µm.

Family: Scinaiaceae

Scinaia furcellata

(Turner) J.Agardh

Scinà's Weed

Appearance: The dark red terete thallus has regularly repeated, dichotomous branches. They are up to 1 mm in diameter and 6.5 cm in length. The alga is hollow and has a basal disc. Branches are pointed at their apices in specimens from Scandinavia and Helgoland, whereas the tips are blunt in other Western European localities. The alga from Scandinavia is referred to a subspecies (subsp. *scandinavica*) by Maggs & Guiry (1982).

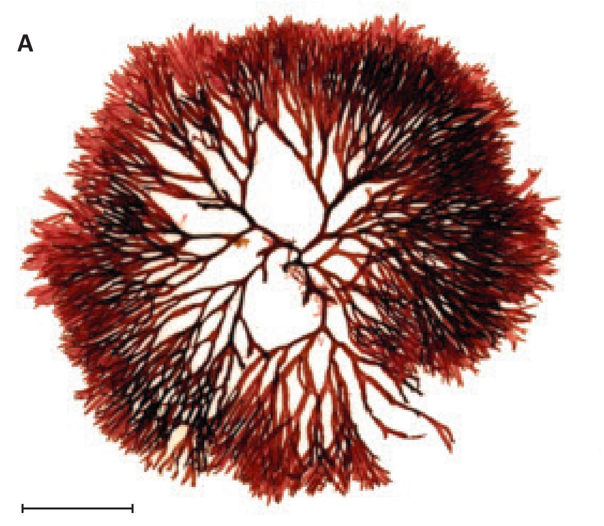
Structure: Multiaxial syntagma with medulla of narrow entangled filaments. The cortex has an inner layer of small, rounded cells with plastids and an outer layer of large colourless cells.

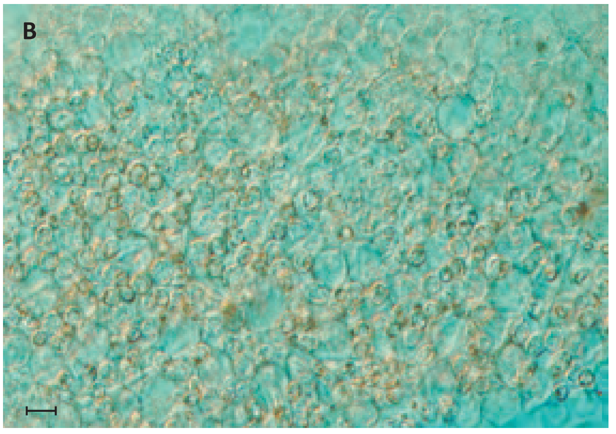
Reproduction: The upright phase is monoecious gametophytes. Antheridia form from the surface of the thallus. Gonimoblasts embedded in the thallus are surrounded by a bowl-shaped pericarp of small cells with an opening to the surface. Tetrasporophytes not known from nature but found in culture and consist of branched, uniseriate filaments with cruciate tetrasporangia.

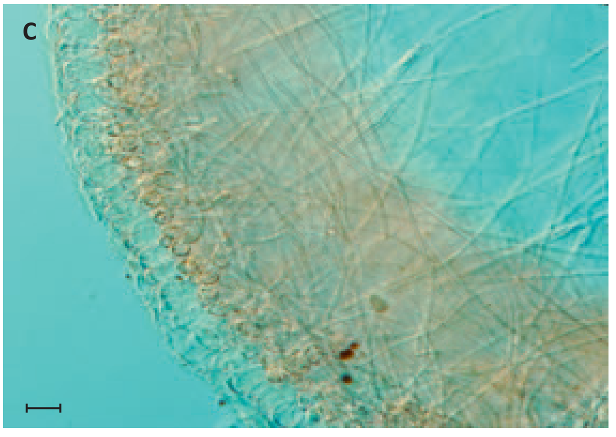
Seasonal variation: Collected in June and August with antheridia, gonimoblasts recorded in August-September.

Habitat: Rare in Danish waters, and only drift specimens recorded.

References: Dixon & Irvine (1977, *S. forcellata*), Kylin (1944), Maggs & Guiry (1982, *S. forcellata* subsp. *scandinavica*), Rosenvinge (1909).







A: *Scinaia furcellata.* Bush-like, terete regularly repeated, dichotomous branches. Stensnæs Flak, Lyngså, drift, 27.8.1975. Scale 2 cm.

B: *Scinaia furcellata.* Surface of small and large rounded cells, seen from outside. Scale 20 µm. B-C: Kandestederne, drift, 9.9.1972.

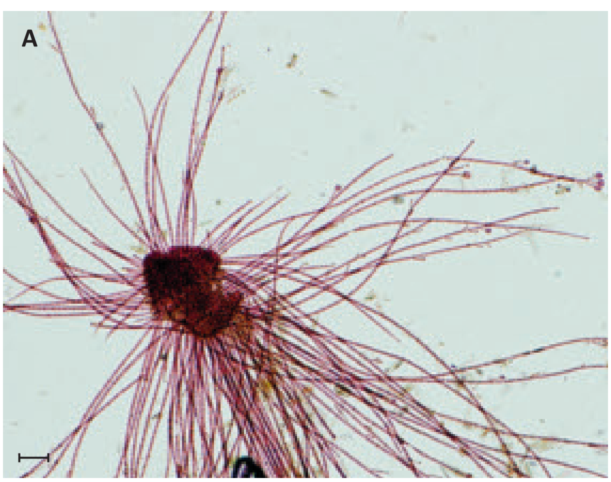
C: *Scinaia furcellata.* Medulla of narrow filaments and surface of small, rounded cells covered by a layer of large colourless cells. Optical transverse section. Scale 20 µm.

Order: Palmariales · Family: Meiodiscaceae

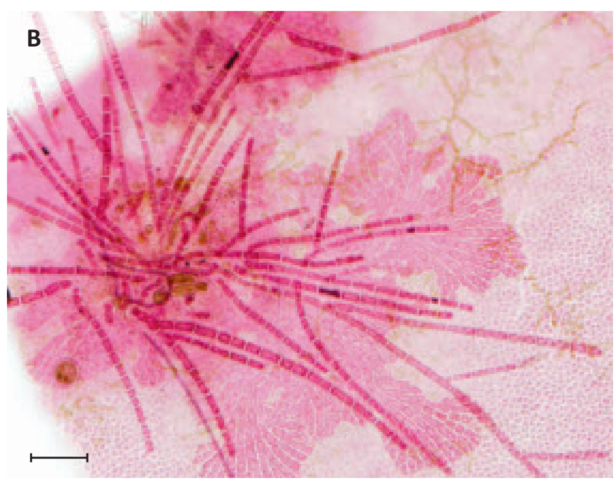
Meiodiscus spetsbergensis

(Kjellman) G.W.Saunders & McLachlan
Disc Tuft

Appearance: A basal disc from which arise scattered upright filaments 0.5-1 mm in height and sparsely branched. Disc Tuft (*Meiodiscus spetsbergensis*) is visible when observed with a magnifying glass as small clear red tufts above the basal disc.
Structure: The basal layer is monostromatic and consists of closely packed radiating filaments with scattered branches and cell fusions. The margin is regular with rounded lobes. The upright filaments are uniseriate, unbranched or with a few scattered branches near the apex. Individuals with repeated branching seldom occur but observed in those with sporangia. The filaments consist of cylindrical cells, 9-12 (-14) µm in width and 1-3.5 times as long as wide. They have both apical and diffuse growth. The cells contain many disc-shaped or oval plastids without pyrenoids.
Reproduction: Cruciate tetrasporangia occur at the apex of main axes and on branches, they are ellipsoid, (21-) 23-25 (-27) µm in width and (25-) 29-32 (-35) µm in height on a few-celled stalk. The upper part of the wall of the sporangia is characteristically thickened. A transverse wall is formed first when the sporangia divide. The following two divisions are perpendicular to the first but usually not in the same plane. New sporangia often develop from the stalk-cell within older emptied sporangial walls. Antheridia may occur on small branches in individuals with tetrasporangia. Culture studies in Canada showed that Disc Tuft (*Meiodiscus spetsbergensis*) had a direct life history (Saunders & McLachlan, 1991). Germinated tetraspores developed into similar individuals to those of the previous generation and formed tetrasporangia.
Seasonal variation: Occurs all year, collected in January-November. Upright filaments with tetrasporangia recorded in May-November and antheridia in June.
Habitat: Epiphytic on various algae including Black Scour Weed (*Ahnfeltia plicata*), Clawed Fork Weed (*Furcellaria lumbricalis*), Stalked Leaf Bearer (*Phyllophora pseudoceranoides*), stipes of Kelp (*Laminaria* sp.), Common Green Branched Weed (*Cladophora rupestris*), Glaucous Brick Weed (*Chaetomorpha melagonium*) and epizoic on hydroids, 5-25 m depth.
Resembles: Superficially resembles Purple Felt Weed (*Rhodochorton purpureum*), but this species has a basal



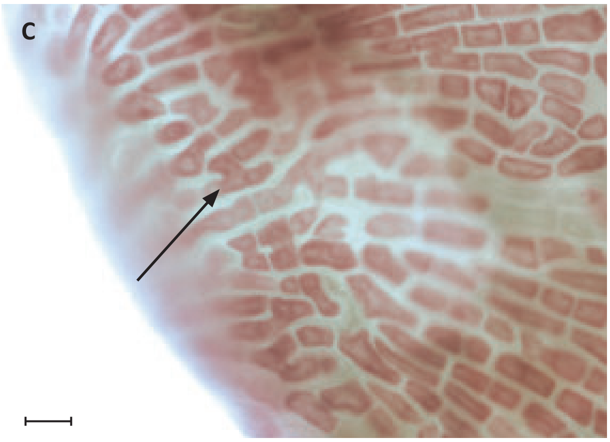
A: *Meiodiscus spetsbergensis*. Tuft of upright filaments from a basal disc. Scale 100 µm. A, D, F: Moselgrund Nord, 9.5 m, 3.8.1994.



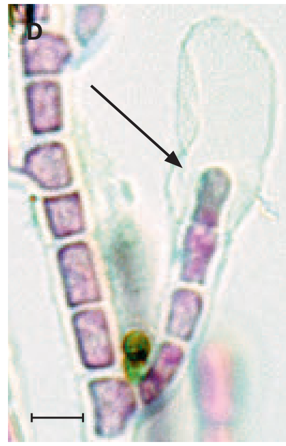
B: *Meiodiscus spetsbergensis*. Basal disc of dense radiating filaments with lobes and scattered upright filaments. Søndre Stenrøn, 14.5 m, 6.9.1993. Scale 25 µm.

system of prostrate filaments, not a disc and the upright filaments are 10-15 µm in width, furthermore the tetrasporangia occur in tufts of apical branchlets in winter.

References: Dixon & Irvine (1977, *Audouinella spetsbergensis*), Rosenvinge (1923-24, *Rhodochorton penicilliforme*), Saunders & McLachlan (1991).



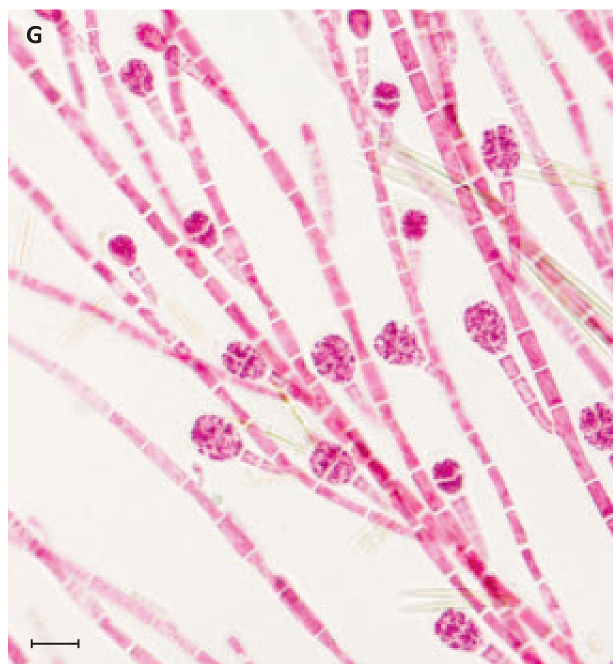
C: *Meiodiscus spetsbergensis*. Cell fusions in the basal disc (arrow). Læsø Trindel, 10.5 m, 27.8.1993. Scale 10 µm.



D: *Meiodiscus spetsbergensis*. A new sporangium formed from the stalk-cell of an emptied sporangium (arrow). Scale 10 µm.

E: *Meiodiscus spetsbergensis*. Vegetative cells of upright filaments, many disc-shaped plastids without pyrenoids (arrow). Ryggen, 13.5 m, 5.3.1997. Scale 10 µm.

F: *Meiodiscus spetsbergensis*. Apical cruciate tetrasporangia with the thickened upper wall (arrow). Scale 10 µm.



G: *Meiodiscus spetsbergensis*. Atypical specimen with many branches and apical cruciate tetrasporangia. Store Middelgrund, 20.5 m, 9.6.1993, Scale 25 µm.

Rubrointrusa membranacea

(Magnus) S.L.Clayden & G.W.Saunders

Membranous Red Intrusion Weed

Appearance: Endozoic in the outer walls (the tough, chitinous perisarc) of hydroids giving the host a clear red colour.

Structure: Uniaxial creeping filaments with opposite or scattered branches. The filaments may be so dense that they form an almost pseudoparenchymatous layer, no cell fusions. Narrow filaments of cylindrical cells occur, 5-6.5 µm in width and 6-10 times as long as wide. In other places the cells are irregularly angular, 13-24 µm in width and 0.7-5 times as long as wide, and often have indentations and a lobed and very irregular appearance. There are many disc-shaped to irregular ribbon-shaped plastids in each cell, but no pyrenoids. Individuals with sporangia have short scattered upright uniseriate filaments.

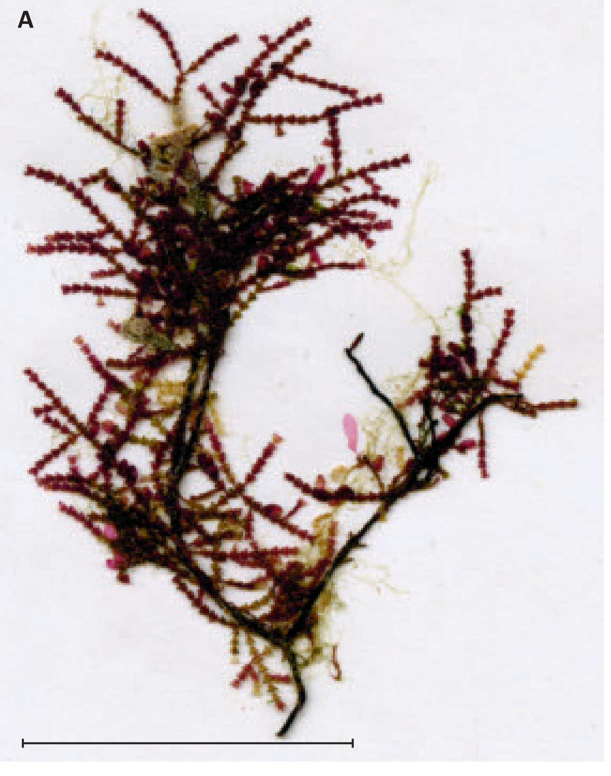
Reproduction: Tetraspores are the only known reproductive structures. The cruciate tetrasporangia are apical on upright filaments, broad ellipsoid, 19-29 µm in width and 31-35 µm in height. At the apex, the content of the sporangia is often contracted slightly from the cell wall to give a lens-shaped structure. In culture studies of Canadian specimens, germinated tetraspores developed into the similar life history phase.

Seasonal variation: Collected in January-November. Tetrasporangia recorded in January-March, June and August-September.

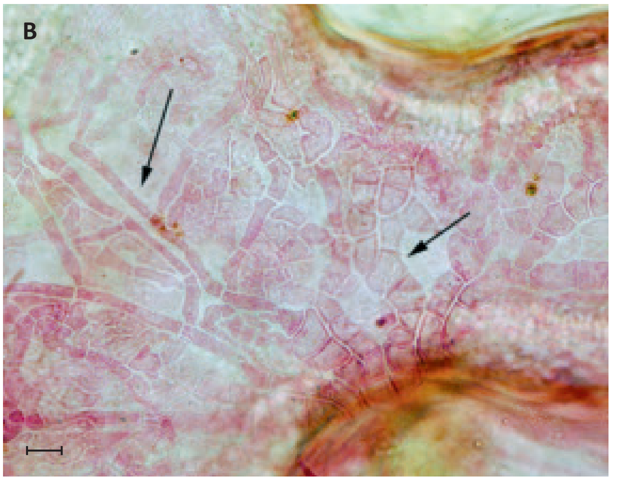
Habitat: Endozoic in the outer walls of hydroids, frequent in *Dynamena pumila*, Sea Fir (*Abietinaria abietina*) and Oaten Pipes Hydroid (*Tubularia indivisa*), 0.5-25 m depth.

Comment: It is likely that the small red algae, endozoic in various hydroids currently referred to *R. membranacea*, will in future turn out to be various species, including *Colaconema* sp. '*obeliae*'.

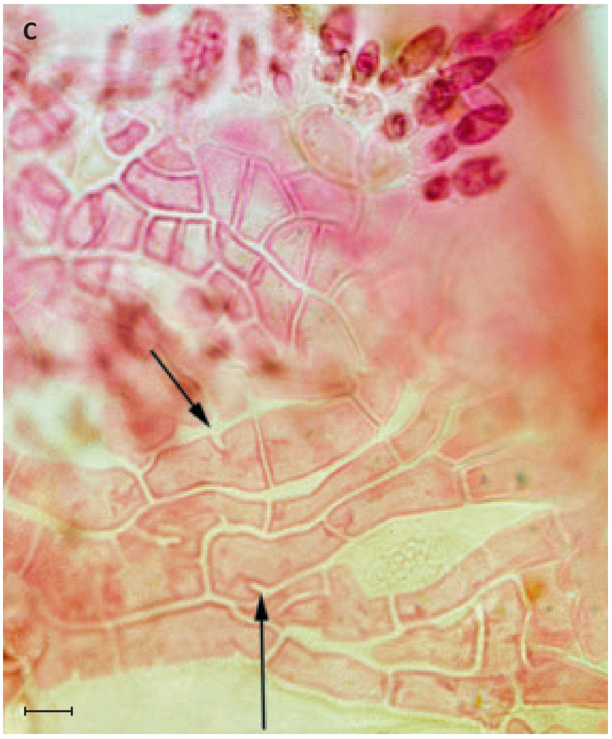
References: Clayden & Saunders (2010), Kornmann & Sahling (1977, *Audouinella membranacea*), Rosenvinge (1923-24, *Rhodochorton membranaceum*).



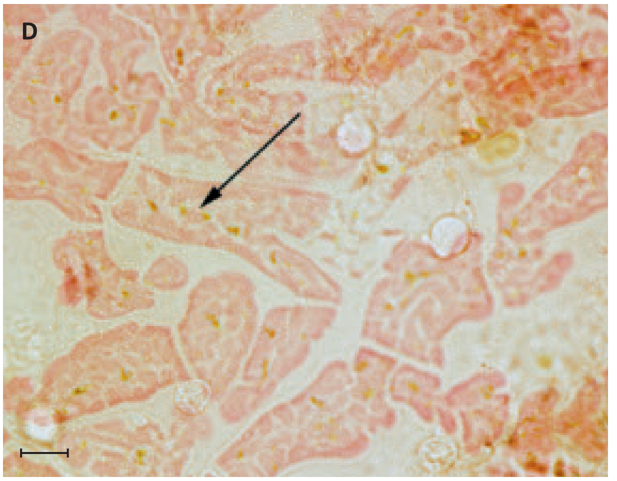
A: *Rubrointrusa membranacea.* In the outer wall of the hydroid *Dynamena pumila*, with a red colour due to the alga. Briseis Flak, 7.5 m, 8.6.1989. Scale 2 cm.



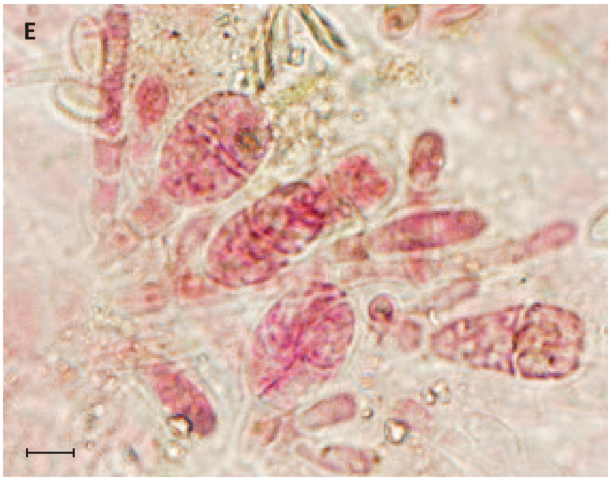
B: *Rubrointrusa membranacea*. Narrow repent filament (left arrow) and thick filament (right arrow) in the hydroid *Dynamena pumila*. Scale 10 µm. B-C, E-F: Jessens Grund, 4 m, 7.3.1997.



C: *Rubrointrusa membranacea*. Filaments of irregularly angular cells with indentation in the margin (arrows). Scale 10 µm.



D: *Rubrointrusa membranacea*. Cells with many plastids without pyrenoids (arrow). Herthas Flak, 15 m, 4.6.1993. Scale 10 µm.



E: *Rubrointrusa membranacea*. Group of short filaments with cruciate tetrasporangia. Scale 10 µm.

F: *Rubrointrusa membranacea*. Cruciate tetrasporangium (arrow) on a longer upright branch. Scale 10 µm.

Family: Palmariaceae

Palmaria palmata

(Linnaeus) F.Weber & D.Mohr

Dulse

Appearance: The blades of the thallus are like thin leather and are a transparent red colour, darker red in shaded localities and lighter red when growing in strong light. The blades have an entire margin and are up to 20 cm in length, seldom longer in Danish waters. The shape may be rounded to oval, almost triangular or ribbon-shaped, sometimes with two or more lobes in the upper end and with new blades from the margin of older ones. The blades develop from a small disc and have a short stipe. Several blades of different age may develop from the same base. The alga with ribbon-shaped blades often occurs as drift at Stevns Klint.

Structure: Blades have a distinct medulla and cortex. The medulla consists of 1-2 layers of large, pale cells. The cortex consists of short dense filaments, that are close together and have cells with a diameter of 8-15 µm in surface view. It is possible to see the cells of the medulla through the cortex under the microscope. The filaments of the cortex in young blades consist of 1-2 cells in length, while older blades or those with sporangia have filaments of up to 10 cells. The cells of the cortical filaments contain many disc-shaped plastids.

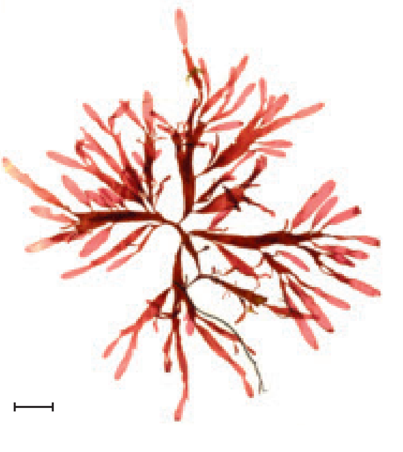
Reproduction: In the life history, the blades are male gametophytes or tetrasporophytes while the female gametophytes are dwarfs known only from culture studies. The antheridia form pale, inconspicuous patches of sori on the surface of both sides of the blades. The tetrasporangia together with filaments of sterile cells form extended patches, also on both sides of the blades. The cruciate tetrasporangia form from scattered cells on the surface. At the first division, a small stalk-cell forms from which a new sporangium might develop within the wall of an emptied sporangium, and this process may repeat several times. The sterile filaments between the tetrasporangia continue to grow, and the sporangia become embedded between filaments of small, rounded cells.

Seasonal variation: The thallus is perennial. Each year an addition of a single set of new blades takes place from the margin of the older blades. New blades

A

B

C

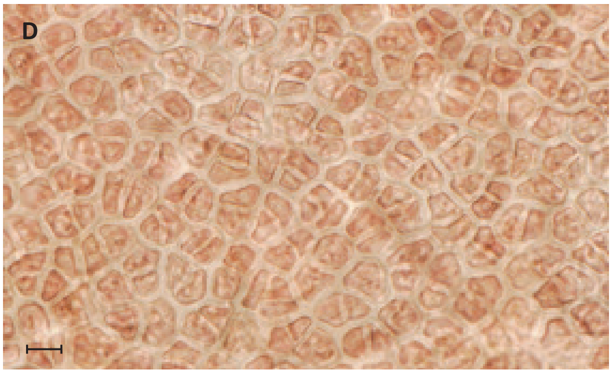


A: *Palmaria palmata*. Elongate oval blades, the young blades arise from the margin of older blades. Schultz's Grund, 7 m, 6.6.1991. Scale 2 cm.

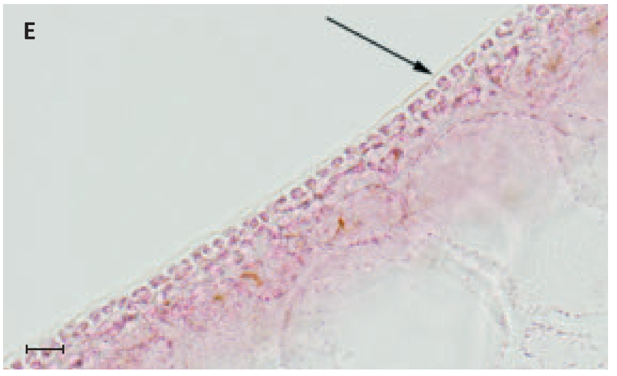
B: *Palmaria palmata*. Triangular blades with many lobes in the upper part. Vengeancegrund, 6 m, 12.9.1991. Scale 2 cm.

C: *Palmaria palmata*. Ribbon-shaped blades, with many light-coloured young ones. Stevns Klint, drift, 13.5.1965. Scale 2 cm.

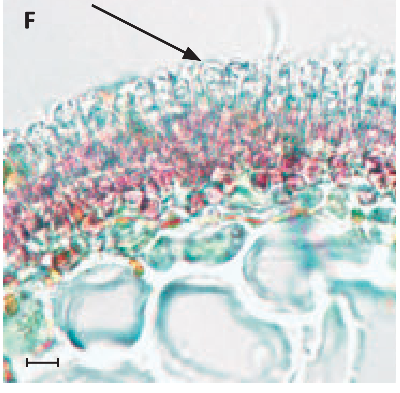
are initiated in autumn and winter and develop during the following spring and summer. The alga lives for three to four years. Antheridia recorded in February-April and mature tetrasporangia in January-April.
Habitat: On stones and boulders and epiphytic on larger algae, particularly the stipes of Oar Weed (*Laminaria digitata*) and Forest Kelp (*L. hyperborea*). Collected by divers from 0.5-18 m depth, and in older collections by dredge to 23.5 m depth. The species is very frequent on shores in the North Atlantic.
Resembles: Dulse (*Palmaria palmata*) is similar to Red Rags (*Dilsea carnosa*), but this species has opaque blades which gradually split longitudinal, and new blades do not form from the margin of older blades. In addition, the medulla in Red Rags (*D. carnosa*) is filamentous and the outer cortical cells are only c. 5 µm in diameter whereas they are 8-15 µm in Dulse (*P. palmata*). Very young blades of Dulse (*P. palmata*) are similar in shape to young blades of Lobed Leaf Bearer (*Coccotylus brodiei*) and Short Leaf Bearer (*C. truncatus*) but can be distinguished by their larger and almost transparent cortical cells.
Comment: The life history was a mystery for many years and only solved when it was possible to follow a green mutant of the female gametophyte in culture. These elegant culture-studies were published by Meer & Todd (1980).
References: Guiry (1974), Irvine & Guiry (1983), Meer & Todd (1980), Rosenvinge (1931, *Rhodymenia palmata*).



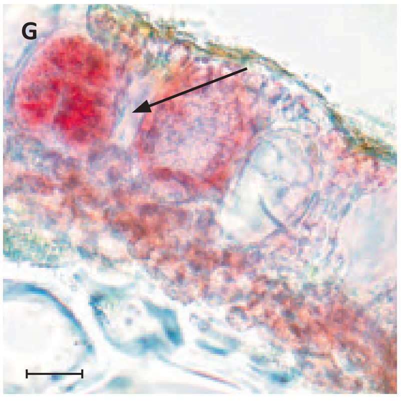
D: *Palmaria palmata*. Surface of relatively large cells. Scale 10 µm. D, E: Tønneberg Banke, 10.5 m, 27.8.2013.



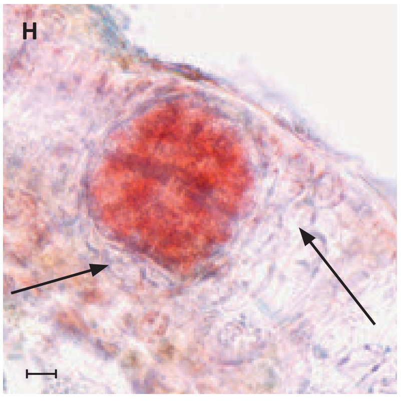
E: *Palmaria palmata*. Medulla of colourless large cells and cortex of small cells (arrow), transverse section. Scale 10 µm.



F: *Palmaria palmata*. Sorus of pale antheridia (arrow) on the surface of male gametophyte. Scale 10 µm. F-H: Fornæs Fyr, drift, 4.2.2016.



G: *Palmaria palmata*. Cruciate tetrasporangium (arrow) in surface layer, transverse section. Scale 20 µm.



H: *Palmaria palmata*. Tetrasporangium with stalk-cell (left arrow) between short filaments (right arrow). Scale 10 µm.

Family: Rhodophysemataceae

Rhodophysema

Appearance: Small crustose alga with a basal layer of confluent radiating filaments.
Structure: The filaments consist of cylindrical cells and have scattered branches. The central part of older crusts is polystromatic with upright filaments while young crusts and the margin of older individuals are monostromatic with small lobes. There are many cell fusions in the basal layer and between cells of the upright filaments. The vegetative cells contain many disc-shaped plastids.
Reproduction: The life history is notable because a tetrasporangium on a stalk-cell forms immediately after the fertilization of the carpogonium. The stalk-cell may repeat formation of tetrasporangia within older, emptied sporangia walls. The relatively large, cruciate tetrasporangia form sori on the surface of the crusts together with few-celled, unbranched, and curved filaments (paraphysis).
Resembles: Superficially reminiscent of Peysonnel's Brick-red Crust (*Peyssonnelia dubyi*), but this species usually has a basal layer of chalk and upright filaments with many (10 or more) cells. Furthermore, the upright filaments arise at branching points from cells with two oblique walls, one for each filament.

Identification key to species of *Rhodophysema*

1a.	Flat, crustose alga on stones, mollusc shells, hydroids and tough algae	*R. elegans*
1b.	Flat or hemispherical crustose alga on leaves of Eelgrass (*Zostera marina*)	*R. georgei*

Rhodophysema elegans

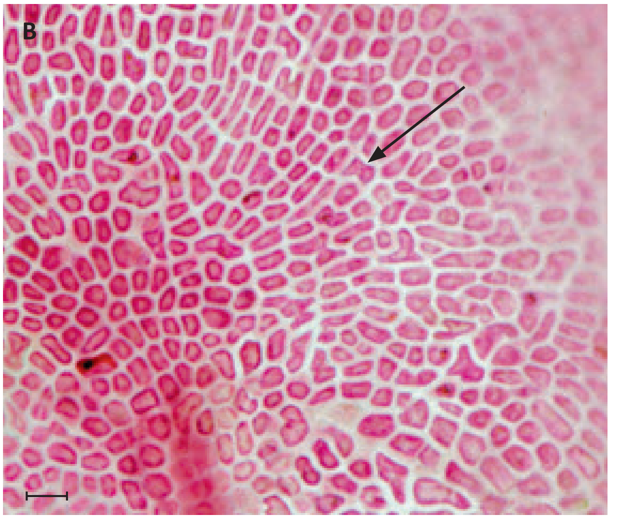
(P.Crouan & H.Crouan ex J.Agardh) P.S.Dixon
Plain Red Crust

Appearance: Thin almost circular spots, 3-5 mm in diameter with a bright red-purple colour.
Structure: The cells of the radial filaments in the basal layer are 5.5-7 µm in width and 1.5-3 times as long as wide. The young alga is monostromatic, but larger individuals become polystromatic in the central part of 2-5 cell layers. The upright filaments are usually unbranched and close together. The marginal area is monostromatic and relatively extensive.
Reproduction: Tetrasporangia are the only reproductive structures reported from Danish waters. They form scattered sori on the surface of the crust together with slightly curved paraphysis that are 3-5 cells long. The cruciate tetrasporangia are ovoid to approximately spherical, 16-20 (-24) µm in width and 24-33 µm in height. They are apical on the upright filaments of the crust on a stalk-cell.
Seasonal variation: Collected in January-September. Tetrasporangia recorded in February-September.
Habitat: On stones, mollusc shells, hydroids and algae, such as Elongate Siphon Weed (*Carradoriella elongata*), Irish Moss (*Chondrus crispus*), haptera and stipe of Kelp (*Laminaria* sp.), Glaucous Brick Weed (*Chaetomorpha melagonium*), on stone reefs, 5-27 m depth.
Comment: Culture studies have revealed that reproduction in this alga from the North Atlantic can be exclusively vegetative, or sexual reproduction may also occur, in which case antheridia form in pairs from surface cells. Female reproductive structures are a single cell with trichogyne. After supposed fertilization, the diploid cell divides into two cells, of which the lower becomes a stalk-cell and the upper a tetrasporangium.

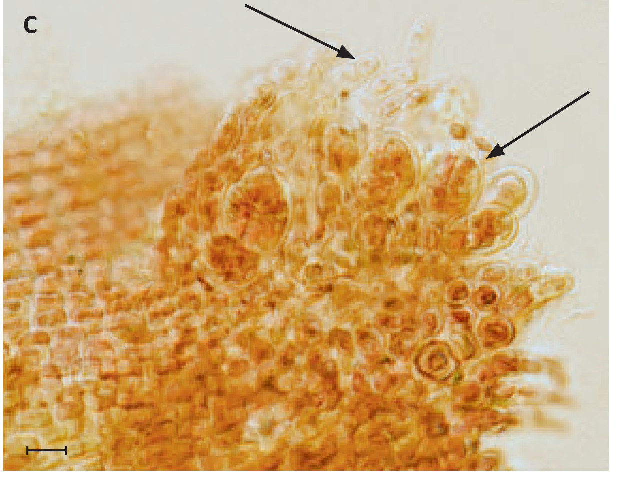
The stalk-cell may repeat the production of tetrasporangia in empty sporangia walls several times. Over time, the wall develops several layers of remnants of the older sporangia walls.

References: Irvine (1983), Maggs (1990), Rosenvinge (1917, *Rhododermis elegans*), Saunders & McLachlan (1989), Saunders et al. (1989).

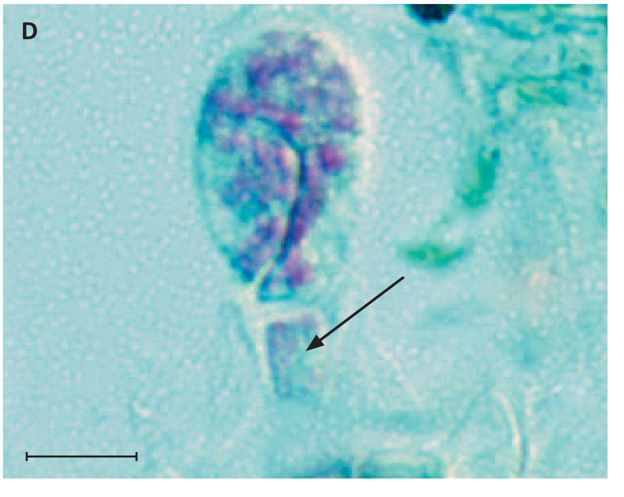
A: *Rhodophysema elegans*. Part of crustose alga of radiating filaments. Scale 20 μm. A-C: Læsø Trindel, 11 m, 8.6.1991.



B: *Rhodophysema elegans*. Basal layer with cell fusions (arrow). Scale 10 μm.



C: *Rhodophysema elegans*. Sorus of cruciate tetrasporangia (right arrow) and curved paraphysis (left arrow). Scale 10 μm.



D: *Rhodophysema elegans*. Stalk-cell (arrow) with cruciate tetrasporangium. Briseis Flak, 7 m, 30.8.1993. Scale 10 μm.

Rhodophysema georgei

Batters

Red Seagrass Crust

Appearance: Flat or slightly raised red spots the size of pinheads, and up to c. 3 mm in diameter.

Structure: A monostromatic layer of confluent radiating filaments growing on the surface of the leaf of Eelgrass (*Zostera marina*). The filaments are 4-6 µm in width and have cell fusions. Older specimens become polystromatic with upright filaments that consist of 4-7 cells, 4-6 µm in width. At the rim of the leaf of the host, many individuals become almost hemispherical and have a medulla of large colourless pyriform cells, and a cortex of small isodiametric cells.

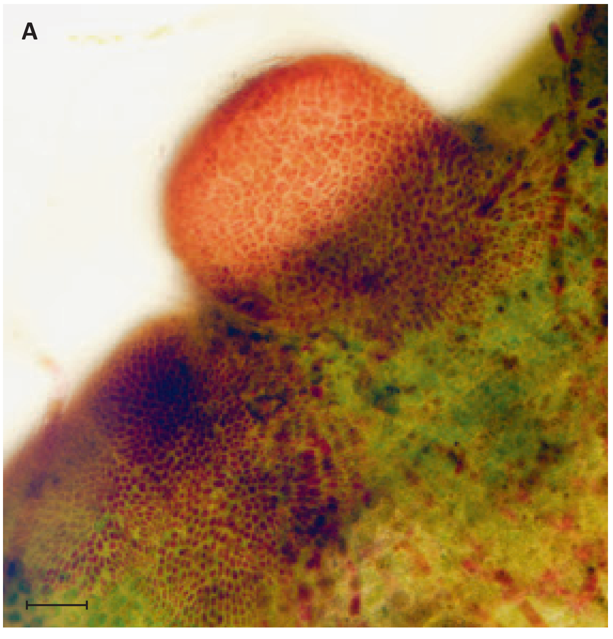
Reproduction: The cruciate tetrasporangia are relatively large and form sori in the centre of the alga together with paraphyses, 3-5 cells long and slightly curved. The sori may occur in a small depression on the flat thalli but form a small bump on the hemispherical thalli. Tetrasporangia are 21-24 µm in width and 26-32 µm in height.

Seasonal variation: Collected in April-August. Antheridia recorded in June and tetrasporangia in May-August.

Habitat: Only known epiphytic on leaves of Eelgrass (*Zostera marina*), often on the rim of old leaves, 0.5-18.5 m depth.

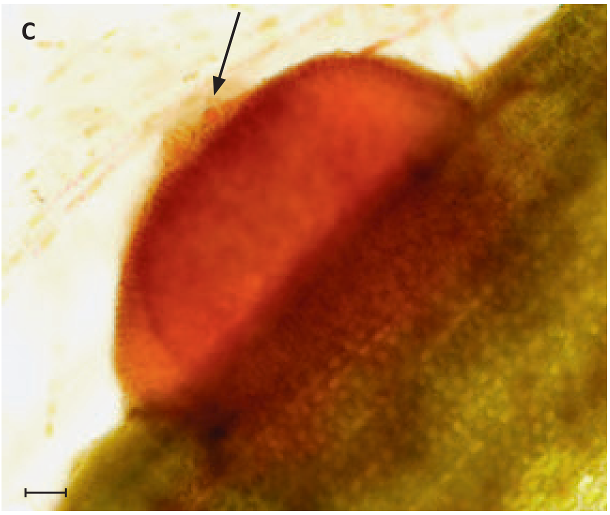
Comment: Studies from the East coast of Canada revealed a direct development from tetraspores to new individuals with tetrasporangia, without sexual reproduction (Saunders & Bird, 1989). Carpogonia reported on the alga from Britain (Irvine & Guiry, 1983). Patches with many small cells, supposed to be antheridia, observed in an alga from Danish waters. The patches occurred on the monostromatic area just outside the area with tetrasporangia.

References: Irvine & Guiry (1983, *Rhodophysema georgii*), Rosenvinge (1917, *R. georgii*), Saunders & Bird (1989, *R. georgii*).

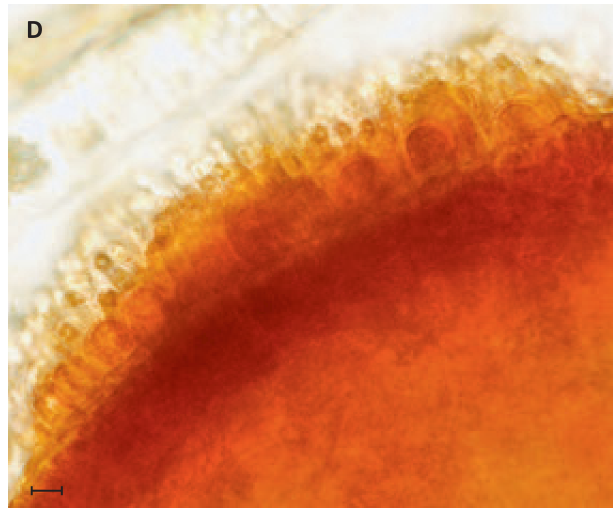


A: *Rhodophysema georgei*. A hemispherical and a flat thallus. Scale 100 µm. A-D, G: On the edges of leaves of Eelgrass (*Zostera marina*). Hirsholm, drift, 14.4.2015.

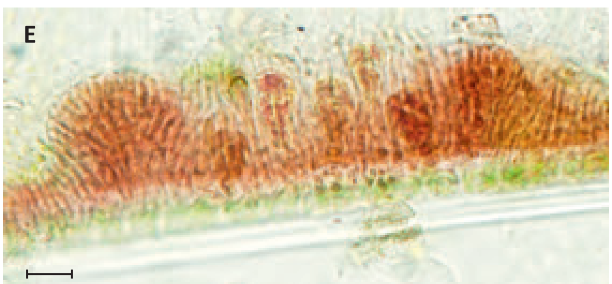
B: *Rhodophysema georgei*. Hemispherical alga with medulla of colourless cells, longitudinal section. Scale 20 µm.



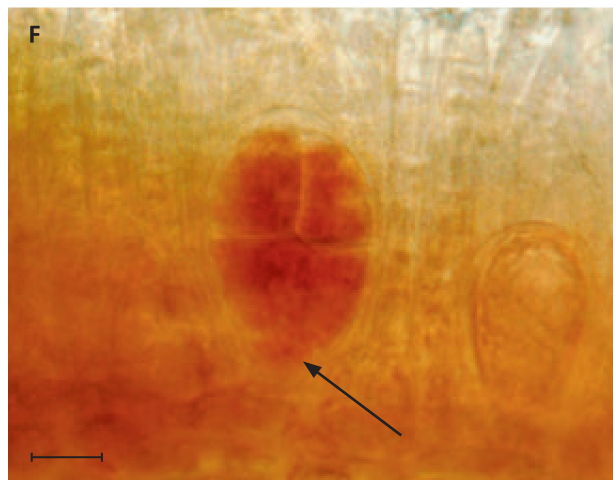
C: *Rhodophysema georgei*. Hemispherical alga with a sorus on the top (arrow). Scale 20 µm.



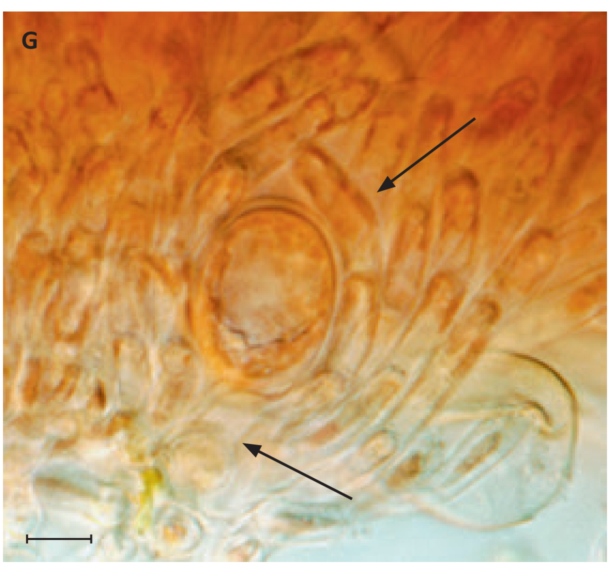
D: *Rhodophysema georgei*. Sorus of tetrasporangia and slightly curved paraphyses. Scale 10 µm.



E: *Rhodophysema georgei*. Flat alga with sorus in a depression (longitudinal section). Nordre Rønner, Læsø, 0.5 m, 15.8.2005. Scale 20 µm.



F: *Rhodophysema georgei*. Cruciate tetrasporangium on short stalk-cell (arrow). Sønder Nyland, Læsø, 0.5 m, 21.6.2013. Scale 10 µm.



G: *Rhodophysema georgei*. Young tetrasporangium with stalk-cell (lower arrow) between curved paraphyses (upper arrow). Scale 10 µm.

Subclass: Rhodymeniophycidae · Order: Atractophorales · Family: Atractophoraceae

Atractophora hypnoides

P.Crouan & H.Crouan

Spindle Weed

Appearance: Terete, dark red-brown alga with whorls of narrow branchlets. Rarely observed in Danish waters, and the specimens only a few mm in height. In the British Isles, it is a soft and much branched thallus, up to 10 cm in length.

Structure: Uprights are a uniaxial syntagma with a central axis covered by a well-developed cortex. Whorled branchlets are initiated a few cells below the apical cell, and are uniseriate with limited growth. A branchlet has a main axis with distichous opposite branches and appears feather-like. The cortex develops from the lower cells of the opposite branches.

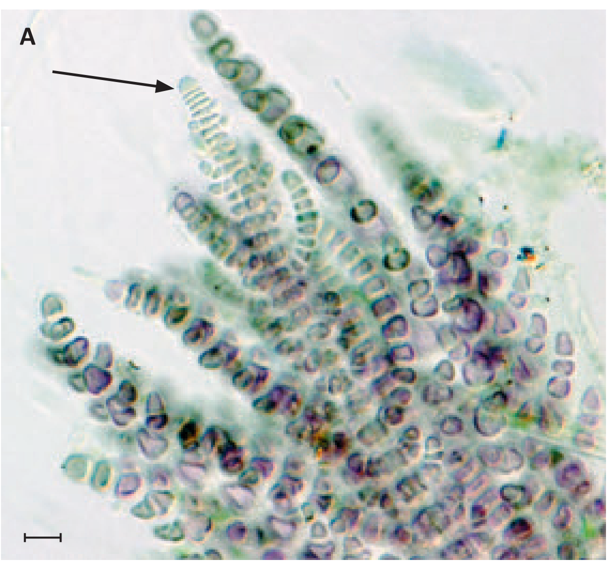
Reproduction: Upright gametophytes and a crustose tetrasporophyte. Gametophytes with reproductive structures and the tetrasporophyte not recorded in Danish waters.

Seasonal variation: Collected in June-July.

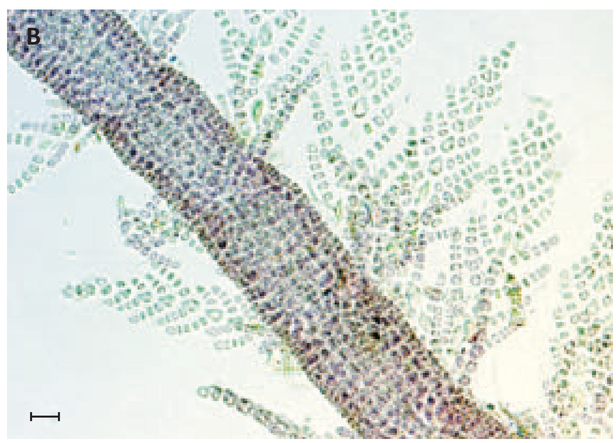
Habitat: On small stones, 2 and 11 m depth.

Comment: Culture studies in the British Isles showed that the life history is heteromorphic and comprises isomorphic gametophytes and a crustose tetrasporophyte, previously known as *Rhododiscus pulcherrimus* P.Crouan & H.Crouan. The tetrasporophyte forms soft carmine red crusts, 8 mm in diameter. It has a basal layer of radiating filaments without cell fusions. Few-celled upright filaments arise from the basal filaments. Regularly cruciate tetrasporangia are apical in slimy patches on the surface of the crusts.

References: Dixon & Irvine (1977), Irvine & Farnham (1983, *Rhododiscus pulcherrimus*), Maggs (1988), Maggs et al. (1983), Rosenvinge (1931).



A: *Atractophora hypnoides.* Apex of uniaxial syntagma with a single apical cell (arrow). Scale 10 µm. A, B: Læsø Trindel, 11 m, 3.6.1993.



B: *Atractophora hypnoides.* Main branch, surface of small cortical cells and whorled branchlets with opposite branches. Scale 20 µm.

Order: Bonnemaisoniales · Family: Bonnemaisoniaceae

Bonnemaisonia asparagoides

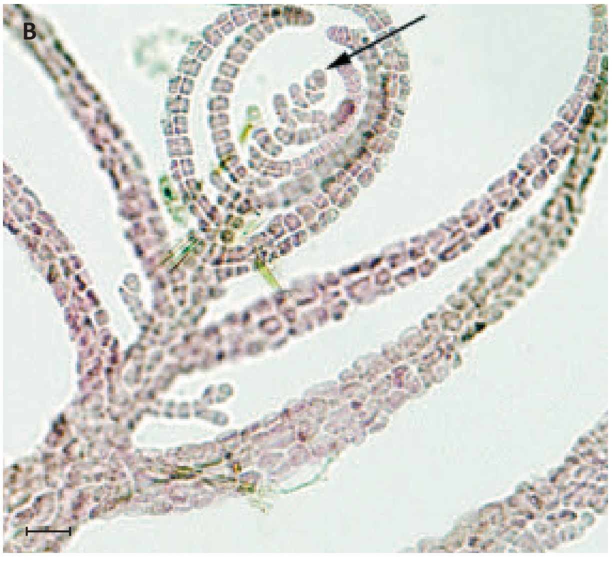
(Woodward) C.Agardh

Bonnemaison's Fern Weed

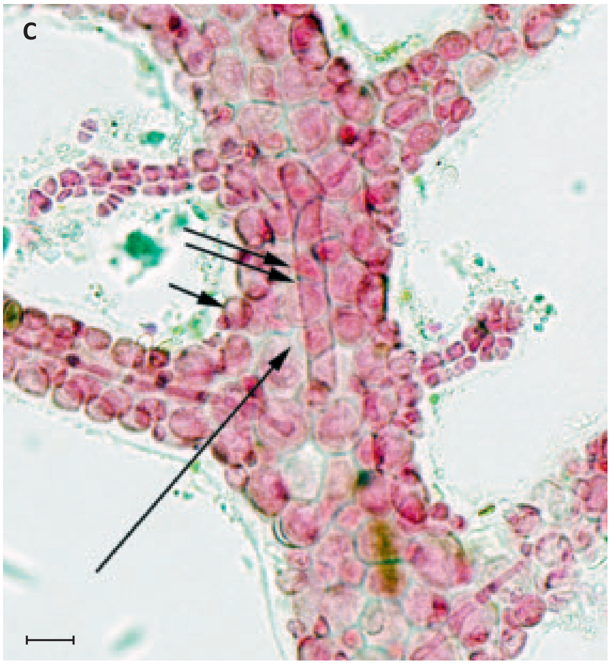
Appearance: The neatly branched thallus has a distinct main axis with opposite, distichous branches of limited growth so the branch systems are flat. The thallus is smooth, 4-12 cm in length with a clear red colour. Opposite branches are unequal in length, a short one always opposite a long one and they alternate so the short one branch alternately turns left then right. The long branches are approximately 3 mm in length. The branches curve inward near the apex whereas they are projecting outward further down. At branching points of main axes, the new branch replaces a short opposite branch. Something similar occurs with the reproductive structures, as they also replace short branches. The thallus has a small attachment disc. The life history comprises upright gametophytes and a prostrate phase, previously known as *Hymenoclonium serpens* (P.Crouan & H.Crouan) Batters. This phase occasionally occurs at the base of upright individuals and consists of dense filaments, with branches in one plane resembling a net.

Structure: Uprights are a uniaxial syntagma. Branches are initiated immediately below the apical cell of the main axis. Further down, each of the cylindrical central axial cells is surrounded by two periaxial cells (Salvador et al., 2008). The periaxial cells are cylindrical, and almost perpendicular to the central axial cells. Three star-shaped cells are cut off from the outer end of the periaxial cells and initiate the cortex, and a tubular cavity develops between the central axial cells and the cortex. The cortex consists of an outermost cell layer of small slightly angular cells that form a reticulate pattern with round larger cells below. Gland cells are transformed surface cells.

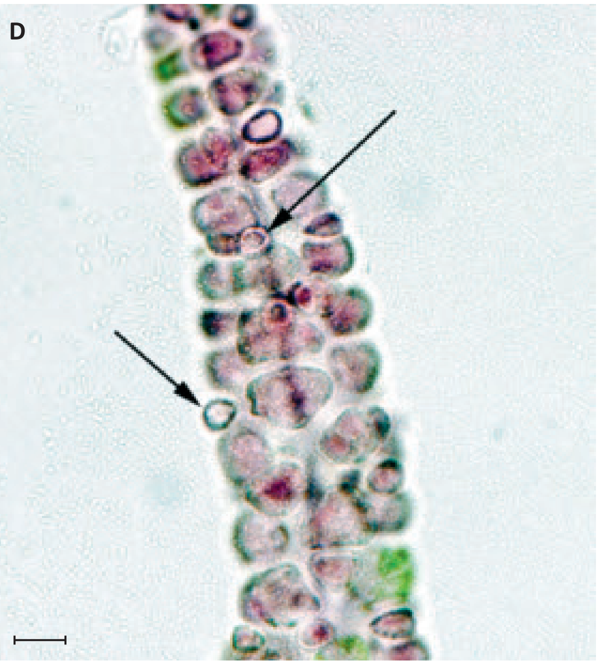
A: *Bonnemaisonia asparagoides.* Main axis and short branches in one plane. Tønneberg Banke, 15 m, 27.8.1993. Scale 2 cm.



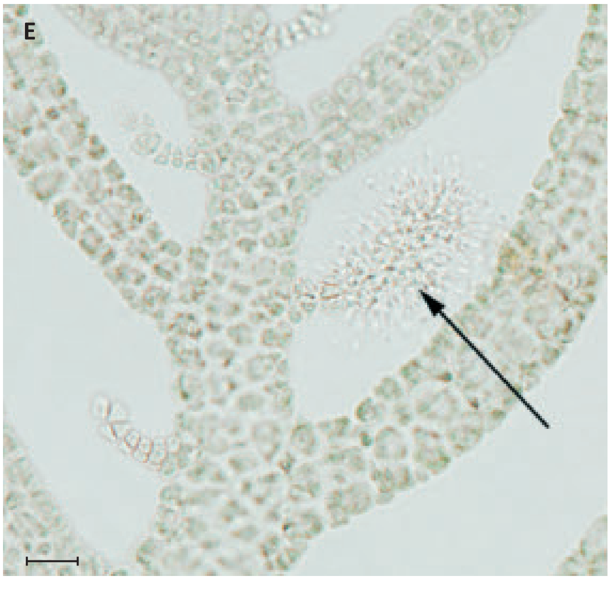
B: *Bonnemaisonia asparagoides.* Uniaxial syntagma, a single apical cell (arrow). Curved distichous branches, a long opposite a short one. Scale 20 µm. B, E-F: Herthas Flak, 13 m, 12.6.1990.



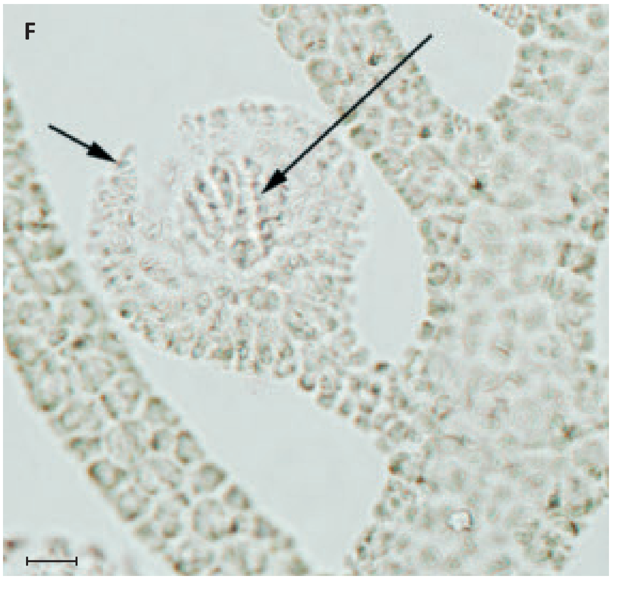
C: *Bonnemaisonia asparagoides.* Cylindrical central axial cell (double arrow) surrounded by a cavity (long arrow) and small rounded cortical cells (short arrow). Cylindrical central axial cells also seen in the branches. Optical longitudinal section slightly pressed. Kims Top, 14.5 m, 4.2.1996. Scale 20 µm.



D: *Bonnemaisonia asparagoides.* Gland cells (arrows) in cortex near the apex, central axial cells visible. Kims Top, 14.5 m, 17.8.1994. Scale 10 µm.



E: *Bonnemaisonia asparagoides.* Spermatangial branchlet (arrow). Scale 20 µm.



F: *Bonnemaisonia asparagoides.* Gonimocarp, comprised of gonimoblast (right arrow) and pericarp (left arrow). Scale 20 µm.

The prostrate phase consists of uniseriate filaments. The radiating main filaments have opposite branches with more or less perpendicular branch angles, the branching pattern repeats a few times, and a net-like plane develops. The main axis has cylindrical cells, on which gland cells may form while the branches lack gland cells (Salvador et al., 2008).

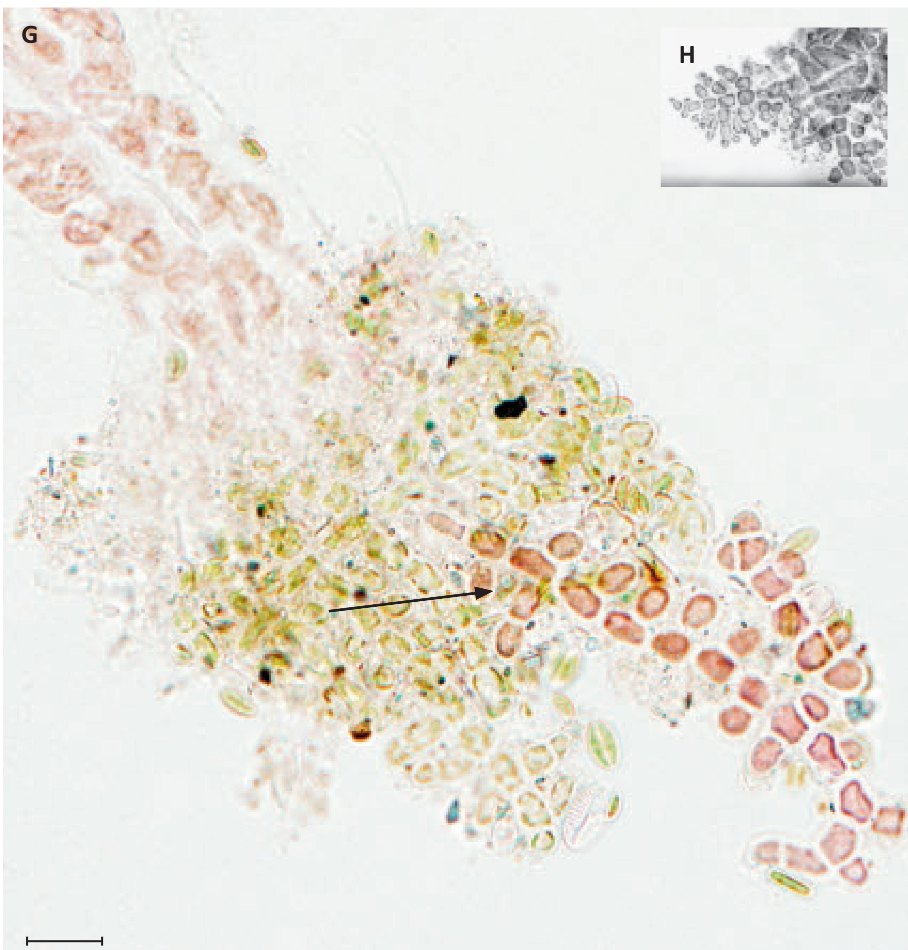
Reproduction: Sexual reproduction with isomorphic monoecious or dioecious gametophytes. Branchlets with the reproductive structures replace short branches. Antheridia are apical on round ellipsoid branchlets that look like small cones. Gonimoblasts occur in urn-shaped pericarps. The prostrate phase is diploid, and after a reduction division in a vegetative cell, upright individuals develop. Tetrasporangia not known.

Seasonal variation: A few individuals 1 mm in length, growing well, collected in January, well-developed in May-August. Antheridia and gonimoblasts recorded in June-August.

Habitat: On solid substratum and epiphytic on Sea Beech (*Delesseria sanguinea*), Stalked Leaf Bearer (*Phyllophora pseudoceranoides*), and epizoic on the bryozoan Horn Wrack (*Flustra foliacea*). Collected by divers, 5-22 m depth.

Comment: The development from the diploid prostrate phase to the upright haploid gametophyte was documented by culture studies of Bonnemaison's Fern Weed (*B. asparagoides*) from the Iberian Peninsula by Salvador Soler et al. (2009).

References: Dixon & Irvine (1977), Salvador et al. (2008), Salvador Soler et al. (2009).



G: *Bonnemaisonia asparagoides*. Prostrate phase with opposite c. 90° branch angles (arrow), at the base of an upright alga. Læsø Trindel, 17 m, 8.6.1991. Scale 20 µm.

H: *Bonnemaisonia asparagoides*. Prostrate phase. Tønneberg Banke, 20.8.1991.

Bonnemaisonia hamifera

Hariot

Bonnemaison's Hook Weed, gametophyte; *Trailliella*-phase, tetrasporophyte

***Trailliella*-phase**

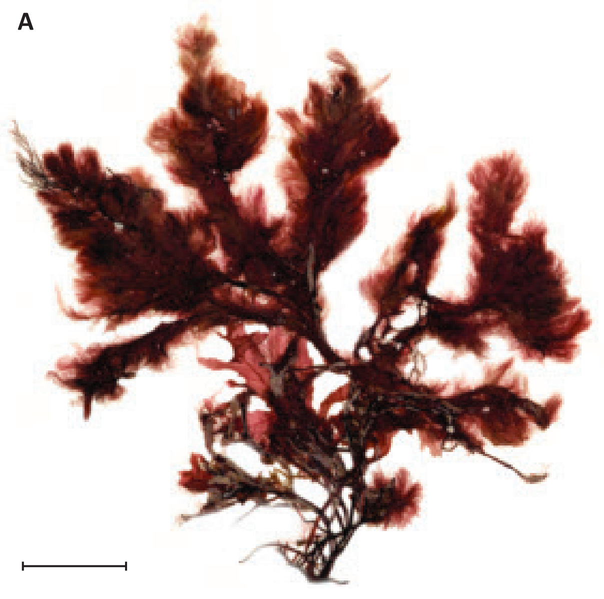
Appearance: Narrow brownish red to red-purple filaments, forming a velvet-like cover or tufts up to 1-2 cm in length.

Structure: Upright uniseriate filaments arise as scattered branches from similar prostrate filaments to form a tuft. Filaments have scattered branches with branch angles of c. 90°. The filaments have an even thickness and consist of cylindrical to barrel-shaped cells, 22-38 µm in width and 1-2.5 times as long as wide. Each cell contains many disc-shaped or slightly elongate plastids. Round, hyaline gland cells form at the distal end of vegetative cells, so it typically appears as if they are placed between the corners of two neighbouring cells. Prostrate filaments attach to the substratum by multicellular attachment pads, which occur on short branchlets but may be apical.

Reproduction: The life history is heteromorphic with isomorphic bush-like gametophytes and the tufts are tetrasporophytes, previously known as *Trailliella intricata* Batters. The gametophytes are 5-20 cm in height and have characteristic hook-shaped branches. So far, they have not been found in Danish waters. Tetrasporophytes have irregularly cruciate tetrasporangia, which are intercalary and develop from vegetative cells at irregular intervals, occurring individually or in short rows. Tetrasporangia seldom recorded in Danish waters. An efficient asexual reproduction occurs from fragments that become loose and grow into new individuals. Culture studies in combination with field observations in the alga from Ireland have shown that tetrasporangia develop under short day condition (day length < 12 hours) and temperature > 11° C (Breeman et. al., 1988).

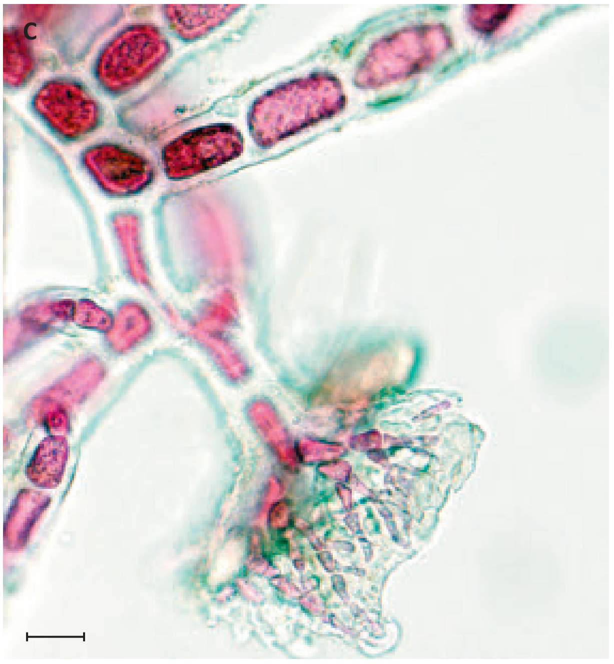
Seasonal variation: Occurs all year. Tetrasporangia recorded in August, October-November.

Habitat: Epiphytic on various algae, epizoic on hydroids and on solid substrata such as mollusc shells, and stones, 0.5-21.5 m depth. Often the dominant species near the depth limit of vegetation on stone reefs.

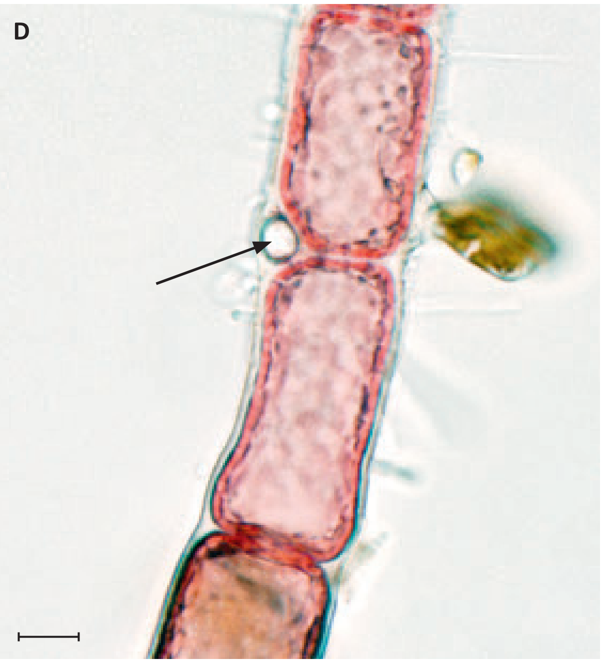


A: *Bonnemaisonia hamifera*. Red tufts on Lobed Leaf Bearer (*Coccotylus brodiei*), with Sea Oak (*Phycodrys rubens*). Lysegrund, 5 m, 15.8.1990. Scale 2 cm.

B: *Bonnemaisonia hamifera*. Scattered branches with c. 90° branch angles, many disc-shaped plastids per cell. Scale 25 µm. B-C, E: Tønneberg Banke, 10.5 m, 27.8.2013.



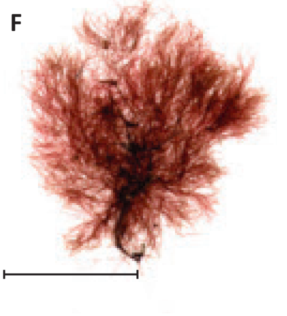
C *Bonnemaisonia hamifera.* Multicellular attachement pad. Scale 25 µm.



D: *Bonnemaisonia hamifera.* Gland cell (arrow) from vegetative cell. Beach north of Vesterø Havn, Læsø, drift, 6.11.2012. Scale 10 µm.

E: *Bonnemaisonia hamifera.* Tetrasporangia. Scale 25 µm.

F: *Bonnemaisonia hamifera.* Characteristic appearance of drift alga. Kims Top, 16 m, 17.8.1994. Scale 1 cm.



Resembles: Creeping Bush Weed (*Spermothamnion repens*) appears similar but has cells, 4-5 times as long as wide, no gland cells, opposite branches may occur and the attachment pads are unicellular.

Comment: Gland cells contain iodine, which react with starch after treatment by acid. Gland cells may be a defence against grazers. Probably introduced to Europe from Japan or its environs, at the end of last century (Guiry in Guiry & Guiry, 2021), first observation in Danish waters in the western part of the Limfjord, 1901. The gametophytes occur at Helgoland, Norway and the British Islets, a young gametophyte observed at Hallands Väderöerne, Sweden (S. Lundsteen personal observation).

References: Breeman et al. (1988), Dixon & Irvine (1977), Guiry in Guiry & Guiry (2021), Kornmann & Sahling (1977), Maggs & Stegenga (1999), Mathiesen (2000), Rosenvinge (1923-24, *Trailliella intricata*).

Order: Ceramiales · Family: Callithamniaceae

Small bush-like thalli of uniseriate repeatedly branched filaments which consist of main branches, branches and branchlets. There is often a branch from each cell of the main branch. Branchlets occur on the branches. Older parts of the main branches may have a filamentous cortex which arises as downward-growing narrow filaments from the lower cells of the branches. Thalli attach to the substratum by prostrate filaments occasionally so dense that they become disc-shaped. There are no gland cells. Young cells contain many disc-shaped plastids which become elongate or ribbon-shaped in older cells. The cells contain a single nucleus in Beautiful Bush Weeds (*Aglaothamnion*) and Chain Seed Bush Weed (*Seirospora*), while the older cells of *Callithamnion* are multinucleate. The nuclei might be visible as "clear" area below the cell walls otherwise covered by plastids. A single nucleus is typically in the middle of the cell. Branching pattern is an important species character and best observed close to the apex.

The life history comprises isomorphic gametophytes and tetrasporophyte. Gonimoblasts are naked, without a pericarp. Tetrasporangia are tetrahedrally divided and without a stalk-cell. The shape and position of the reproductive structures are important characters for species identification, but the vegetative characters are of priority in the identification keys.

References: Bird & McLachlan (1992), Choi et al. (2008), Hommersand et al. (2006), L'Hardy-Halos & Rueness (1990), Maggs & Hommersand (1993), Rosenvinge (1920, 1923-24).

Identification key to species of Callithamniaceae (*Aglaothamnion, Callithamnion, Gaillona* and *Seirospora*)

1a.	Thallus with complanate branch systems, branchlets distichous	2
1b.	Thallus with branches on all sides	3
2a.	Branches level with apical cell of main branch, the two lowest branchlets are adaxial on the branches	*A. bipinnatum*
2b.	Branches do not reach the apical cell of the main branch, the lower cells of the branches typically without branchlets, parasporangia	*G. hookeri*
3a.	Branchlets with conical pointed apical cells	*C. tetragonum*
3b.	Branchlets with cylindrical blunt apical cells	4
4a.	Upper part of thallus with repeated pseudodichotomous branching	5
4b.	Upper part of thallus with distinct main branches and scattered branches	6
5a.	Distal branches close together in semi-umbelliferous tufts. Many nuclei in older cells. Cortical filaments arise individually	*C. corymbosum*
5b.	Distal branches not close together. The outline of the upper part of branch-systems is conical. A single nucleus per cell, in all cells. Three cortical filaments typically arise from the same cell	*S. interrupta*
6a.	Cortex is sparse and not densely attached to the main branch. Cells of the branches are 4-12 times as long as wide. Gonimoblasts with conical lobes	*A. tenuissimum*
6b.	Cortex well-developed on lower part of main branches. Cells of the branches short. Gonimoblasts rounded	7
7a.	Branching very dense with many branchlets	*G. gallica*
7b.	Branching open, the lower cells of the branches without branchlets	*G. rosea*

Aglaothamnion bipinnatum

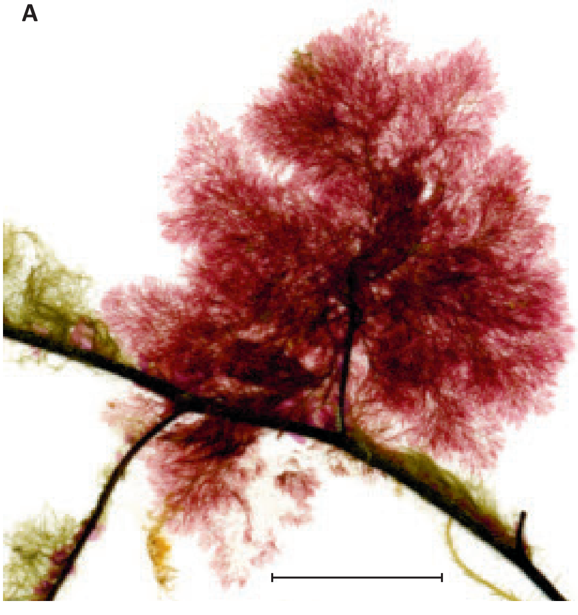
(P.Crouan & H.Crouan) Feldmann & G.Feldmann

Twice-pinnate Beautiful Bush Weed

Appearance: Delicate rose bushy thallus, up to 2 cm in height, youngest branch systems complanate. One or several uprights arise from a small attachment disc. **Structure:** Distichous branches alternate and reach to the apex of the main branch, making the outline of the apex appear round. Lower one or two branchlets arise on the adaxial side of the branches. The following branchlets alternate with the first an abaxial branch. No record of red algal hairs. Young individuals attach by radiating narrow filaments, almost confluent to form a small disc. Later, downward-growing narrow filaments arise from the lower cells of the main branch. These may form a narrow cortex and also contribute to the attachment. New upright branches may arise from these cortical filaments.

Reproduction: Gametophytes are monoecious. Antheridial branchlets occur individually on the lower cells of the branches. They have a few-celled stalk with distal antheridia. Young gonimoblasts are rounded to heart-shaped, eventually becoming a broad conical shape with several lobes. Tetrasporangia form rows on the adaxial side of the branches with a single sporangium per cell. Individuals with both antheridia and tetrasporangia occasionally occur, and in rare instances, young gonimoblasts are also noticed. Antheridial branchlets and tetrasporangia replace branchlets in fertile individuals.
Seasonal variation: Collected in February, May-August. Antheridia and gonimoblasts recorded in February, May-August and tetrasporangia in May-August.
Habitat: Epiphytic on Desmarest's Prickly Weed (*Desmarestia aculeata*), and epizoic on bryozoans and hydroids, 12-24.5 m depth. In older collections by dredge, 30 m depth.
References: Maggs & Hommersand (1993), Rosenvinge (1923-24, *Callithamnion* sp.), 1935a, *C. bipinnatum*), J. Rueness & M. Rueness (1980, *C. bipinnatum*).

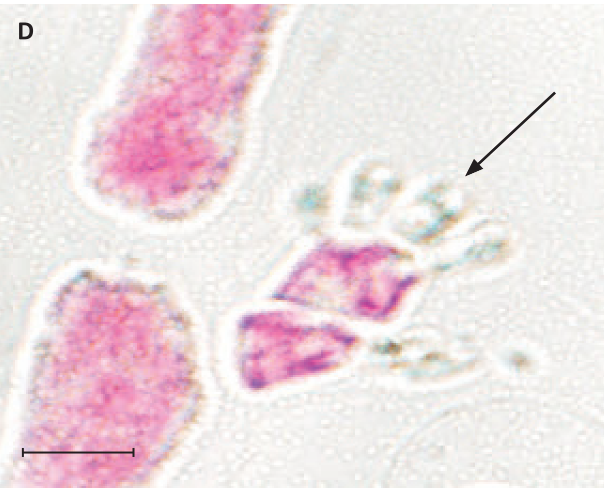
A



A: *Aglaothamnion bipinnatum*. Bush-like alga on Desmarest's Prickly Weed (*Desmarestia aculeata*). Herthas Flak, 12 m, 30.5.1992. Scale 1 cm.

B: *Aglaothamnion bipinnatum*. Apex with a rounded outline. The lower one or two branchlets on the adaxial side of branches (arrows), and the following branchlets regularly alternating. Herthas Flak, 20 m, 21.8.1991. Scale 50 µm.

C: *Aglaothamnion bipinnatum*. Antheridial branchlet (long arrow), young gonimoblasts (short arrow) and tetrahedrally divided tetrasporangia. Scale 50 µm. C-D: Herthas Flak, 18 m, 4.6.1993.



D: *Aglaothamnion bipinnatum*. Antheridia (arrow), part of figure C. Scale 10 µm.

E: *Aglaothamnion bipinnatum*. Gonimoblasts with rounded lobes, one heart-shaped (arrow). Herthas Flak, 13 m, 28.8.1993. Scale 50 µm.

Aglaothamnion tenuissimum

(Bonnemaison) Feldmann-Mazoyer

Slender Beautiful Bush Weed

Appearance: Delicate pink bushy thalli, up to 2 cm in height, rarely up to 4 cm in height. Much branched with branches on all sides. Uprights arise individually or several together from prostrate filaments.

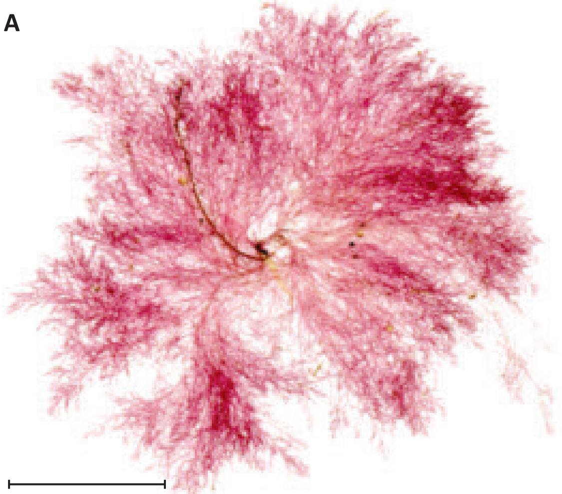
Structure: Main branch distinct throughout the thallus although not much different in size from other branches at the apex. Branches are scattered on all sides. At the apex they reach the apical cell or slightly overtop it. Branches are repeatedly branched with a branchlet from almost every cell, giving the thallus a very bushy appearance. Cells are 1.5-2 times as long as wide in the lower part of the alga, and 4-12 times as long as wide in the upper part, rarely longer. Red algal hairs are narrow and relatively short but very rare. At the lower part of main branches many downward-growing narrow filaments form a sparse cortex, loosely surrounding the branch. There are also downward-curved branches from which new upright branches may arise.

Reproduction: Gametophytes are dioecious. Antheridial branchlets form series at the adaxial side of branches, single or 2-3 on each cell. They have a stalk of 3-5 cells, upright or slightly curved towards the branch and may have short branches. Antheridia form from each of the stalk-cells. Gonimoblasts are irregular with several conical lobes, each terminating in an apical cell. Tetrasporangia are in series at the adaxial side of the branches with one or two sporangia per cell. Bisporangia also reported, they occur in the same way as the tetrasporangia.

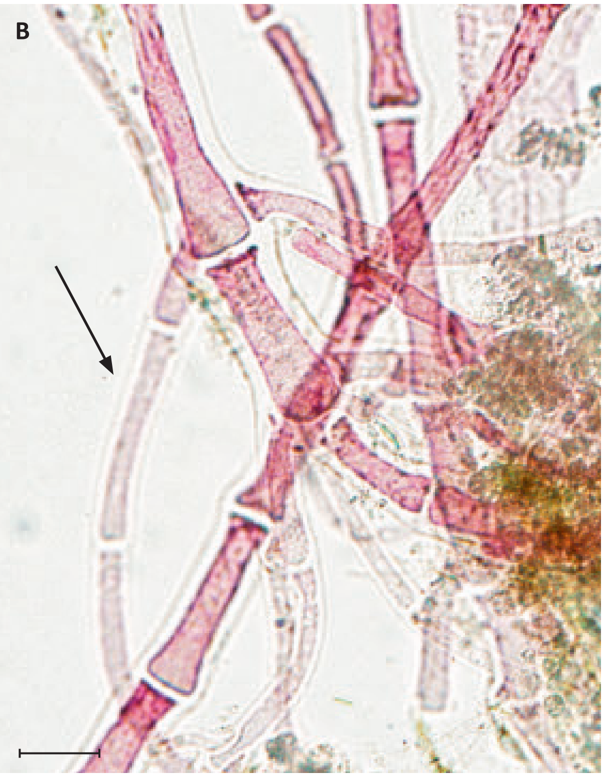
Seasonal variation: Collected in April-November. Antheridia recorded in May-September, gonimoblasts and tetrasporangia in June-October and bisporangia in May-July and September.

Habitat: Epiphytic on larger algae, collected at harbour jetties and stone reefs, 1-24.5 m depth.

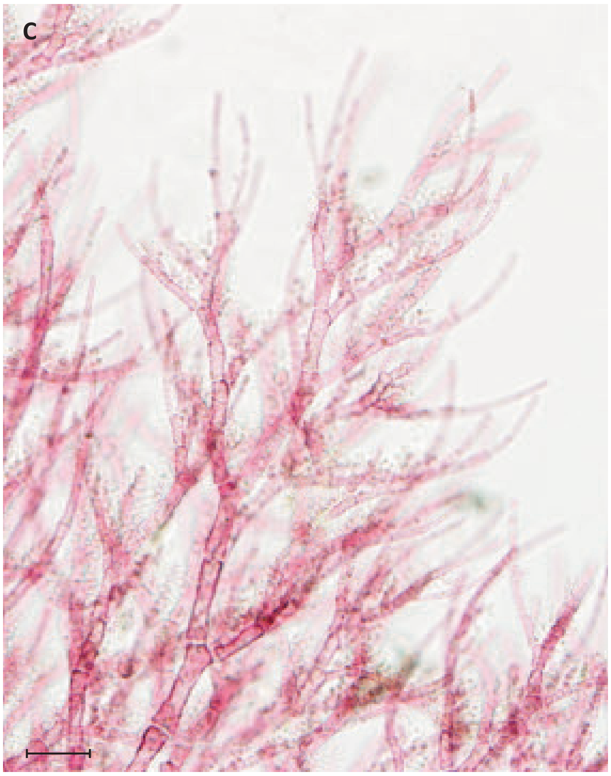
References: Furnari et al. (1998), Kylin (1907, *Callithamnion furcellariae*), L'Hardy-Halos & Rueness (1990, *A. byssoides*), Maggs & Hommersand (1993, *A. byssoides*), Rosenvinge (1923-24, *C. furcellariae*), J. Rueness & M. Rueness (1980, *C. byssoides)*.



A: *Aglaothamnion tenuissimum*. Delicate, much branched bushy alga. Briseis Flak, 11 m, 8.6.1989. Scale 1 cm.



B: *Aglaothamnion tenuissimum*. Lower part of main branch with downward-growing narrow filaments (arrow). Paludans Flak, 9 m, 11.9.1993. Scale 50 µm.

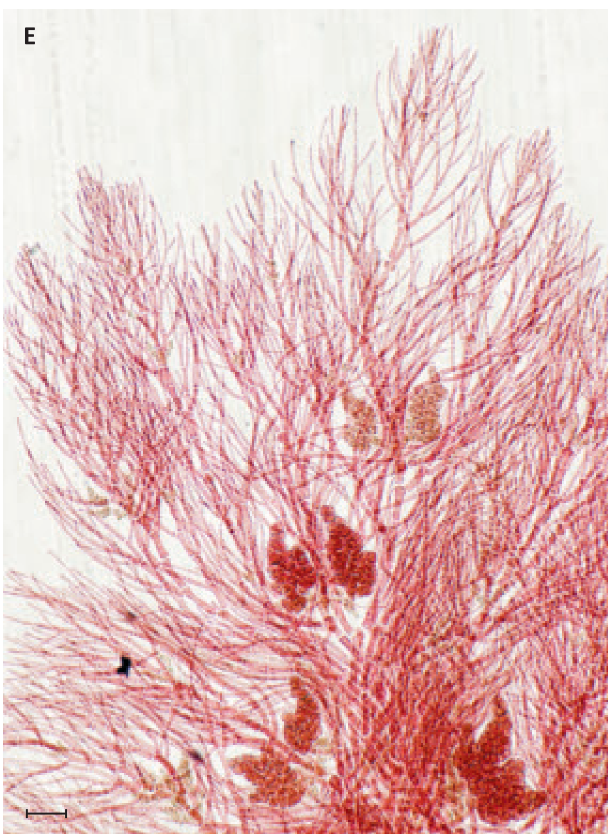


C: *Aglaothamnion tenuissimum*. Male gametophyte, scattered branches with series of antheridia. Læsø Trindel, 8 m, 19.8.1994. Scale 50 µ.

D: *Aglaothamnion tenuissimum*. Branches with two upright antheridial branchlets per cell. Scale 10 µm. D-E: Læsø Trindel, 8 m, 20.8.1991.

E: *Aglaothamnion tenuissimum*. Female gametophyte, gonimoblasts with several conical lobes. Scale 100 µm.

F: *Aglaothamnion tenuissimum*. Tetrahedrally divided tetrasporangia on adaxial side of branch. Kims Top, 15 m, 28.8.2013. Scale 20 µm.

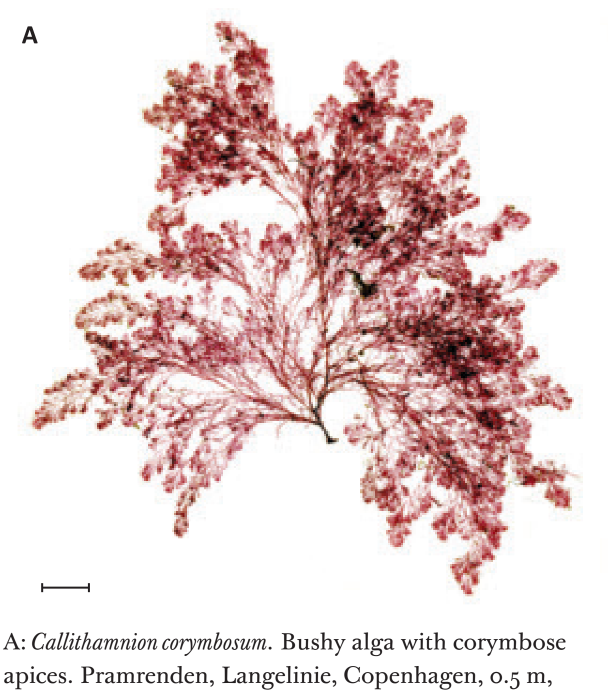


Callithamnion corymbosum

(Smith) Lyngbye

Delicate Bush Weed

Appearance: Delicate, much branched bushy thalli, bright brick-red or rose. They are typically 2-5 cm in height, but occasionally up to 10 cm. Distinct main branch with branches on all sides. Uprights typically arise individually from a discoid base. The uppermost branches are often corymbose and form clusters.
Structure: The upper part of the thallus is repeatedly pseudodichotomously branched on all sides. Branches terminate at about the same height, are dense and often with apical red algal hairs. Cortical filaments arise from the lowest cells of the branches and grow downwards, covering the basal part of the main branches completely and might contribute to the attachment of the thallus. New branches may arise from the cortical filaments. Older cells contain many small nuclei, the formation of which often begins immediately after the first pseudodichotomous branching, but in brackish water, it may start further down.
Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Antheridial stands are sessile on the adaxial side of branchlets, typically several on each cell and forming a coherent cushion of antheridia. Gonimoblasts are rounded with several spherical lobes in pairs of equal size. Tetrasporangia occur individually at the lower part of branchlets and appear as if they are in the corners of the branchlets.
Seasonal variation: Occurs all year, but best developed in summer and autumn month. Antheridia recorded in April-September, gonimoblasts in June-October and tetrasporangia in June-January.
Habitat: On larger algae, seagrass, and on solid sub-



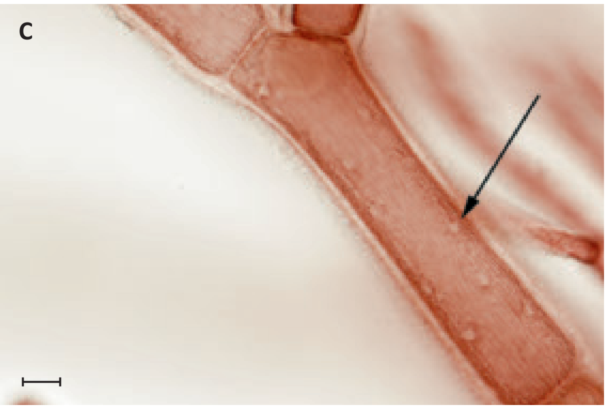
A: *Callithamnion corymbosum*. Bushy alga with corymbose apices. Pramrenden, Langelinie, Copenhagen, 0.5 m, 20.9.2007. Scale 2 cm.

B: *Callithamnion corymbosum*. Apex of dense pseudodichotomous branches. Scale 100 µm. B, E-F: Paludans Flak, 9 m, 11.9.1993.

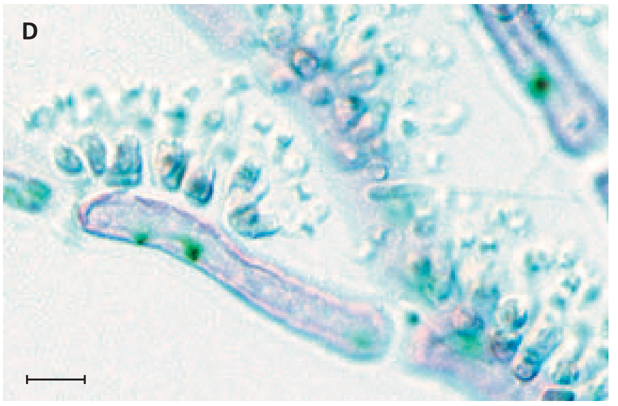
stratum. Collected at shallow water and by divers to 10 m depth. Collected by dredge to 31 m depth in the North Sea.

Comment: The name "corymbosum" means corymb and refers to the upper branch tufts.

References: Maggs & Hommersand (1993), Rosenvinge (1923-24).



C: *Callithamnion corymbosum*. Older cell with many nuclei (arrow). Fiskerihavn Nord, Copenhagen, 0.5 m, 21.9.2007. Scale 20 µm.



D: *Callithamnion corymbosum*. Cushion-forming antheridia on the adaxial side of branchlets. Lysegrund, 6 m, 23.8.1996. Scale 10 µm.

E: *Callithamnion corymbosum*. Gonimoblasts with almost spherical lobes. Scale 20 µm.

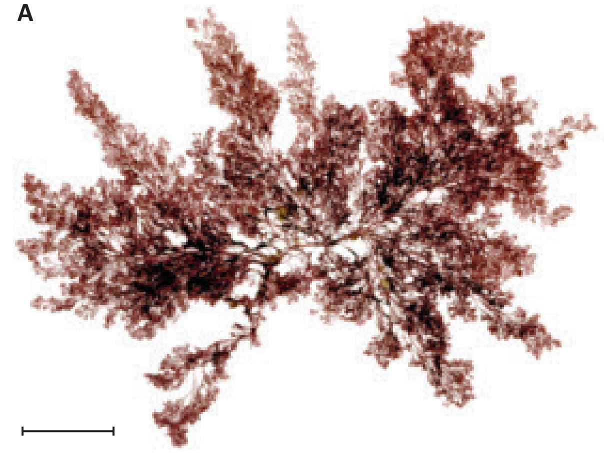
F: *Callithamnion corymbosum*. Tetrahedrally divided tetrasporangia, appears as if at branching points. Scale 50 µm.

Callithamnion granulatum
(Ducluzeau) C.Agardh

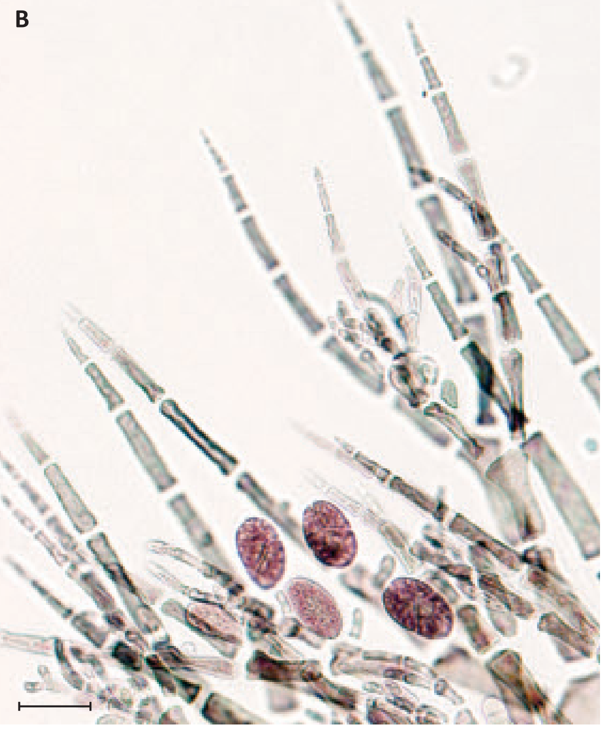
The species does not grow attached in Danish waters, but there is a report of a small individual with antheridia. It was found at the basal part of drift Thong Weed (*Himanthalia elongata*) on the beach at Tversted, 1904 (Rosenvinge, 1905 p. 90-91, 97).

Callithamnion tetragonum
(Stackhouse) S.F.Gray
Red Cloud Bush Weed

Appearance: Densely branched brownish red bushy alga, with distinct main branches. Uprights appear compact with very close branches on all sides. The branches taper upwards to give the apex a conical appearance. On stone reefs near Frederikshavn, the Northern Kattegat the alga is only 1.5-2 cm in height, whilst in the waters around the island of Samsø, at Gilleleje and the northern part of the Sound it is up to 7 cm in height. A single upright arises from the discoid base.
Structure: Branches on all sides grow above the apical cell of the main branch. The upper branchlets might be distichous. They consist of 6-7 cylindrical to barrel-shaped cells, which attenuate towards the pointed apical cells. There are several nuclei per cell. A well-developed cortex typically develops at the lower part of main branches. It consists of narrow filaments, growing downward from the lower cells of the branches. Secondary branches form from the cortex. There are no red algal hairs.
Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Antheridial branchlets have an axis of short cells and look like hemispherical cushions on the adaxial sides of the branches. Gonimoblasts have rounded to heart-shaped lobes. Tetrasporangia are adaxial on the lower cells of branchlets, single or rarely two on the same cell. They are obovate to ellipsoid.
Seasonal variation: Collected in March-September. Sexual reproductive structures recorded in May-September, gonimoblasts in July-October and tetrasporangia in March, May-September.
Habitat: Epiphytic on larger algae and on solid substratum, 0.5-20 m depth.
References: Maggs & Hommersand (1993), Rosenvinge (1923-24), J. Rueness & M. Rueness (1985).

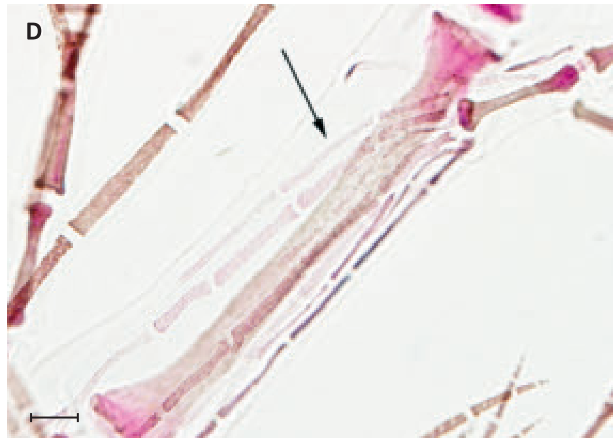


A: *Callithamnion tetragonum*. Distinct main axes with dense branches, apexes conical. Scale 1 cm. A-B: Briseis Flak, 6.5 m, 10.8.1992.

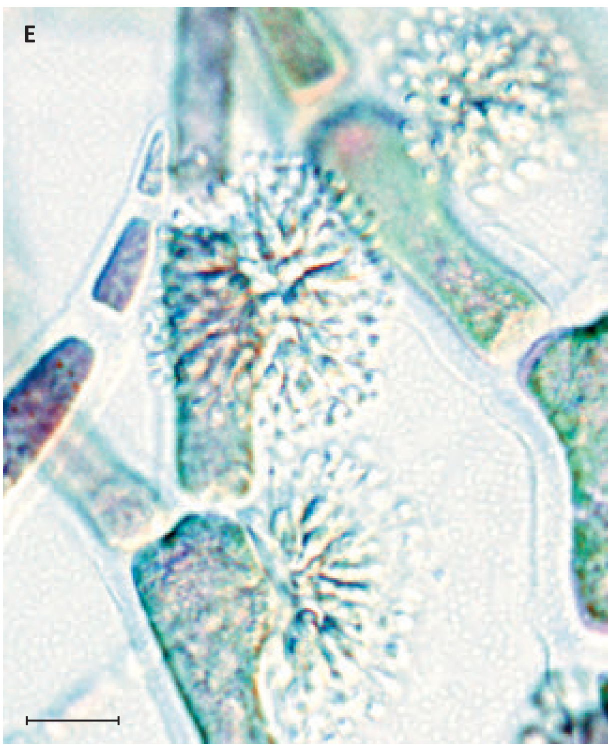


B: *Callithamnion tetragonum*. Branches with pointed apical cells. Scale 50 µm.

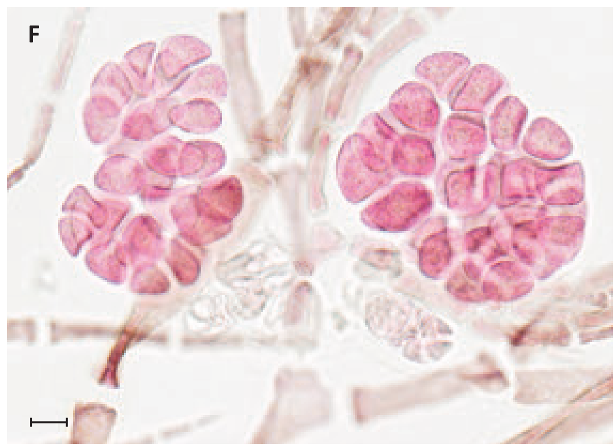
C: *Callithamnion tetragonum*. Apex of branch with pointed apical cell and several nuclei per cell (arrow). Exposed side of eastern harbour jetty, Gilleleje, 0.5 m, 29.4.2014. Scale 10 µm.



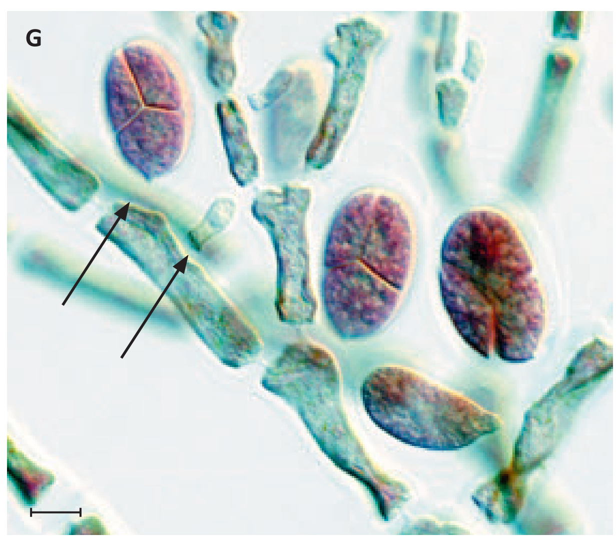
D: *Callithamnion tetragonum*. Cortical filaments from the lower cell of a branch (arrow). Scale 50 µm. D-G: Briseis Flak, 5 m, 10.8.1992.



E: *Callithamnion tetragonum*. Hemispherical cushions of antheridia. Scale 20 µm.



F: *Callithamnion tetragonum*. Rounded lobes of gonimoblasts. Scale 20 µm.



G: *Callithamnion tetragonum*. Tetrahedrally divided tetrasporangia, a young and an older on the same cell (arrows). Scale 20 µm.

Gaillona gallica

(Nägeli) Athanasiadis

Recent synonym: ***Aglaothamnion gallicum*** **(Nägeli) Halos ex Ardré**

Pyramidal Bush Weed

Appearance: Delicate red-brown bushy alga with a narrow conical to pyramidal outline or fan-shaped, up to 1-1.5 cm in height. Uprights arise individually or several from densely connected prostrate filaments.

Structure: Distinct main branches with scattered branches on all sides. Branches are relatively short, giving the thallus an elongate to pyramidal outline. Branches often have a small projecting branchlet from the lower cell, or the lowest two cells are unbranched with the following branchlets alternating. Many short red algal hairs may be present at the apex. The lower part of the main branches may have a well-developed cortex from which new uprights may arise.

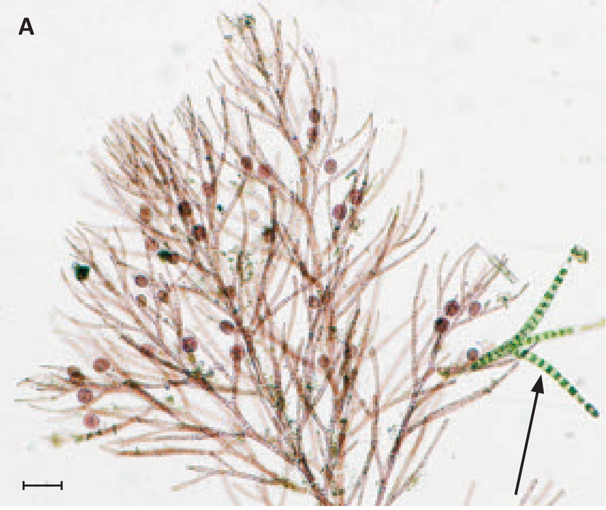
Reproduction: Gametophytes are dioecious. Antheridial branchlets have a few-celled axis curving towards the branch. They develop at the adaxial side of branches with 1-2 antheridial branchlets on each of several consecutive cells. Antheridial branchlets aggregated when mature into a continuous layer on the upper side of projecting branches. Gonimoblasts have rounded lobes. Young tetrasporangia are pyriform and become spherical at maturity. They are individual or in short series on the adaxial side of the distal branchlets.

Seasonal variation: Collected in July-August with antheridia, gonimoblasts and mature tetrasporangia.

Habitat: Epiphytic on Clawed Fork Weed (*Furcellaria lumbricalis*) and other red algae and drift on Thong Weed (*Himanthalia elongata*) at Tversted.

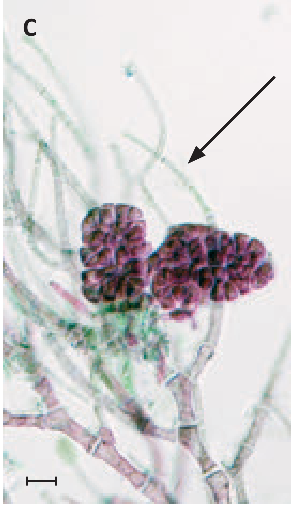
Comment: Mentioned by Rosenvinge (1923-24) as *Callithamnion brodiaei*, according to Maggs & Hommersand (1993).

References: Maggs & Hommersand (1993, *Aglaothamnion gallicum*), Rosenvinge (1923-24, *Callithamnion brodiaei*).



A: *Gaillona gallica*. Tetrasporophyte with sphaerical tetrasporangia. Epiphytic propagule of Small Brown Feather Weed (*Sphacelaria cirrosa*) (arrow). Læsø Trindel, 10.5 m, 28.8.1993. Scale 100 µm.

B: *Gaillona gallica*. Apex with apical red algal hairs (arrow). Scale 20 µm. B-C: Tønneberg Banke, 14.5 m, 20.8.1994.



C: *Gaillona gallica*. Female gametophyte with rounded gonimoblasts. Many branchlets getting slender towards the apex (arrow). Scale 10 µm.

Gaillona hookeri

(Dillwyn) Athanasiadis

Recent synonym: ***Aglaothamnion hookeri*** **(Dillwyn) Maggs & Hommersand**

Hooker's Bush Weed

Appearance: Delicate red-brown bushy thalli, up to 1-2 (3) cm in height. They have a distinct main branch and dense branches. Uprights arise individually or several together from a base of densely matted filaments.

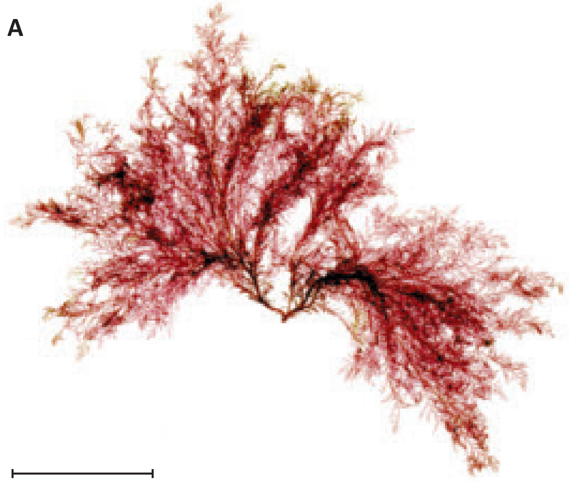
Structure: Main branch distinct all through the thallus with distichous alternating branches. The branching is relatively open without many branchlets. Branches are typically short and do not reach the apex of the main branch giving the thallus apex a triangular outline. Branching may be irregular, with branches on all sides particularly in the lower part of older individuals. The lower cells of branches are typically without lateral branches. Cells are relatively short, 2-4 times as long as wide. The basal part of main branches covered by confluent downward-growing narrow filaments that make a well-developed cortex in older thalli. New uprights may arise from the cortical filaments. No records of red algal hairs.

Reproduction: Asexual reproduction by paraspores. Parasporangia are sessile as irregularly rounded cell clusters on the adaxial side of short branches. Germinated spores develop to identical offspring with parasporangia. Mature tetrasporangia are almost globular, but tetrasporangia are seldom observed in this alga from Danish waters and sexual structures are not recorded.

Seasonal variation: Collected in January-September and November. Parasporangia recorded in January-February, May-September and November, tetrasporangia in June and August-September.

Habitat: Epiphytic on larger algae, and on stone. Collected by divers to 18 m depth. In older collections by dredge to 30 m depth.

Comment: Cells may contain many angular crystals after fixation in formaldehyde, something we have not observed in other algae from Danish waters.

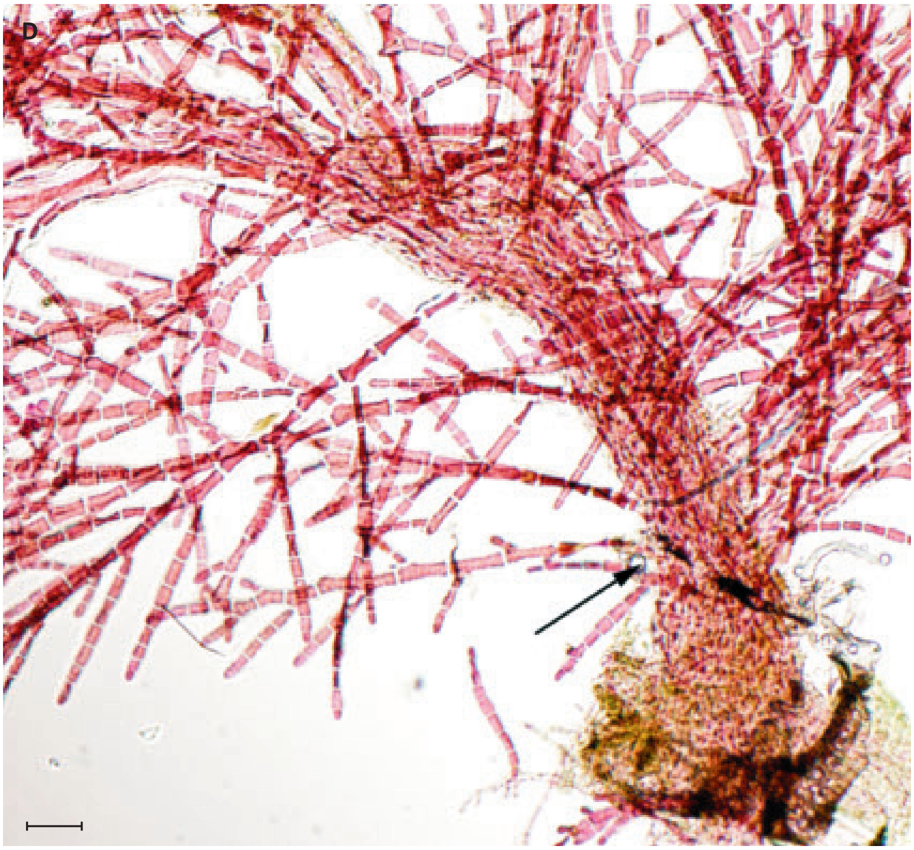


A: *Gaillona hookeri.* Bushy thalli with distinct main branches and bristly branches. Borfeld, Nordre Rønner, Læsø, 6.5 m, 22.5.1988. Scale 1 cm.

B: *Gaillona hookeri.* Apex with open branching, alternating branches and parasporangia. Schultz's Grund, 4 m, 6.9.1993. Scale 50 µm.

References: Kylin (1907, *Callithamnion hookeri*), Maggs & Hommersand (1993, *Aglaothamnion hookeri*), Rosenvinge (1923-24, *C. hookeri*), M. Rueness & J. Rueness (1978, *C. hookeri*).

C: *Gaillona hookeri*. Cells with crystals (arrow) after formalin fixation. Lysegrund, 6 m, 23.8.1996. Scale 10 µm.



D: *Gaillona hookeri*. Lower part of main branch with well-developed cortex, from where new branches arise (arrow). Schultz's Grund, 7 m, 1.9.1993. Scale 100 µm.

Gaillona rosea

(Roth) Athanasiadis

Recent synonym: ***Aglaothamnion roseum*** **(Roth) Maggs & L'Hardy-Halos**

Rose-red Bush Weed

Appearance: Delicate red to bordeaux-red bushy thalli with distinct main branches. A single or several uprights arise from a base of densely matted prostrate filaments. The alga is typically 3-5 cm in height, occasionally up to 10 cm in height.

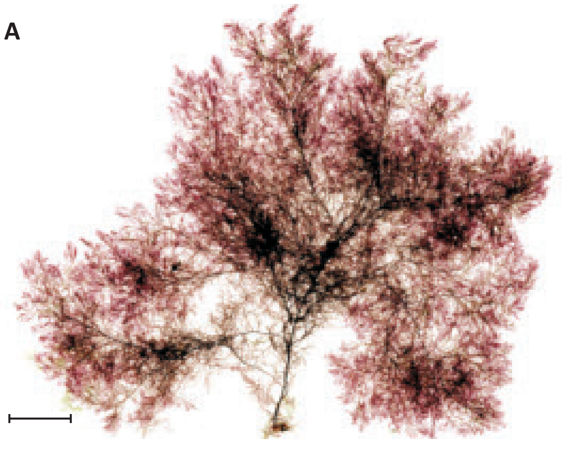
Structure: Main branch with scattered branches on all sides. The lower 4 to 6 cells of the branches typically without branchlets, while a branchlet arises on each of the following cells. The branches may alternate, particularly in the lower part of main branches. Cortical filaments arise from the lower cells of the branches and form a dense relatively thick cortex completely covering the main branches. Branches may develop from cortical cells, but not secondary main branches. Older cells of the main branches are up to 5 times as long as wide. The plastids are disc-shaped in young cells and irregularly elongate in older cells. Red algal hairs may occur, but are not frequent.

Reproduction: Gametophytes are dioecious. Antheridial branchlets form series on the adaxial side of branches and consist of a stalk with a dense cluster of antheridia at the top. Opposite carpogonia develop from the same cell of the main branch. Rounded to slightly irregular or ovoid gonimoblasts develop after fertilization. Tetrasporangia and bisporangia form series on the adaxial side of branches, typically with a single sporangium per cell.

Seasonal variation: Collected in January, March-November. Antheridia recorded in July-August, gonimoblasts in July-September, tetrasporangia in June-September and bisporangia in September.

Habitat: Epiphytic and on solid substratum. On stone reefs, 3-20 m depth, and on harbour jetties in the Northern Kattegat and The Sound, 0.5-1.5 m depth.

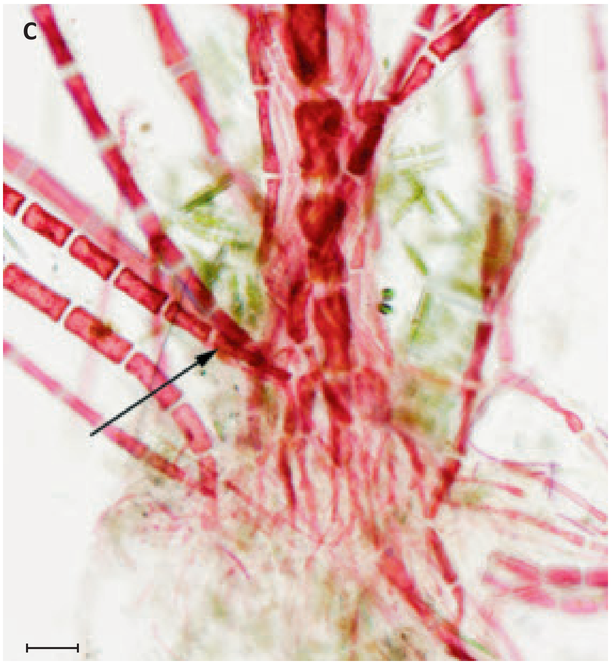
Comment: It seems that *G. rosea* has increased in Danish waters. Collected in the Limfjord, the Northern Kattegat and the Sound before 1930, while recently



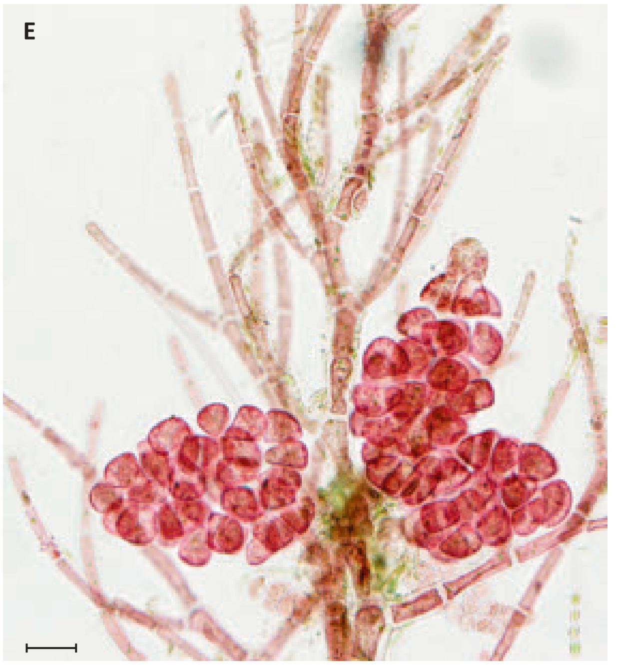
A: *Gaillona rosea.* Much branched delicate alga with distinct main branches. Sheltered side of northern harbour jetty near the outer end, Frederikshavn, 0.5 m, 15.9.1984. Scale 1 cm.

B: *Gaillona rosea.* Upper part of alga, scattered branches on all sides and lower cells of main branches without branches. Broen, 9 m, 28.7.1994. Scale 100 µm.

collected from most districts except the North Sea, Skagerrak and the archipelago South of Funen.
References: Maggs & Hommersand (1993, *Aglaothamnion roseum*), Maggs & L'Hardy-Halos (1993), Rosenvinge (1923-24, *Callithamnion roseum*), Wærn (1952, *C. roseum*).



C: *Gaillona rosea*. Lower part of main branch, well-developed cortex of downward-growing filaments from which branches arise (arrow). Broen, 11 m, 10.9.1991. Scale 50 µm.



E: *Gaillona rosea*. Apex of female gametophyte with ovoid gonimoblasts. Tønneberg Banke, 15 m, 20.8.1994. Scale 20 µm.

D: *Gaillona rosea*. Antheridial branchlet, stalk with a cluster of antheridia on top. Vegetative cell with a single nucleus (arrow). Schönheyders Pulle, 7 m, 25.9.1992. Scale 10 µm.

F: *Gaillona rosea*. Bisporangia on adaxial side of branch. Gedser Rev, 7 m, 25.9.1992. Scale 50 µm.

Gaillona seposita

(Gunnerus) Athanasiadis

Recent synonym: ***Aglaothamnion sepositum*** **(Gunnerus) Maggs & Hommersand**

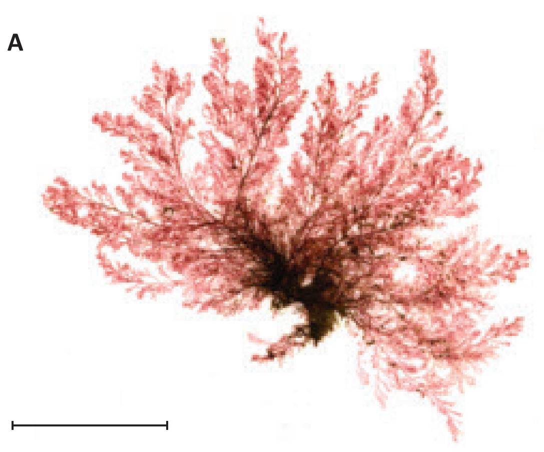
Delicate bushy thallus with dense branching, purple to brownish red. The species is not recorded attached in Danish waters but collected as an epiphyte on drift Egg Wrack (*Ascophyllum nodosum*) and Wrack Siphon Weed (*Vertebrata lanosa*) at Thyborøn, 1904.
References: Rosenvinge (1905, *Callithamnion arbuscula*).

Seirospora interrupta

(Smith) F.Schmitz

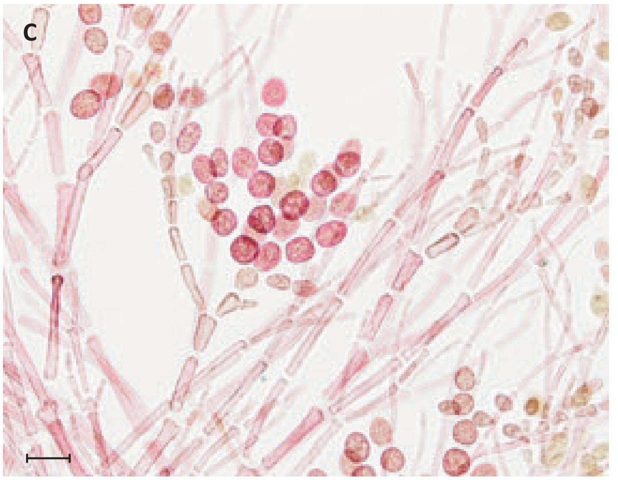
Chain Seed Bush Weed

Appearance: Delicate rose bushy alga with distinct main branches with branches on all sides. The alga has a rounded or pyramidal outline and is 6.5-10 (-16) cm in height.
Structure: Branches on all sides, which in the upper part are pseudodichotomous or otherwise scattered. Branching is relatively open without tufts of branches. Branchlets arise from each cell of the branches. A well-developed cortex covers the basal part of the main branches. Cortical filaments arise from the basal cells of the branches with up to three filaments from a single cell. There is only one nucleus per cell. Plastids are disc-shaped to elongate and may have small lobes. Red algal hairs only reported on female gametophytes.
Reproduction: Isomorphic dioecious gametophytes and separate individuals with sporangia. Gametophytes not recorded in Danish waters. Tetrasporangia are ellipsoid, typically sessile but occasionally have a stalk-cell. They form series of up to 4 sporangia on the adaxial side of the distal branches. Bisporangia occur on other algae, in the same way as the tetrasporangia. Bisporangia are transversely divided or have an oblique wall, and typically with an additional small cell at the base of the sporangium. Asexual reproduction also takes place by seirospores, a type of mono-



A: *Seirospora interrupta.* Bushy alga with distinct main branches and pyramidal apices. Scale 2 cm. A-B: Sheltered side of southern harbour jetty, near the distal end, Frederikshavn, 0.5 m, 2.7.1991.

B: *Seirospora interrupta*. Three downward-growing cortical filaments from a single basal cell of a branch. (1, 2, 3). Scale 20 µm.



C: *Seirospora interrupta*. Pseudodichotomous branches and seirosporangia. Gjeller Odde, at Hygum Church, 3.5 m, 23.8.2000. Scale 50 µm.

spore formed in special branches of uniseriate series of sporangia forming clusters in the upper part of the alga.

Seasonal variation: Collected in May-October with seirosporangia.

Habitat: On stones and boulders and epiphytic on larger algae. Collected in the western part of the Limfjord, 2.5-4 m depth and in the Northern Kattegat on harbour jetties in Frederikshavn, 0.5 m depth. In older collections on stone reefs, 15-22 m depth.

References: Bird & McLachlan (1992), Maggs & Hommersand (1993), Rosenvinge (1923-24, *S. griffithsiana*).

Familie: Ceramiaceae

Antithamnion

Shrublets

Appearance: Delicate rose to brownish red tufts, up to a few centimetres in height. Uprights arise from prostrate filaments and the alga becomes tufted. The apical part of branches is typically like a small paint brush because the branches grow above the apex of the main axis.

Structure: The thallus consists of uniseriate, branched filaments without cortex. Main branches have continuous growth, while branches and branchlets have restricted growth. Opposite branch pairs arise from each cell of the main branch. Branch pairs are displaced approximately 90° in relation to the former branch pairs, so the branches occur in 4 rows. Secondary main branches are scattered. They arise from the basal cell of a branch or from a cell of the main branch. The new main branch replaces an opposite branch pair. The basal cells of the branches are short, and about as long as wide. The following cells are cylindrical and their diameter decreases towards the apex to a more or less pointed apical cell. Branchlets are opposite or scattered. Vegetative cells contain many disc- to ribbon-shaped plastids. Hyaline gland cells occur on few-celled branchlets. The gland cells are oval in longitudinal section with the long axis parallel to the branch. Creeping filaments arise from the basal cells of the lower branches. New uprights arise as opposite branches from the creeping filaments. Short downward-growing filaments with attachment pads of several cells arise from the basal cells of the uprights.

Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Cruciate tetrasporangia are ellipsoid have a 1- or 2-cells long stalk and replace branchlets. No record of gametophytes in Danish waters.

Comment: *Antithamnion cruciatum* and *A. villosum* were previously considered a single species, as varieties of *A. cruciatum* (Athanasiadis, 1986), but considered separate species by Maggs & Hommersand (1993). Rosenvinge referred both species to *A. cruciatum* and the prostrate individuals to *A. cruciatum* var. *radicans* J.Agardh (Rosenvinge, 1923-24).

References: Athanasiadis (1986, *Antithamnion tenuissimum* var. *scandinavicum*, 1996), Maggs & Hommersand (1993), Rosenvinge (1923-24).

Identification key to species of *Antithamnion*

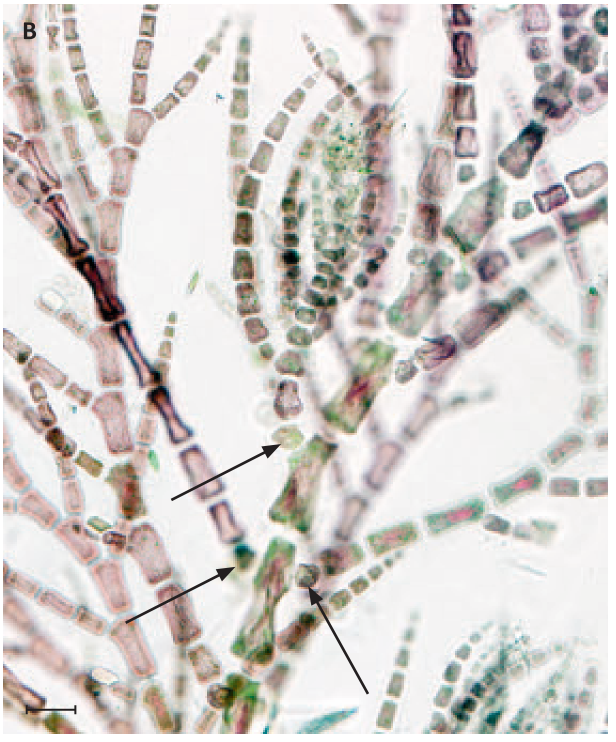
1a.	Cells of the branches are 2.5-4 times as long as wide. Branchlets are scattered, distichous or opposite. Gland cells cover 2-3 cells	*A. cruciatum*
1b.	Cells of the branches are 4-7 times as long as wide. Branchlets are scattered on all sides, occasionally in short series. Gland cells cover 1-2 cells	*A. villosum*

Antithamnion cruciatum

(C.Agardh) Nägeli

Appearance: The alga is bright brownish red, 2-2.5 cm in height.
Structure: Branches consist of cylindrical cells, 2.5-4 times as long as wide. There are opposite or scattered distichous branchlets. Opposite branchlets are typically in the lower part of branches. Gland cells occur at branchlets, 3-4 (-5) cells long and cover 2-3 vegetative cells. Secondary main branches alternate and arise from the carrying main branch at intervals of 7-8 cells according to Maggs & Hommersand (1993).
Reproduction: In Swedish culture studies by Athanasiadis (1986), reproduction was mainly by fragments. Tetraspores only germinated in a single strain and grew into dioecious gametophytes.
Seasonal variation: Collected in March and August-September, tetrasporangia recorded in August-September.
Habitat: Epiphytic on other algae, 1-14 m depth.

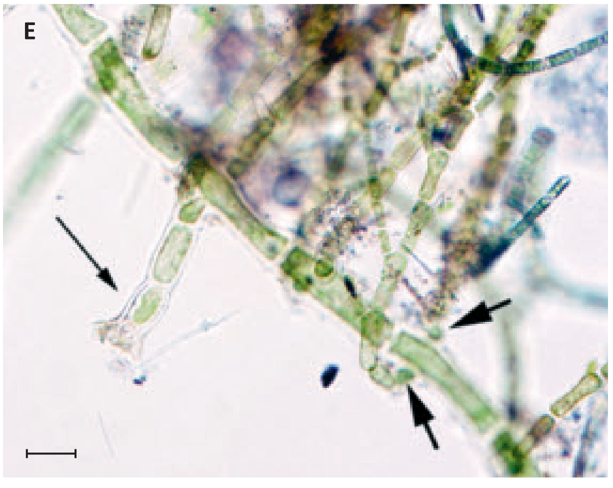
A: *Antithamnion cruciatum*. Epiphytic tuft on Clawed Fork Weed (*Furcellaria lumbricalis*). Scale 2 cm. A, F: Kalundborg Fjord, 3 m, 23.9.1992.



B: *Antithamnion cruciatum*. Main branch with opposite branches having short basal cells (lower arrows) and scattered distichous branchlets. A secondary main branch (upper arrow) replaces opposite branches. B, D-E: Schultz's Grund, 4.5 m, 25.3.1992. Scale 50 µm.

C: *Antithamnion cruciatum*. Branch with opposite branchlets. Gland cells cover 3 cells (arrow). Schultz's Grund, 4 m, 26.8.1992. Scale 50 µm.

D: *Antithamnion cruciatum*. Gland cell covers 3 cells of a branchlets (arrow). Scale 10 µm.



E: *Antithamnion cruciatum*. Prostrate branch with opposite upright branches (right arrows). A downward-growing branch with a multicellular attachment pad (left arrow) arise from a basal cell of an upright branch. The alga greenish after fixation in formalin for more than a year. Scale 50 µm.

F: *Antithamnion cruciatum*. Cruciate tetrasporangia on unicellular stalk-cells. Scale 10 µm.

Antithamnion villosum

(Kützing) Athanasiadis in Maggs & Hommersand

Appearance: Delicate rose tufts, up to 4 cm in height. Branches terminate in a tuft.
Structure: Branches, 17-21 µm in width with cells, 3.5-5 times as long as wide. Branchlets are scattered and alternate or in short unilateral series on the adaxial side of the opposite branches. Secondary main branches alternate and arise at variable intervals of 3-10 cells on the main branch according to Maggs & Hommersand (1993). Gland cells occur on branchlets of 2-4 cells and cover 1-2 vegetative cells, but they are often sparse or lacking.
Reproduction: Swedish culture studies by Athanasiadis (1986) showed that reproduction mainly took place by fragments and monospores.
Seasonal variation: Collected in June-September. Tetrasporangia recorded in July-August.
Habitat: Epiphytic on larger algae, Eelgrass (*Zostera marina*) and on stones and boulders in sheltered localities with a thin cover of detritus, 0.5-7 m depth.

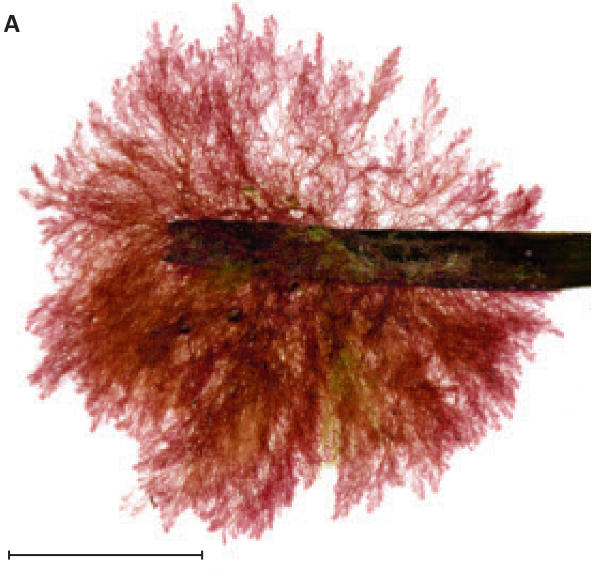
A: *Antithamnion villosum*. Epiphytic well-developed tuft on Eelgrass (*Zostera marina*). Sillerslev Øre, Mors, 0.5 m, 7.8.1969. Leg.: T. Christensen. Scale 2 cm.

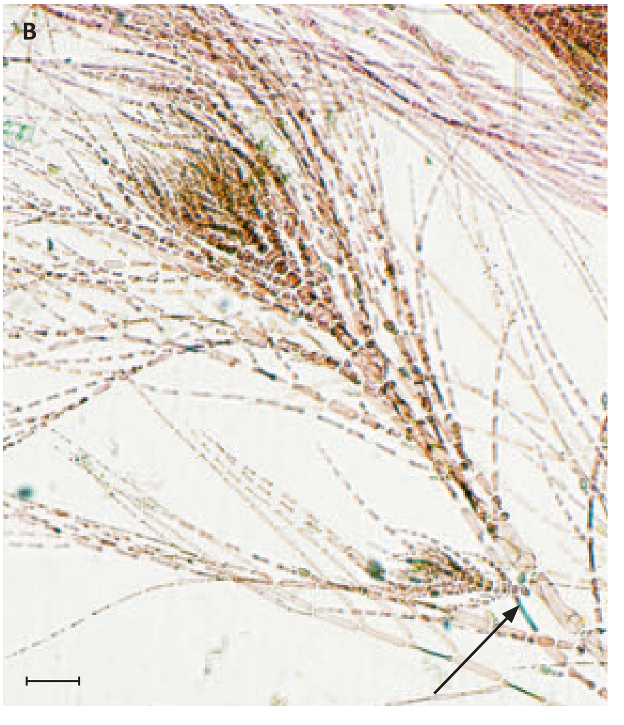
B: *Antithamnion villosum*. Paint brush-like apex with opposite branches longer than the main branch. Secondary main branch replaces opposite branches (arrow). Scale 100 µm. B-F: Stone reef outside Frederikshavn, 6.7.1992.

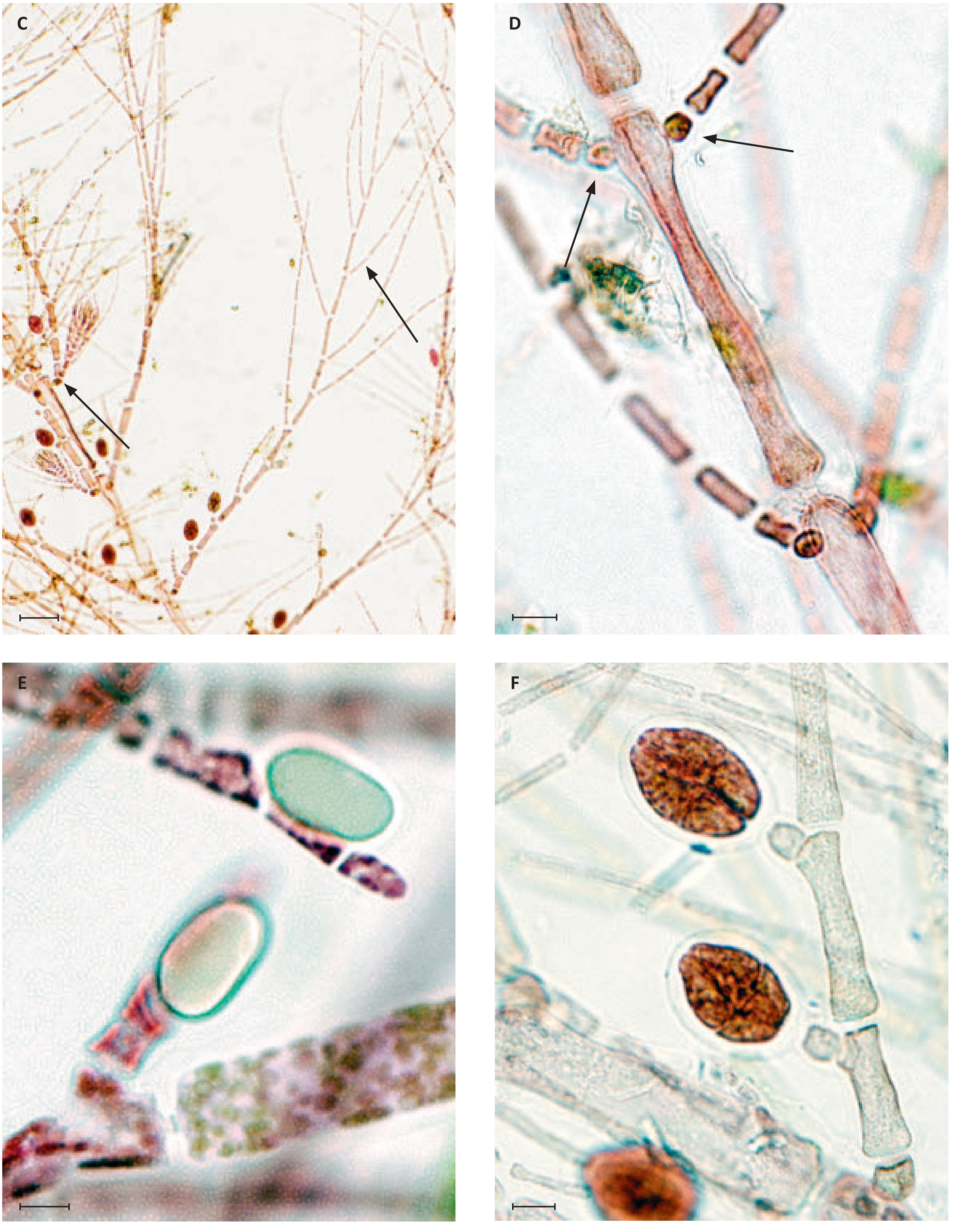
C: *Antithamnion villosum*. Main branch with opposite branches. Secondary main branch arises from a short basal cell (left arrow). Branch with scattered distichous branchlets (right arrow) and tetrasporangia on stalk-cells. Scale 100 µm.

D: *Antithamnion villosum*. Opposite branches with short basal cells (arrows). Scale 20 µm.
E: *Antithamnion villosum*. Gland cells on branchlets. Scale 10 µm.

F: *Antithamnion villosum*. Cruciate tetrasporangia on unicellular stalk-cells. Scale 10 µm.



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Antithamnionella floccosa

(O.F.Müller) Whittick

Regular Seafeather, Little Shrublet

Appearance: Delicate branched dark bordeaux-red bushy alga of flat uprights, up to 7 cm in height. Distinct main branch of unlimited growth with short opposite branches of limited growth. On the main branch there are also scattered distichous and alternating branches with unlimited growth. The uprights arise from prostrate filaments.

Structure: Uniseriate, branched filaments with opposite branches in a single plane, so the alga is flat and without cortex. Short opposite branches arise from each of the cells in the main branch. They are unbranched and consist of 1-12 cells. The basal cell is shorter than the rest of the cells, and the apical cell rounded or pointed. Lateral main branches develop regularly from just below the apex at an interval of three cells on the carrying main branch. A new main branch replaces one of the short opposite branches at the branching point. The basal cell of the main branches has no or only a single branch. Gland cells not present.

Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte; only tetrasporophytes recorded in Danish waters. The cruciate tetrasporangia are ellipsoid to spherical, with stalks that might be branched and from which small clusters with 3 tetrasporangia may develop.

Seasonal variation: Only a few Danish collections in June with tetrasporangia.

A

Habitat: Epiphytic on larger algae. Rare in Danish waters, only collected at Kims Top, 14-22 m depth.

References: Jacobsen et al. (1991), Maggs & Hommersand (1993,), Whittick (1980).

A: *Antithamnionella floccosa*. Dark red bushy alga with branches in one plane. Kims Top, 14.5 m, 5.6.1993. Scale 1 cm.

B: *Antithamnionella floccosa*. Apex with alternating main branches, and short opposite branches. Kims Top, 22 m, 5.6.1993. Scale 50 µm.

C: *Antithamnionella floccosa*. Cruciate tetrasporangium on a stalk-cell (arrow) from which two branches arise with young sporangia at the apex. Kims Top, 18 m, 5.6.1993. Scale 20 µm.

Ceramium

Banded Pincer Weed

Appearance: Bush-like thallus of terete, pseudodichotomous main branches on all sides. Secondary lateral branches may develop, and are unilateral, distichous or on all sides. Branches might be uniformly red or banded with alternating dark and bright bands in all or part of the thallus.

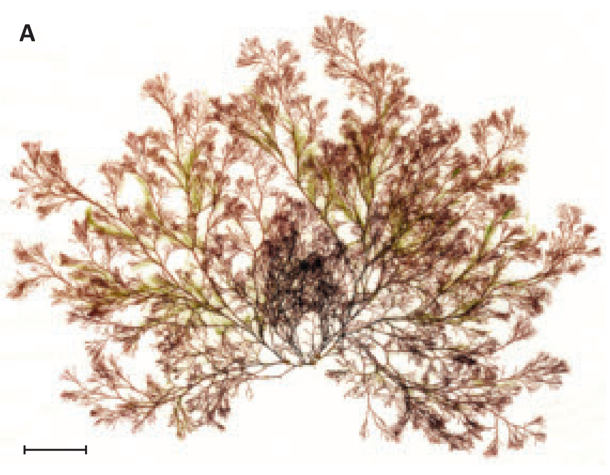
Structure: The thallus is a uniaxial syntagma with growth from an apical cell and composed of uniform segments. A segment consists of a relatively large axial cell surrounded by smaller cells that may cover the axial cell completely or in part as entire cortex or separate cortical bands. Axial cells are spherical to barrel-shaped or cylindrical. Between the cells of the same filament there are distinct pit connections. Four or more periaxial cells arise from the upper part of the axial cells and form a whorl around the axial cell. Periaxial cells are more or less spherical and smaller than the axial cell. From each periaxial cell, 1-3 cortical filaments arise and grow up or down along the axial cell, forming a cortex. Periaxial cells are the inner and the largest cells of the cortex while other cells of the cortex are smaller and decrease in size away from the periaxial cells. In some species the cortical filaments are confluent from one segment to the next and the branches have a uniform colour. Other species have distinct bands of cortical filaments in all or parts of the thallus. Branches of these species are banded with dark cortical bands alternating with bright bands without cortex. The structure of the cortex changes from the apex of the thallus and downwards. Growth of the cortical filaments might be almost equal in up and downward directions or take place mainly in one direction. The cortical bands have dentate margins in the direction of growth and are regular when the growth is less. Cell divisions of the cortex takes place in several directions in many species in which the cortex becomes multilayered, the outer smallest cells might form a rosette pattern around the larger cells in the inner part of the cortex. Other species have a thin cortex consisting of a single or a few cell layers and the cells may elongate along with the longitudinal stretching of the axial cells. Gland cells occur in a few species, are hyaline and refract the light. They develop from surface cells in the cortical bands. They contain protein but the function of the gland cells is unknown. Some species have uni- or multicellular spines, but these structures do not occur in species known in Danish waters. Pseudodichotomous branches form by division of the cell just below the apical cell. The new cell grows into a branch with the same appearance as the main branch, except that it is one segment shorter from the beginning and therefore a pseudodichotomous rather than a dichotomous branch. Lateral secondary branches might form further down in the thallus. The number of segments between the pseudodichotomies varies. In some species the number varies considerably within single individuals, while there is a uniform distance between the ramifications in other species. The algae attach to the substratum by small attachment pads on narrow filaments (rhizoids). The rhizoids arise from the cortex- or periaxial cells and are uni- or multicellular. Uprights arise from prostrate filaments in some species.

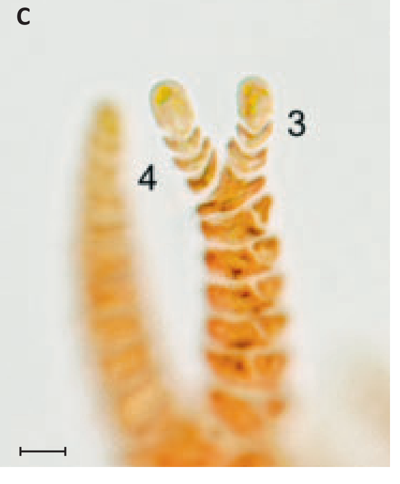
Reproduction: Dioecious gametophytes and tetrasporophyte which are isomorphic although the tetrasporophyte is typically larger and more vigorous than the gametophytes with straight apical branches. Male gametophytes are often smaller than female gametophytes, which are commonly irregularly and much branched with curved apical branches. Reproductive structures develop in the cortical bands. Antheridia form as the outer cells in very short branches of small cells and appear like a cover of colourless cells over the cortical bands. Carpogonia with trichogyne form on special carpogonial branches. Gonimoblasts consist of one or a few spherical lobes of dark cells and each cell becomes a carposporangium. Gonimoblasts typically occur as if they replace one of the branches at a pseudodichotomous branching point. Gonimoblasts are surrounded by short branches (involucral branches) and without a pericarpium. Tetrasporangia are tetrahedrally divided and occur singly or several together to form a single or several whorls per cortical band. Tetrasporangia might be naked or in part covered by cortical filaments or embedded in the cortex. Asexual reproduction takes place from parasporangia with the appearance of irregularly placed clumps of dark cells. They are lateral on the cortex and without involucral branches as opposed to the gonimoblasts. *Ceramium tenuicorne* may have special vegetative propagules.

Comment: The genus is one of the most species rich among the red algae and easy to recognize but there is still much uncertainty in delimiting some of the species, not least because the morphological variation within individual species is large. Furthermore, many early descriptions of the species were not very precise and lacked knowledge as to which features characterized the species best and which varied according to physical conditions. Furthermore, the naming in many cases has been rather confused. A single species may have been described several times under various names and conversely, different species were mixed up and described as a single species. Several revisions have taken place in recent years after culture studies and genetic analyses. In the Baltic Sea, ecological various forms of *C. tenuicorne* were considered to be various species (Gabrielsen et al. 2002, 2003). In other cases, similarly-looking algae were found to be genetically different from DNA sequence analysis but were morphologically similar (cryptic) species. This applies to *C. rubrum* (Hudson) C.Agardh (Maggs et al. 2002) which was an aggregate of species.

Henning E. Petersen has undertaken the most comprehensive investigations of Banded Pincer Weed (*Ceramium* sp.) in Danish waters and his observations were published in 1908, 1911, 1923-24, 1925 and 1929. He described several new species, many subspecies and forms. Only a few species of the Danish Banded Pincer Weed (*Ceramium* sp.) have been studied by modern investigations so there is still much to do to determine how many of Petersen's taxa are good entities and to find out how many species we really have in Danish waters. Species with an entire cortex previously referred to *C. rubrum*, are particularly problematic.

References: Christensen (1966, 1980, 1994), Gabrielsen et al. (2002, 2003), Kylin (1907, 1924, 1944), Maggs & Hommersand (1993), Maggs et al. (2002), Petersen (1908, 1911, 1925, 1929), Petersen in Rosenvinge (1923-24), Wolf et al. (2011).





A: *Ceramium* sp. Vesterø Havn, Læsø, 0.5 m, 21.5.2005. Scale 2 cm.

B: *Ceramium diaphanum*. Apex with curved branches, apical cell (right arrow) carpogonial branch with carpogonium and trichogyne (left arrow). Cortical band (lower left arrow). Thisted Bredning, 2.5 m, 18.8.2008. Scale 20 µm.

C: *Ceramium cimbricum*. Pseudodichotomous branching, one branch with 4 cells the other with 3 cells. Thisted Bredning, 3.5 m, 18.8.2008. Scale 10 µm.

Identification key to species of *Ceramium*

1a.	Separated cortical bands in all parts of the alga	2
1b.	Entire cortex in all or part of the alga	6
2a.	Rose or red delicate bushy thallus with 4-5 periaxial cells. Very narrow cortical bands, rarely more than 3 cells in height, no gland cells. Tetrasporangia unilateral on the adaxial side of branches not covered by cortex	3
2b.	Coarser bush-like thallus with (4-) 5-6 (-7) periaxial cells, cortical bands more than 3 cells in height	4
3a.	Straight or slightly curved apical branches, long axial cells	*C. cimbricum*
3b.	Curved apical branches	*C. sungminbooi*
4a.	Dark brownish red to greyish purple bush-like thallus with straight apical branches. Narrow cortical bands with regular margins. Tetrasporangia in a single whorl only in part covered by cortex and protruding from the branches	*C. deslongchampsii*
4b.	Red to brownish red bush-like thallus with straight to curved apical branches	5
5a.	Apical branches curved typically with dentate outer edges. Cortical bands appear like cuffs around the axial cells. Gland cells occur. Tetrasporangia in series on the abaxial side of branches, in part covered by cortical filaments and bulge from the cortex	*C. diaphanum*
5b.	Apical branches are straight. Cortex without gland cells. Cortical filaments mainly growing upward and the lower margin regular. Lower axial cells mainly pyriform. Tetrasporangia embedded in the cortex in one or several whorls. Parasporangia frequent	*C. tenuicorne*
6a.	Separated cortical bands in upper half of the alga and entire cortex in the lower part. The dichotomous branching points with regularly short distances or the main branch with alternating branches. Apical branches curved. Cortical bands with both up- and downward-growing filaments, and dentate at both upper and lower margins	*C. pallidum*
6b.	Cortex almost entire in all part of the algae, although narrow lines without cortex may occur in the upper parts	7
7a.	Downward-growing cortical filaments with larger cells than upward-growing filaments	*C. arborescens*
7b.	Cells of cortical filaments of equal size in both up and downward directions	8
8a.	Apical branches slightly or very curved. There are 6-8 periaxial cells. Cortex consists of relatively coarse angular cells in young branches. Cortex is multilayered in older branches with characteristic rosette pattern. Scattered gland cells	*C. secundatum*
8b.	Apical branches straight or slightly curved. There are 6-7 periaxial cells. Cortex consists of relatively small cells. Cortical bands near the apex have regular margins both at the upper and lower edges and may be separated by short almost linear area. No gland cells. Rosette pattern occurs in older branches with multilayered cortex	*C. virgatum*

Ceramium arborescens
J.Agardh

Appearance: Robust dark red bush-like thallus up to 17-18 cm in length with conspicuous dichotomous main branches and many lateral branches. Towards the top the branches are often in semi-umbelliferous stands. The apical branches are straight or slightly curved and resemble a pair of long narrow pincers.
Structure: There are 10-20 segments between the dichotomous branching points. Cortication is entire in the lower part of the alga and up to more than half of the length. Separate cortical bands occur in the upper part, with short intervals without cortication below the apex. The cortical filaments grow both up- and downwards. The cells of the downward-growing filaments are conspicuously larger than the cells of the upward-growing filaments.

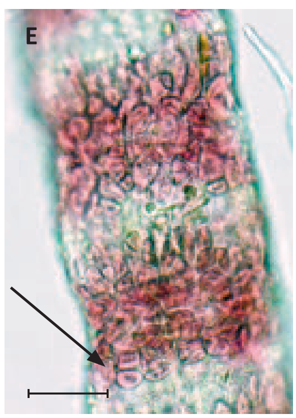
Reproduction: Tetrasporangia completely embedded in the cortex in 1-2 whorls. Gonimoblasts develop in the upper part of the alga and have 3-4 involucral branches.
Seasonal variation: Collected in April-September. Gonimoblasts and tetrasporangia recorded in May-June.
Habitat: Epiphytic and on solid substratum, 0.5-8 m depth.
Resembles: Sandy Banded Pincer Weed (*Ceramium secundatum*) and Common Banded Pincer Weed (*C. virgatum*) are similar-looking algae. They both have cortical cells of equal size in up- and downward-growing filaments and Sandy Banded Pincer Weed (*C. secundatum*) has gland cells.
Comment: According to Kylin (1944) *Ceramium rubriforme* Kylin is young specimens of *C. arborescens*. *Ceramium danicum* H.E.Petersen, *C. scandinavicum*

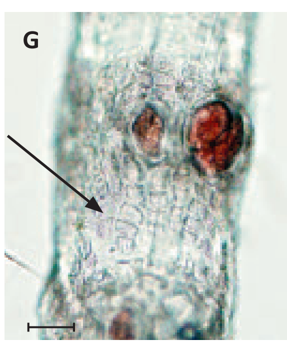
A, B: *Ceramium arborescens*. Female gametophyte (A) and tetrasporophyte (B) identified by H.E. Petersen. Hirtshals, 0.5 m, 22.5.1902. Scale 2 cm.

H.E.Petersen and *C. septentrionale* H.E.Petersen have cortical bands where the downward-growing filaments have larger cells than the upward-growing filaments and therefore probably synonyms of *C. arborescens*, as also supposed by Kylin (1944). Petersen (1908, p. 49) mentioned the presence of gland cells in *C. arborescens*, but we did not observe such in the algae from Hirtshals, which were identified by Petersen (figures A and B), and none in newer collections referred to this species.

References: Kylin (1944), Petersen (1908, 1911), Petersen in Rosenvinge (1923-24).

C: *Ceramium arborescens*. Epiphytic on Desmarest's Prickly Weed (*Desmarestia aculeata*). Scale 2 cm. C, E-F: Læsø Trindel, 8 m, 3.6.1993.





D: *Ceramium arborescens*. Apical branch, attenuates towards the top, separated cortical bands (arrow) and red algal hairs. Scale 50 µm. D, G: Vejrø, 5 m, 2.6.1989.

E: *Ceramium arborescens*. Separate cortical bands just below apex, with large cells in downward-growing filaments (arrow). Scale 50 µm.

F: *Ceramium arborescens*. Almost entire cortex in the lower part of a branch, large cells in downward-growing filaments and small elongate cells in upward-growing filaments. Scale 50 µm.

G: *Ceramium arborescens*. Tetrasporangia, embedded in cortex. Downward-growing cortical filaments of large cells (arrow). Scale 50 µm.

Ceramium cimbricum

H.E.Petersen

Cimbri Banded Pincer Weed

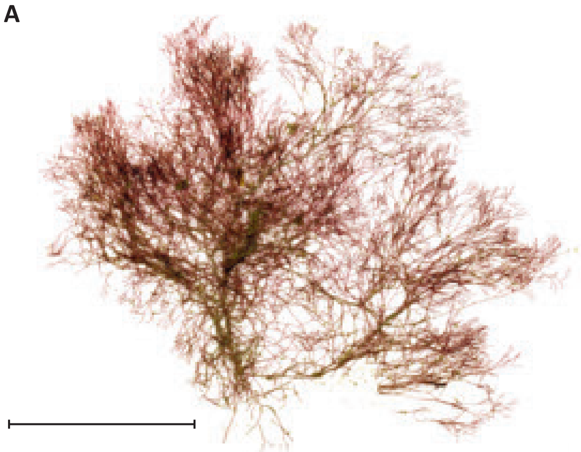
Appearance: Delicate, bright purple bushy thalli up to 2-3.5 cm in height. Branches have narrow separated cortical bands. The apical pair of branches straight or slightly curved with regular outer edge, the two typically unequal in length. Uprights arise from prostrate filaments with attachment pads on rhizoids.

Structure: Regularly pseudodichotomous branches with 5-17 segments between the branching points. Axial cells are approximately spherical at the apex but stretch and become cylindrical, 5-7 times as long as wide. Branches are 32-40 µm in width at the apex, and slightly broader at the base. Cortical bands best developed in the lower part of the alga. The cortical bands are only 2-3 cells in length with relatively large cells and have a regular edge both at the upper and lower margin they have 4-5 periaxial cells. In the oldest branches at the basal part of the alga, two up- and two downwards filaments arise from each periaxial cell. The cortical bands may reach 25-50 µm in height and 60-100 µm in width. Gland cells not present. Multicellular rhizoids with attachment pads arise from periaxial or cortical cells.

Reproduction: Antheridia occur at the adaxial side of the youngest branches. Gonimoblasts are spherical and c. 150 µm in width, surrounded by 1-4 straight involucral branches. Tetrasporangia are in series on the adaxial side of the youngest branches. They are sessile outside the cortical bands and not covered by cortical filaments. Parasporangia observed in a single collection.

Seasonal variation: Collected in July-August. Antheridia and gonimoblasts recorded in August and tetrasporangia in July-August, parasporangia in July.

Habitat: Epiphytic on larger algae, on the Knotted



A: *Ceramium cimbricum*. Delicate bushy alga with straight apical branches and separate cortical bands. Thisted Bredning, 3.5 m, 18.8.2008. Scale 2 cm.

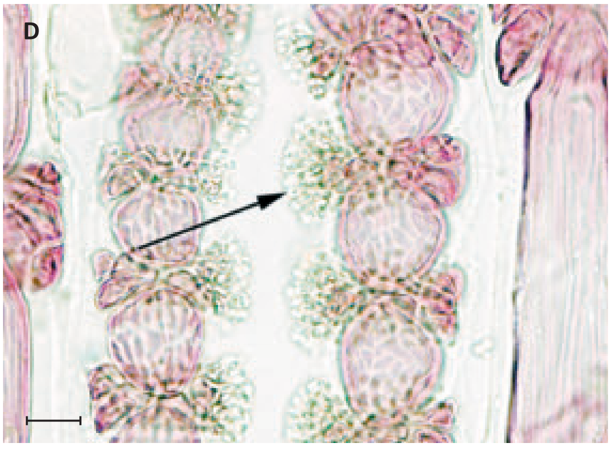
B: *Ceramium cimbricum*. Apical branches unequal in length. Axial cells cylindrical below the apex. In addition, a narrow filament of Common Red Hair Weed (*Erythrotrichia carnea*). Scale 50 µm. B, G: Røsnæs Nord, 9.5 m, 27.7.1994.

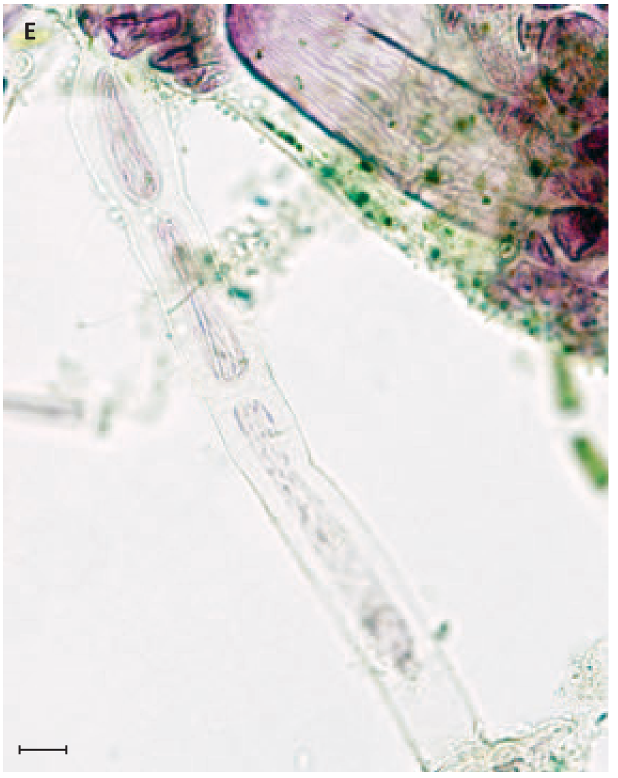
C: *Ceramium cimbricum*. Cortical band, 2 of 4 periaxial cells visible (arrow) with few-celled upward-growing filaments. Scale 10 µm. C-F: Geller Odde outside Hygum Church, 3.5 m, 23.8.2000.

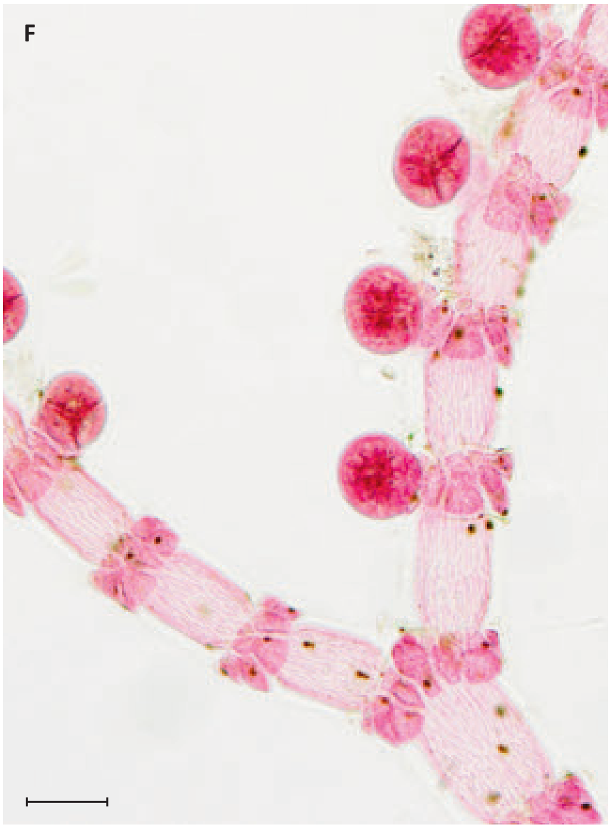
Thread Hydroid (*Obelia geniculata*) and on stones, 2.5-17 m depth.

Resembles: *Ceramium sungminbooi* is similar but has curved apical branches whereas they are straight or slightly curved in Cimbri Banded Pincer Weed (*C. cimbricum*).

References: Hughey & Boo (2016), Petersen in Rosenvinge (1923-24), Rueness (1992).







D: *Ceramium cimbricum.* Male gametophyte with antheridia (arrow). Scale 20 µm.

E: *Ceramium cimbricum.* Multicellular rhizoid with attachment pad arising from a cortical cell. Scale 10 µm.

F: *Ceramium cimbricum.* Series of tetrasporangia on the adaxial side of branches, not covered by cortical filaments. Scale 50 µm.

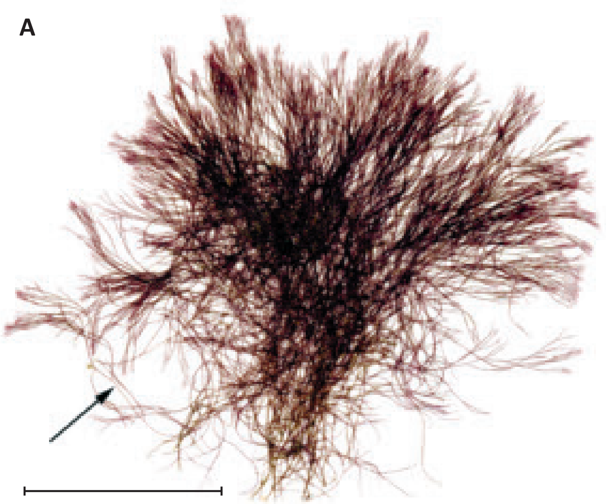
G: *Ceramium cimbricum.* Parasporangia. Scale 20 µm.

Ceramium deslongchampsii

Chauvin ex Duby

Straight Tip Banded Pincer Weed

Appearance: Straight, dark red-brown to greyish brown bush-like thallus. Uprights, 6-10 cm in height, arise from prostrate branches. The pseudodichotomous branches have acute branch angles and slightly incurved apical branches. Banded all over the thallus, the cortical bands are shorter or about as long as wide.
Structure: Pseudodichotomous branches occur at an interval of 6-30 segments. Cortical bands have 5 periaxial cells, each with 2 up- and 2 downward-growing cortical filaments, cortical bands are 6-7 cells in height. The margins are typically regular but occasionally dentate in the lowest part of the branches. No gland cells. Rhizoids from the prostrate branches and cortical cells are multicellular.
Reproduction: Antheridia cover the cortical bands on the youngest branches of male gametophytes. Mature gonimoblasts consist of 1-3 spherical lobes of different age, typically surrounded by 1-4 straight involucral branches. Spherical tetrasporangia bulge out from the cortex, only half covered by cortical filaments. There is a single or up to 5 sporangia in a whorl in each cortical band.
Seasonal variation: Collected in January and April-August. Antheridia recorded in July, gonimoblasts in January, June-August and tetrasporangia in June-August.
Habitat: Occurs only with certainty at the harbour of Frederikshavn, both at the exposed and the sheltered side of the northern harbour jetty. In the algal herbarium, Natural History Museum, of Denmark there is a collection from the harbour of Nykøbing Mors, 1897, but no later collections from there.
Comment: Parasporangia reported by Rosenvinge (1923-24), but not observed in recent years.
References: Petersen (1908, 1929), Rosenvinge (1923-24).

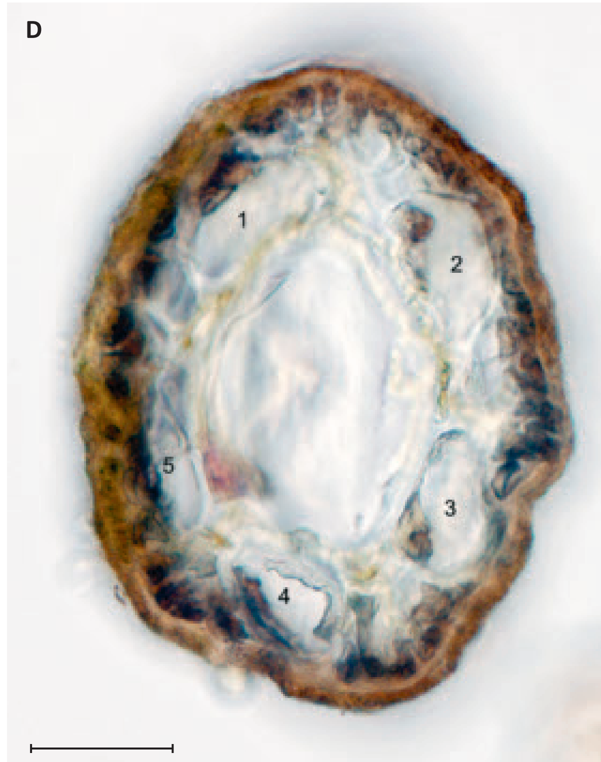


A: *Ceramium deslongchampsii.* Dense bush-like alga with straight dark branches, acute branch angles and separate cortical bands (arrow). Northern harbour jetty, Frederikshavn, 0.5 m, 29.8.1984. Scale 2 cm.

B: *Ceramium deslongchampsii.* Apex with straight to slightly curved pseudodichotomous branches, separate cortical bands. B-C, E: Northern harbour jetty, Frederikshavn, 0.5 m, 24.6.2000. Scale 50 µm.

C: *Ceramium deslongchampsii.* Cortical band with regular margins and a multicellular rhizoid, basal part of alga. Scale 50 µm.

E: *Ceramium deslongchampsii.* Tetrahedrally divided tetrasporangia in whorls and protruding from the cortical bands. Scale 50 µm.



D: *Ceramium deslongchampsii.* Cortical band with 5 periaxial cells, transverse section. Northern harbour jetty, Frederikshavn, 0.5 m, 15.1.1977. Scale 50 µm.

Ceramium diaphanum

(Lightfoot) Roth

Diaphanous Banded Pincer Weed

Appearance: Delicate loosely attached pink to red bush-like thallus with many uprights with banded branches. Branches typically dense and up to 3-8 (-10) cm in height. Regular pseudodichotomous branching, the branch angles open with curved apical branches. Many lateral branches. Uprights arise from prostrate branches.

Structure: Between the pseudodichotomous branching points there are 6-12 segments. Apical branches curved inwards with a dentate outer edge of large cells. Cortical bands sharply delimited in both the upper and lower direction. They typically bulge from the axial cells and resemble cuffs on the branches. There are 5-7 periaxial cells, each with 2 up- and 2-3 downward-growing cortical filaments. Cortical cells are relatively small with continued growth in both up- and downward directions. Gland cells may occur on some of the outer cortical cells, with 1 or 2 gland cells in each of the cortical bands, but not always present. Prostrate branches attach by multicellular rhizoids.

Reproduction: Antheridia start to develop at the abaxial side of the branches, but eventually the cortical bands become completely covered by the small colourless antheridia. Gonimoblasts are spherical and surrounded by a few involucral branches. Tetrasporangia form short series on the abaxial side of the branches with a single tetrasporangium in each cortical band. The tetrasporangia bulge from the cortical band, with only the lower half covered by cortical filaments.

Seasonal variation: Occurs all year, best developed in summer and only 1-2 cm in height in the winter. Antheridia recorded in July-August, gonimoblasts in July-September and tetrasporangia in July-August.

Habitat: Epiphytic on various algae and Eelgrass (*Zostera marina*), 0.5-24 m depth.

Comment: The species name is applied in agreement with Maggs & Hommersand (1993), mentioned as *C. tenuissimum* by Rosenvinge (1923-24). The alga Petersen (1908) and Rosenvinge (1923-24) referred to *C. diaphanum* is identical with *C. tenuicorne* according to

A: *Ceramium diaphanum*. Epiphytic algae with slender, regular pseudodichotomous branches and separate cortical bands. Tile works, Helligsø, 2 m, 25.8.2009. Scale 2 cm.

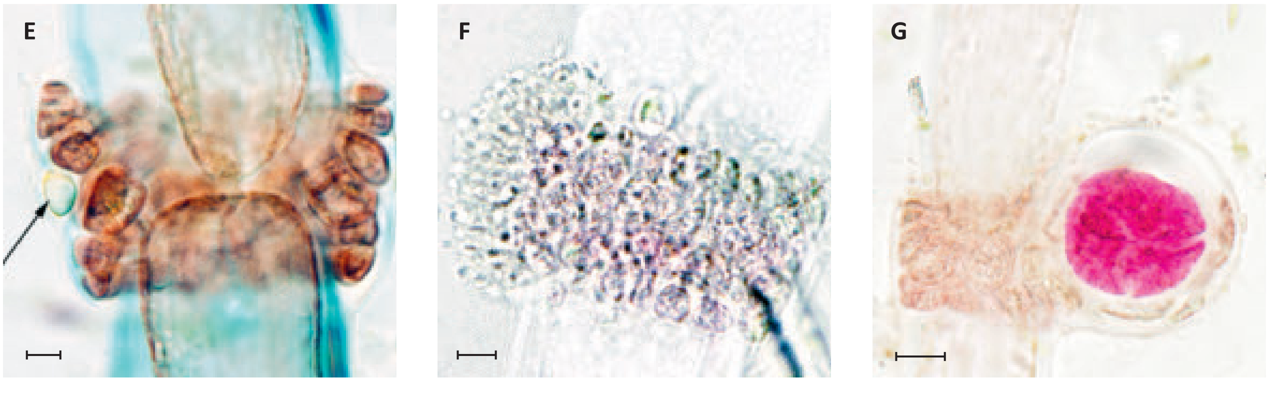
Gabrielsen et al. (2003). British collections of *Ceramium diaphanum* sensu Harvey are identical with *C. polyceras* (Kützing) Zanardini according to Wolf et al. (2011).

References: Gabrielsen et al. (2003), Maggs & Hommersand (1993), Petersen (1908, *C. tenuissimum*), Rosenvinge (1923-24, *C. tenuissimum*), Rueness & Boo (1994), Wolf et al. (2011).

B: *Ceramium diaphanum*. Branch with separate cuff-like cortical bands and incurved apical branches. Scale 50 µm.
B-G: Western side of Nordre Rønner, Læsø, 5 m, 19.8.2005.

C: *Ceramium diaphanum*. Apex with incurved branches and dentate outline. Scale 20 µm.

D: *Ceramium diaphanum*. Cortical band with 6 periaxial cells, transverse section. Scale 10 µm.



E: *Ceramium diaphanum*. Cortical band with gland cell (arrow). Scale 10 µm.

F: *Ceramium diaphanum*. Cortical band with antheridia. Scale 10 µm.

G: *Ceramium diaphanum*. Tetrasporangium in part covered by cortical filaments. Scale 20 µm.

Ceramium pallidum

(Kützing) Maggs & Hommersand

Regular Banded Pincer Weed

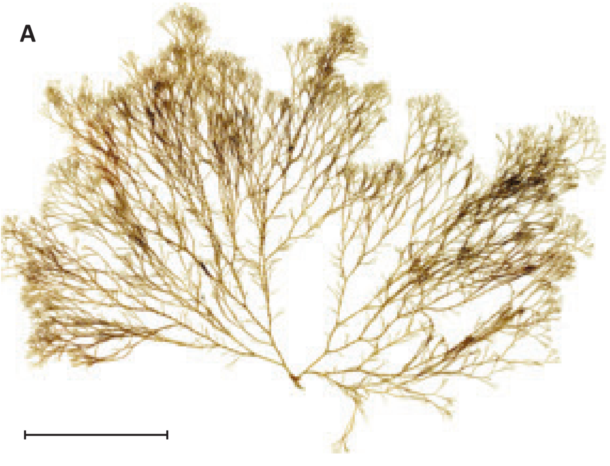
Appearance: Bush-like thallus with regular short intervals between the pseudodichotomous branches, but the intervals become longer lower down, simultaneously with stretching of the cells. Apical branches curved. Uprights may be regularly dichotomously branched and fan-shaped or have a conspicuous main branch with alternating lateral branches. The alga is brownish red and up to 3-12 cm in height with both entire cortex and separate cortical bands.

Structure: Pseudodichotomous branching points occur regularly at an interval of 6-12 segments. The segments typically have 6 periaxial cells, but in British studies the number varied between 5 and 8. Periaxial cells each have 2 up- and 2 downward-growing cortical filaments. Cortical bands at the apex consist of small cells in filaments that grow in all directions, up and down the central axis and outwards. Cortication is complete or banded in all or part of the thallus, typically complete at the apex, and banded a little below with narrow bands in between. Cortical bands towards the apex have dentate edges both at the upper and lower margin. Further down, cortication is complete, well-developed and multilayered with a tendency to form in a rosette pattern. The middle part of the axial cells is covered by a thin layer of up- and downward-growing filaments of elongated cells.

Reproduction: Antheridia cover the branches with an extended pale area. Gonimoblasts have 2-3 spherical lobes, surrounded by 2-5 slightly curved involucral branches. Tetrasporangia form a single whorl in cortical bands in young branches but are irregularly placed in broader cortical bands on old branches, and the fertile cortical bands are slightly swollen.

Seasonal variation: Collected in May and August. Gonimoblasts and tetrasporangia recorded in August.

Habitat: Epiphytic on Bladder Wrack (*Fucus vesiculosus*), Brown Sea Oak (*Halidrys siliquosa*) and Eelgrass (*Zostera marina*), 0.5 m depth.



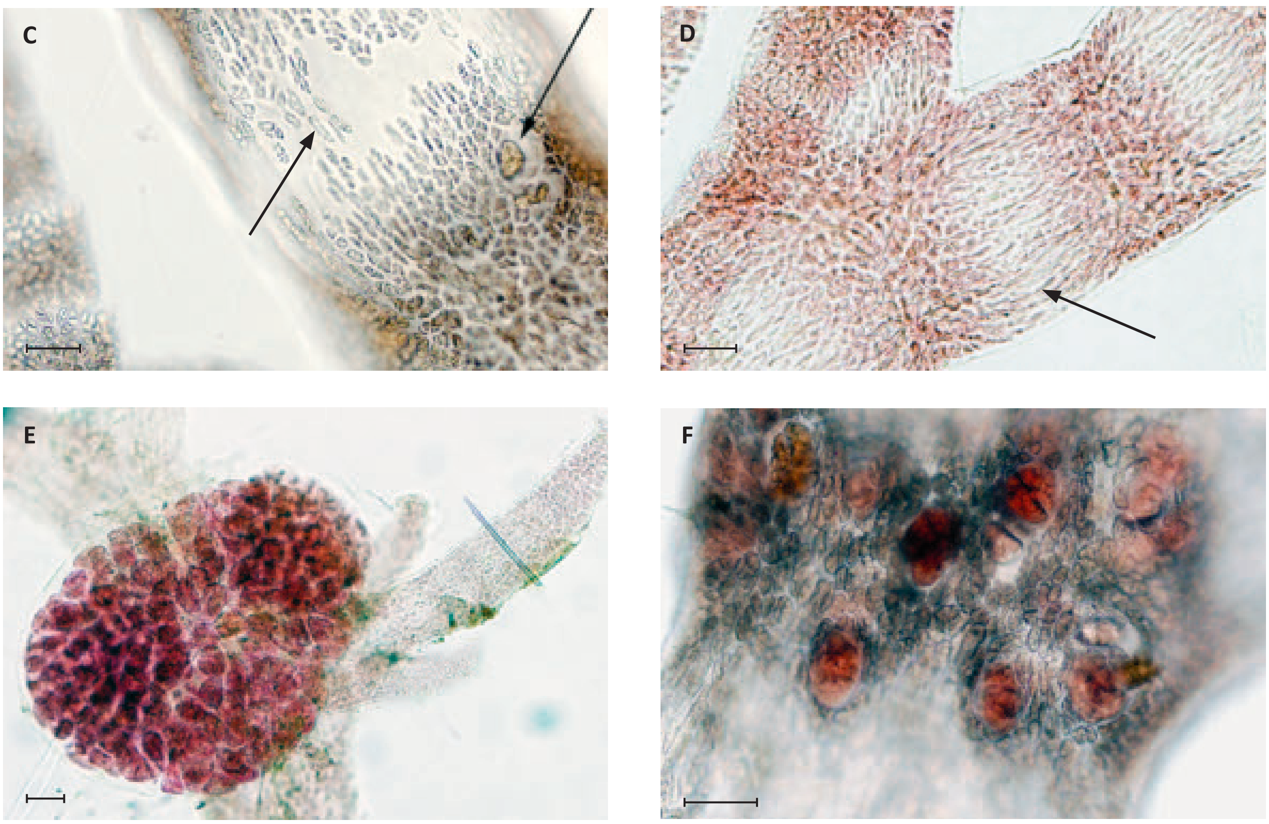
A: *Ceramium pallidum*. Regular short distances between the pseudodichotomous branches. Scale 2 cm. A-D: On Brown Sea Oak (*Halidrys siliquosa*), Nordre Rønner, Læsø, 0.5 m, 15.8.2005.

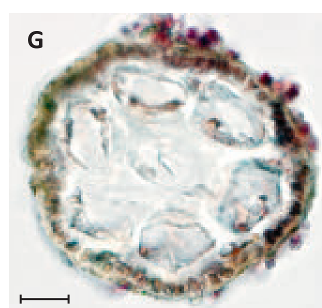
B: *Ceramium pallidum*. Curved apical branches, 6-7 segments between pseudodichotomous branching points. Cortical bands of small cells in up- and downward-growing filaments (arrow). Scale 50 µm.

Comment: Danish specimens referred to *C. abyssale* H.E.Petersen, *C. boergesenii* H.E.Petersen and *C. rosenvingii* H.E.Petersen by Petersen (1911) and Rosenvinge (1923-24) and maintained in the algal herbarium, Natural History Museum of Denmark were examined. The morphology and the cortical bands were found to agree with the cortex of *C. pallidum*. We therefore suppose that these species are synonyms of *C. pallidum*. This statement requires confirmation by future studies comprising genetic examinations.

Specimens from Danish waters, previously referred to *C. recissum* Kylin, probably also belong in *C. pallidum* because the cortex develops similarly. *Ceramium fruticulosum* f. *penicillatum* (Areschoug) H.E.Petersen and *Ceramium rubrum* f. *fasciculata* H.E.Petersen both have alternating lateral branches and possibly also belong in *C. pallidum*.

References: Maggs & Hommersand (1993), Maggs et al. (2002), Petersen (1908, 1911), Rosenvinge (1923-24).





C: *Ceramium pallidum*. Along the branches, cortical bands are separated with dentate margins and have up- and downward-growing filaments (left arrow). Tetrasporangia completely embedded in the cortex (right arrow). Scale 50 µm.

D: *Ceramium pallidum*. Lower part of branches with complete cortex, the middle part of the axial cell covered by a thin layer of elongate cortical cells (arrow). Scale 50 µm.

E: *Ceramium pallidum*. Gonimoblast with 3 spherical lobes (slightly pressed) and 3-4 slightly curved involucral branches. Scale 50 µm. E-G: On Bladder Wrack (*F. vesiculosus*), Nordre Rønner, Læsø, 0.5 m, 15.8.2005.

F: *Ceramium pallidum*. Wide irregular band of tetrasporangia, embedded in the cortex. Scale 50 µm.

G: *Ceramium pallidum*. Transverse section of branch with 6 periaxial cells. Scale 50 µm.

Ceramium secundatum

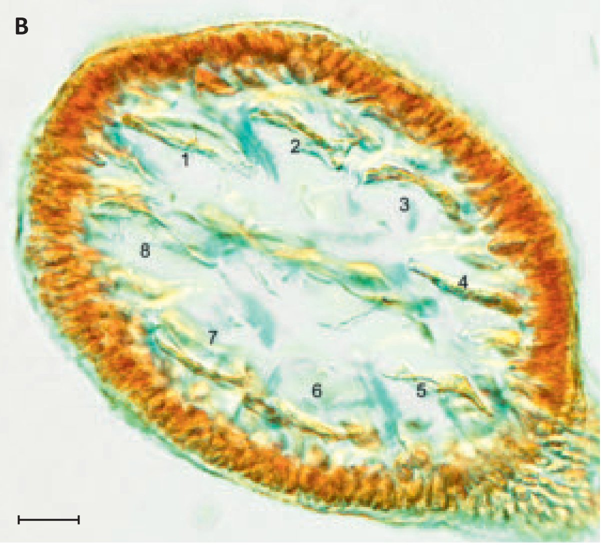
Lyngbye

Sandy Banded Pincer Weed

Appearance: Red or brownish red bush-like alga with distinct dichotomous main branches and many secondary branches. The distance between the dichotomous branching points is regular with increasing length towards the base. Apical branches are straight or slightly curved. In shallow water at wave-exposed localities is it characteristic that the apical branches are curved, and the alga has many small secondary branches. These branches might be on all sides adpressed to the main branch or unilateral on the adaxial side of the branches and grow upwards. Such individuals are 7-10 cm in length and branches may be in one plane. In more sheltered localities and at greater depth the alga is up to 15 cm in height and secondary branches relatively long on all sides and not adpressed to the main branches.

A: *Ceramium secundatum*. Alga with short lateral branches, from shallow water at wave-exposed locality. Scale 2 cm. A-B: Hirtshals, 0.2 m, 19.10.1977.

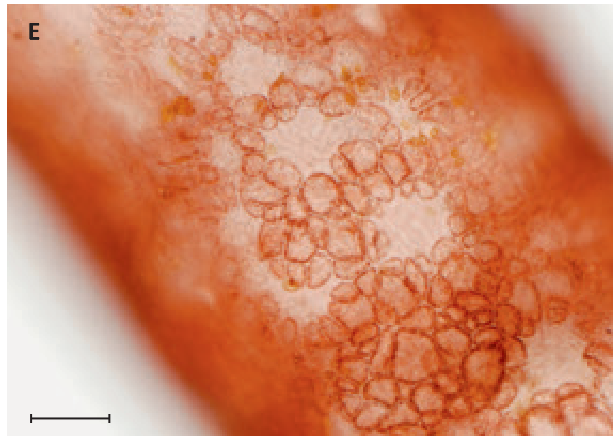
Structure: Between the pseudodichotomous branching there are 8-16 segments and the distance increases by stretching in the lower part. In the alga from Danish waters, 6-8 periaxial cells are observed, but the number varies and up to 9 in the species from the



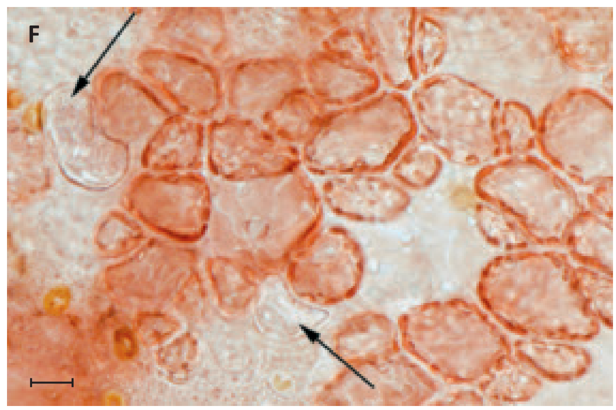
B: *Ceramium secundatum*. 8 periaxial cells transverse section of the same alga as in figure A. Scale 50 µm.

C: *Ceramium secundatum*. The alga, from which Hansen (2011) extracted DNA that matched DNA of *C. secundatum* from Germany and the British Isles. Scale 2 cm. C, E-F, J: Gilleleje Flak, 4 m, 8.10.2009. Leg.: L. Hansen.

D: *Ceramium secundatum*. Apex, slightly curved branches, large apical cell, and young cortical bands separated by narrow lines without cortex (arrow). Vejrø, 9 m, 28.5.1992. Scale 50 µm.



E: *Ceramium secundatum*. Multilayered cortex with rosettes of small cells around older and larger cortical cells. Scale 50 µm.



F: *Ceramium secundatum*. Kidney-shaped gland cells (arrows) between small cortical cells. Scale 10 µm.

British Isles. Cortical filaments growth both up- and downwards. The cortex is typically complete, but very narrow bands without cortex sometimes occur near the apex. The apical cell is large and from it relatively large and slightly angular cells are cut off just below the apical cell. The outermost cortical cells are 8-12 µm in width. The cortex is multilayered further down in the branches and the outer and smallest cells form characteristic rosette patterns round older and larger cortical cells or round the tetrasporangia. Gland cells are frequent or scarce and visible as hyaline kidney-shaped refractive cells in the outer cortical layer. In fertile male gametophytes the surface structures are hidden by small reproductive antheridial branchlets.

Reproduction: Antheridia cover the surface in male gametophytes with small colourless cells. Gonimoblasts have 1-3 spherical lobes at different age surrounded by 2-5 involucral branches. Tetrasporangia are embedded in the cortex, in 1-2 whorls, and surrounded by small cortical cells, and often slightly protruding from the branches.

Seasonal variation: Collected in February, April, June-October. Antheridia recorded in July and September, gonimoblasts and tetrasporangia in June-August and October.

Habitat: In wave-exposed localities epiphytic on

G: *Ceramium secundatum*. Apex with large apical cell and separate cortical bands of relatively large angular cells. Scale 20 µm. G-I: Tangen, 7.5 m, 15.9.1996.

H: *Ceramium secundatum*. Apex of male gametophyte. Scale 20 µm.

I: *Ceramium secundatum*. Antheridia, branch in optical longitudinal section. Scale 20 µm.

J: *Ceramium secundatum*. Spherical gonimoblast with slightly curved involucral branches (arrow). Scale 50 µm.

K: *Ceramium secundatum*. Tetrasporophyte with whorls of tetrasporangia embedded in cortex and protruding from the branch. Hastens Grund, 3.5 m, 26.8.1992. Scale 50 µm.

Black Scour Weed (*Ahnfeltia plicata*) and on boulders, 0.2-1 m depth. In sheltered localities and deeper water, epiphytic on algae such as Sea Oak (*Phycodrys rubens*) and Stalked Leaf Bearer (*Phyllophora pseudoceranoides*) and on boulders and stones, 0.2-8 m depth.

Comment: Reliable identification is only possible by use of genetic investigations in many cases. Thus, the identification of *C. secundatum* on the east coast of Canada was possible only after genetic examination, according to Bruce & Saunders (2015). Hansen (2011) undertook genetic investigations of Danish *Ceramium* as part of her Master's study. She found that the molecular sequence of specimens with gland cells matched that for *C. secundatum* from the British Isles and France while the sequence data for an alga with smaller cortical cells and no gland cells matched the sequence of *C. virgatum* from Ireland and the epitype from Germany. Hansen also examined the lectotype of *C. secundatum* from the Faroe Islands and found a gland cell (Hansen 2011). This indicates that it is possible to identify *C. secundatum* morphologically when gland cells are present.

Ceramium furcatum H.E.Petersen and *C. vendlicum* H.E.Petersen both have gland cells and the morphology of their cortex resembles *C. secundatum*. The species from shallow water at exposed localities mentioned by Petersen (1908, 1911, 1923-24 (in Rosenvinge), 1929) as *C. rubrum* f. *secundata* is likely to be *C. secundatum*. Taxa from deeper water mentioned by Petersen as *C. rubrum* f. *prolifera secundata* (Petersen 1908, 1911 legend for plate [Tavle] III figures 13-15), *Ceramium rubrum* var. *proliferum*, *Ceramium rubrum* f. *pedicellatum* and *Ceramium rubrum* f. *pedicellata-virgata* H.E.Petersen (1908, 1911, 1923-24 (in Rosenvinge), 1929) probably also belong in *C. secundatum*.

Resembles: *Ceramium virgatum* is similar in general appearance but the cortex has smaller cells and no gland cells. *C. secundatum* is distinquished by the presence of gland cells, relatively large cortical cells and protruding tetrasporangia. The two species also resemble *C. arborescens*, but in this species, the downward-growing cortical cells are much larger than the other cortical cells.

References: Boo & Rueness (1994), Bruce & Saunders (2015), Cocquyt et al. (2005), Hansen (2011), Maggs et al. (2002), Petersen (1908, 1911, 1929), Petersen in Rosenvinge (1923-24, *C. rubrum* f. *secundata, C. rubrum* f. *prolifera secundata*, part of *C. rubrum* var. *proliferum*).

Ceramium sungminbooi

J.R.Hughey & G.H.Boo

The species was described recently and characterised by slightly curved apical branches, 5 periaxial cells, narrow cortical bands and gonimoblasts without or with two involucral branches. Tetrasporangia occur on the adaxial side of branches with a single sporangium at each cortical band. (Hughey & Boo, 2016).

Comment: Genetic analyses, undertaken by Hughey & Boo (2016), showed that the lectotype of *C. cimbricum* from the western part of the Limfjord was different from the species in the Pacific Ocean, previously identified as *C. cimbricum*, and was described as *C. sungminbooi*. Analyses of algae from elsewhere showed that *C. sungminbooi* occurs in many localities. It is a new species in European waters and it was reported from Hirsholm by Hughey & Boo (2016). Future investigations are needed to reveal the distribution in Danish waters.

References: Hughey & Boo (2016).

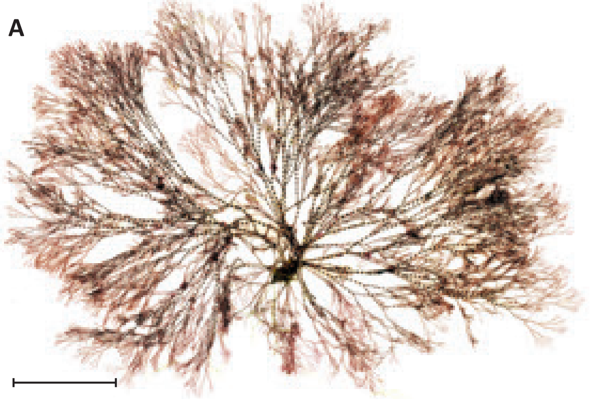
Ceramium tenuicorne

(Kützing) Waern

Appearance: Red to brownish red bush-like thallus banded branches and 3-10 cm in height. Main branches are regularly and repeatedly pseudodichotomously branched. Apical branches are straight or slightly curved. Lateral branches may occur especially in female gametophytes. Basal part of the alga often entangled.

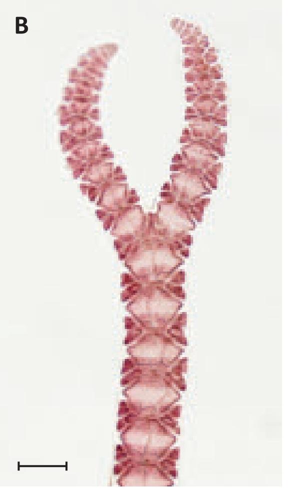
Structure: Main branches are 120-250 µm in width in the lower part and slightly tapering towards the apex. The outline of the apical part of the branches are smooth or slightly dentate. Between the pseudodichotomous branching points are 7-18 segments. Axial cells in the lower part of the alga are typically constricted just below the cortical bands and appear pyriform. The number of periaxial cells varies, there are often 6 but slender individuals might have only 4 or 5. There are 2 up- and 2 downward-growing cortical filaments from each of the periaxial cells. Cortical filaments grow mainly upwards and the upper margin is dentate while the lower margin is regular. The pyriform central axial cells with upward-growing filaments are particularly characteristic for the species, and best developed in the lower part of alga. Rhizoids have one or several cells.

The walls of the axial cells in specimens previously referred to *C. vertebrale* H.E.Petersen, might be very thick and refracting.



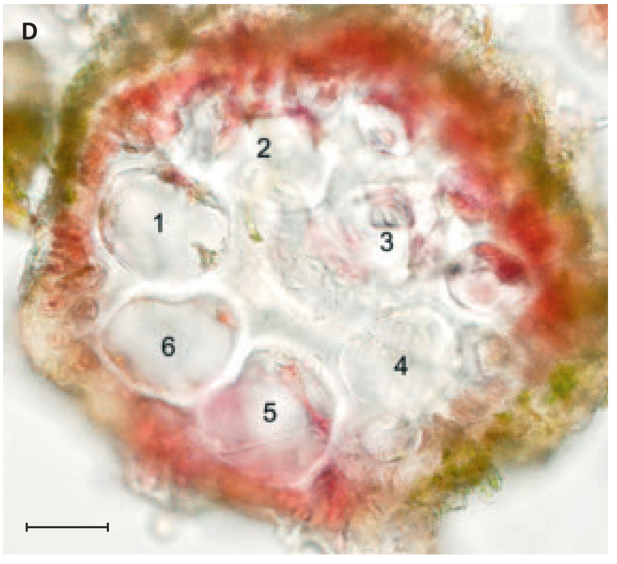
A: *Ceramium tenuicorne*. Well-developed alga, branches with separate cortical bands. Pramrenden, Langelinie, Copenhagen, 0.5 m, 20.9.2007. Scale 2 cm.

Reproduction: Antheridia form at the end of small branchlets arising from the periaxial cells in male gametophytes. Antheridia cover the cortical bands as a pale layer of small cells. Gonimoblasts have spherical

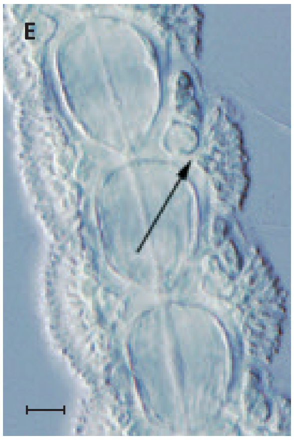


B: *Ceramium tenuicorne*. Slightly curved apical branches and separate cortical bands. Scale 50 µm. B-C, G: Gyldenløves Flak, 7 m, 4.9.1997.

C: *Ceramium tenuicorne*. Pyriform cell from basal part of alga, cortical band with upward-growing filaments, the upper margin dentate the lower margin regular. Scale 50 µm.



D: *Ceramium tenuicorne*. Branch with 6 periaxial cells, oblique transverse section. Scale 50 µm. D-F, H: Breakwater near the ferry berth, Vesterø Havn, Læsø, 0.5 m, 2.7.2008.

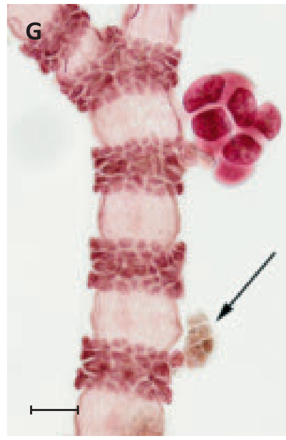


E: *Ceramium tenuicorne*. Male gametophyte with antheridia. Antheridial branchlets arise from a periaxial cell (arrow). Optical longitudinal section. Scale 20 µm.

F: *Ceramium tenuicorne*. Spherical gonimoblast with straight involucral branches. Scale 50 µm.

lobes and are surrounded by up to 6 involucral branches. Tetrasporangia form a single or several whorls and are covered by cortical cells and might bulge out from the branches. Asexual reproduction by paraspores and propagules. Parasporangia occur as clumps of dark cells, usually one per cortical band. Paraspores in culture germinate and grow into thalli with parasporangia. Propagules, also mentioned as 'Gobi's monosporangia', are large dark cells in the apices of branches. When mature the branch degenerates, and the dark red cells are released and function like monospores. Asexual reproduction becomes increasingly frequent towards the Baltic Sea. Gametophytes are most common in populations from Skagerrak, but male gametophytes have only been observed a few times in Danish waters. Parasporangia are common on the alga from Kattegat and propagules on those from areas further towards the Baltic Sea. Propagules in the alga from Danish waters are only recorded in those from the Sound.

Seasonal variation: Collected in May-September. Antheridia recorded in July-August, gonimoblasts in July-September, tetrasporangia in April-May, July-September, parasporangia in May, July-September and propagules in June.



G: *Ceramium tenuicorne*. Young (arrow) and older parasporangium. Scale 50 µm.

H: *Ceramium tenuicorne*. Tetrasporangia in whorls, embedded in cortex and protruding from the branch. Scale 100 µm.

I: *Ceramium tenuicorne*. Propagule with dark red cells. Rehydrated herbarium material. Dragør harbour, the Sound, 0.5 m, 7.6.1998, Leg.: L. Düwel. Scale 50 µm.

Habitat: Epiphytic on larger algae and on solid substratum, 0-10 m depth, rarely at greater depth.

Comment: A large number of individuals from Kattegat and the Baltic Sea have been studied in culture and with genetic analyses by Gabrielsen et al. (2002, 2003). These studies showed that it is likely that *C. diaphanum* sensu Areschoug, *C. diaphanum* sensu H.E.Petersen, *C. gobii* Waern, *C. strictum* sensu Kylin,

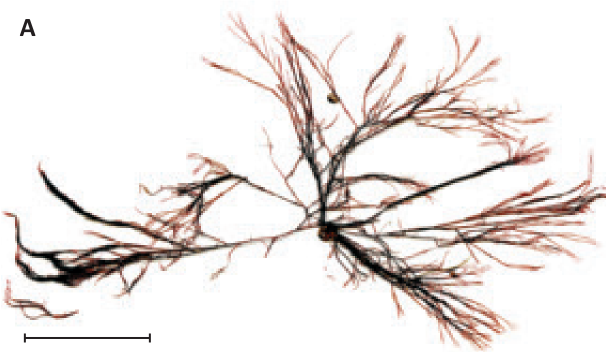
C. strictum sensu H.E.Petersen, *C. tenuicorne* and *C. vertebrale* in the Skagerrak-Baltic Sea region belong into a single species (Gabrielsen et al. 2003). The valid name for this species is *C. tenuicorne* (Gabrielsen et al. 2003).
References: Gabrielsen et al. (2002, 2003), Kylin (1944, *C. strictum*, *C. diaphanum* f. *strictoides*, *C. corticatulum*), Petersen (1908, *C. diaphanum*, *C. strictum, C. vertebrale*), Rosenvinge (1923-24, *C. diaphanum*, *C. strictum, C. vertebrale*), Rueness (1978), Rueness et al. (2002), Wolf et al. (2011), Wærn (1952, 1992, *C. gobii*).

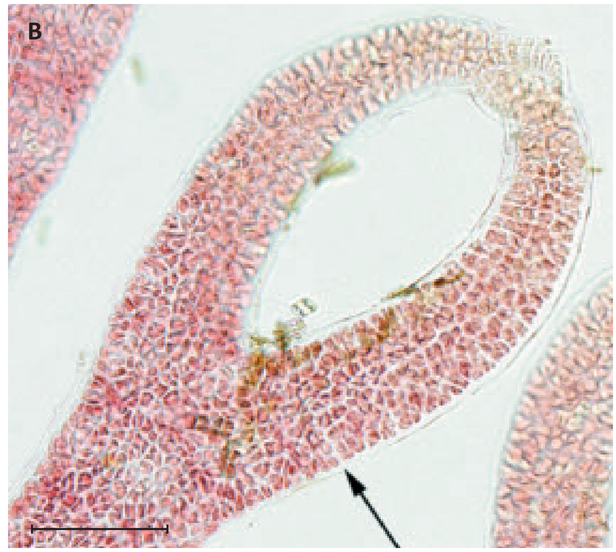
Ceramium virgatum

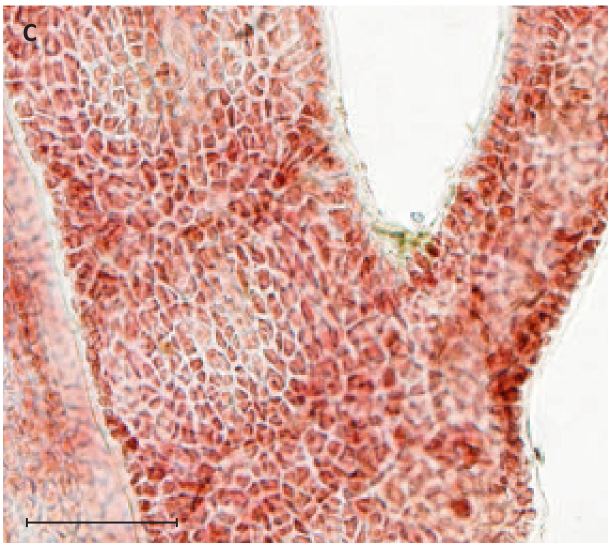
Roth

Common Banded Pincer Weed

Appearance: Red or brownish red relatively coarse bush-like thallus, 3-30 cm in height with branches at irregular intervals. Main branches are distinctly pseudodichotomously branched and have lateral branches. Uprights arise from dense prostrate branches with many rhizoids. The cortex is typically complete, but in the upper part and in young algae, narrow lines without cortication may occur. Apical branches more or less straight or only slightly curved.
Structure: The outline of the apical branches is regular. In the alga from Danish waters, 5-20 segments observed between the pseudodichotomous branching points. The number varies from 4 to 30, in this species from the British Isles, with a large variation even within a single individual. There are 6-7 periaxial cells with 2 upward- and 2-3 downward-growing cortical filaments. The cortex is typically complete except for very narrow bands without cortication near the apex. When cortical bands are separate, they have regular margins both at the upper and lower edges, and the area without cortex is only a line or a very narrow rectangle. A rosette pattern of small cells might develop around larger and older cells that are deeper in the cortex. No report of gland cells in type material or in the alga from the British Isles. Rhizoids on prostrate branches are multicellular.
Reproduction: Antheridia cover all the branches in fertile male gametophytes. Gonimoblasts are spherical, 30-45 µm in width, with angular carposporangia, and have 3-5 involucral branches banded or with confluent cortex. Tetrasporangia, (40-) 55-70 (-85) µm in diameter are embedded in the cortex. The first formed occur in a single whorl from the periaxial cell, later they occur irregularly in an upper and a lower whorl in the cortex.
Seasonal variation: Present all year. Gonimoblasts recorded in May, and tetrasporangia in June-July and October.
Habitat: On rocks and epiphytic on perennial algae in the littoral zone to 1 m depth. The depth distribution is probably larger, but this has to be documented by future investigations.
Comment: Many *Ceramium*-species, with confluent cortex were referred to *C. rubrum* C.Agardh by the latest generation of Danish phycologists. Similar practice took place in other North Atlantic areas. In the British Isles intensive modern studies revealed that several species were confused. Nomenclatural problems were also revealed. It turned out that *C. rubrum* and the later used *C. nodulosum* (Lightfoot) Ducluzeau are invalid names. The name *C. virgatum* is now in use and well defined with selection of type material, which has been studied both by morphological and genetic methods (Maggs et al., 2002). Similar comprehensive studies have, unfortunately not been undertaken for Common Banded Pincer Weed (*C. virgatum*) from Danish waters. Therefore, we do not have exact information about seasonal variation and distribution. Hansen (2011) undertook some genetic studies of Danish Banded Pincer Weed (*Ceramium*), as part of her Master's project. She found an individual with similar morphology and molecular sequence (*rbc*L) to the type material of Common Banded Pincer Weed (*C. virgatum*) from Germany and to the alga from Ireland, studied by Maggs et al. (2002). See morphological detail of the apex and cortical band of this alga in figures A-D.
References: Hansen (2011), Maggs et al. (2002), Petersen (1908), Petersen in Rosenvinge (1923-24), Silva et al. (1996, *C. rubrum*).



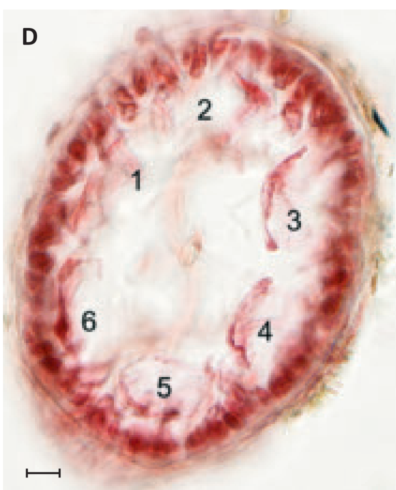


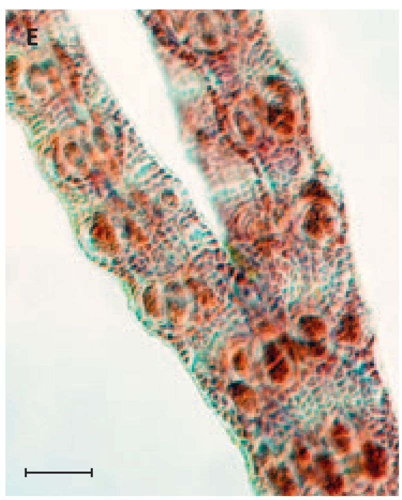


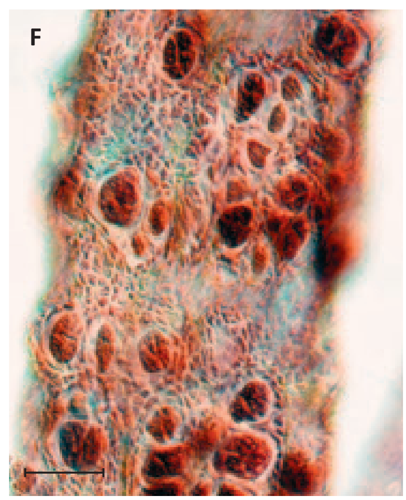
A: *Ceramium virgatum*. The alga from which Hansen (2011) extracted DNA that matched DNA from type material of *C. virgatum*. Scale 2 cm. A-D: The same alga, Gilleleje, 1 m, 20.10.2009. Leg. L. Hansen.

B: *Ceramium virgatum*. Apex with slightly curved branches, complete cortex of small cells, except lines without cortex (arrow). Scale 100 µm.

C: *Ceramium virgatum*. Complete cortex at the basal part of the alga. Scale 50 µm.







D: *Ceramium virgatum*. Axial cell surrounded by 6 periaxial cells and cortex of small cells. Scale 20 µm. Transverse section and photo by L. Hansen.

E: *Ceramium virgatum*. Upper part of tetrasporophyte with small cortical cells, tetrasporangia in a single whorl in each cortical band. Scale 100 µm. E-F: Breakwater near the ferry berth, Vesterø Havn, Læsø, 2.7.2008.

F: *Ceramium virgatum*. Lower part of tetrasporophyte with irregular bands of tetrasporangia embedded in cortex. Scale 100 µm.

Pterothamnion plumula

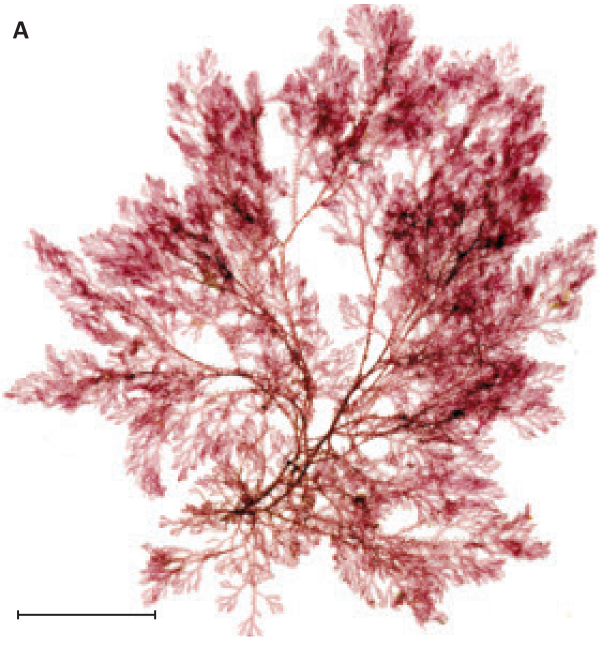
(J.Ellis) Nägeli

Bushy Feather Weed

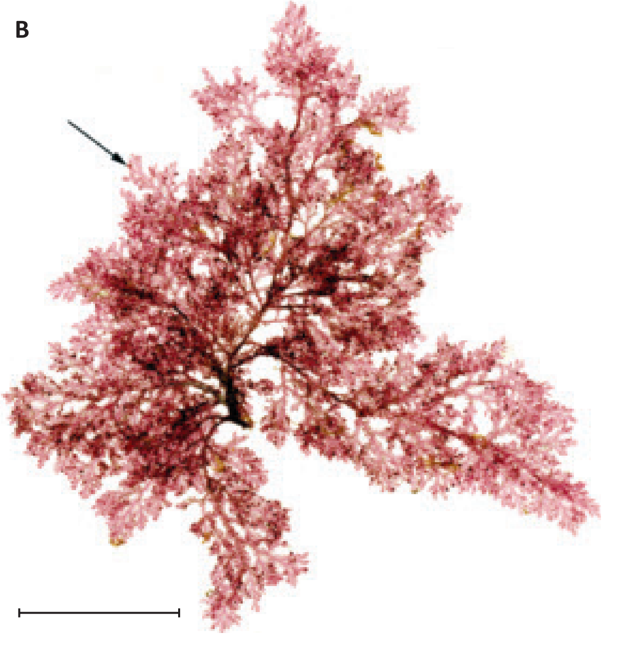
Appearance: Delicate rose bushy fronds in one plane that can be 9.5 cm in height but are usually less than 4 cm in height.

Structure: The upright bushy fronds consist of branched uniseriate filaments without cortex, mainly with branches in one plane. Main branches are conspicuous and repeatedly pseudodichotomously branched. Lateral branches short, opposite, arise from each cell of the main branch. Some individuals have four branches in a whorl. The basal cells of the branches are the same height as the following cells or only slightly shorter. Short unbranched branchlets are unilateral on the adaxial side of the opposite branches, with a single branchlet from each cell of the opposite branches. Occasionally, a few opposite branchlets occur at the lowest opposite branches. New main branches replace an opposite branch, and at such a branching point two additional unbranched opposite branchlets occur perpendicular to the plane of other branches. New main branches may also arise from the basal cell of a branch. Apical cells of the branches may be pointed. The cells contain many disc-shaped plastids, that become ribbon-shaped in old cells. Gland cells occur individually on vegetative cells of the opposite branches or on the branchlets. They are relatively large with the long axis perpendicular to the length of the branch. The thallus attaches to the substratum by many narrow filaments that arise from the lower cells of the upright branches. The branching pattern varies considerably, with some individuals having several main branches and relatively short cells, 1.5-2 times as long as wide so these thalli become rather dense. The branches of other individuals have relatively long cells, 3-4 time as long as wide so they have a larger distance between the branches and appear more open. *Pterothamnion plumula* ssp. *verticillatum* Athanasiadis has 4 branches in whorls and appears even more bushy than dense *P. plumula* ssp. *plumula*.

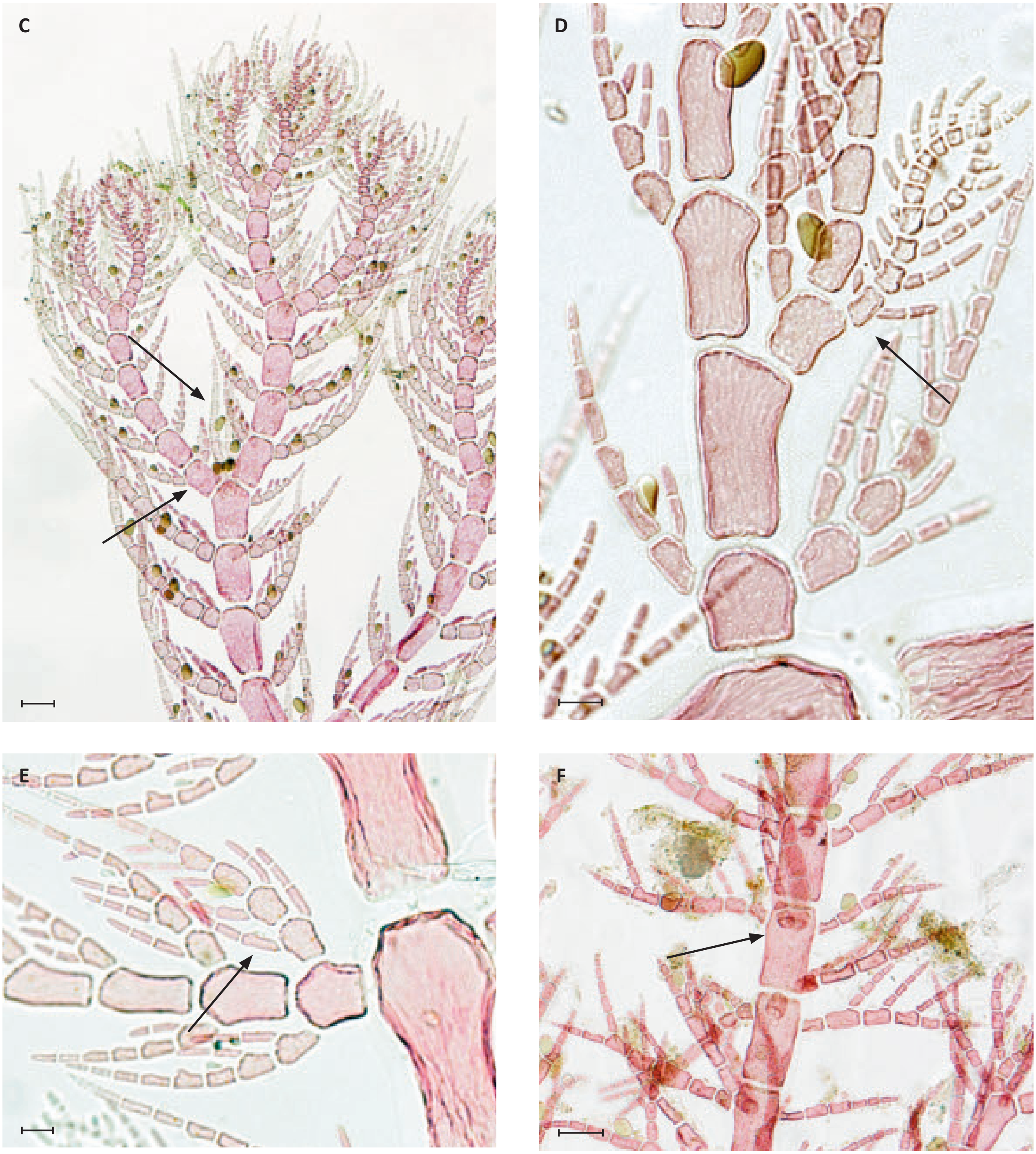
Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Stalked antheridial branchlets replace branchlets and form small bushes on the



A: *Pterothamnion plumula*. Open branched bushy thallus with branches in one plane. Herthas Flak, 2.8.1957. Leg.: J.B. Hansen. Scale 2 cm.



B: *Pterothamnion plumula*. Female gametophyte with dense branches and dark dot-like gonimoblasts (arrow). Herthas Flak, 13 m, 21.8.1991. Scale 2 cm.



C: *Pterothamnion plumula*. Pseudodichotomous main branches. Opposite branches with unilateral branchlets on the inner side. Main branches replace one opposite branch at branching points (lower arrow) with two additional branchlets (upper arrow). Scale 50 µm. C-E: Kims Top, 14.5 m, 5.6.1993.

D: *Pterothamnion plumula*. Main branch arising from the basal cell of a branch (arrow). Scale 20 µm.

E: *Pterothamnion plumula*. Opposite branchlets (arrow) on lower cells of opposite branches. Scale 20 µm.

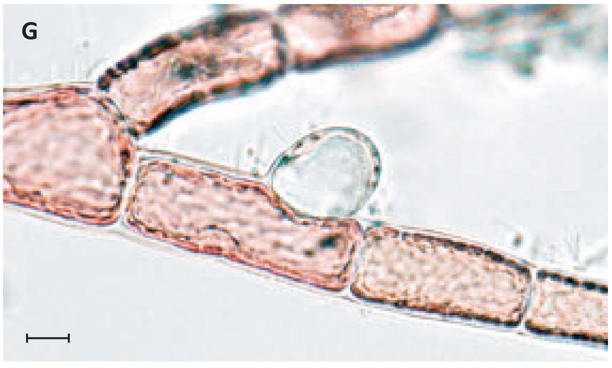
F: *Pterothamnion plumula*. Four branches in whorls (arrow). Kims Top, 14.5 m, 25.8.1993. Scale 50 µm.

adaxial side of the opposite branches. Carpogonial branches form on the outer (abaxial) side of the opposite branches near the apex. Gonimoblasts have several rounded lobes. The cruciate tetrasporangia on stalks are in series on the adaxial side of the opposite branches. Their stalks may have branches with more tetrasporangia appearing as small clusters. The sporangia are ellipsoid, 32-47 µm in height and 25-33 µm in width.

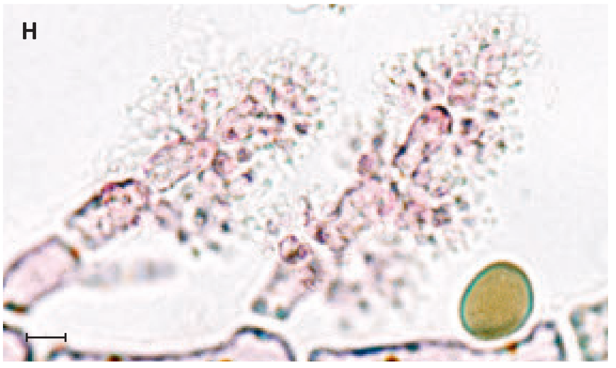
Seasonal variation: Basal systems, completely overgrown by epiphytes, and probably overwintering observed in January-February with a few upright cells. Well-developed individuals collected in April-October. Antheridia recorded in June-September, gonimoblasts in August-September and tetrasporangia in June-August.

Habitat: At shallow water, 1 m depth on a concrete wall in the harbour, Frederikshavn and at Thyholm. Otherwise in deeper water, epiphytic on other algae, epizoic on Common Whelk (*Buccinum undatum*), bryozoans and hydroids, 5-20.5 m depth.

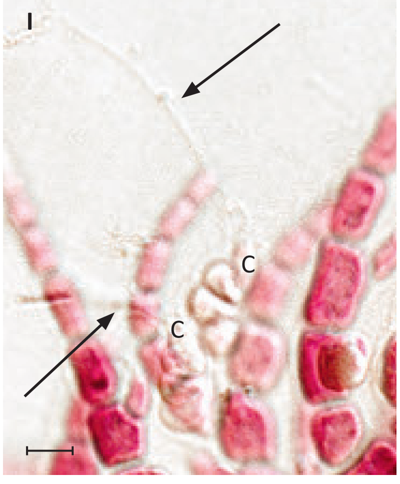
References: Athanasiadis (1986), Maggs & Hommersand (1993), Rosenvinge (1923-24, *Antithamnion plumula*).



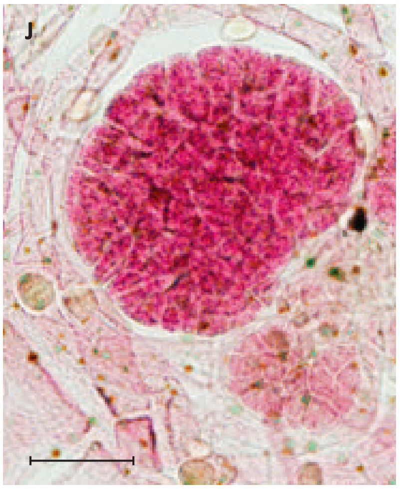
G: *Pterothamnion plumula*. Gland cell. Hirsholm, drift, 25.5.2010. Scale 10 µm.



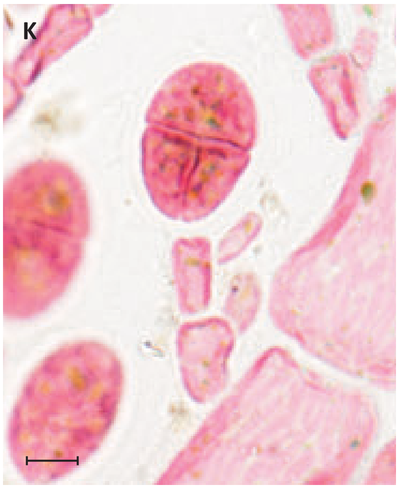
H: *Pterothamnion plumula*. Antheridial branchlets and a gland cell. Scale 10 µm. H, J: Boblerev at Nordre Rønner, Læsø, 10 m, 17.8.2004.



I: *Pterothamnion plumula*. Female gametophyte with two carpogonial branches, carpogonia (c) and trichogynes (arrows). Tønneberg Banke, 13 m, 20.8.2001. Scale 10 µm.



J: *Pterothamnion plumula*. Gonimoblast with rounded lobes. Scale 50 µm.



K: *Pterothamnion plumula*. Cruciate tetrasporangium on branched stalk. Munkegrunde, 11 m, 4.8.1994. Scale 10 µm.

Scagelothamnion pusillum

(Ruprecht) Athanasiadis

Scagel's Cloud Weed

Appearance: Delicate branched red to light red bushy fronds with two varieties in Danish waters. One of them, *S. pusillum* var. *droebackense* (Sundene) Athanasiadis, is reminiscent of red tennis balls in the water, and grows to 10 cm in height, at shallow water in winter and spring. The other, *S. pusillum* var. *pusillum*, is up to 3 cm in height and occurs mainly in deep water in summer months.

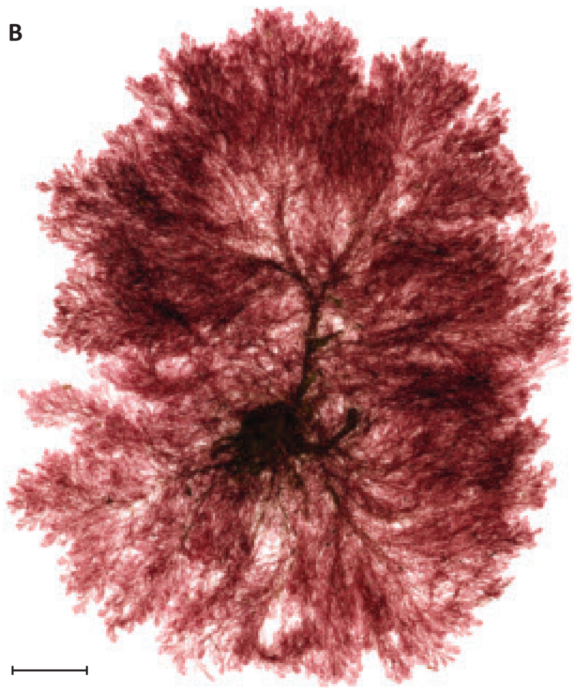
Structure: Branched uniseriate filaments without cortex. The distinct main branches are irregularly alternately branched with cells, 3-5 times as long as wide. Opposite branches arise from each cell of the main branches, seldom three around the axis. Each pair of opposite branches is slightly unequal in length and they have cylindrical cells of equal height except the basal cell which is shorter than the rest of the cells. The branches are irregularly displaced from one branching point to the next, so the branches are not in one plane. Branchlets with restricted growth are often in series on the adaxial side of the branches, but also occur scattered on the abaxial side and a few opposite branchlets are occasionally observed. Gland cells only cover a single cell. They are lens-shaped with the long axis parallel with the branch. The upright thallus attaches to the substratum by downward-growing filaments that arise from the lowest cells of the main branch. They might have a small multicellular attachment pad.

Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Antheridia occur as small, rounded cells at the apex of branchlets and have also been observed to occur with tetrasporangia on the same thallus. There are no reports of female reproductive structures on this species from Danish waters. Cruciate tetrasporangia are ellipsoid and sessile

A

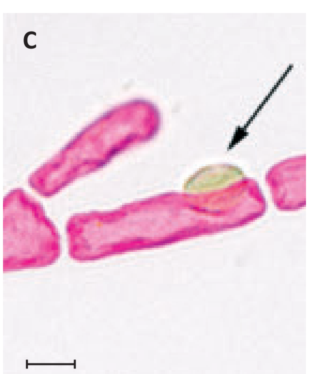
A: *Scagelothamnion pusillum* var. *pusillum*, small epiphytes. Falske Bolsaks, 15 m, 13.9.1991. Scale 2 cm.

B

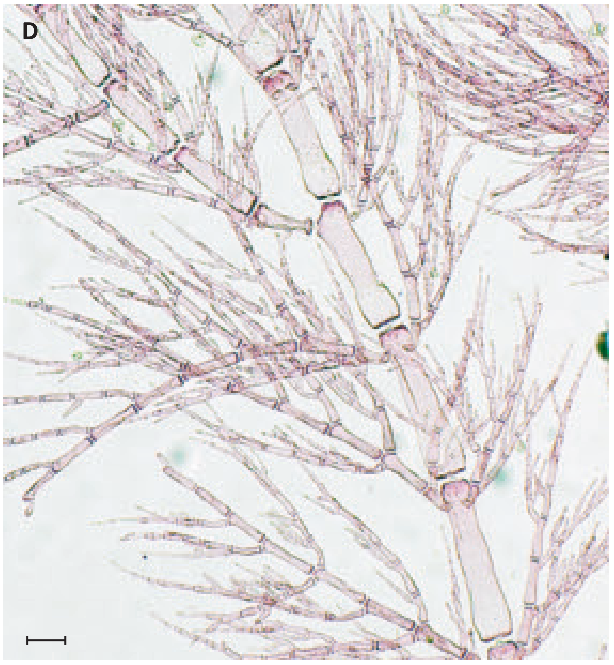


B: *Scagelothamnion pusillum* var. *droebackense*. Large much branched red bush. Scale 2 cm. B, D, F: Østerby Havn, Læsø, 1 m, 24.3.2002.

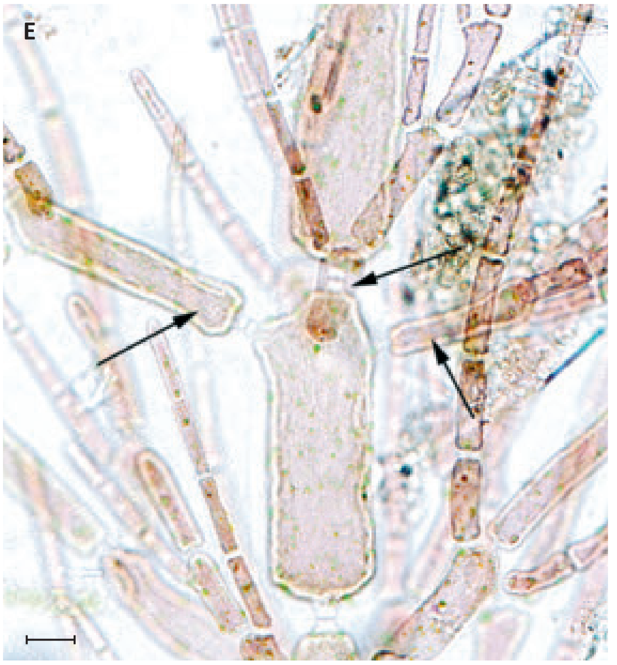
C



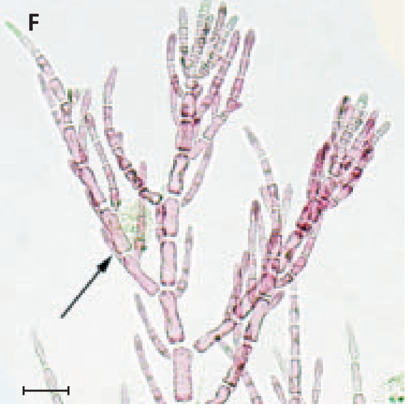
C: *Scagelothamnion pusillum*. Lens-shaped gland cell (arrow). Scale 10 µm. C, H: Kims Top, 14.5 m, 5.6.1993.



D: *Scagelothamnion pusillum*. Main branch with opposite branches of unequal length, basal cells cylindrical and branchlets with additional branchlets. Scale 100 µm.



E: *Scagelothamnion pusillum*. Main branch with three branches around axis (arrows). Vejrø, 9 m, 26.3.1992. Scale 20 µm.

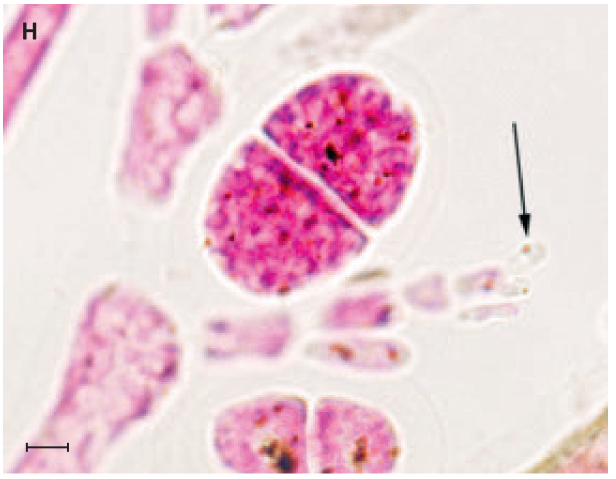


F: *Scagelothamnion pusillum*. Apical part, main branch with opposite branches of unequal length, with adaxial branchlets and a single abaxial branchlet (arrow). Scale 50 µm.

G: *Scagelothamnion pusillum*. Basal part, downward-growing filaments from main branch, with attachment pads (arrows). Scale 50 µm. G: Vejrø, 19 m, 5.6.1991.

in short series on the adaxial side of branchlets. They typically measure 60-85 µm in height and 35-50 µm in width, and in individuals from Fænø the tetrasporangia were 46-49 µm in height and 35 µm in width according to Rosenvinge (1923-24, as *Antithamnion boreale*).

Seasonal variation: *Scagelothamnion pusillum* var. *droebackense* collected in January-May. *Scagelothamnion pusillum* var. *pusillum* collected in January, April-September. Antheridia and tetrasporangia recorded in April-September.



H: *Scagelothamnion pusillum*. Antheridia (arrow) on alga, also with tetrasporangia. Scale 10 µm.

I: *Scagelothamnion pusillum*. Cruciate tetrasporangia (arrow) sessile on adaxial side of opposite branches. Herthas Flak, 14 m, 9.6.1991. Scale 50 µm.

Habitat: *Scagelothamnion pusillum* var. *droebackense* occurs on boulders, seldom epiphytic, 1-6 m depth. Scagelo*thamnion pusillum* var. *pusillum* epiphytic on other algae such as Lobed Leaf Bearer (*Coccotylus brodiei*), Sea Beech (*Delesseria sanguinea*), and Sea Oak (*Phycodrys rubens*), collected by divers, 5-18.5 m depth, and by dredge at Bornholm, 21.5 m depth.

Resembles: The irregularly placed branchlets are reminiscent of *Antithamnion villosum*, but in this species, the basal cells in opposite branches are much shorter than the rest of the cells and gland cells cover 2-3 cells on short branchlets.

Comment: Species delimitation within *Scagelia* is largely unresolved. This particularly concerns species and varieties where sexual reproduction is unknown. According to Athanasiadis (1996), *S. pusillum* is a hybrid between *Scagelia* and *Pterothamnion*.

References: Athanasiadis (1996), Athanasiadis & Rueness (1992), Maggs & Hommersand (1993, *Scagelia pusilla*), Rosenvinge (1923-24, *Antithamnion boreale*), Sundene (1962, *A. boreale*).

Family: Dasyaceae

Algae with distinct terete main branches, with unlimited growth surrounded by branchlets of limited growth.

The main branches are constructed as uniaxial syntagma with segments that consist of axial cells surrounded by equally high periaxial cells and a cortex of smaller cells. Growth is sympodial, the apical cell develops into a branchlet while the cell below continues the growth of the main branch. The branchlets are uniseriate and pseudodichotomously branched, except in *Heterosiphonia*, where the lower part of the branchlets have segments of more cells (polysiphonous). The branchlets appear dichotomously branched but in the youngest branching points, it appears that one of the branches is a lateral branch to the other, thus the branching is pseudodichotomous. New main branches arise from the lower part of branchlets or from cortical cells. Isomorphic dioecious male and female gametophytes and tetrasporophyte. The tetrahedrally divided tetrasporangia are in whorls in modified branchlets (stichidia).

References: Christensen (1980), Kim (2012), Kylin (1956), Maggs & Hommersand (1993).

Identification key to species of Dasyaceae

1a.	Robust alga, main branches 25-75 cm in height and 1-2 mm in width with small red branchlets on all sides	*Dasya baillouviana*
1b.	Slender alga with distichous branchlets, alternating to the right and left side of branches	2
2a.	4 periaxial cells. Uniseriate branchlets from each segment	*Dasysiphonia japonica*
2b.	6 or 8 periaxial cells. Branchlets arise every 2-3 segments, their lower part polysiphonous	*Heterosiphonia plumosa*

Dasya baillouviana

(S.G.Gmelin) Montagne

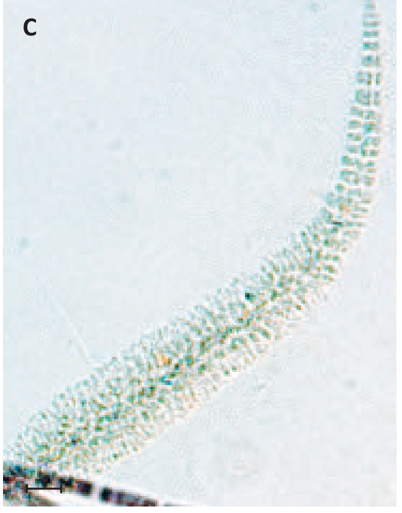
Recent synonym: ***Dasya pedicellata*** **(C.Agardh) C.Agardh**

Stalked Tree Weed

Appearance: Large much branched thalli, up to 25-75 cm in height are bright red. The long main branches are terete, 1-2 mm in width, with scattered branches, on all sides. Narrow red branchlets that look like clusters of hairs cover the main branches and give the alga

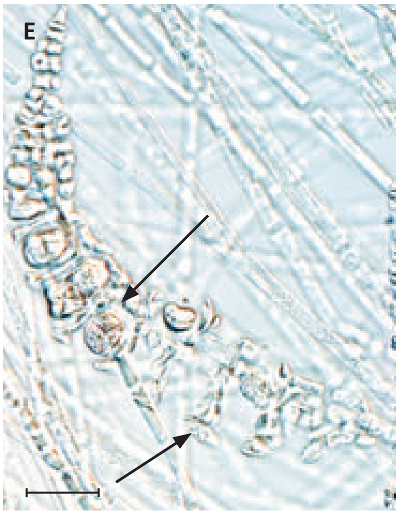
A: *Dasya baillouviana*. Long main branches surrounded by branchlets looking like clusters of hairs. Scale 2 cm. A-D: On wooden pole, Lillestranden, Kerteminde, 0.2 m, 21.9.2009.

B: *Dasya baillouviana*. Apex with sympodial growth, the apical cell initiates a branchlet (right arrow), and a new apical cell (left arrow) is cut off from the cell below. Young branchlets are clearly pseudodichotomously branched. Periaxial cells form from the axial cells immediately below the apex.



C: *Dasya baillouviana.* Stichidium covered by antheridia. Scale 20 µm

D: *Dasya baillouviana.* Young gonimocarp on a branchlet with an apical tuft of filaments. Scale 100 µm.



E: *Dasya baillouviana.* Stichidium with tetrahedrally divided tetrasporangia (upper arrow) and empty sporangia each with a small cover cell (lower arrow). Margretheholms Havn, Copenhagen, 0.5 m, 11.9.2003. Scale 50 µm.

a shaggy appearance. The main branch arises from a small attachment disc.

Structure: The frond is a uniaxial syntagma and consists of segments with 5-6 periaxial cells. A well-developed cortex of small cells covers the branches from just below the apex. Narrow filaments grow between the periaxial cells in older branches. The red pseudodichotomous branchlets occur on all sides and arise both from the axial, periaxial, and cortical cells. They consist of uniseriate long cylindrical cells, c. 15 µm in width in the distal end and with a more or less pointed apical cell. The branchlets soon overtop the apical cell of the main branch.

Reproduction: Isomorphic dioecious male and female gametophytes and tetrasporophyte. The Reproductive structures develop on the branchlets. The antheridia are small colourless cells that cover the surface of a special branchlet with a series of sterile cells at the apex (stichidium). Gonimoblasts develop on a small branch that appears like a short stipe (pedicel). They have a pericarp with a small opening. The branches associated with this structure have a tuft of uniseriate filaments at the apex. The tetrahedrally divided tetrasporangia are in whorls around the axial cells of stichidia and surrounded by small cover cells, best seen after extrusion of the tetraspores. Asexual reproduction by fragments, and even small fragments of the red branchlets may be the start of new individuals.

F: *Dasya baillouviana.* Branch with well-developed cortex and many branchlets. Scale 500 µm. F-G: Alsund, 5 m, 6.6.2009.

G: *Dasya baillouviana.* Young pseudodichotomously branched branchlet from cortical cell (arrow). Scale 200 µm.

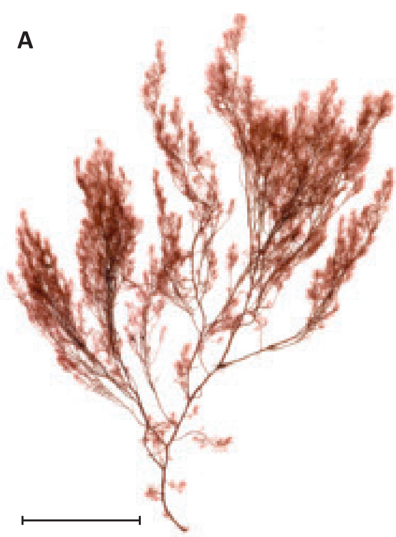
Seasonal variation: Collected in February-March, June-December, probably perennial and best developed in summer and autumn months. The branchlets are lost late in the growing season.
Habitat: Localities with shelter, on solid substratum such as harbour jetties, gravel, wooden poles and Blue Mussel (*Mytilus edulis*), 0.2-12 m depth.
Comment: The first specimen in Danish waters was a drift alga in the Great Belt, 1961. Attached specimens were first collected in 1989 from the Little Belt area. The dispersal is efficient due to regrowth from fragments of the thallus.
References: Christensen (1980, 1994), Maggs & Stegenga (1999), Nielsen & Mathiesen (2005), Stegenga & Karremans (2015, *D. pedicellata*), Stegenga & Mol (1983).

Dasysiphonia japonica

(Yendo) H.-S.Kim
Siphoned Japan Weed

Appearance: Light rose to brownish red bush-like fronds with delicate branches, up to 17 cm in height. The main branches scattered and repeatedly branched on all sides. They have delicate distichous branchlets resulting in young specimens and the apical parts of the older specimens are in one plane. The branchlets easily decay so older individuals lack branchlets on the lower parts of branches. A single or a few uprights arise from a basal disc.
Structure: Main branches constructed as a segmented uniaxial syntagma with 4 periaxial cells per segment. Cortical filaments arise from the lower part of periaxial cells at some distance from the apex and cover the branches. A single branchlet arises from each segment of the main branch. The branchlets are slightly curved, alternate in distichous series and have 2-3 dichotomies. They consist of uniseriate cylindrical cells, 2.5 times as long as wide with a pointed apical cell.
Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Only individuals with tetrasporangia collected in Danish waters. Tetrasporangia develop in stichidia on the branchlets. They have segments, with 4 tetrasporangia in a whorl per segment and a series of sterile cells at the apex. The tetrahedrally divided tetrasporangia are spherical. Asexual reproduction by fragments is a frequent and efficient dispersal mechanism.
Seasonal variation: Collected in March, May and

A

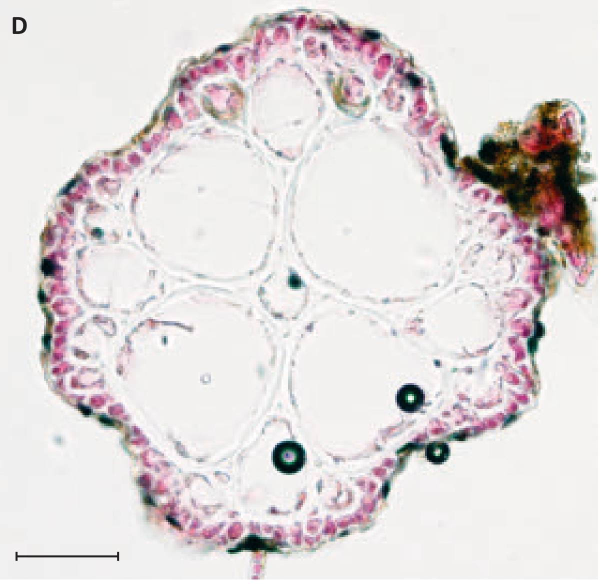


B

A: *Dasysiphonia japonica*. Main branches (dark axes) repeatedly branched on all sides with delicate branchlets. Thisted Bredning, 1.5 m, 24.8.2005. Leg.: S. Rønhede & M. Laursen. Scale 2 cm.

B: *Dasysiphonia japonica*. Small specimen with bright delicate young branches, and distichous branchlets. Thisted Bredning, 5 m, 18.8.2008. Leg.: J. Deding. Scale 2 cm.

C: *Dasysiphonia japonica*. Apex of uniaxial syntagma, main branch of segments, each with 4 periaxial cells and alternating uniseriate branchlets with pointed apical cells. Scale 100 µm. C, E: Boblerev between Hirsholm and Frederikshavn, 8 m, 23.8.2004.



D: *Dasysiphonia japonica*. Axial cell, 4 periaxial cells and cortex, transverse section (black circles are air bubbles). Visby Bredning, the Limfjord, 3 m, 19.8.2008. Scale 100 µm.

E: *Dasysiphonia japonica*. Stichidium with tetrahedrally divided tetrasporangia and a series of vegetative cells at the apex. Main branch with cortical filaments (arrow). Scale 100 µm.

July-August. Tetrasporangia observed in May and August. The species is perennial in the Netherlands and Norway, probably also in Danish waters.

Habitat: On small stones and epiphytic on various algae such as Sea Oak (*Phycodrys rubens*) and Wire Weed (*Sargassum muticum*). Often growing unattached around other algae, 1.5-25 m depth.

Resembles: Brongniart's Thread Weed (*Vertebrata byssoides*) may look similar with its coloured trichoblasts, but it has 7 periaxial cells and no cortex.

Comment: A species which originated from Japan and has spread in the North Atlantic. First collected in Danish waters in 2004. Collected in Flensborg Fjord and Vejle Fjord, 2021.

References: Bjærke & Rueness (2004, *Heterosiphonia japonica*), Lein (1999), Maggs & Stegenga (1999, *Dasysipohonia* sp.), Sjøtun et al. (2008, *H. japonica*).

Heterosiphonia plumosa

(J.Ellis) Batters

Siphoned Feather Weed

Appearance: Bush-like frond with a clear red colour, up to 10 cm in height. Main axis conspicuous, repeatedly branched with scattered branches that have distichous alternating branchlets in one plane. The main branches are thick and slightly cartilaginous, while the branchlets are narrow and delicate giving the alga a bushy appearance. A single or several uprights arise from a disc-shaped holdfast.

Structure: The main branches are constructed as uniaxial syntagma, the segments have relatively thick axial cells and 6-8 periaxial cells. Cortical filaments grow down from the periaxial cells and make a thick layer of cortication at the lower part of the alga. The apex of the main branches is uniseriate and zigzag-shaped. The sympodial growth is easy to see, the apical cell continues as a lateral branch and growth of the main branch continues from the cell below. The alternating branchlets arise from the main branch every 2-3 cells. Branchlets consist of short cells, each with a pointed apical cell. They are uniseriate at the apex but have segments with periaxial cells in the lower part. They curve upward. Secondary branches may develop in the lower part of old individuals.

Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Reproductive structures develop on the branchlets. Antheridia form a cover of small pale cells in the central part of uniseriate branchlets that terminate in a series of vegetative cells. Gonimocarps are urceolate and sessile at the adaxial side of the branchlets. The stichidia with tetrasporangia are conical. They have a polysiphonous stalk followed by 12 or more segments with whorls of tetrahedrally divided tetrasporangia.

Seasonal variation: Perennial, collected in January-March, June-September. Antheridia, gonimoblasts and tetrasporangia recorded in August, young gonimoblasts in July.

Habitat: On gravel and boulders, 15-18 m depth. Older collections by dredge, 30 m depth.

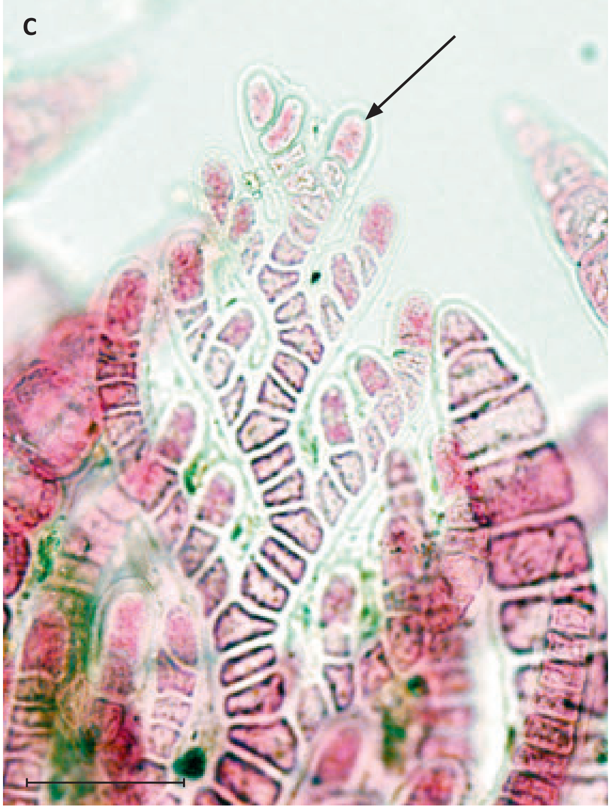
References: Christensen (1980, 1994), Maggs & Hommersand (1993), Rosenvinge (1923-24), Stegenga & Mol (1983).

A

A: *Heterosiphonia plumosa*. Plane thallus, conspicuous main branches and alternating distichous branchlets. A, E: Østerby Havn, Læsø, drift, 6.9.2002. Scale 2 cm.

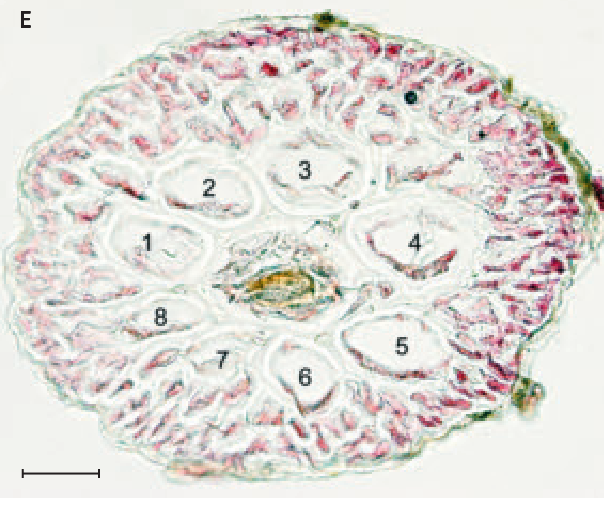
B

B: *Heterosiphonia plumosa*. Old, dark red specimen from winter, with bright new branches. Scale 2 cm. B-C: Kims Top, 19 m, 15.1.1997.

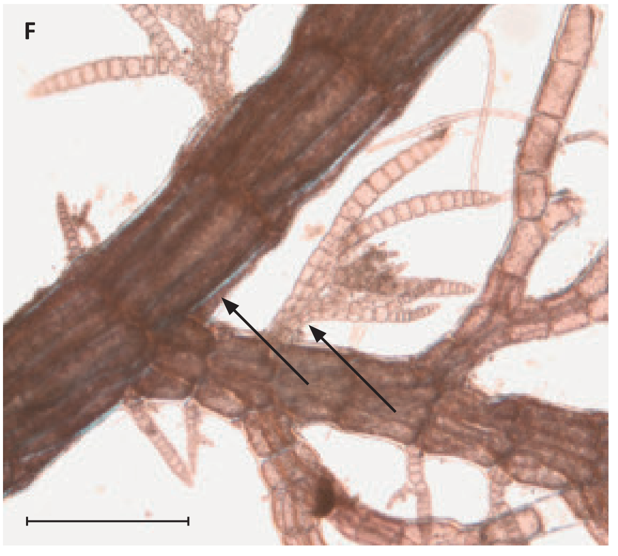


C: *Heterosiphonia plumosa*. Zigzag-shaped uniseriate apex. Sympodial growth, the former apical cell grows into a branchlet and a new apical cell occurs (arrow). Scale 50 µm.

D: *Heterosiphonia plumosa*. Stichidium with tetrahedrally divided tetrasporangia (arrow). Scale 200 µm. D-F: Kims Top, 19 m, 18.8.2015.

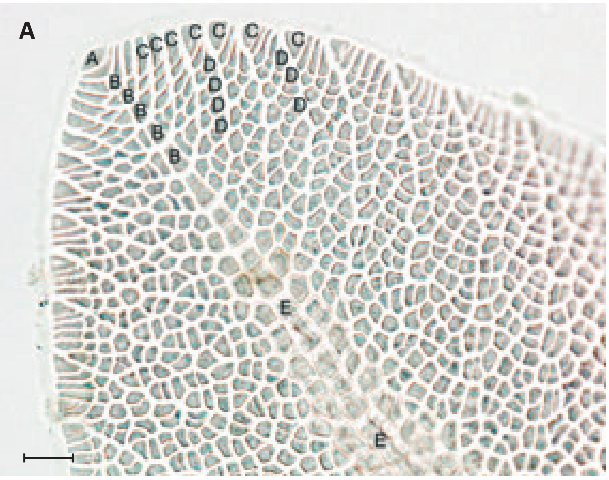


E: *Heterosiphonia plumosa*. Axial cell surrounded by 8 periaxial cells and cortex of small cells. Transverse section. Scale 50 µm.



F: *Heterosiphonia plumosa*. Main branches with many periaxial cells and cortical filaments (left arrow) and a later-formed lateral branch (right arrow). Scale 500 µm.

Family: Delesseriaceae



A: *Delesseria sanguinea*. Apex of blade, apical cell (A), axial cells (B), apical cells of first order lateral filaments (C), apical cells of second order lateral filaments (D). Initiation of cortex (E) round axial cells that become midrib. Tønneberg Banke, 14.5 m, 16.1.1997. Scale 20 µm.

Appearance: Perennial species with membranous blades with a central midrib and lateral veins that are visible with the naked eye or by microscopic examination.

Structure: Thallus constructed as a flat uniaxial syntagma with monostromatic blades. The construction of the algae is best seen at the apices. Growth by the apical cell forms a central axial cell row that is visible below in the thallus. Each axial cell is surrounded by 4 periaxial cells. The membranous blade develops from two of the four opposite periaxial cells. From each of them first order lateral filaments develop and from these arise second order lateral filaments with a single filament from each of the cells in the first order lateral filaments. This process continues a variable number of times. The filaments are dense and form the pseudoparenchymatous monostromatic blade. From the other two opposite of the 4 periaxial cells a cortex develops by oblique cell divisions. The cortex forms the midrib along the axial cells. In some cases, there are also very narrow filaments in the midrib. The cells and the following filaments that form from a single axial cell make a blade segment. There may be intercalary cell divisions within the filaments and secondary pit connections between cells of the blade. The apical cells of the first order lateral filaments are typically in the upper, outer corner of each segment. There may also be apical cells from one or more of the following orders of filaments at the margin of the blade. The pattern for the development of the lateral filaments is stable and of systematic importance.

The lateral veins form when small cortical cells develop on some of the first order lateral filaments. Veins may develop in the same way on the following orders of filaments. Veins without cortex occur as elongated cells in the lateral filaments in Veined Tongue Weed (*Apoglossum ruscifolium*) and as the lateral veins in Winged Weed (*Membranoptera alata*).

Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte with tetrahedrally divided tetrasporangia.

References: Christensen (1980), Maggs & Hommersand (1993), Rosenvinge (1923-24), Wynne (1996, 1997, 2001), Wynne & Saunders (2012).

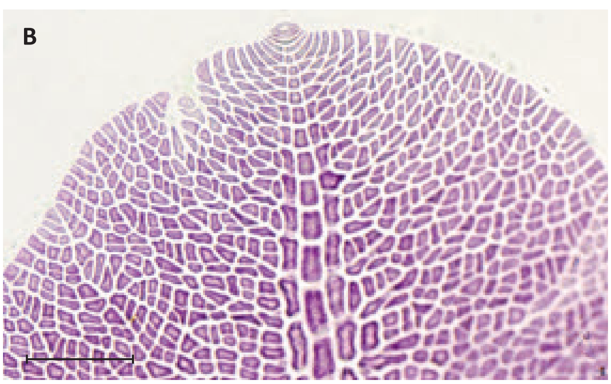
Identification keys to species of Delesseriaceae
Macroscopic characters

1a.	Margin of blades indented, with dentate, rounded lobes or narrow linear parts. Young blades arise from the margin of older blades	2
1b.	Margin of blades entire, oval to lanceolate, sometimes ruffled. Young blades arise from the midrib of older blades	3

2a.	Sections of blades of an even width (few mm) with distinct midrib, lateral veins inconspicuous and only visible with a magnifying glass	*Membranoptera alata*
2b.	Margin of blade with lobes, dentate or irregular indentations, lateral veins visible by eye	*Phycodrys rubens*
3a.	Small algae, a few cm in length, blades oval, veins microscopic. Colour red-violet	*Apoglossum ruscifolium*
3b.	Large algae, lanceolate to oval blades, well-developed midrib and veins. Colour clear red or brownish red	*Delesseria sanguinea*

Microscopic characters at the apex

4a.	Axial cells transversely divide by longitudinal growth of the blade simultaneously with other cells of the blades, making the lateral filaments and segments difficult to distinguish from each other	*P. rubens*
4b.	Axial cells elongate by longitudinal growth of the blade. Lateral filaments and segments distinct. From the cells of first order lateral filaments, second order lateral filaments grow downwards (abaxial)	5
5a.	Veins consist of long cells without cortex	*A. ruscifolium*
5b.	Veins with cortex	6
6a.	Transverse cell divisions of periaxial cells and blade cells	*D. sanguinea*
6b.	No transverse cell divisions of periaxial cells	*M. alata*

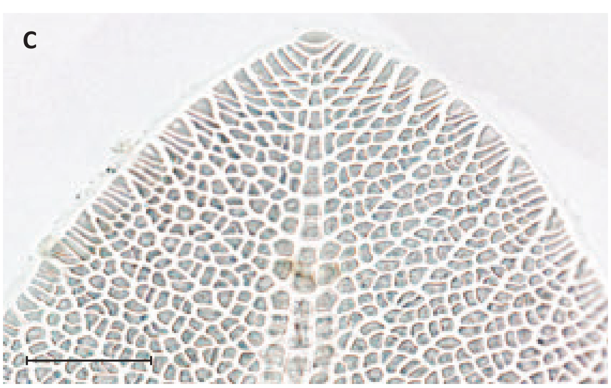


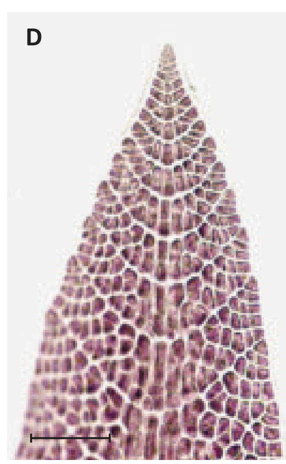
B: Veined Tongue Weed (*Apoglossum ruscifolium*). Tønneberg Banke, 13.5 m, 16.1.1997. Scale 50 µm.

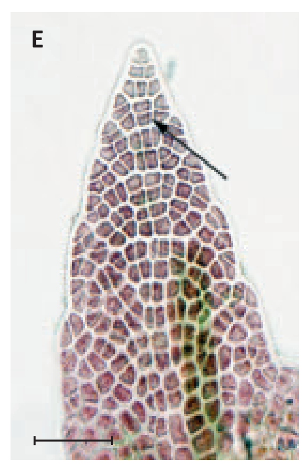
C: Sea Beech (*Delesseria sanguinea*). Tønneberg Banke, 14.5 m, 16.1.1997. Scale 50 µm.

D: Winged Weed (*Membranoptera alata*). Møns Klint, 17 m, 2.9.2004. Scale 50 µm.

E: Sea Oak (*Phycodrys rubens*), first axial cell transversely divided (arrow). Vejrø, 13 m, 27.3.1992. Scale 50 µm.







Apoglossum ruscifolium

(Turner) J.Agardh

Veined Tongue Weed

Appearance: The oval tongue-shaped dark red-violet blades, up to 2 cm in height are often growing close together. The blades have a small stipe and a regular, sometimes slightly wavy margin. The apex is acute, or the apical cell is slightly retracted from the margin. The midrib is conspicuous while the veins are barely visible. New blades form from the midrib of older blades. Individual blades are approximately 0.4 mm in width. The lower part of older blades sometimes decay, leaving the midrib as an extension of the stipe.

Structure: Thallus is a flat, uniaxial syntagma, both the axial and the periaxial cells elongate during growth without transverse division (figure B p. 201). The midrib develops from axial and periaxial cells which become covered with a multilayered cortex of small cells below the apex. The cortex also extends slightly over the otherwise monostromatic blade. Segments of the blade are regularly constructed with the first order lateral filaments at the top of each segment. Second order lateral filaments usually grow downwards (abaxial), while the third order lateral filaments grow upwards (adaxial). There are more orders of lateral filaments further down in the blade. Veins develop without cortex from cells of the first and following orders of lateral filaments in which the cells elongate and the veins appear as a branched net of long cells between smaller angular cells.

Reproduction: Antheridia form sori of small pale cells between the veins. The gonimocarps develop on the midrib. Pericarps have a protruding exit tube. Tetrahedrally divided tetrasporangia develop along the midrib on both sides of the blade.

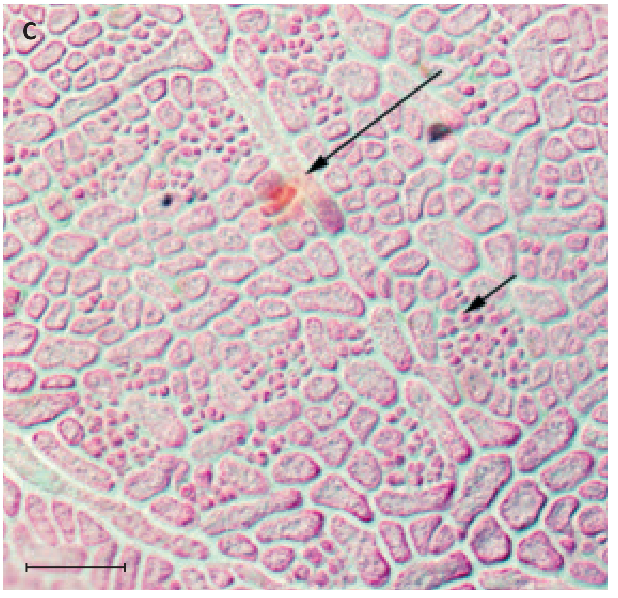
Seasonal variation: Collected in January, February and April-August. Antheridia, gonimocarps and tetrasporangia recorded in August.

Habitat: On boulders, epiphytic on haptera and stipes of Forest Kelp (*Laminaria hyperborea*) on stone reefs, 10-21 m depth.

References: Lin et al. (2012).

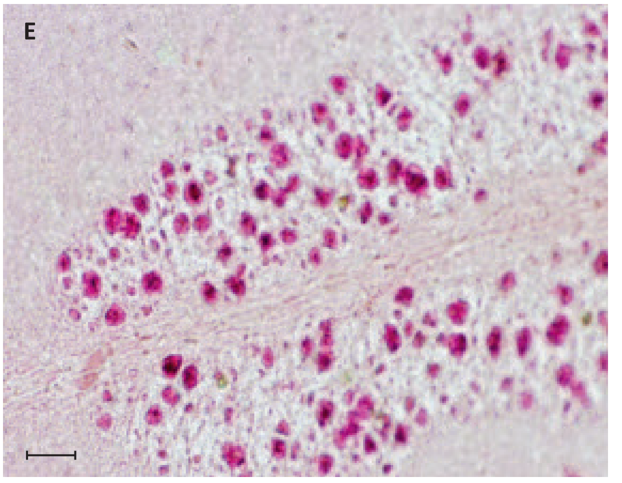
A: *Apoglossum ruscifolium*. Small, elongated blades with rounded apices. Young blades from the midrib of older blades and from prostrate branches. Tønneberg Banke, 13 m, 27.8.1993. Scale 2 cm.

B: *Apoglossum ruscifolium*. Young blade from midrib of old blade. Tønneberg Banke, 12 m, 11.6.1990. Scale 50 μm.



C: *Apoglossum ruscifolium*. Antheridia (lower arrow) between veins of the blade (upper arrow). Tønneberg Banke, 12 m, 12.8.1990. Scale 50 μm.

D: *Apoglossum ruscifolium*. Gonimocarp from midrib of blade. Pericarp with ostiole on a small exit tube (arrow). Tønneberg Banke, 14 m, 27.8.2013. Scale 100 µm.



E: *Apoglossum ruscifolium*. Tetrasporangia on both sides of the midrib. Tønneberg Banke, 15 m, 12.8.1990. Scale 100 µm.

Delesseria sanguinea

(Hudson) J.V.Lamouroux

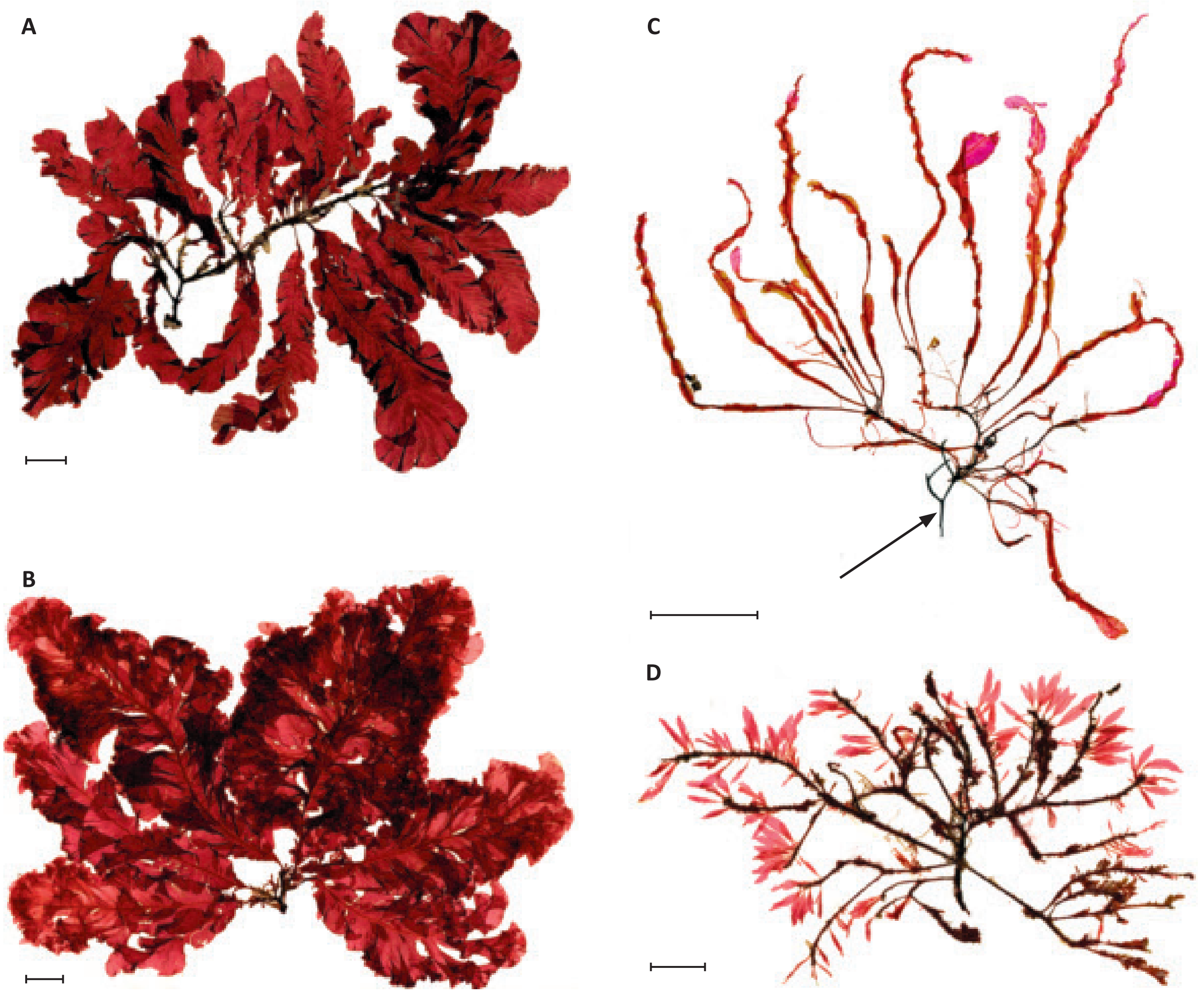
Sea Beech

Appearance: Red lanceolate to oval blades, up to 30 cm in height. The blades have a short stipe and a prominent midrib with opposite veins. Older blades may have secondary veins growing downwards in relation to the apex of the blade. The older and lower part of blades often decay leaving the midrib as a continuation of the stipe. The blades are flat, wavy or ruffled along the margin. Thalli are branched several times with new blades arising from the midrib of older blades. Individuals attach to the substratum by a small disc-shaped base. The size and the shape of individual blades varies according to the locality. Generally, the size decreases towards Bornholm, where the specimens are relatively small with narrow ribbon-shaped blades. Large individuals with several generations of blade are frequent in the deeper parts of the Great Belt. In the Northern Kattegat and in the Great Belt Area individual blades become 7-18.5 cm in height and 1.5-7.5 cm in width.

Structure: Thallus constructed as a flat, uniaxial syntagma, axial cells elongate with the longitudinal growth of the blades, and cortical cells on the axial cells form a midrib. There is a secondary partition of periaxial and other cells in the blade. Formation of segments of the blade develop regularly with first order lateral filaments at the top of each segment. Second order and following orders of filaments usually grow downwards (abaxial). Cortical cells also form on first and second orders of lateral filaments and they become veins, growing downwards in the blade (figure C p. 201).

Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. The reproductive structures form on small blades along the midribs of old decayed blades in autumn and winter. Antheridia develop on both sides of the blade along the midrib, but gradually cover the small blade. Gonimocarps develop singly in the middle of the small blade, appear spherical and have a protruding ostiole at maturity. Tetrahedrally divided tetrasporangia form on both sides of elongated oval small blades. Antheridia and tetrasporangia occasionally observed on the same individual.

Seasonal variation: Perennial, new blades arise from the midrib of decayed specimens, usually in January-March and are well-developed in June. Commonly overgrown by other algae in summer months and decaying in August-September, with only the midribs



A: *Delesseria sanguinea*. Relatively long lanceolate blades. Herthas Flak, 13 m, 12.6.1990. Scale 2 cm.

B: *Delesseria sanguinea*. Wide wavy blades. Briseis Flak, 8 m, 8.6.1989. Scale 2 cm.

C: *Delesseria sanguinea*. Narrow ribbon-shaped blades. Epiphytic on Black Scour Weed (*Ahnfeltia plicata*) (arrow). Christiansø, 15 m, 16.9.2009. Leg.: S. Krogsbøl. Scale 2 cm.

D: *Delesseria sanguinea*. Young light red blades from the previous year's midribs. Sheltered side, northern harbour jetty, Lynæs, 0.5 m, 15.2.1993. Leg.: H. Gøtzsche, P. Corfixen & R. Nielsen. Scale 2 cm.

remaining in the winter months. The reproductive structures develop from the overwintering midribs in autumn and winter. Antheridia recorded in September, gonimocarps in September, January-May, and tetrasporangia in November, January-April.

Habitat: On boulders and epiphytic on other perennial algae such as Stalked Leaf Bearer (*Phyllophora pseudoceranoides*), stipe and holdfast of Kelp (*Laminaria* sp.). Collected by divers, 1.5-24.5 m depth, and in older collections by dredge, 45 m depth, probably a drift individual.

Comment: Culture studies have documented the occurrence of special brackish water forms in the Baltic Sea with growth rate adapted to the low salinity (Rietema, 1993).

References: Lundsteen (1980), Rietema (1993).

E: *Delesseria sanguinea*. Tetrasporophyte, small blades of dark tetrasporangia. Scale 2 cm. E-F: Gilleleje, drift, 30.1.1964. Leg. & det.: T. Christensen.

F: *Delesseria sanguinea*. Female gametophyte, small spherical blades with gonimocarps (arrow). Scale 2 cm.

G: *Delesseria sanguinea*. Blade of male gametophyte, completely covered by antheridia. Hatter Barn, 7 m, 18.9.1993. Scale 100 µm.

Membranoptera alata

(Hudson) Stackhouse

Winged Weed

Appearance: Blades deeply incised with narrow lobes with entire margins, typically 2 mm in width, occasionally up to 4.5 mm in width, and up to 14 cm in height. Young blades are pink or light red, later become brownish red. The midrib is wide, slightly raised and there are slender, barely visible veins. The lobes of the blades develop at the apex, which often appears pseudodichotomously divided. In new lobes the adaxial side is narrower than the outer side. New blades develop from the base and from the margin of older eroded blades. The alga is attached by a disc-shaped holdfast. In the inner districts towards Bornholm the species is small and has blades with very narrow lobes.

Structure: Thallus constructed as a flat, uniaxial syntagma, where the axial and the periaxial cells elongate with the longitudinal growth of the blades and simultaneously with the formation of the cortex (figure D p. 201). The cortex spreads from the midrib over the inner part of the blade causing the midrib to appear continuous with the blade membrane, although there is always a border of the blade without cortex. In the lateral cell rows, the cells elongate and some form narrow veins in the blade, a few with cortex. The formation of segments is regular with first order lateral filaments at the top of each segment. The direction of the following rows of lateral filaments is mainly downwards (abaxial). There are no intercalary cell divisions (figure D p. 201). The new lobes develop from scattered first order lateral filaments where the apical cell grows above the margin of the blade and becomes the apical cell of the new lobe.

Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Reproductive structures develop in the upper part of blades or on special small blades. Antheridia cover the surface except for a narrow vegetative border. Gonimocarps develop singly, are rounded without a protruding ostiole. Tetrasporangia develop at the distal part of blades on both sides of the midrib.

Seasonal variation: Perennial, growth begins in early spring and ceases in summer month. Antheridia recorded in September-November, gonimocarps and tetrasporangia in December-April. Young individuals collected in July.

Habitat: On boulders and coarser algae such as Clawed Fork Weed (*Furcellaria lumbricalis*), Lobed Leaf Bearer (*Coccotylus brodiei*), Stalked Leaf Bearer (*Phyllophora pseudoceranoides*), Oar Weed (*Laminaria digitata*) and Forest Kelp (*L. hyperborea*). Collected by divers, 1-21 m depth and in older collections by dredge, 27 m depth.

Resembles: Appearance of young individuals similar to young Northern Tooth Weed (*Odonthalia dentata*) but in this species the cortex reaches the margin of the thallus very early on. Furthermore, the apical cells of the first order lateral filaments are in the lower part of the segments. The border of the blades in Winged Weed (*M. alata*) are monostromatic with apical cells in the upper part of the segments.

Comment: Growth experiments have documented brackish water forms in the Baltic Sea (Rietema, 1993).

References: Christensen (1980), Maggs & Hommersand (1993), Rietema (1993), Rosenvinge (1923-24).

A

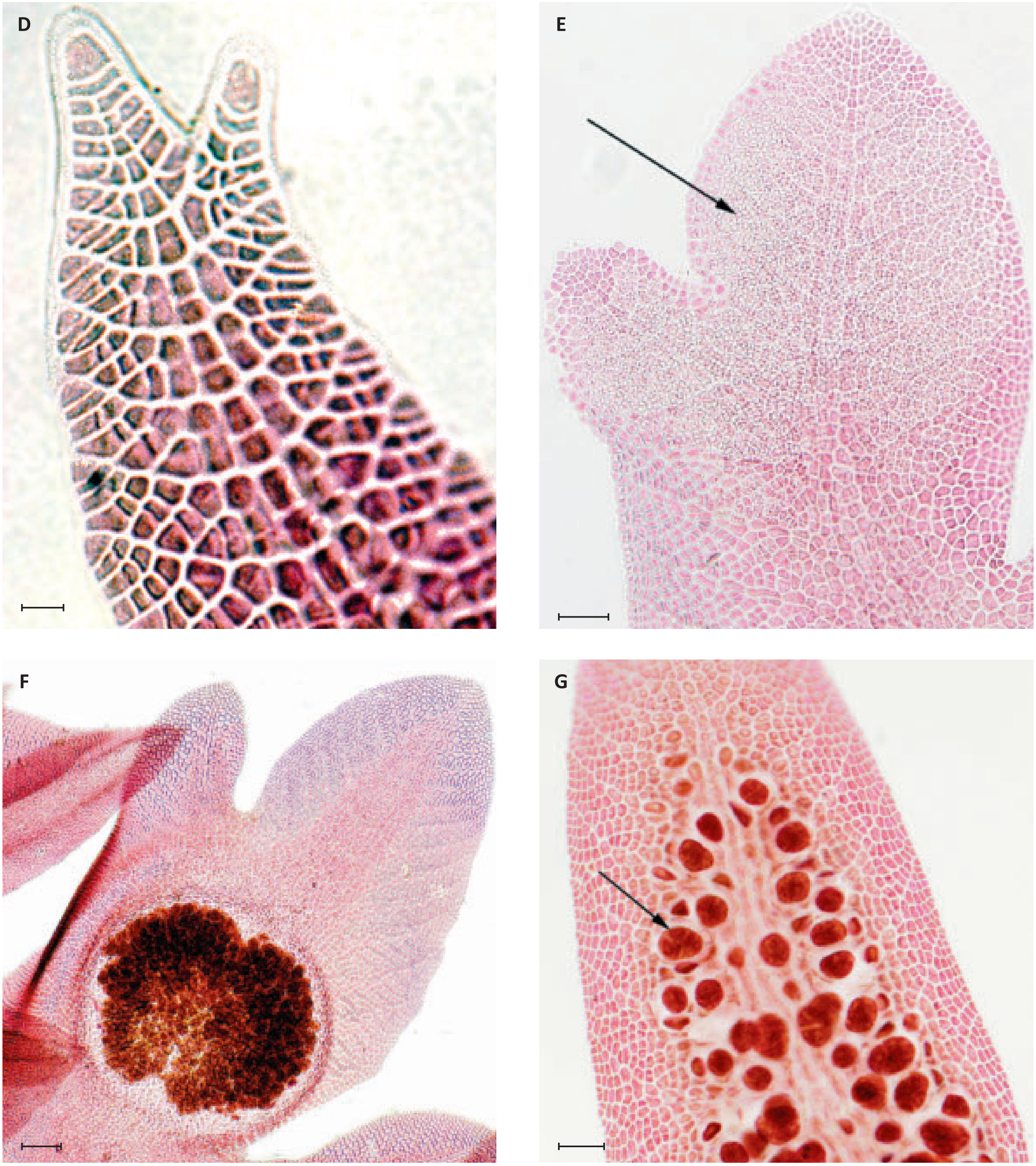
B

C

A: *Membranoptera alata*. Blades in one plane with ribbon-shaped lobes. Ebbeløkke, 11 m, 26.7.1994. Scale 2 cm.

B: *Membranoptera alata*. Specimens with very narrow lobes. Møns Klint, 17 m, 2.9.2004. Scale 2 cm.

C: *Membranoptera alata*. Tetrasporophyte with dark patches of tetrasporangia on lobe apices (arrow). Hirsholm, drift, 22.3.1989. Scale 2 cm.



D: *Membranoptera alata*. Apex with a new lobe. Scale 10 µm. D-E: Hatter Barn, 7 m, 18.9.1993.

E *Membranoptera alata*. Male gametophyte, area of pale antheridia (arrow). Scale 50 µm.

F: *Membranoptera alata*. Female gametophyte, gonimocarp on a lobe. Stålhage, Hirsholm, 5.5 m, 3.2.1996. Scale 100 µm.

G: *Membranoptera alata*. Tetrasporophyte, tetrahedrally divided tetrasporangia (arrow) on both sides of midrib. Hirsholm, drift, 27.12.1985. Scale 50 µm.

Phycodrys rubens

(Linnaeus) Batters

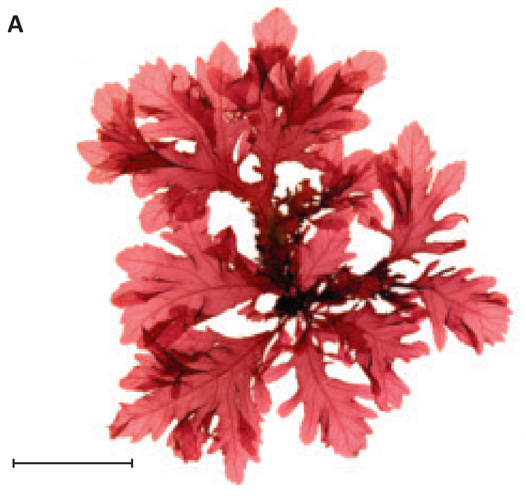
Sea Oak

Appearance: Red to brownish red alga, blades with a lobed outline resembling oak leaves, up to 18 cm in height. The blades have a midrib and opposite or slightly displaced veins. Older broad blades may have secondary veins growing upwards and downwards in relation to the apex of the blade. New light-coloured blades develop from the margin of older decayed blades, often in continuation of midribs and veins. The first blade in very young individuals often has a smaller blade growing from the stipe. The alga attaches to the substratum by a small disc-shaped holdfast. The lobes of the blades are typically rounded but they can be elongate. The variable shape includes thalli with narrow lobes from the tip or margin of the blades, these may develop small branch systems or rhizoid-like filaments. They entangle the alga together or attach them to other algae. Even secondary holdfasts may develop from the margin of old blades. In the inner waters towards the Baltic Sea the alga is very delicate with narrow blades.

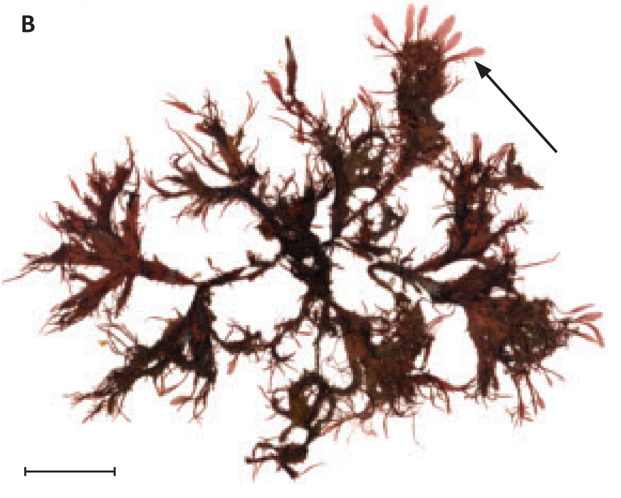
Structure: Thallus constructed as a flat, uniaxial syntagma, the axial and periaxial cells divide simultaneously with the longitudinal growth of the blades. From the first order lateral filaments second order lateral filaments grow downward, with a few of them in an upward direction. There are many intercalary cell divisions, making the filaments and blade segments difficult to follow (figure E p. 201). Cortical cells around the central axial cells form the midrib. Veins are formed by cortical cells around the lateral filaments. The margin is dentate except in very young individuals where it is typically regular.

Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Reproductive structures form at the border of the blades sometimes in special lobes or small blades. Antheridia form a colourless area in small lobes with a vegetative margin. Gonimocarps develop at the margin of blades or in small lobes, they are rounded to spherical structures without a protruding ostiole. Tetrasporangia develop from cortical cells on both sides of small lobes.

Seasonal variation: Perennial, blades decay in autumn months. The midribs, veins and part of the blades remain in winter. The growth of new blades begins in early spring from the margin of the old thallus. Antheridia recorded in September, November

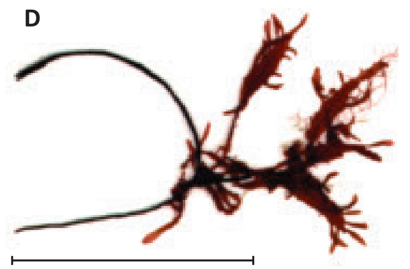


A: *Phycodrys rubens.* Light red in spring, blades like oak-leaves, midrib and veins visible. Vejrø, 8 m, 19.4.1989. Scale 2 cm.

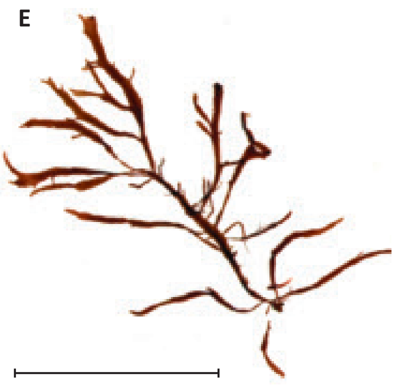


B: *Phycodrys rubens.* Dark old blades with narrow lobes from the margin and new light red blades (arrow). Søndre Stenrøn, 12 m, 7.9.1993. Scale 2 cm.

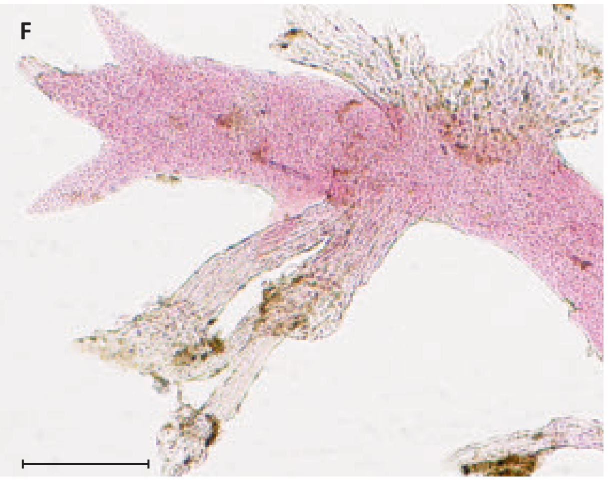
C: *Phycodrys rubens*. Young light red blades on dark old alga. Vejrø, 16.5 m, 2.6.1989. Scale 2 cm.



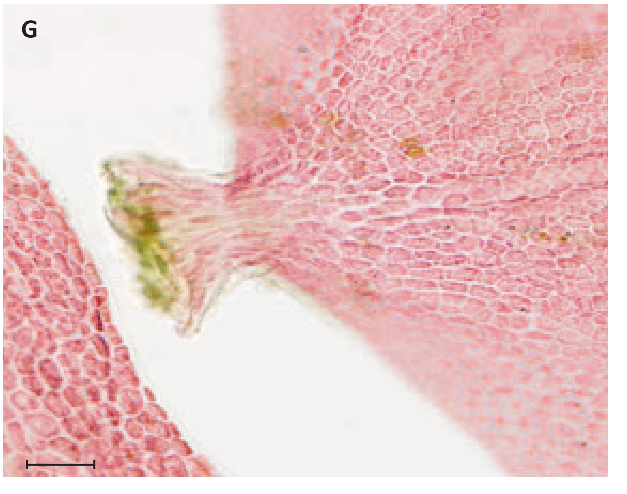
D: *Phycodrys rubens*. Delicate small alga on Clawed Fork Weed (*Furcellaria lumbricalis*). Hasle, Bornholm, 15 m, 25.8. 2008. Leg.: C. Darling. Scale 2 cm.



E: *Phycodrys rubens*. Very narrow blades. Hulle Havn, Bornholm, 17 m, 19.6.2008. Leg.: C. Darling. Scale 2 cm.



F: *Phycodrys rubens*. Apex of narrow lobe of blade with outgrowths for secondary attachment. Munkegrunde, 11 m, 4.8.1994. Scale 250 µm.



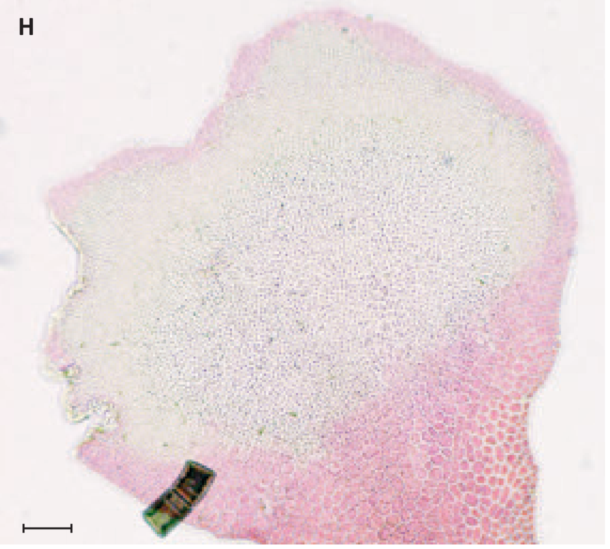
G: *Phycodrys rubens*. Secondary holdfast from edge of blade. Kims top, 15.5 m, 15.1.1997. Scale 50 µm.

and January, gonimocarps in March and tetrasporangia in December-May.

Habitat: On solid substrata of boulders and mollusc shells and epiphytic on coarser algae such as Clawed Fork Weed (*Furcellaria lumbricalis*), Lobed Leaf Bearer (*Coccotylus brodiei*), Stalked Leaf Bearer (*Phyllophora pseudoceranoides*), stipe and holdfast of Oar Weed (*Laminaria digitata*) and Forest Kelp (*L. hyperborea*). In the Northern Kattegat, 1.5-21 m depth, in shallow water only at shaded places. In the inner water districts only below 3 m depth.

Comment: Growth experiments have documented brackish water forms from the Baltic Sea (Rietema, 1991).

References: Maggs & Hommersand (1993), Rietema (1991), Rosenvinge (1923-24), Wynne (1997).



H: *Phycodrys rubens.* Pale antheridia on small lobe. Lysegrund, 6.5 m, 19.1.1997. Scale 100 µm.

I: *Phycodrys rubens.* Female gametophyte with gonimocarps on small lobes (arrow). Scale 2 cm. I, K: Albatros, 7.5 m, 8.3.1997.

J: *Phycodrys rubens.* Lobe with gonimocarp (slightly pressed). Jessens Grund, 8 m, 7.3.1997. Scale 100 µm.

K: *Phycodrys rubens.* Tetrasporophyte with small dark lobes of tetrasporangia (arrow). Scale 2 cm.

L: *Phycodrys rubens.* Lobe with tetrahedrally divided tetrasporangia (arrow). Tønneberg Banke, 14.5 m, 16.1.1997. Scale 100 µm.

Family: Rhodomelaceae · Subfamily: Rhodomeloideae · Tribe: Chondrieae

Chondria dasyphylla

(Woodward) C.Agardh

Diamond Cartilage Weed

Appearance: A single or a few upright branches arise from a disc-shaped base. They are transparent, light purplish red or light reddish brown and up to 5-8 (-14) cm in height. The thallus has a main branch with scattered branches on all sides. The branches have a narrow base and are short cylindrical to club-shaped, 1-10 mm in length.

Structure: The axial cells of the uniaxial syntagma are easily seen in optical section by microscopic examination. The apical cell is at the base of a small depression, from which protrude pseudodichotomous trichoblasts without plastids. There are 5 periaxial cells, from where a few cell layers are cut off towards the surface. The outermost layer is a monostromatic cortex of small cells with many secondary pit connections. The cortex covers a medullary layer of larger cells. In the lower part of the thallus the medullary cells and the periaxial cells are woven together by narrow filaments.

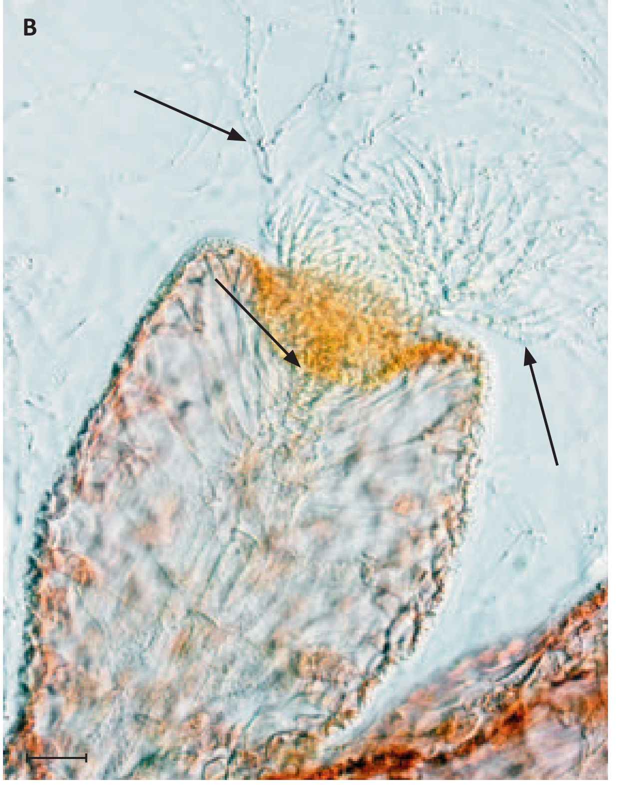
Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Antheridia form from the surface cells of small plate-shaped branchlets with relatively large cells at the margin. Gonimocarps are sessile or on short stalks on branches in the upper part of the thallus. The pericarps are ellipsoid to sphaerical, almost transparent and without a protruding ostiole. Tetrahedrally divided tetrasporangia occur among the cortical cells in club-shaped branches.

Seasonal variation: Collected in June-September, antheridia and gonimocarps recorded in August and tetrasporangia in August-September.

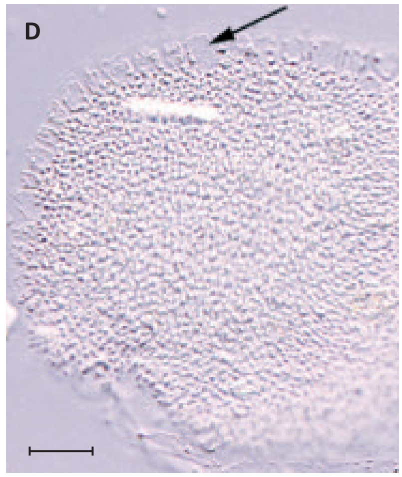
Habitat: On pebbles and boulders, 0.5-1.5 m depth.

References: Falkenberg (1901), Gordon-Mills (1987), Kylin (1944), Maggs & Hommersand (1993), Nielsen (2002), Rosenvinge (1923-24).

A: *Chondria dasyphylla*. Short club-shaped branches on main branches. Horneks Odde, Læsø, 0.5 m, 24.8.2016. Leg.: K.L. Krabbe. Scale 2 cm.



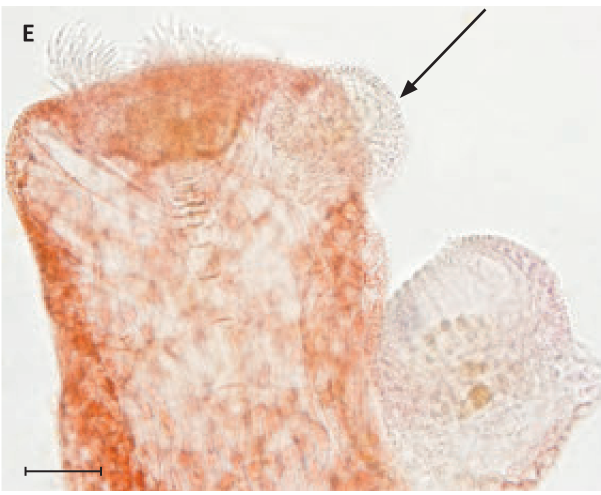
B: *Chondria dasyphylla*. Club-shaped branch, apical depression with the apical cell (lower left arrow) and pseudodichotomous trichoblasts (upper arrows). Optical longitudinal section. Scale 50 µm. B, D-F: Kallestrup, 1 m, 25.8.2009. Leg.: J. Deding.

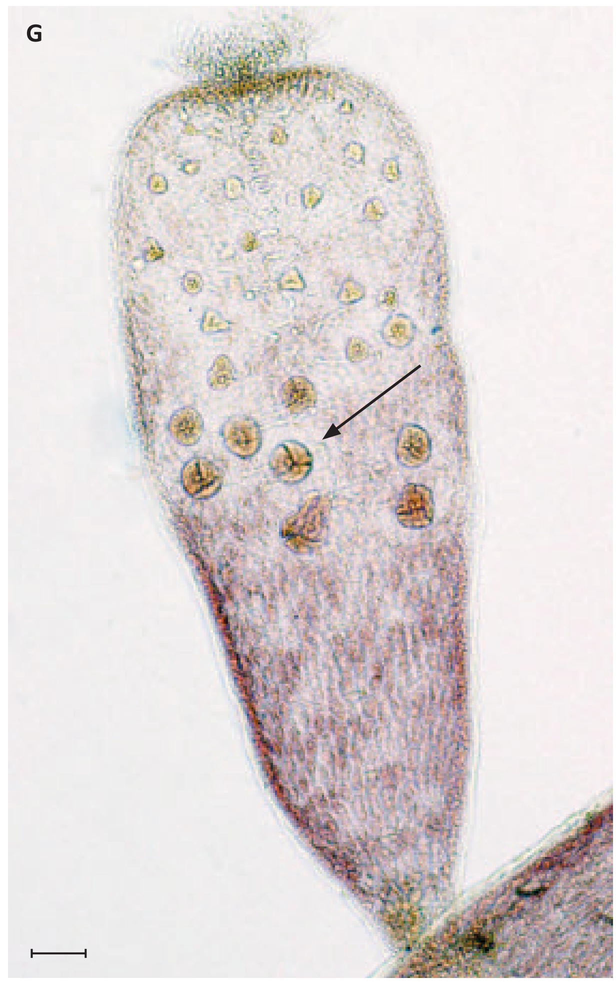


C: *Chondria dasyphylla*. Axial cell, 5 periaxial cells and surface of small cortical cells. Transverse section. Scale 50 µm. C, G: Beach south of Vesterø Havn, Læsø, drift, 13.9.2001.

D: *Chondria dasyphylla*. Disc-shaped male branchlet with relatively large cells at the margin (arrow). Antheridia cover the surface. Scale 50 µm.

E: *Chondria dasyphylla*. Apex of female gametophyte with young gonimocarp (arrow). Scale 100 µm.





F: *Chondria dasyphylla*. Gonimoblast with transparent pericarp. Scale 100 µm.

G: *Chondria dasyphylla*. Tetrahedrally divided tetrasporangia (arrow) in club-shaped branch. Scale 100 µm.

Tribe: Laurencieae

Osmundea oederi

(Gunnerus) G.Furnari

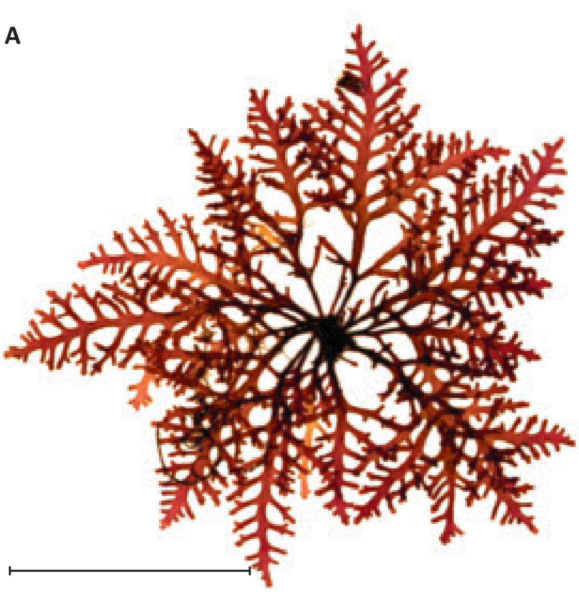
Flat Fern-weed

Appearance: Cartilaginous, stiff red-brown bush-like thalli, up to 5 cm in height, with one or several upright main branches arising from a disc-shaped base. There is a conspicuous main branch with distichous alternating branches. The branches may be 1-1.5 mm in width and in one plane, but oval in transverse section. The apex is obtuse with a slight depression. Young branches are cigar-shaped or cylindrical with a constricted base.

Structure: Uniaxial syntagma with a well-developed cortex. The axial cells only visible at the apex just below the apical cell at the base of the depression. Pale, pseudodichotomously branched trichoblasts protrude from the depression. Cortical cells are irregularly rounded with secondary pit connections between them.

Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. The apex of the branches in male gametophytes are bowl-shaped with dense antheridial filaments at the base. The antheridia are small spherical cells, lateral on unbranched, uniseriate upright filaments with a balloon-shaped apical cell. The gonimocarps are spherical with an exit pore but no protruding ostiole. Tetrahedrally divided te-

A



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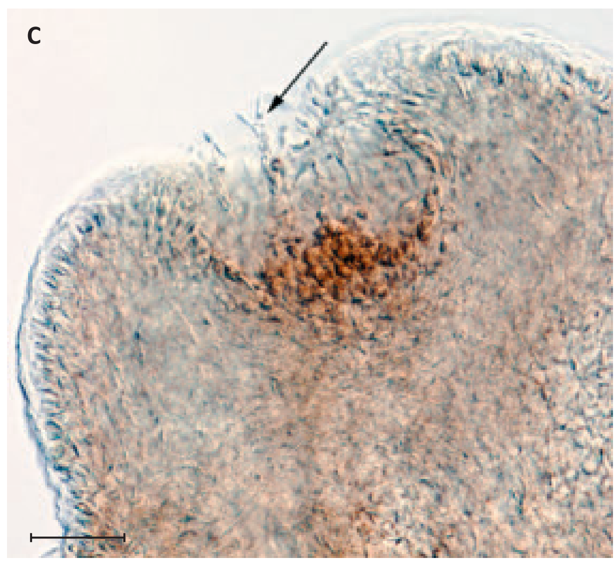


A: *Osmundea oederi*. Several upright main branches from a disc-shaped base. Beach south of Vesterø Havn, Læsø, drift, 7.4.1985. Scale 2 cm.

B: *Osmundea oederi*. Alga with flat branches. Tile works, Helligsø, drift, 27.10.1974. Scale 2 cm.

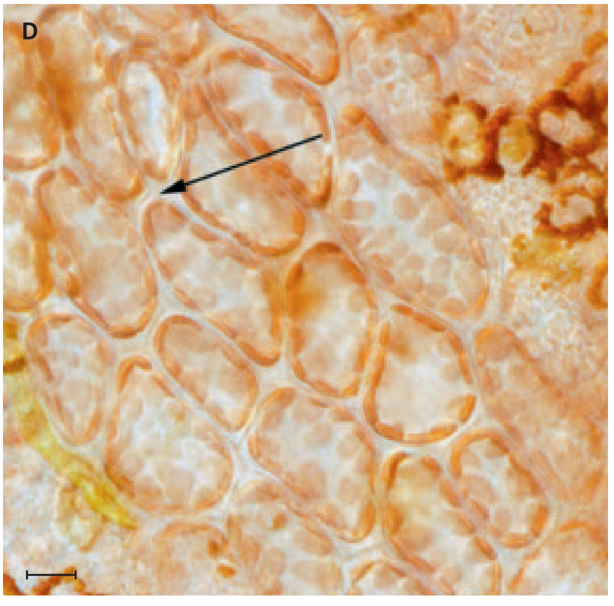
C: *Osmundea oederi*. Apical cell at the bottom of the depression with trichoblasts (arrow), optical longitudinal section. Scale 50 µm. C, K: Præstebugten, Hirsholm, 0.5 m, 9.7.1999.

trasporangia occur scattered between the surface cells in the youngest branches.

Seasonal variation: Collected all year. Antheridia recorded in May-October, December, gonimocarps in June-August, December and tetrasporangia in May-September, December.

Habitat: Commonly epiphytic on Serrated Wrack (*Fucus serratus*) and Bladder Wrack (*F. vesiculosus*), coarse red algae and on small stones. Collected by hand, 0.5-2.5 m depth. In older collections by dredge to 10 m depth.

Comment: *Osmundea* was separated from *Laurencia* by Nam et al. (1994). The collections from Danish waters in the algal herbarium, Natural History Museum of Denmark previously referred to *L. pinnatifida* (Hudson) J.V.Lamouroux, were studied and reidentified to *O. truncata*. Nam et al. (2000) separated *O. oederi* (as *O. ramosissima* Athanasiadis) from *O. truncata*. Later



E

F

G

D: *Osmundea oederi.* Surface cells with many disc-shaped plastids and secondary pit connections between cells (arrow). Hirsholm, 0.5 m, 14.4.2015. Scale 10 µm.

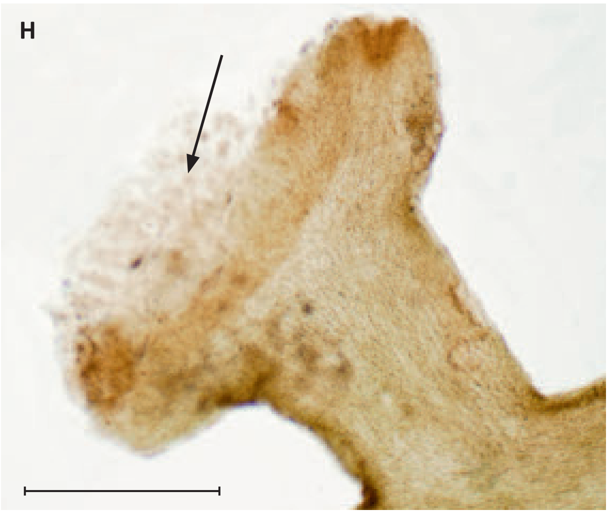
E: *Osmundea oederi.* Male gametophyte, apex of branches bowl-shaped. Scale 2 cm. E-G: Tile works, Helligsø, 0.5 m, 30.12.1971. Leg.: T. Christensen.

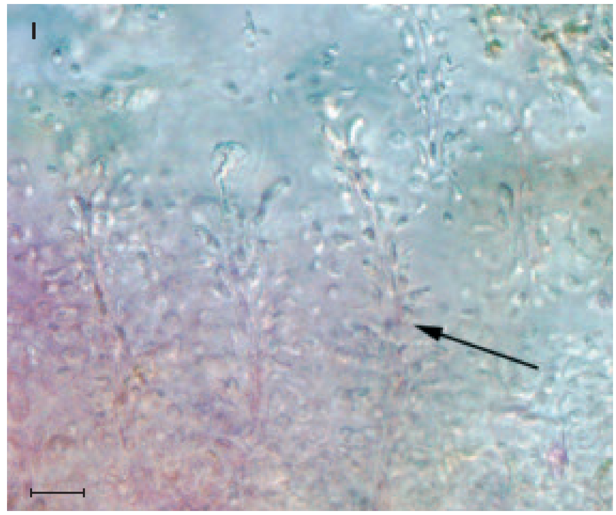
F: *Osmundea oederi.* Female gametophyte, apex of branches rugged. Scale 2 cm.

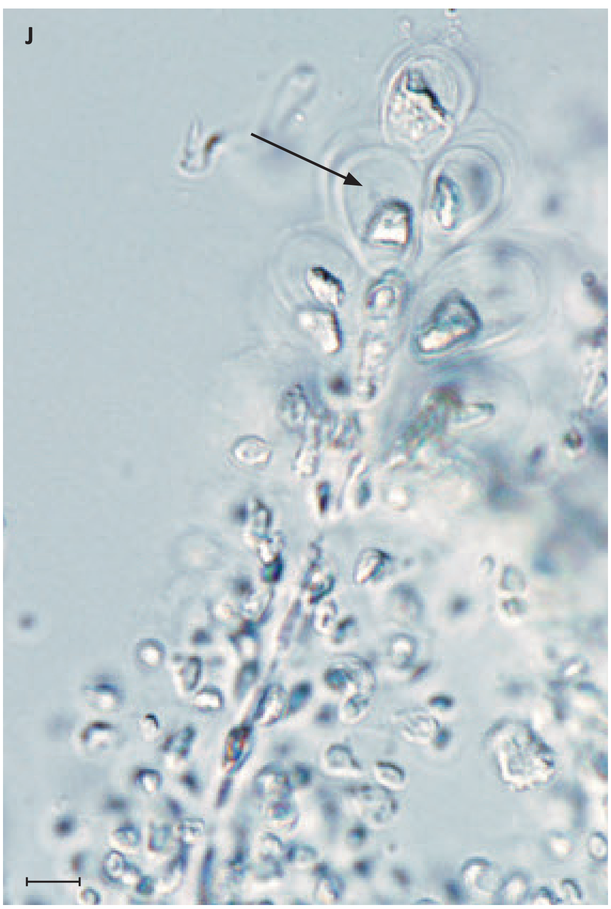
G: *Osmundea oederi.* Tetrasporophyte, apex of branches thick and short. Scale 2 cm.

O. ramosissima Athanasiadis was found to be illegal and *O. oederi* proposed as a replacement by McIvor et al. (2002). The combination *O. oederi* first published by Furnari in Serio et al. (2008).

References: McIvor et al. (2002), Nam et al. (1994, *O. truncata*), Nam et al. (2000, *O. ramosissima*), Rosenvinge (1923-24, *Laurencia pinnatifida*), Serio et al. (2008).







H: *Osmundea oederi.* Bowl-shaped apex with antheridial filaments (arrow). Tile works, Helligsø, 1 m, 10.8.1998. Leg.: L. Knudsen. Scale 500 µm.

I: *Osmundea oederi.* Dense antheridial filaments (arrow). Scale 20 µm. I-J: Nordre Rønner, Læsø, 0.5 m, 24.5.2005.

J: *Osmundea oederi.* A single antheridial filament with lateral antheridia and balloon-like apical cells (arrow). Scale 10 µm.

K: *Osmundea oederi.* Spherical gonimocarp with exit pore (right arrow). A small branch with apical depression (left arrow). Scale 100 µm.

Tribe: Polysiphonieae

Carradoriella, Leptosiphonia, Melanothamnus, Polysiphonia and *Vertebrata*

Siphon Weeds

Appearance: Much and repeated branched bush-like algae, 2-25 cm in height. In some species all the branches are alike while other species have a distinct main branch with slender branches. The base consists of prostrate filaments matted together with an open branching pattern or merged and disc-shaped.

Structure: Uniaxial syntagma of similar segments. Each segment consists of a cylindrical central axial cell surrounded by 4-20 periaxial cells all the same height as the axial cell. The number of periaxial cells is species-specific and an important key character. A cortex of small cells arises from the periaxial cells in some species. The cortex may have several cell layers and completely cover the lower part of branches. The prostrate branches are attached to the substratum by small attachment pads on short rhizoids that arise from the periaxial cells or from down growing cortical filaments. The vegetative cells contain many disc-shaped to oval or irregularly-shaped plastids. Trichoblasts are uniseriate branches that form a spiral at the apex with a single trichoblast per segment. They are pseudodichotomously branched or unbranched with relatively long, narrow cylindrical cells and in most cases colourless. They are frequent at the apex of the alga when growing vigorously. The basal cell of the trichoblasts is round and persists as a scar cell after the trichoblasts are cast off. The primary branches develop at the apex. In some species these are as a replacement for trichoblasts and in other species develop in the axil of a trichoblast. Secondary branches form further down the branches. They develop from the scar cells of trichoblasts or from the axial cells (endogenous).

Reproduction: Isomorphic dioecious male and female haploid gametophytes and a diploid tetrasporophyte. On the male gametophytes, the antheridia are surface cells in special antheridial branchlets that develop on or replace the trichoblasts. They are cylindrical or slightly conical with or without sterile cells at the apex. In the female gametophytes, carpogonia develop with trichogynes on branchlets (carpogonial branches). After fertilization the diploid carposporophyte develops as a dense clump of cells (gonimoblast) with elongate or club-shaped carposporangia at maturity. The gonimoblast is surrounded by a pericarp that develops, from the haploid female gametophyte. The tetrasporophyte has a single tetrasporangium per segment, often in several consecutive segments and the tetrasporangia occur in straight or spirally twisted series. Tetrasporangia are spherical and tetrahedrally divided.

Comment: The group contains a great number of species in several genera, but the genus delimitation is difficult. Generic concepts have often changed and the revision continues with morphological characters supported by genetic data (Díaz-Tapia et al., 2017, Savoie & Saunders, 2019). This has caused many name changes of the genera. For species in Danish waters, this particularly concerns those previously referred to *Polysiphonia*.

References: Batten (1923), Choi et al. (2001), Díaz-Tapia & Bárbara (2013), Díaz-Tapia et al. (2017), Falkenberg (1901), Kim & Lee (1999), Kjellman (1883), Kornmann & Sahling (1977), Kylin (1944), Maggs & Hommersand (1993), Rosenvinge (1923-24), Rueness (1977), Savoie & Saunders (2019), Stuercke & Freshwater (2008).

Identification key to species of Polysiphonieae

(*Carradoriella, Leptosiphonia, Melanothamnus, Polysiphonia* and *Vertebrata*)

1a.	Red permanent trichoblasts with plastids	*V. byssoides*
1b.	Trichoblasts typically without plastids or not present	2
2a.	4-5(-6) periaxial cells	3
2b.	6 or more periaxial cells	10
3a.	4 periaxial cells	4
3b.	5-6 periaxial cells, with cortex. Bush-like red alga with a tufted growth of ascending filaments from extended prostrate branches. Rhizoids cut off from periaxial cells by a cross wall. The primary branches arise in the axil of trichoblasts	*P. kieliana*
4a.	One upright main branch from the base, pseudodichotomous main branches. Primary branches replace trichoblasts	5
4b.	One or more upright main branches from the base, scattered branches	6
5a.	Coarse bush-like alga with a cone-shaped base, branches straight and cortex well-developed. Branches with a narrow base	*C. elongata*
5b.	Delicate alga with a disc-shaped base, branching regularly repeated. Often with bisporangia	*C. elongella*
6a.	Branches without cortex	7
6b.	Branches with cortex	8
7a.	Uprights arise from extended prostrate branches and become tufts or bush-like of narrow branches. Rhizoids not separated from periaxial cells by a cross wall. Primary branches replace trichoblasts	*P. stricta*
7b.	Uprights arise from a dense base and form much branched bush-like alga. Rhizoids separated from periaxial cells by a cross wall. Primary branches arise in the axil of trichoblasts (in the Limfjord)	*P. orthocarpa*
8a.	Bush-like alga with conspicuous main branches and well-developed cortex	9
8b.	Bush-like alga without conspicuous main branches. Segments 4-7 times as long as wide, with sparse cortex	brackish water forms of *C. elongata* and *L. fibrillosa*
9a.	Much branched dark red-brown coarse bush-like alga or slender red bush-like alga. Periaxial cells appear transparent without plastids along the outer walls, only along radial walls. Primary branches replace trichoblasts	*M. harveyi*
9b.	Much branched dark red-brown to straw-yellow bush-like alga with slender scattered branches. Periaxial cells with plastids along the outer walls. Primary branches arise from the axil of trichoblasts	*L. fibrillosa*

10a.	6-8 periaxial cells. Conspicuous main branch with fascicles of short branches in the upper part of the alga. Primary branches arise from the axil of trichoblasts. Lower littoral on wave-exposed localities	*L. brodiei*
10b.	10 or more periaxial cells	11
11a.	Tufts on *Ascophyllum nodosum,* 2-3 cm in height. Pseudodichotomous branches with 20 or more periaxial cells without cortex and no trichoblasts. Only records of drift algae in Danish waters	*V. lanosa*
11b.	Main and lateral branches, there are 10-20 periaxial cells	12
12a.	Branches with cortex, which may be sparse but visible at the base. Main branches often with distichous alternating branches at the apex. (10-) 12-17 (-20) periaxial cells. Primary branches replace trichoblasts	*V. fucoides*
12b.	Branches without cortex. Conspicuous main branches commonly 'S-shaped' curved at the apex. Short adpressed branches in small fascicles. (8-) 9-13 periaxial cells. Primary branches arise from the axil of trichoblasts.	*V. nigra*

Carradoriella elongata

(Hudson) Savoie & G.W.Saunders

Recent synonym: ***Polysiphonia elongata*** **(Hudson) Sprengel**

Elongate Siphon Weed

Appearance: Well-developed specimens are typically coarse, stiff, red to brownish red and bush-like. They have a hemispherical outline and up to 30-40 cm in height. Other individuals can be open branched, have an elongate outline and a strong red colour, such algae mainly occur in the Great Belt and the archipelago of Smålandshavet, between Sealand (Sjælland) and Lolland. The alga has a single, upright main branch from a conical base. The main branch is up to 1.5 mm in width at the base and gradually taper in thickness to the apex. The lower 1-2 cm of the main branch lacks lateral branches. The main branch above this part is often one or several times pseudodichotomously branched and has many scattered lateral branches on all sides. The branches are straight and taper towards the apex. Herbarium specimens commonly become dark when dry. Very slender bush-like specimens in which it is difficult to distinguish between main and lateral branches occur in brackish water towards the Baltic Sea. Rosenvinge (1923-24) referred to them as *Polysiphonia elongata* f. *schuebeleri* (Foslie) Rosenvinge and *P. elongata* f. *baltica* Rosenvinge.

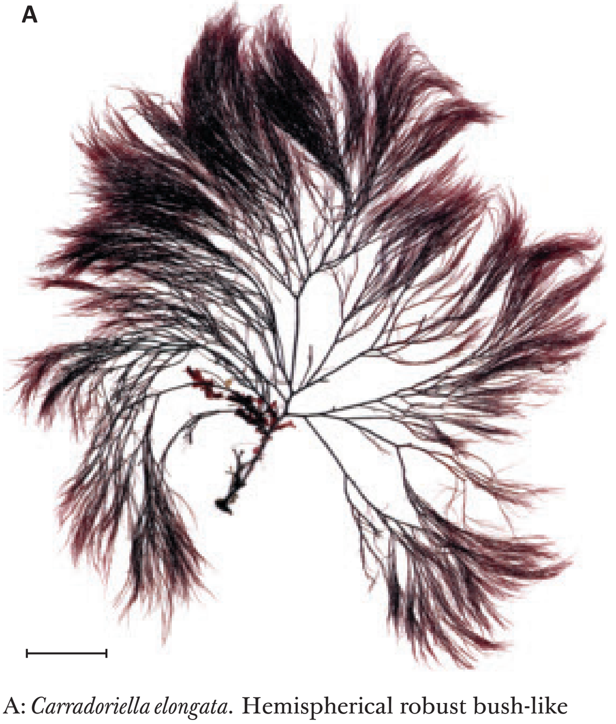
Structure: The branches consist of segments with 4 periaxial cells, 0.3-2 times as long as wide. Trichoblasts develop 4-5 segments below the apical cell, occurring in a spiral with a single trichoblast per segment and each with 1-3 branching points. Primary branches replace trichoblasts and form at intervals of (4-) 5 (-6) segments. Secondary branches are sparse and occur at irregular intervals. Lateral branches become narrower towards the apex and are frequently constricted at the base. Well-developed cortex with the first cortical cells just below the apex. The young cortical cells are elongate and cut off by a wall that runs approximately parallel to the longitudinal wall of the periaxial cell. The cortical cells typically arise from the middle or lower part of the periaxial cells. A secondary pit connection to a periaxial cell in the segment below frequently occurs. The cortical cells initiate the growth towards the apex, but soon after continue growth towards the base. Over time, the branches become completely covered by several layers of elongated cortical cells. The conical base of the alga consists of aggregated cortical filaments or rhizoids terminating in small attachment pads.

Reproduction: Antheridial branchlets develop as one of the branches at the first and sometimes the second and third branching points in modified trichoblasts. They are cylindrical or slightly conical and sometimes slightly curved. The gonimocarps are ovoid and have rows of angular pericarp cells that decrease in size towards the opening, which is bordered by relatively large cells. Tetrasporangia form long spiral series in lateral branches with narrow bases.

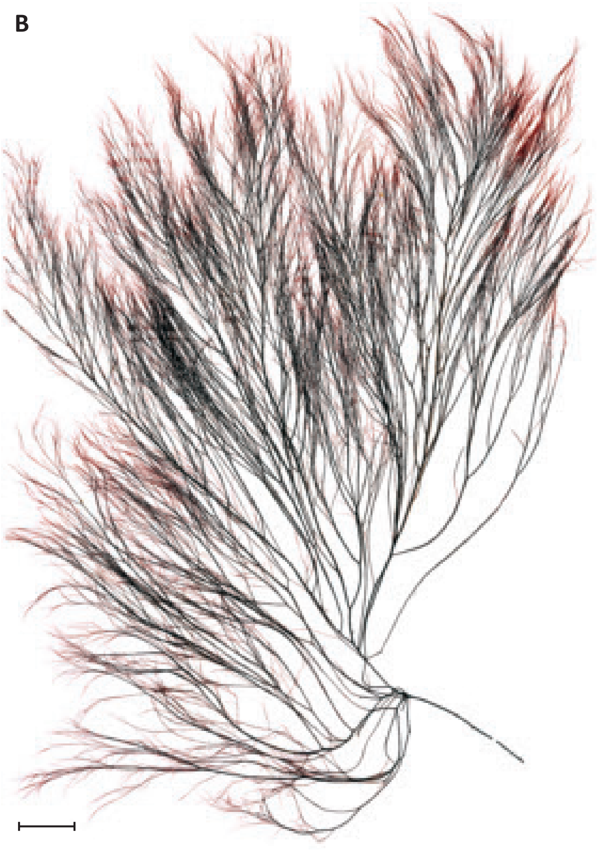
Seasonal variation: Perennial, the young branches worn away in the autumn, sometimes to such an extent that only a single unbranched branch remains. In the winter, new light-coloured branches appear from the upper part along old branches. The growth continues during summer when new individuals also appear. Antheridia recorded in January, March-June, August, gonimocarps in May-September and mature tetrasporangia in May-August.

Habitat: On boulders and epiphytic on coarse perennial red and brown algae such as Lobed Leaf Bearer (*Coccotylus brodiei*), and fronds of Oar Weed (*Laminaria digitata*). Common in the open vegetation of gravel seabeds. Collected by divers, 1-23 m depth.

A

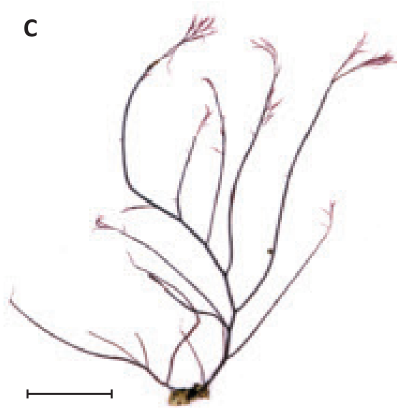


B

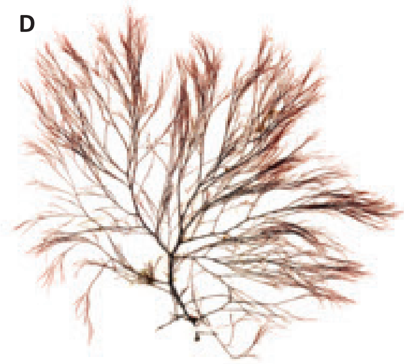


A: *Carradoriella elongata*. Hemispherical robust bush-like alga, main branches straight, pseudodichotomously branched with branches that become very narrow towards the apex. Briseis Flak, 9 m, 11.8.1990. Scale 2 cm.

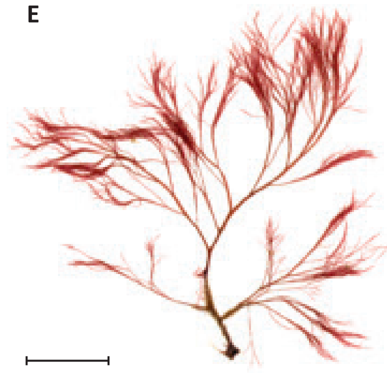
B: *Carradoriella elongata*. Very elongate alga with clear red branches. Kirkegrund, 13 m, 9.8.1992. Scale 2 cm.



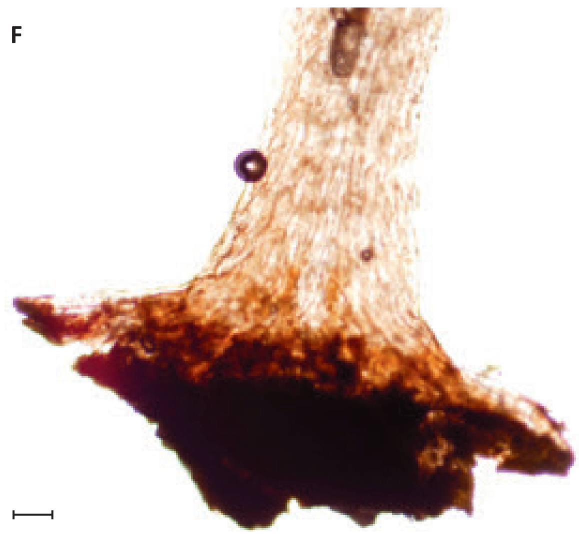
C: *Carradoriella elongata*. Decayed winter alga, with regrowth from the upper part. On a small bivalve shell. Tønneberg Banke, 14.5 m, 16.1.1997. Scale 2 cm.



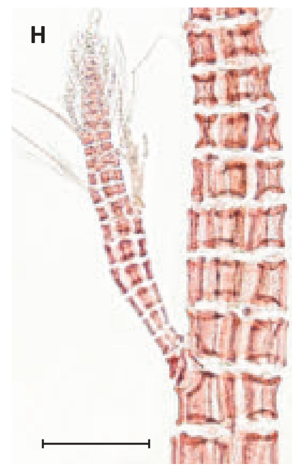
D: *Carradoriella elongata*. Relatively short alga with open branch angles, in shape intermediate between the specimens in figure A and B. Moselgrund Nord, 9 m, 3.8.1994.
Scale 2 cm.



E: *Carradoriella elongata*. Young alga. Store Middelgrund, 14 m, 4.6.1992. Scale 1 cm.



F: *Carradoriella elongata*. Conical base of an old alga, of aggregated cortical filaments with small attachment discs. Kims Top, 18.5 m, 15.1.1997. Scale 100 µm.



G: *Carradoriella elongata*. Apex, primary branch (arrow) replaces trichoblast. Herthas Flak, 20.5 m, 28.8.1993. Scale 100 µm.

H: *Carradoriella elongata*. Branch with narrow base. Hanklit, Thisted Bredning, 0.5 m, 19.8.2008. Leg.: J. Sund. Scale 50 µm.

f. *baltica*

Brackish water form of soft clear red bush-like individuals, much branched on all sides, up to 20 cm in height. The branches have an even thickness, 140-280 µm in diameter with segments, 4-7 times as long as wide. The cortex is sparse and branches are incompletely covered by the cortex. Cortical cells are cut off from the lower part of periaxial cells with a long, oblique wall. Trichoblasts are in general unbranched, but in rare cases have a single dichotomy, they contain pink plastids. Primary branches replace trichoblasts as in the typical form but might occur from basal cells of trichoblasts that still persist. Lateral branches not constricted at the base. Recorded from the area round Møn and Bornholm by Rosenvinge (1923-24).

f. *schuebeleri*

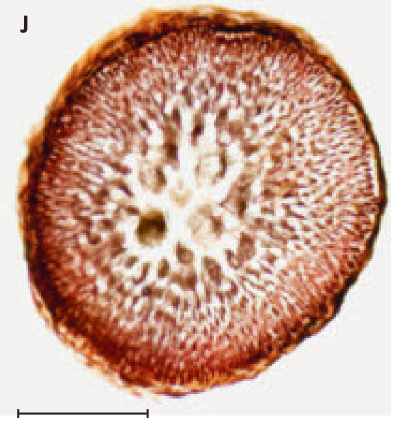
Brackish water form that is similar to f. *baltica*, but has main branches, 300-660 µm in width, and dichotomous branched trichoblasts. Recorded from the Great Belt by Rosenvinge (1923-24).

Resembles: The forms f. *baltica* and f. *schuebeleri* are similar in morphology to f. *tenuis* which is also found in brackish water and referred to *Leptosiphonia fibrillosa* (as *Polysiphonia violacea*) by Rosenvinge (1923-24). Primary branches in Elongate Siphon Weed (*C. elongata*) replace trichoblasts while the primary branches of Purple Siphon Weed (*L. fibrillosa*) are in the axil of trichoblasts, which is the same for the tiny forms.

Comment: The taxonomic status of the different forms, particularly the slender forms of the Baltic Sea, needs clarification using genetic analysis.

References: Kapraun & Rueness (1983, *Polysiphonia elongata*), Maggs & Hommersand (1993, *P. elongata*), Rosenvinge (1923-1924, *P. elongata*), Savoie & Saunders (2019), Schiffner (1939, *P. elongata*), Wærn (1952, *P. elongata*).

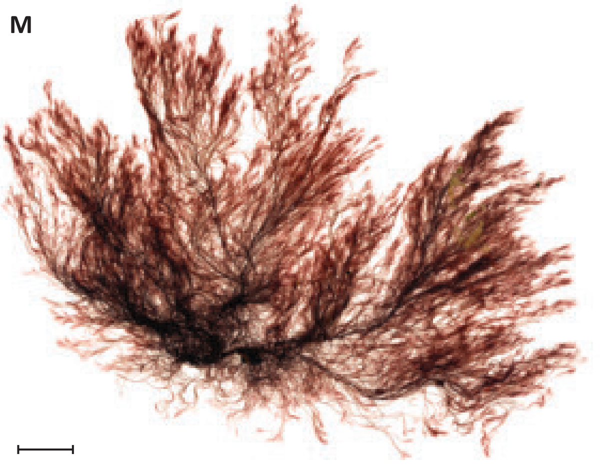
I: *Carradoriella elongata*. Young cortical cell (arrow), walls parallel to the periaxial cells. Alsund, the Little Belt, 5 m, 6.6.2009. Scale 200 µm. Photo by S. Lundsteen.



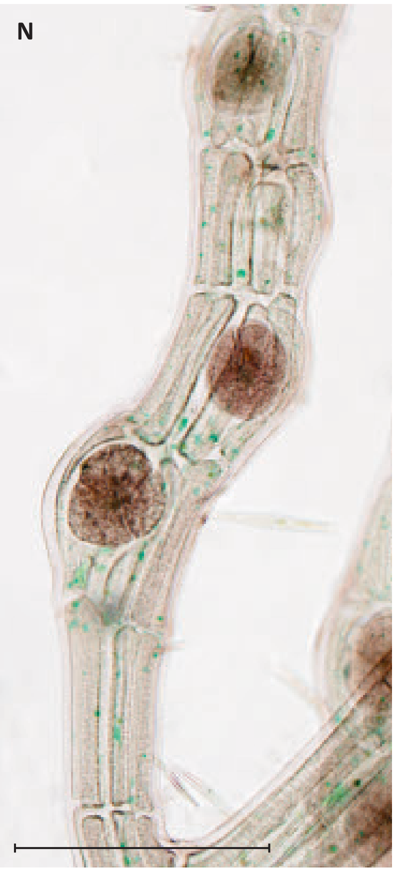
J: *Carradoriella elongata*. Axial cell, 4 periaxial cells and well-developed cortex, transverse section near the base. Beach north of Vesterø Havn, Læsø, drift, 25.3.2008. Scale 500 µm.

K: *Carradoriella elongata*. Apex of male gametophyte with slightly curved and conical antheridial branchlets. Arise from the 1 and 2 branching point of modified trichoblasts (arrow). Pullerterne NE of Hjelm, 8 m, 7.3.1997. Scale 50 µm.

L: *Carradoriella elongata*. Gonimocarp. Pericarp with large angular cells and a wide opening. Store Middelgrund, 9 m, 10.6.1991. Scale 100 µm.



M: f. *baltica*. Much branched bush-like alga with narrow scattered branches on all sides. Broens Odde, Bornholm, 9 m, 7.6.1990. Leg.: L. Mathiesen. Scale 2 cm.



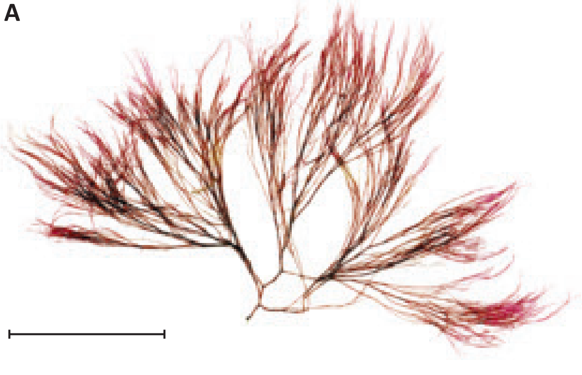
N: *Carradoriella elongata*. Branch with tetrahedrally divided tetrasporangia. Schultz's Grund, 8 m, 9.5.2000. Scale 100 µm.

O: f. *baltica*. Apex with unbranched trichoblasts (arrow) and primary branches replacing trichoblasts. Part of the same alga as in figure M. Scale 50 µm.

Carradoriella elongella

(Harvey) Savoie & G.W.Saunders
Recent synonym: *Polysiphonia elongella* Harvey
Fine Elongate Siphon Weed

Appearance: Delicate bush-like alga with a single upright main axis from a disc-shaped base. It is 2.5-6 cm in height, light red at the apex and slightly darker below. Branches on all sides, pseudodichotomous with a similar distance between the branching points, therefore the alga looks as if constructed in levels.
Structure: Uniaxial syntagma with 4 periaxial cells per segment, 1-3 times as long as wide. Transversely divided periaxial cells occasionally observed. The distance between the branching points varies from a few to 10 segments. The primary branches replace trichoblasts. Secondary branches seldom occur. The cortex is sparse with the first cortical cells occurring at 4 or more branching points below the apex. Cortical cells arise from the lower end of the periaxial cells and cut off by a curved wall. The disc-shaped base consists of matted cortical filaments with small attachment pads.
Reproduction: *Polysiphonia*-life history, but only bi-



A: *Carradoriella elongella.* Delicate pseudodichotomously branched alga, the youngest branches form soft tufts. Kims Top, 18 m, 18.8.2014. Scale 2 cm.

B: *Carradoriella elongella.* Apex, primary branch replaces trichoblast. Herthas Flak, 13 m, 14.8.2007. Scale 25 µm.

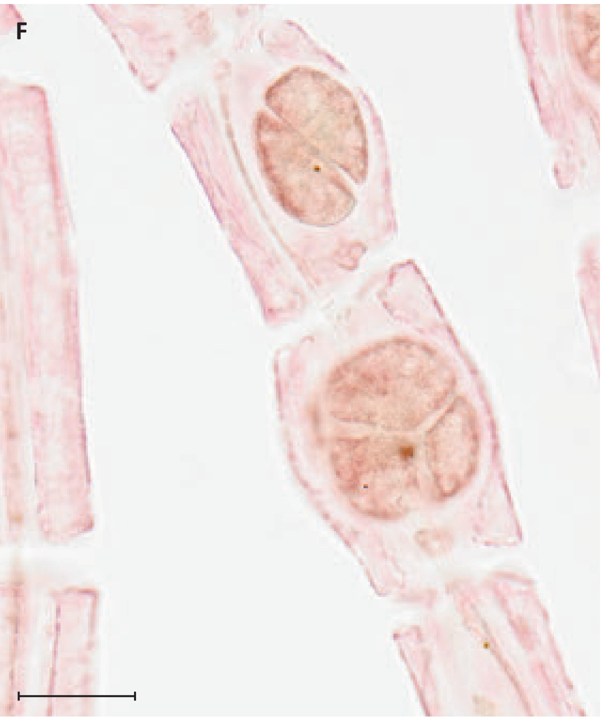
C: *Carradoriella elongella.* Uniform branching in upper part of alga, segments of 4 periaxial cells, still without cortex. Kims Top, 18 m, 18.8.2013. Scale 200 µm.

and tetrasporangia recorded on alga from Danish waters. The sporangia form spiral series in the youngest branches with a single sporangium per segment.
Seasonal variation: Few collections from Danish waters in August with bi- and tetrasporangia. Perennial in the British Isles where the fronds are worn to become denuded in winter and recover in spring.
Habitat: On small stones and epiphytic on Sea Beech (*Delesseria sanguinea*) and Sea Oak (*Phycodrys rubens*) on stone reefs, 14-21 m depth.
References: Lundsteen et al. (2008, *Neosiphonia elongella*), Maggs & Hommersand (1993, *Polysiphonia elongella*), Savoie & Saunders (2019).

D: *Carradoriella elongella.* First cortical cell (long, upper arrow) and cortical cells growing down the branch (short, lower arrow) (after the 8th branching point below apex). Herthas Flak, 20 m, 16.8.2008. Scale 50 µm.

E: *Carradoriella elongella.* Sporangia form spiral series in young branches. Kims Top, 16 m, 28.8.2013. Scale 200 µm.

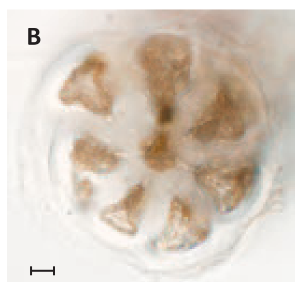
F: *Carradoriella elongella.* Bisporangium and tetrahedrally divided tetrasporangium. Kims Top, 18.5 m, 10.8.2004. Scale 50 µm.

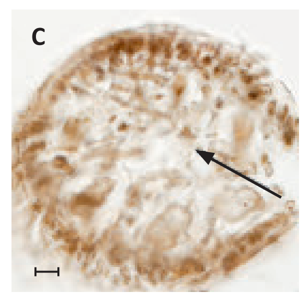


Leptosiphonia brodiei

(Dillwyn) Savoie & G.W.Saunders
Recent synonym: *Polysiphonia brodiei* (Dillwyn) Sprengel
Brodie's Siphon Weed

Appearance: Bush-like alga of several upright branches, up to 20 cm in height. They are delicate and soft brownish red or faded to straw-yellow in strong light. The main branches conspicuous approximately 0.5 mm across at the base. The branches scattered on all sides and in the upper part form fascicles of small branchlets. Basal system of dense short prostrate branches matted together to become disc-shaped.
Structure: Branches consist of segments with 6-8 periaxial cells, 1-2 times as long as wide. The main branches have a well-developed cortex of relatively long cells, while the outer small branches lack cortex. There are very narrow filaments between the axial cells and the periaxial cells in the lower part of thick branches. The primary branches develop in the axil of trichoblasts. The prostrate branches lack trichoblasts. The alga attaches by rhizoids separated by a cross wall from the periaxial cells or cortical cells in the lower part of upright branches.
Reproduction: Reproductive structures form at the branchlets in fascicles in the upper part of the alga. Antheridial branchlets develop as one of the branches at the first dichotomy of trichoblasts. They are cylindrical to slightly conical with a rounded apex without vegetative cells. Gonimoblasts develop on few-celled





A: *Leptosiphonia brodiei.* Bush-like alga of several uprights from a disc-shaped base. Main branches with fascicles of branchlets. Southern harbour jetty, Hirsholm, 0.2 m, 4.7.1984. Scale 2 cm.

B: *Leptosiphonia brodiei.* Axial cell and 7 periaxial cells, transverse section of young branch without cortex. Scale 10 µm. B-I: Rehydrated herbarium material. Southern harbour jetty, Hirsholm, 0.2 m, 11.7.2000.

C: *Leptosiphonia brodiei.* Narrow filaments (arrow) between axial cell and periaxial cells in lower part of older branch, transverse section. Scale 50 µm.

D: *Leptosiphonia brodiei.* Cortex of long cells, lower part of old branch. Scale 50 µm.

branches at the axil of trichoblasts. The ellipsoid to spherical pericarps have a wide opening and consist of cells in series, the upper ones delimiting the opening clearly larger than the rest. The tetrasporangia are in spiral series in the small branchlets which turn thick and dark.

E: *Leptosiphonia brodiei.* Rhizoids arise from cortical cells in lower part of upright branch. Scale 50 µm.

F: *Leptosiphonia brodiei.* Fascicle of branchlets with young gonimocarps. Scale 100 µm.

G: *Leptosiphonia brodiei.* Branchlet with tetrahedrally divided tetrasporangia (arrow). Scale 100 µm.

H: *Leptosiphonia brodiei.* Apex of male gametophyte, antheridial branchlets in the first dichotomy of a trichoblast (arrow). Scale 50 µm.

I: *Leptosiphonia brodiei.* Gonimocarp, optical longitudinal section. Scale 100 µm.

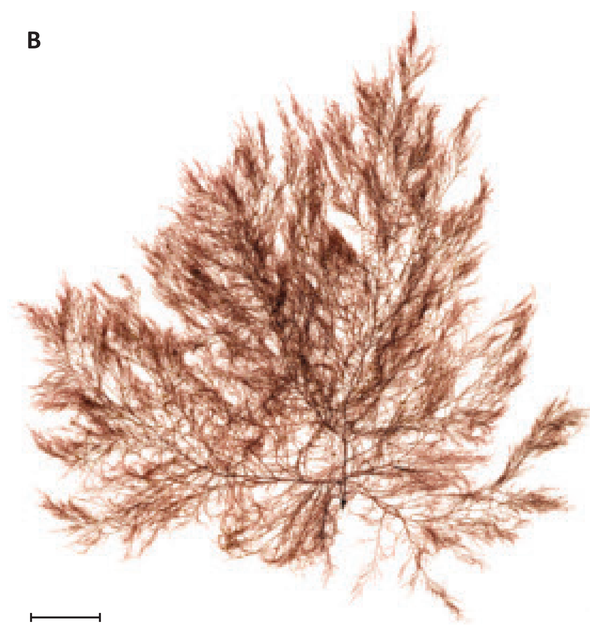
Seasonal variation: Probably a summer alga in Danish waters. Recorded in May-September with antheridia in May-September, gonimocarps and tetrasporangia in July-September.
Habitat: On boulders between Acorn Barnacles (*Semibalanus balanoides*) in the lower part of the littoral zone at wave-exposed coasts.
References: Kapraun & Rueness (1983, *Polysiphonia brodiaei*), Maggs & Hommersand (1993, *P. brodiaei*), Rosenvinge (1923-24, *P. brodiaei*), Savoie & Saunders (2019).

Leptosiphonia fibrillosa

(C.Agardh) Savoie & G.W.Saunders
Recent synonym: *Polysiphonia fibrillosa* (C.Agardh) Sprengel
Purple Siphon Weed

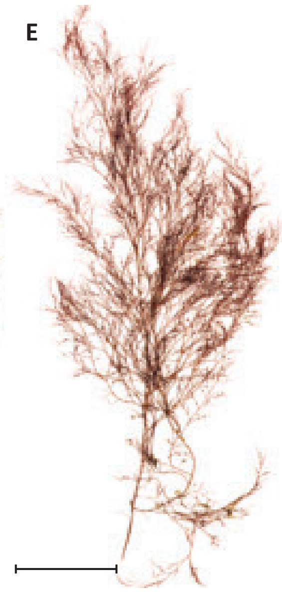
Appearance: Densely branched bush-like alga with one or several upright axes. Fronds arise from matted prostrate branches so dense that the base becomes disc-shaped. The thallus, up to 20 cm in height, is soft and delicate red-brown or faded to a straw-yellow colour. The uprights are up to 750 µm in width at the base, gradually getting narrower towards the apex. The main branch is usually obvious with many scattered branches on all sides from the base to the apex. The youngest branches are very fine. Slender forms, where the main branch is difficult to tell apart from other branches, were referred to f. *tenuis* by Rosenvinge (1923-24, as *Polysiphonia violacea* f. *tenuis* (Roth) Rosenvinge). Rosenvinge (1923-24) also mentioned f. *aculeata* (as *P. violacea* f. *aculeata* (C.Agardh) Rosenvinge). This form is loose growing with spreading branches.
Structure: The branches consist of segments with 4 periaxial cells that are 1-5 times as long as wide.

A: *Leptosiphonia fibrillosa*. A single upright main branch, branches on all sides. Læsø Trindel, 5 m, 20.8.1991. Scale 2 cm.



B: *Leptosiphonia fibrillosa*. Several upright main branches from the base, much branched on all sides. Main branches obvious but diminish towards apex. Røsnæs Nord, 12 m, 27.7.1994. Scale 2 cm.

C: *Leptosiphonia fibrillosa.* On top of several layers of vegetation, epiphytic on Sea Oak (*Phycodrys rubens*) on Stalked Leaf Bearer (*Phyllophora pseudoceranoides*). Store Middelgrund, 14 m, 4.6.1992. Scale 2 cm.



D: *Leptosiphonia fibrillosa.* Epiphytic on Bootlace Weed (*Chorda filum*). Briseis Flak, 7 m, 30.8.1993. Scale 2 cm.

E: *Leptosiphonia fibrillosa.* Delicate alga, main branch visible, tending towards f. *tenuis.* Scale 2 cm. E, K: Munkegrunde, 13 m, 4.8.1994.

Trichoblasts are numerous at the apex, they make a spiral on the branches and have 2-4 pseudodichotomies but are often shed early leaving the rounded basal cell (scar cell). Primary branches develop in the axil of trichoblasts often at a distance of 4-5 segments; but may occur a few after each other at consecutive segments. Secondary branches develop from the scar cells of trichoblasts and are usually numerous on old branches. Cortical cells arise from the lower part of periaxial cells and are cut off by an oblique wall, giving the first cortical cell a triangular outline. The alga has attachment pads on rhizoidal filaments that arise from periaxial cells and cut off by a cross wall. Ascending branches might occur from prostrate branches.

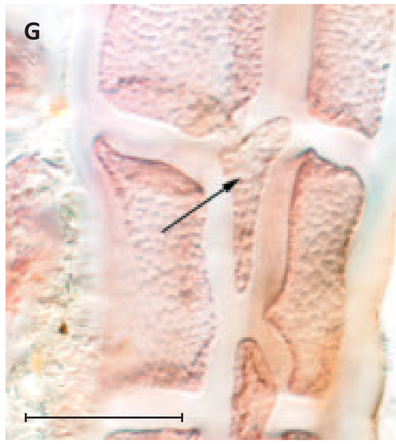
Reproduction: Antheridial branchlets occur as one of the branches at the first pseudodichotomy of trichoblasts. They are cylindrical without sterile cells at the apex. The gonimocarps are ovoid to spherical and turn inward against the branch. The pericarp cells are in series and decrease in size towards the apex, except the relatively large upper cells surrounding the opening. Tetrahedrally divided tetrasporangia form short spiral series in the youngest branches.

Seasonal variation: Several generations probably replace each other during the summer month. The species grows fast, as shown by epiphytic individuals on Bootlace Weed (*Chorda filum*) which itself develops in spring and the first summer months. The growth stops in the autumn month and the frond is worn away. Growth recommences the following spring from individuals that survived the winter as prostrate filaments. Antheridia, gonimocarps and tetrasporangia recorded in May-September.

Habitat: On small stones, empty mollusc shells and other solid material and epiphytic on various coarse red and brown algae, 0.5-20.5 m depth. Purple Siphon Weed (*L. fibrillosa*) is often a member of the upper layer in vegetation of several layers of various algae on stone reefs.

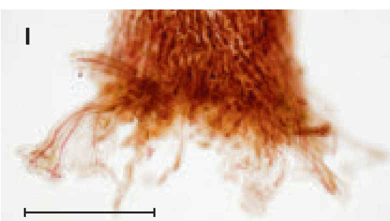
The loose growing f. *aculeata* is almost without cortex and has secondary branches perpendicular to the

F: *Leptosiphonia fibrillosa.* Apex, primary branch in axil of trichoblast (arrow). Scale 50 µm. F, H-I: Beach south of Vesterø Havn, Læsø, drift, 28.3.2008.



G: *Leptosiphonia fibrillosa.* The first cortical cell cut off by an oblique wall (arrow) from lower part of a periaxial cell, growth towards base. Boblerev, Nordre Rønner, Læsø, 10 m, 17.8.2004. Scale 50 µm.

H: *Leptosiphonia fibrillosa.* Axial cell, 4 periaxial cells and smaller cortical cells, transverse section. Scale 50 µm.



I: *Leptosiphonia fibrillosa.* Base with branched attachment pads on rhizoids. Scale 500 µm.

J: *Leptosiphonia fibrillosa.* Cylindrical antheridial branchlets without sterile cells at apex arise as one branch at the first dichotomy of trichoblast. Halskov Rev, 10 m, 25.9.1997. Scale 100 µm.

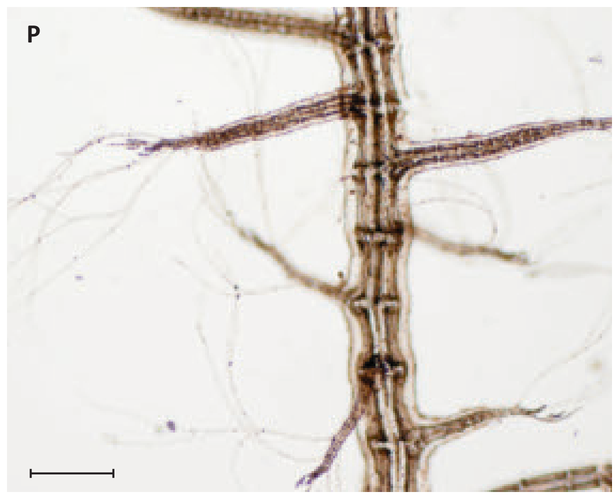
K: *Leptosiphonia fibrillosa.* Gonimocarp with pericarp filaments of cells, that decrease in size to the enlarged apical cells. Scale 100 µm.

L: *Leptosiphonia fibrillosa.* Branch with tetrahedrally divided tetrasporangia in spiral series. Vejsnæs Flak, 7.5 m, 30.7.1994. Scale 100 µm.

N: f. *tenuis*. Branch of long segments and sparse cortex. Scale 100 µm.

O: f. *tenuis*. First cortical cell cut off by an oblique wall (arrow). Scale 10 µm.

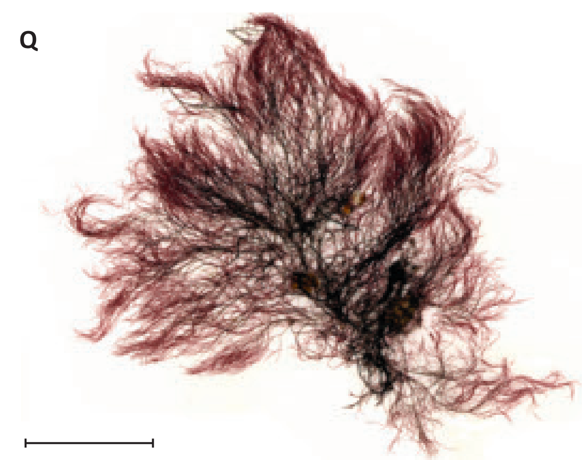
M: f. *tenuis*. Apex, a branch in the axil of an unbranched trichoblast (arrow). Scale 50 µm. M-O, Q: Schönheyders Pulle, 7 m, 6.9.1997.

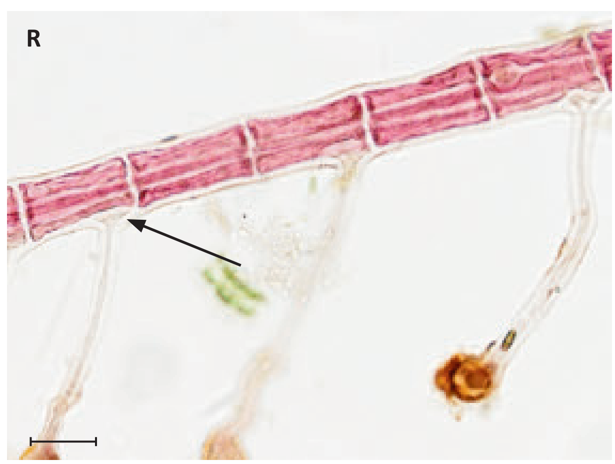


P: f. *aculeata*. Main branch with perpendicular branches. Bay of harbour, Hirsholm, loose lying, 0.5 m, 11.7.1999. Scale 200 µm.

Q: f. *tenuis*. Candyfloss-looking alga from brackish water. Scale 2 cm.

R: f. *tenuis*. Branch with many rhizoids cut off from periaxial cells with a wall (arrow). Søndre Stenrøn, 6.5 m, 6.9.1993. Scale 100 µm.





main branches. It occurs in sheltered localities at shallow water. Reproductive structures not observed.

Bush-like fronds of *P. violacea* f. *tenuis* resemble candyfloss and it is difficult to distinguish the main and other branches from each other. The segments are (4-) 6-9 times as long as wide with sparse cortex. The trichoblasts are often unbranched.

Resembles: Slender forms of Elongate Siphon Weed (*C. elongata*) and Purple Siphon Weed (*L. fibrillosa*) in the Baltic Sea are very similar. They can be distinguished by the primary branches replacing trichoblasts in Elongate Siphon Weed (*C. elongata*) and arise from the axil of trichoblasts in Purple Siphon Weed (*L. fibrillosa*). Furthermore, the youngest cortical cells are elongate in Elongate Siphon Weed (*C. elongata*), but short with a triangular outline in Purple Siphon Weed (*L. fibrillosa*).

References: Kapraun & Rueness (1983, *Polysiphonia violacea*), Maggs & Hommersand (1993, *P. fibrillosa*), Rosenvinge (1923-1924, *P. violacea*), Savoie & Saunders (2019), Schiffner (1939, *P. violacea*), Wærn (1952, *P. violacea*).

Melanothamnus harveyi

(Bailey) Díaz-Tapia & Maggs

Harvey's Siphon Weed

Appearance: Much branched light red or red brown bush-like alga, up to 11 cm in heigh. The alga becomes relatively dark with age, stiff and develops short, spine-like branches. Main branches conspicuous, 0.2-0.6 mm across at the base and becoming gradually narrower towards the apex. The branches scattered on all sides. The alga attaches by slender, downward-growing matted filaments that form a disc or with age form prostrate branches.

Structure: The upright branches have short segments with 4 periaxial cells. The youngest branches 20-30 segments below the apex are 30 µm in diameter, the segments are 0.7-1 times as long as wide. It is peculiar that the plastids in the periaxial cells are along the radiating lateral walls and not below the outer walls, making the cells appear transparent. The pseudodichotomous trichoblasts are shed early and only present at the apex. Primary branches replace trichoblasts while secondary branches develop from the scar cells of trichoblasts. The cortex develops differently, it may be sparse or absent or very well-developed particularly at the lower part of the alga. The cortical cells are cut off from the lower part of periaxial cells with an oblique wall. The prostrate filaments have attachment pads on rhizoids, cut off from the periaxial cells with a crosswall.

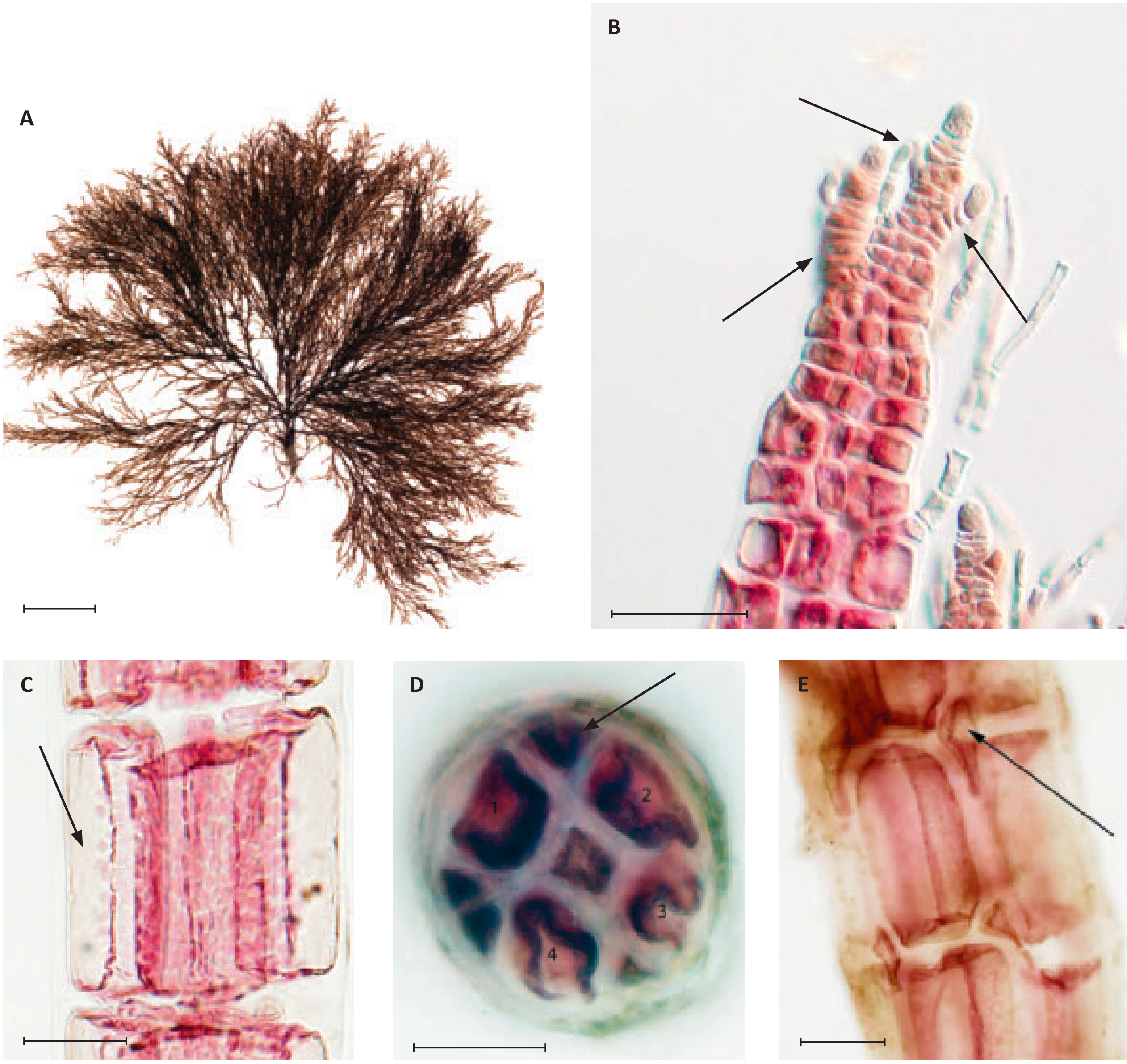
Reproduction: Antheridial branchlets form as one of the branches at the first dichotomy of trichoblasts. They are cylindrical or cone-shaped with a sterile cell at the apex. Gonimocarps have a short, thick stalk. They are ovoid when young and become spherical at maturity. The cells of the pericarp are in straight series and decrease in size towards the wide opening which is surrounded by transparent cells. The tetrasporangia form spiral rows in the upper branches and in secondary branches in older specimens.

Seasonal variation: Collected in July-September. Antheridia recorded in July-August, gonimocarps in August and tetrasporangia in August-September.

Habitat: On stones, epiphytic on Irish Moss (*Chondrus crispus*) and various brown algae, 0.5-4 m depth.

Comment: Harvey's Siphon Weed (*M. harveyi*) is considered an invasive species in the North Atlantic, probably originating in Japan (Maggs & Hommersand, 1990, 1993, Maggs & Stegenga, 1999, McIvor et al., 2001). The first Danish collection was in the western part of the Limfjord, 1980 (Koch, 1986 as *Polysiphonia fibrillosa*).

References: Choi et al. (2001), Díaz-Tapia et al. (2017), Kim & Lee (1999), Koch (1986, *P. fibrillosa*), Kornmann & Sahling (1977, *P. violacea*), Maggs & Hommersand (1990, 1993, *P. harveyi*), Maggs & Stegenga (1999, *P. harveyi*), McIvor et al. (2001, *P. harveyi*), Nielsen (2005a, *Neosiphonia harveyi*).

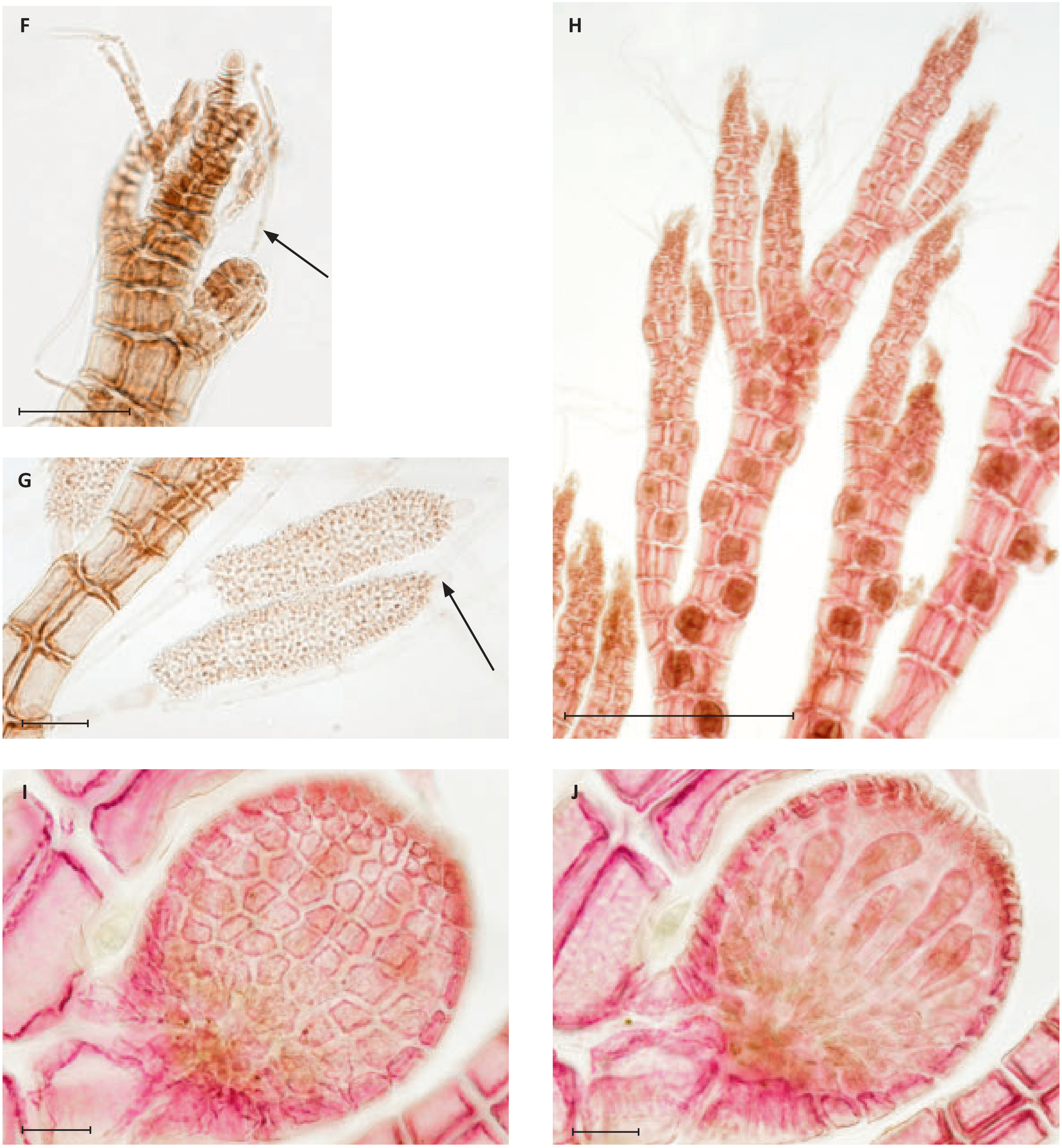


A: *Melanothamnus harveyi*. Robust dark alga with scattered branches on all sides. Tile works, Helligsø, 0.5 m, 2.8.1980. Scale 2 cm.

B: *Melanothamnus harveyi*. Apex, primary branches (lower arrows) replace trichoblasts (upper arrow). Scale 50 µm. B-C, E-J: Tile works, Helligsø, 3.5 m, 2.8.2000.

C: *Melanothamnus harveyi*. Branch segment with 4 periaxial cells without cortex. Periaxial cells appear transparent without plastids along the outer walls (arrow). Scale 50 µm.

D: *Melanothamnus harveyi*. Axial cell surrounded by 4 periaxial cells (1-4) and a few cortical cells (arrow). Beach north of Vesterø Havn, Læsø, drift, 25.3.2008. Scale 50 µm.



E: *Melanothamnus harveyi*. Short segment and first cortical cells (arrow). Scale 100 µm.

F: *Melanothamnus harveyi*. Young gonimoblast with trichogyne (arrow). Scale 50 µm.

G: *Melanothamnus harveyi*. Antheridial branchlets with a sterile cell at the apex (arrow). Scale 50 µm.

H: *Melanothamnus harveyi*. Branches with tetrasporangia in spiral series. Scale 50 µm.

I: *Melanothamnus harveyi*. Pericarp with cells in rows. Scale 50 µm.

J: *Melanothamnus harveyi*. Mature gonimoblast with pericarp, same as in fig. I, optical longitudinal section. Scale 50 µm.

Polysiphonia kieliana

Kaminski & Nizamuddin

Appearance: Dense bright red bush-like alga up to 8-9 cm in height. It consists of several upright axes with scattered or pseudodichotomously divided branches on all sides, main and lateral branches uniformly thick. The base consists of dense matted prostrate filaments from where many ascending branches arise.

Structure: The branches consist of segments with 5-7 periaxial cells. The segments are 3-5 times as long as wide in the middle part of the thallus. The primary branches arise from the axil of trichoblasts. The cortex is sparse and only covers the periaxial cells in part. The first cortical cells cut off from the lower part of the periaxial cells with an oblique wall. Prostrate filaments attach to the substratum with rhizoids separated from periaxial cells by a cross-wall.

Reproduction: Only tetrasporophytes observed in Danish waters. Tetrasporangia form spiral series in the youngest branches.

Seasonal variation: Recorded in November-March. Young tetrasporangia observed in December.

Habitat: On stones at the lower part of the littoral zone in protected localities.

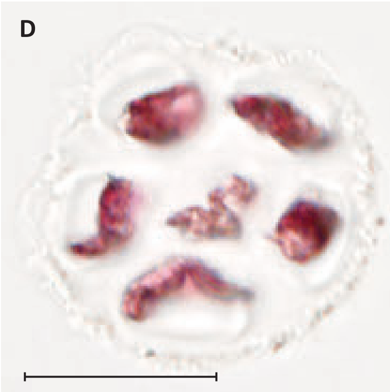
Comment: Danish algae were erroneously referred to *Polysiphonia denudata* (Dillwyn) Greville ex Harvey by Nielsen & Lundsteen (2019a).

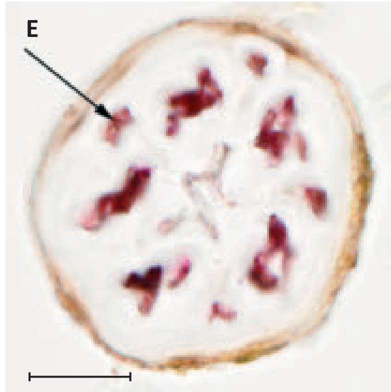
References: Kaminski & Nizamuddin (1975), Nielsen (2008), Nielsen & Lundsteen (2019a).

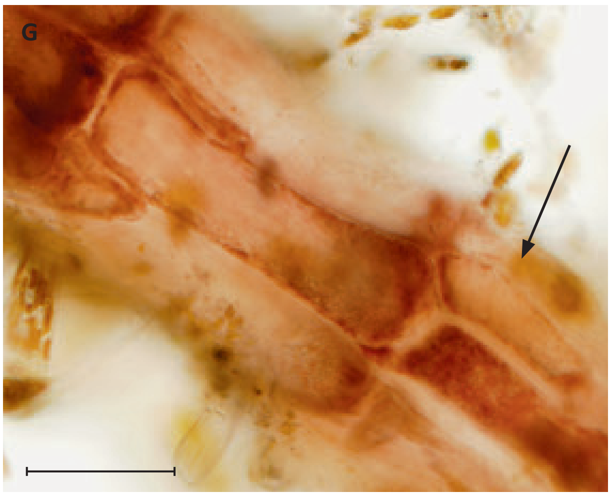
A: *Polysiphonia kieliana*. Clear red bush-like alga, branches of equal thickness. Scale 2 cm. A, D-E, H: Protected side of harbour jetty Margretheholms Havn, Copenhagen, 0.5 m, 9.12.2003.

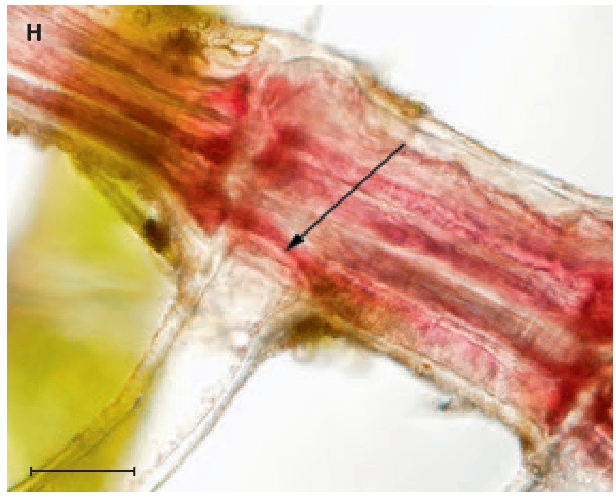
B: *Polysiphonia kieliana*. A single ascending branch from short prostrate branch, attached by rhizoids (arrow). Studstrup Havn, Kalø Vig, 0.5 m, 3.2.1975. Leg.: L. Mathiesen. Scale 2 cm.

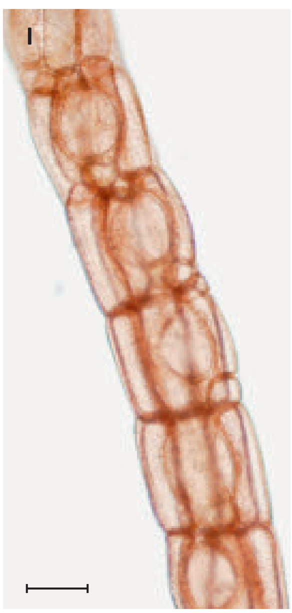
C: *Polysiphonia kieliana*. Apex with primary branch in the axil of trichoblast (arrow). Scale 50 µm. C, G: Protected side of harbour jetty Margretheholms Havn, Copenhagen, 0.5 m, 19.2.2008.

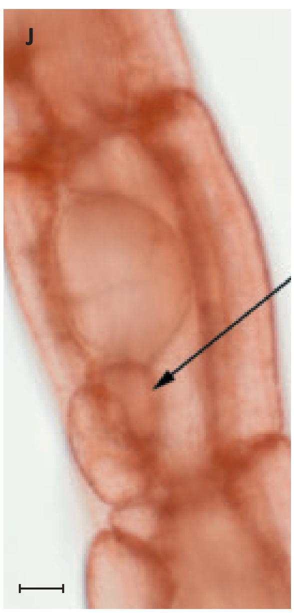












D: *Polysiphonia kieliana*. Axial cell and 5 periaxial cells, transverse section. Scale 50 µm.

E: *Polysiphonia kieliana*. Axial cell, 5 periaxial cells and cortex (arrow), transverse section. Scale 50 µm.

F: *Polysiphonia kieliana*. Axial cell and 6 periaxial cells, transverse section. North-eastern part of Refshaleøen, Copenhagen, 0.5 m, 4.11.2008. Scale 20 µm.

G: *Polysiphonia kieliana*. First cortical cell (arrow). Scale 50 µm.

H: *Polysiphonia kieliana*. Rhizoid cut off from periaxial cell of prostrate filament by a cross-wall (arrow). Scale 50 µm.

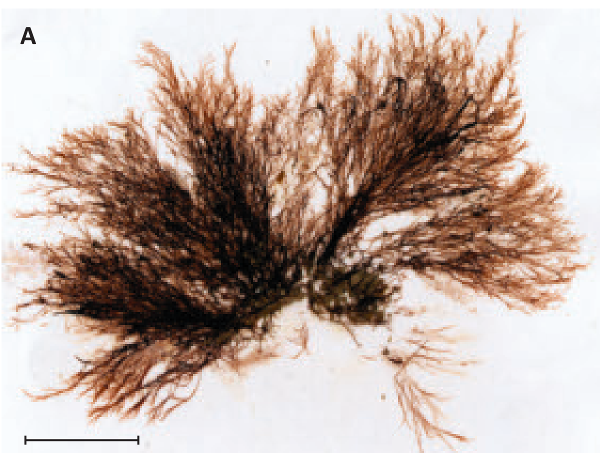
I: *Polysiphonia kieliana*. Young or aborted tetrasporangia in a spiral series. Scale 50 µm. I-J: Sheltered side of harbour jetty Margretheholms Havn, Copenhagen, 0.5 m, 4.11.2008.

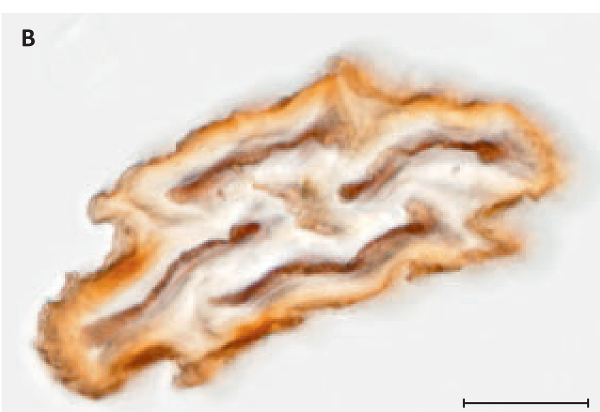
J: *Polysiphonia kieliana*. A single sporangium on stalk-cell (arrow). Scale 20 µm.

Polysiphonia orthocarpa

Rosenvinge

Appearance: Bush-like red-brown alga of narrow branches, up to 7 cm in height. There is a basal system of matted branches with several upright branches. Main branches approximately 150 µm in width at base and have scattered branches on all sides.
Structure: The branches consist of segments with 4 periaxial cells without cortex. In the middle part of the thallus the segments are 3-6 times as long as wide. The primary branches develop in the axil of trichoblasts. Secondary branches not present. The prostrate branches attach by rhizoids. Numerous rhizoids also arise both from the upper and lower part of the periaxial cells in the basal part of the upright branches, separated from them by a cross wall.
Reproduction: Antheridial branchlets not known. Gonimocarps are approximately spherical with large pericarp cells decreasing in size towards the apical opening. The gonimocarps occur in continuation of the stalk-cell. Tetrasporangia form spiral rows in the youngest branches.
Seasonal variation: Collected in July-August, gonimocarps recorded in August and tetrasporangia in July.
Habitat: Stones in localities with sandy seabed, 0-4 m depth.
Comment: There are no later collections than the original by Rosenvinge, 1893 in the algal herbarium, Natural History Museum of Denmark. The species appears to be closely related to *Leptosiphonia fibrata* (Dillwyn) A.M.Savoie & G.W.Saunders, according to Maggs & Hommersand (1993 p. 333 as *Polysiphonia fibrata* (Dillwyn) Harvey).
References: Maggs & Hommersand (1993), Rosenvinge (1923-24).





A: *Polysiphonia orthocarpa*. Densely branched alga. Scale 2 cm. A-C: Amtoft Rev, the Limfjord, dredge 4-0 m, 28.8.1893. Leg. & det.: Rosenvinge.

B: *Polysiphonia orthocarpa*. Axial cell surrounded by 4 periaxial cells, no cortex, transverse section. B-C: Rehydrated herbarium material. Scale 50 µm.

C: *Polysiphonia orthocarpa*. Apex with primary branch in axil of trichoblast (arrow). Scale 50 µm.

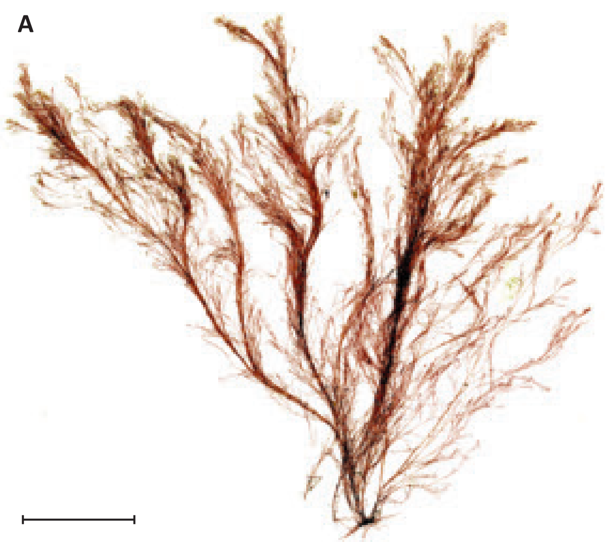
Polysiphonia stricta

(Mertens ex Dillwyn) Greville

Pitcher Siphon Weed

Appearance: Bush-like alga with narrow branches on all sides, up to 20 cm height. Several uprights develop from prostrate basal branches that are loosely woven together, often as an open network. Branches are of an even thickness without conspicuous main branches. The alga is clear red in spring when growth is active, becoming red-brown later in the year.

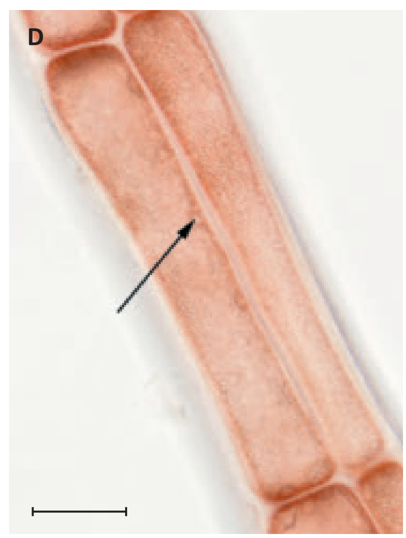
Structure: The upright axes are c. 100 µm in width at the base and 50 µm near the apex. The branches consist of segments with 4 periaxial cells without cortex. The segments are 1-1.5 (-3) times as long as wide often with a series of very short cells below the apical cell. Trichoblasts are in a spiral at the apex, but with a variable density and frequently not present. They are usually separated by several segments and have a single nucleus per cell. The primary branches replace trichoblasts. Secondary branches form occasionally in the lower part of the alga, arising from central axial cells (endogenous branches). The prostrate branches have attachment pads on rhizoids. These develop from periaxial cells and remain in open connection with them. The uprights develop as endogenous branches or as ascending filaments from the prostrate branches.



A: *Polysiphonia stricta*. Well-developed alga in spring. Vejrø, 8 m, 9.4.1989. Scale 2 cm.

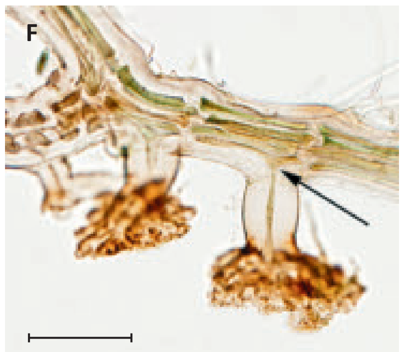
B: *Polysiphonia stricta*. Tuft of short uprights from a dense matted base. Store Middelgrund, 20.5 m, 9.6.1993. Scale 2 cm.

C: *Polysiphonia stricta*. Apex with trichoblasts, 1 nucleus per cell (arrow). The wave-exposed side, Margretheholms Havn, Copenhagen, 0.5 m, 19.2.2008. Scale 50 µm.



D: *Polysiphonia stricta*. Segment with 4 periaxial cells, 2 of them visible and have several nuclei (arrow). Scale 50 µm. D-E: Eastern harbour jetty Gilleleje, 0.5 m, 3.5.2008.

Reproduction: Antheridial branchlets are unbranched and develop near the apex of male gametophytes. They are long cylindrical to slightly conical with a series of sterile cells at the apex. The gonimocarps are urn-shaped with a small spout, the pericarp cells are in straight rows, with the opening surrounded by relatively large cells. The tetrahedrally divided tetrasporangia form straight series in the youngest branches.
Seasonal variation: Perennial, decaying in winter and thalli surviving as one to a few centimetres in height. Growth greatest in spring where the largest thalli occur in April-May. Antheridia recorded in January-August, gonimocarps in April-September and tetrasporangia in May-September.
Habitat: Often on stones and other solid material, on stone reefs epiphytic on coarse red algae and haptera of Forest Kelp (*Laminaria hyperborea*) 0.5-23 m depth.
Comment: It is the type species for the genus *Polysiphonia*.
References: Díaz-Tapia et al. (2017), Kim et al. (2000), Maggs & Hommersand (1993), Rosenvinge (1923-1924, *P. urceolata*), Savoie & Saunders (2019).



E: *Polysiphonia stricta*. Central axial cell and 4 periaxial cells without cortex, transverse section. Scale 50 µm.

F: *Polysiphonia stricta*. Prostrate branch, rhizoids with attachment pads in open connection with periaxial cells (arrow). Scale 100 µm. F, I: Schultz's Grund, 9 m, 9.8.1992.

G: *Polysiphonia stricta*. Antheridial branchlets, apex with a series of sterile cells (arrow). Klokkegrund, 3.5 m, 6.3.1997. Scale 50 µm.

H: *Polysiphonia stricta*. Mature gonimocarp, pericarp urn-shaped with small spout. Store Middelgrund, 9 m, 10.6.1991. Scale 100 µm.

I: *Polysiphonia stricta*. Tetrahedrally divided tetrasporangia in a straight series. Scale 100 µm.

Vertebrata byssoides

(Goodenough & Woodward) Kuntze

Brongniart's Thread Weed

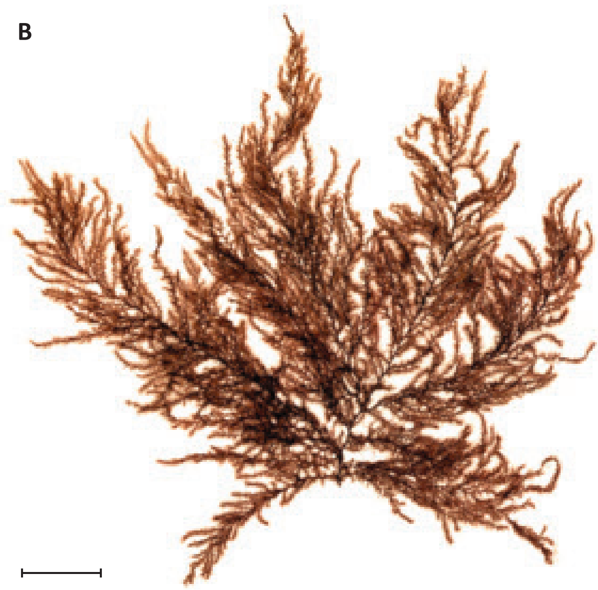
Appearance: Repeatedly branched bush-like alga with conspicuous main branches with branches on all sides, up to 23 cm in height. All branches have so many red trichoblasts that they appear shaggy and the species may look like red Christmas trees. Well-developed thalli are brownish red while small young individuals are light red or light purple in late spring. The upright branches arise from prostrate branches fixed to the substratum with attachment pads.

Structure: The main branches consist of segments with 7 periaxial cells without cortex. The apices and prostrate branches have 4-6 periaxial cells. Between the axial cells and the periaxial cells there are very narrow filaments. A pigmented trichoblast arises from each of the segments. The trichoblasts are permanent and the cells contain many disc-shaped plastids. Primary branches develop from the basal cells of the trichoblasts. Secondary branches are rare. The prostrate branches lack trichoblasts and arise from cells in the basal part of main branches. They have attachment pads on rhizoids cut off from periaxial cells by a cross wall.

Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Antheridial branchlets replace trichoblasts in the upper part of male gametophytes. They are cylindrical to club-shaped on a stalk of 1-2 cells. Gonimocarps form on special branches with two segments at the base and continue into a uniseriate trichoblast with few branches. The gonimoblast develops on the second segment and becomes ovoid to spherical and the pericarp has a small spout. The tetrahedrally divided tetrasporangia form a spiral series in the youngest branches with a single sporangium per segment.

Seasonal variation: Overwinters as short prostrate branches and probably also as spores. Old dark prostrate branches with new bright branches collected in January and spring. Young thalli a few centimetres

A: *Vertebrata byssoides*. Shape like a Christmas tree with conspicuous main branches. Middelflak, 9 m, 15.9.1991. Scale 2 cm.



B: *Vertebrata byssoides*. Dense bush-like specimen, branches shaggy with red trichoblasts. Lysegrund, 9.5 m, 13.8.1990. Scale 2 cm.

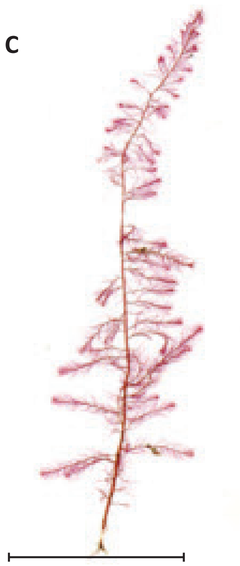
in height appear in April-June and the alga is well-developed in June-November. Antheridia recorded in July-October, gonimocarps and tetrasporangia in July-November. The alga decays later in the autumn.

Habitat: Epiphytic on various red and brown algae, Eelgrass (*Zostera marina*), hydroids, tunicates and on small stones and boulders, 2-23 m depth.

Resembles: Siphoned Japan Weed (*Dasysiphonia japonica*) and Siphoned Feather Weed (*Heterosiphonia plumosa*), particularly the tiny Siphoned Japan Weed (*D. japonica*), have alternating branchlets resembling the pigmented trichoblasts in Brongniart's Thread Weed (*V. byssoides*). The two species have cortex, which is not present in Brongniart's Thread Weed (*V. byssoides*).

Comment: The species accepted as a *Vertebrata* by Díaz-Tapia et al. (2017), was previously known as *Brongniartella byssoides* (Goodenough & Woodward) F.Schmitz.

References: Díaz-Tapia et al. (2017), Kornmann & Sahling (1977, *Brongniartella byssoides*), Kylin (1944, *B. byssoides*), Maggs & Hommersand (1993, *B. byssoides*), Parsons (1980, *B. byssoides*), Rosenvinge (1923-24, *B. byssoides*) Savoie & Saunders (2019).

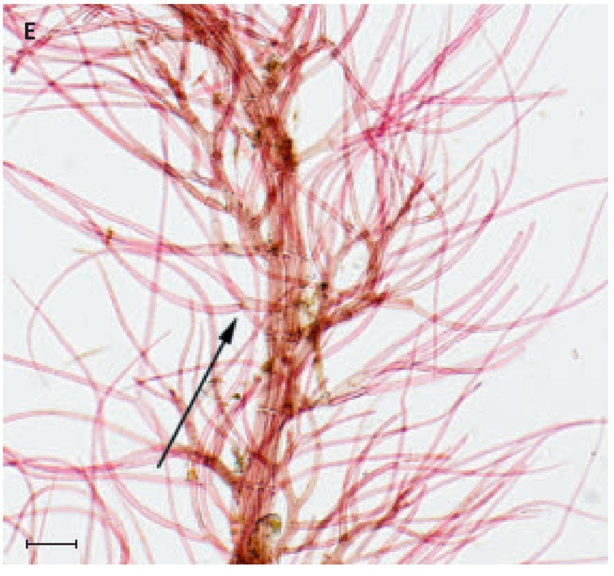


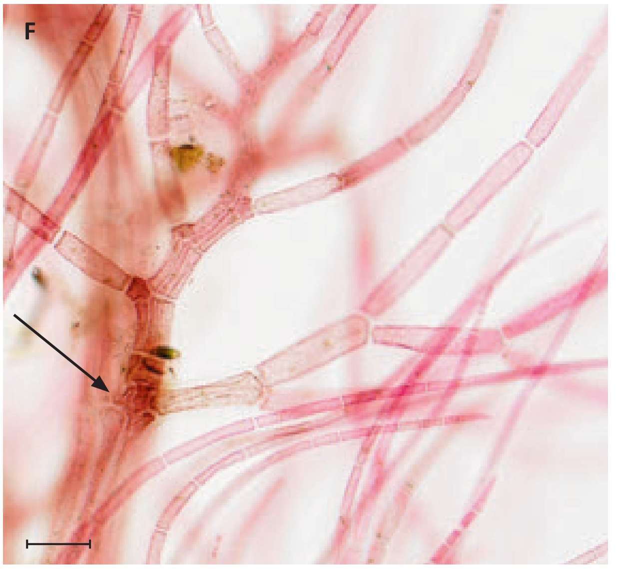
C: *Vertebrata byssoides.* Young, light purple alga. Kims Top, 22 m, 5.6.1993. Scale 1 cm.

E: *Vertebrata byssoides.* Main branch and branches with periaxial cells and uniseriate red pseudodichotomous trichoblasts (arrow). Scale 100 µm. E, F: Tangen, 7.5 m, 15.9.1996.

F: *Vertebrata byssoides.* Branch from basal cell of trichoblast (arrow). Scale 100 µm.

D: *Vertebrata byssoides.* Attachment pad on short rhizoid cut off from a periaxial cell with a cross wall (arrow), on a prostrate branch. Schultz's Grund, 11 m, 18.2.1997. Scale 50 µm.



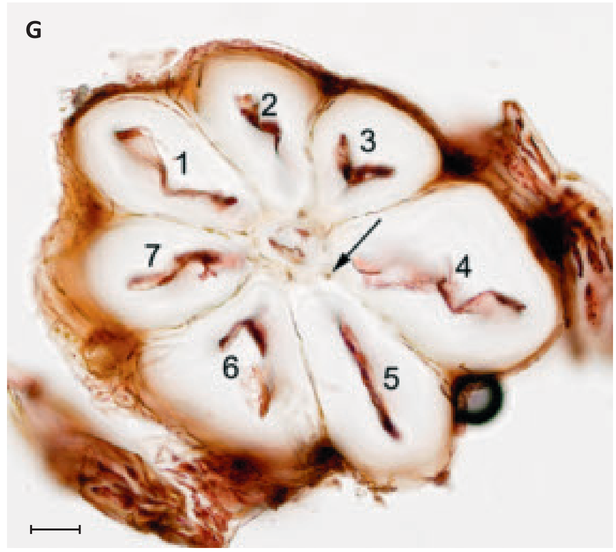


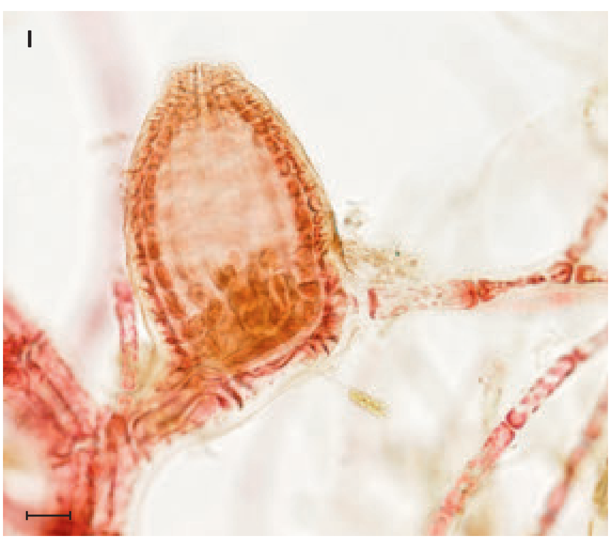
G: *Vertebrata byssoides.* Central axial cell, 7 periaxial cells, and narrow filaments between the axial cell and the periaxial cells (arrow), transverse section. West of Endelave, 3 m, 22.8.1998. Scale 50 µm.

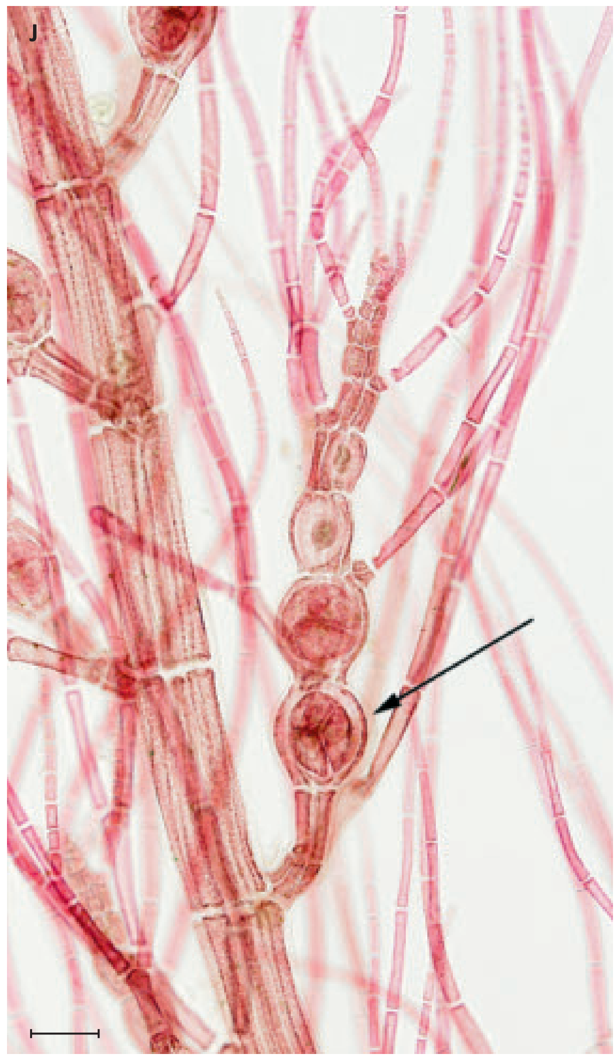
H: *Vertebrata byssoides.* Antheridial branchlets. Ebbeløkke, 9 m, 26.7.1994. Scale 20 µm.

I: *Vertebrata byssoides.* Gonimocarp. Scale 50 µm. I-J: Moselgrund Nord, 9.5 m, 3.8.1994.

J: *Vertebrata byssoides.* Tetrahedrally divided tetrasporangia (arrow). Scale 50 µm.







Vertebrata fucoides

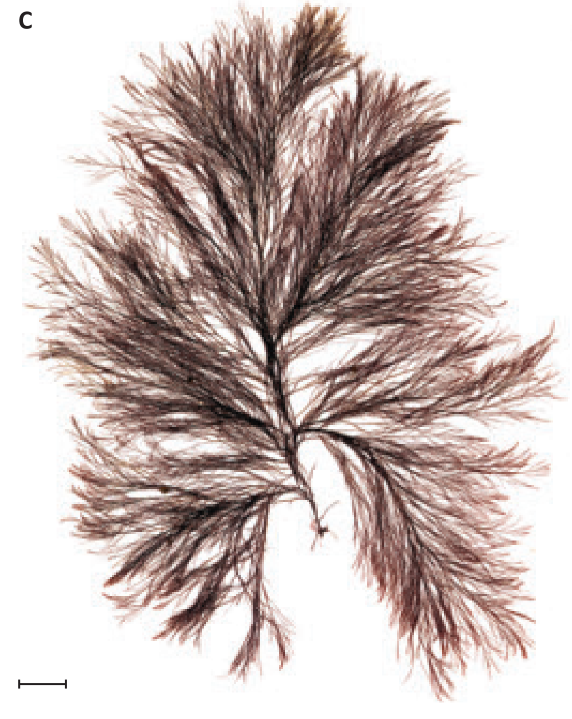
(Hudson) Kuntze

Black Siphon Weed

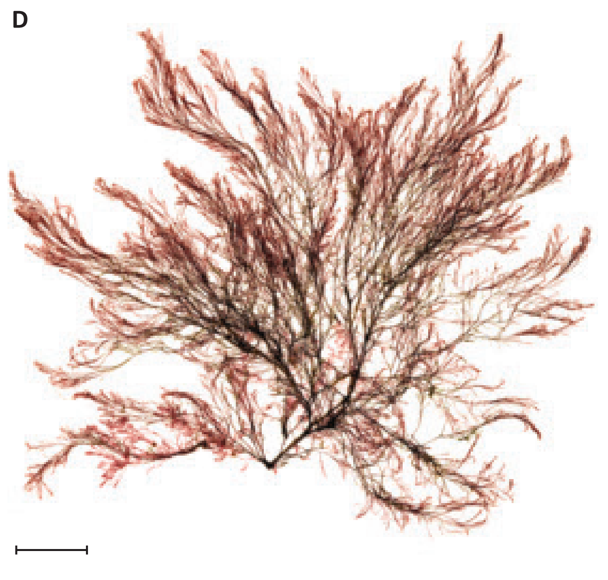
Appearance: Dark red-brown bush-like alga, 3-26 cm in height and much branched on all sides. Several upright main branches arise from a disc-shaped base of matted branches and rhizoids with attachment pads. The main branches are usually conspicuous and repeatedly branched, and are 100-700 µm in width at the base. It is common in older thalli for the lower part of the branches to have only a few short lateral branches. The branches are scattered on all sides, but

A: *Vertebrata fucoides.* Densely branched dark alga with feather-like branches (arrow). Northern harbour jetty, Frederikshavn, 0.2 m, 6.6.2003. Scale 2 cm.

B: *Vertebrata fucoides.* Alga with bright apical branches in spring. Older part of the main branches only have short lateral branches. Store Middelgrund, 9 m, 12.4.1991. Scale 2 cm.

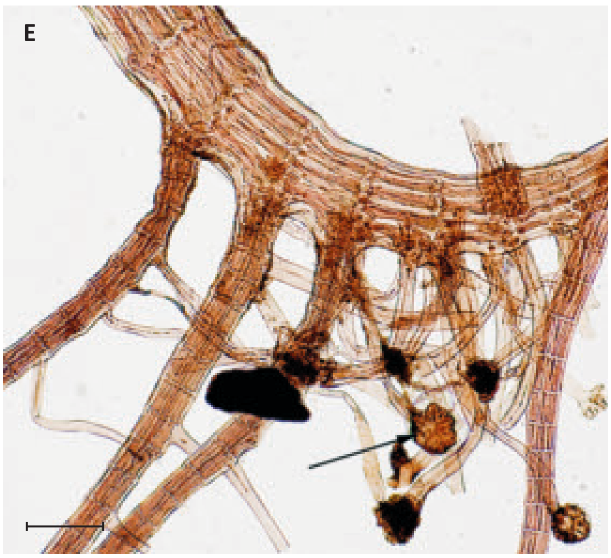


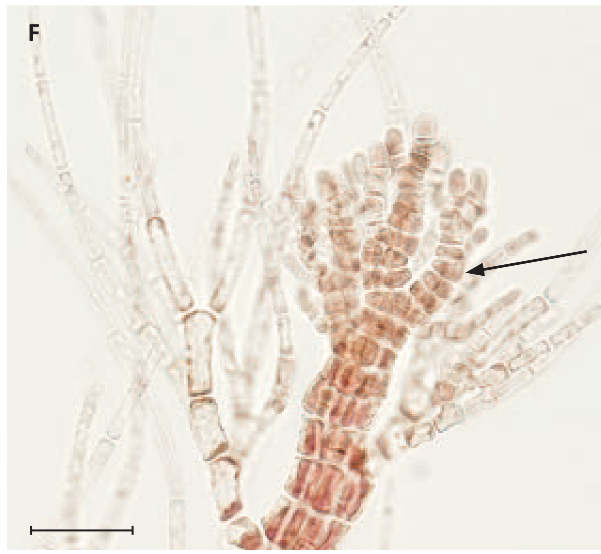
C: *Vertebrata fucoides.* Dark bush-like thallus without feather-like branches. Venegrund, 5 m, 26.9.1992. Scale 2 cm.



D: *Vertebrata fucoides.* Slender alga with growth in bright apical parts. Vedbæk, 6 m, 15.3.1993. Leg.: K. Anthony. Scale 2 cm.

some forms have alternating distichous branches at the apex in one plane with a feather-like appearance. When dry the alga turns dark to almost black.
Structure: Branches consist of segments with (10-) 12-17 (-20) periaxial cells, straight or slightly spirally twisted. The segments are 0.5-3 times as long as wide. Pseudodichotomous trichoblasts are frequent at the actively growing apex of the alga (February-June). The trichoblasts have 3-4 branching points and occur from each segment or irregularly at intervals of more than one segment. Primary branches replace trichoblasts. Secondary branches may arise from scar cells of trichoblasts, or from central axial cells (endogenous branches) in the axil of older branches or at the lower part of main branches. The cortex consists of relatively short cells cut off from the basal end of periaxial cells. The cortex might be sparse but is present at least in the lower part of the alga. The base consists of matted masses of prostrate branches and attachment pads on numerous rhizoids cut off from the periaxial cells by cross walls. The upright branches may arise as endogenous branches from the prostrate branches or be ascending.
Reproduction: Antheridial branchlets develop as one





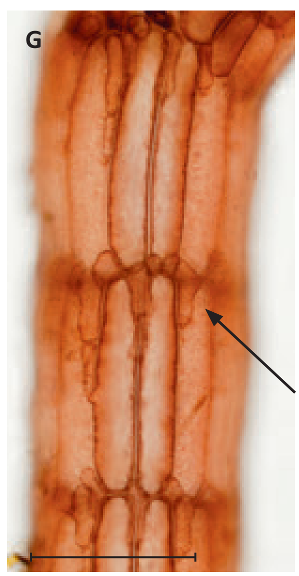
E: *Vertebrata fucoides*. Ascending branch from basal system. Prostrate branches with attachment pads (arrow) on rhizoids. Vejsnæs Flak, 9 m, 30.7.1994. Scale 200 µm.

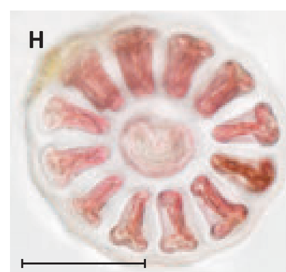
F: *Vertebrata fucoides*. Apex of uniaxial syntagma, apical cell, first periaxial cells, primary branch (arrow) and pseudodichotomous trichoblasts. Beach north of Vesterø Havn, Læsø, drift, 28.3.2008. Scale 50 µm.

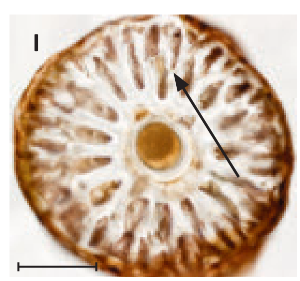
G: *Vertebrata fucoides*. 6 periaxial cells visible on the upper side of a branch, first cortical cells (arrow). Sanddobberne, Nekselø Bugt, 0.5 m, 25.2.2008. Leg.: H. Kristensen & C. Madsen. Scale 200 µm.

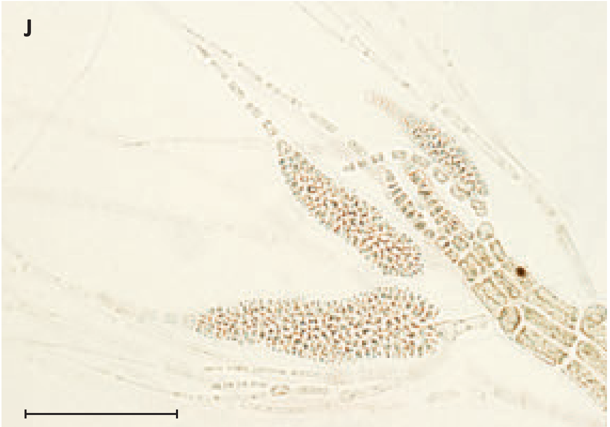
H: *Vertebrata fucoides*. 12 periaxial cells, transverse section just below the apex. Scale 50 µm. H-I: Beach south of Vesterø Havn, Læsø, drift, 16.3.2008.

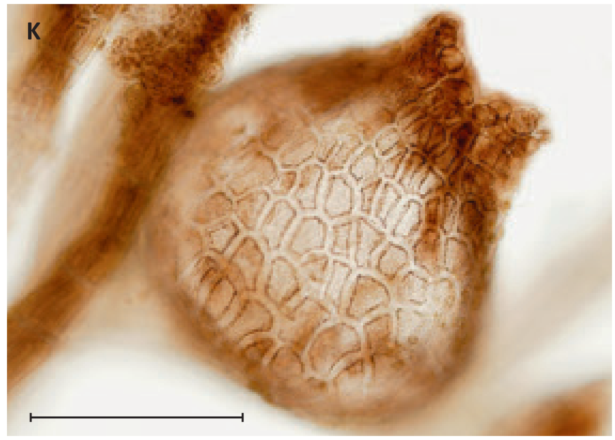
I: *Vertebrata fucoides*. Many periaxial cells and cortex, pit connections (arrow) between periaxial cells and cortical cells, transverse section at lower part of branch. Scale 200 µm.











J: *Vertebrata fucoides.* Antheridial branchlets with a series of sterile cells at the apex. Schultz's Grund, 8 m, 9.5.2000. Scale 100 µm.

K: *Vertebrata fucoides.* Gonimocarp with angular pericarp cells. Large, rounded cells delimit the opening. Hirsholm, 7.5 m, 15.6.1998. Scale 200 µm.

L: *Vertebrata fucoides.* Tetrahedrally divided tetrasporangia in a spiral series in a young branch. Schultz's Grund, 8 m, 9.5.2000. Scale 100 µm.

branch at the first dichotomy of trichoblasts. They are slightly conical with a series of sterile cells at the apex. Mature gonimoblasts are broad, ovoid, with a conical top. Pericarp cells are angular and decrease in size towards the short ostiole. The opening is bordered by slightly enlarged cells. Tetrahedrally-divided tetrasporangia form spiral series in the upper branches.

Seasonal variation: Perennial, well-developed thalli present all year. The largest growth of new bright branches occurs in spring while the growth almost stops in winter. Branches with reproductive structures decay, but even though some thalli appear emaciated, growth continues the following spring. Antheridial branchlets recorded in January-February, May-September, gonimocarps in January, May-September, and tetrasporangia in April-September.

Habitat: Black Siphon Weed (*Vertebrata fucoides*) is a component in 'the red algal belt' at shallow water on wave-exposed shores in Skagerrak and the Northern Kattegat. Common on stones and epiphytic on stone reefs, 0.5-21 m depth.

Comment: The morphological variation reflects the growth at different seasons and local conditions in relation to wave-exposure, depth and salinity and revealed by the description of various forms (Kylin, 1944). Rosenvinge (1923-24) mentions four, as forms of *Polysiphonia nigrescens* (Hudson) Greville ex Harvey as occurring in Danish waters. Common is *P. nigrescens* f. *fucoides* J.Agardh with distichous branches. The dense and dark *P. nigrescens* f. *pectinata* (C.Agardh) J.Agardh occurs at wave-exposed localities in the North Sea, Skagerrak and the Northern Kattegat. Towards the Baltic Sea, the slender, soft *P. nigrescens* f. *reducta* Svedelius is found, and in deeper water *P. nigrescens* f. *flaccida* (Areschoug) Kylin occurs, without distichous branches, and is a clear red colour.

References: Díaz-Tapia et al. (2017), Kapraun & Rueness (1983, *Polysiphonia nigrescens*), Kylin (1944, *P. nigrescens*), Maggs & Hommersand (1993, *P. fucoides*), Rosenvinge (1884, 1923-24, *P. nigrescens*).

Vertebrata lanosa

(Linnaeus) T.A.Christensen

Wrack Siphon Weed

Appearance: Densely branched dark red-brown almost black tufts, 2-5 (-8) cm in height, on Egg Wrack (*Ascophyllum nodosum*). The largest branches up to 0.5 mm wide at the base, gradually narrower towards the apex.

Structure: Pseudodichotomously branched uprights with very short segments, approximately 0.5 times as long as wide. Segments with (12-) 20-24 periaxial cells without cortex. The axial cells have thick walls, occupying nearly half the diameter of the segments. No trichoblasts. Prostrate branches with rhizoids that grow down into the host.

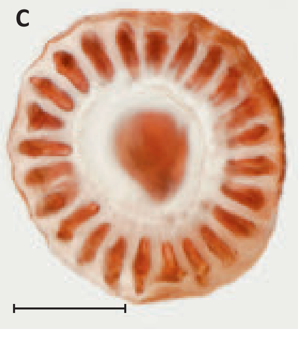
Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Antheridial branchlets in dense clusters at the apex of branches, are cylindrical, rounded at the apex without sterile cells. The gonimocarps are ovoid and the pericarps have irregular rows of cells that decrease in size towards the opening. Tetrasporangia form spiral series in the youngest branches.

Seasonal variation: Perennial with reproductive structures all year according to Kapraun & Rueness (1983) and Maggs & Hommersand (1993).

Habitat: Host-specific on Egg Wrack (*Ascophyllum nodosum*). Frequent in the drift algae at the beaches of the North Sea and Skagerrak, but not recorded on attached Egg Wrack (*A. nodosum*) in Danish waters. Common in the littoral of the North Atlantic.

Comment: The genus was previously referred to Siphon Weed (*Polysiphonia*), but re-established as a genus of its own, *Vertebrata* by Christensen (1967), and supported genetic by studies by Choi et al. (2001).

References: Choi et al. (2001), Christensen (1967), Kapraun & Rueness (1983, *Polysiphonia lanosa*), Kylin (1956), Maggs & Hommersand (1993, *P. lanosa*), Nielsen (1982a, b), Rosenvinge (1884, 1905. *P. fastigiata*).



A: *Vertebrata lanosa*. On Egg Wrack (*Ascophyllum nodosum*). Scale 2 cm. A-C: Skiveren, drift, 14.1.1976.

B: *Vertebrata lanosa*. Pseudodichotomous apex. Branches with short segments and many periaxial cells, no trichoblasts. Scale 100 µm. B-C: Rehydrated herbarium material.

C: *Vertebrata lanosa*. 24 periaxial cells without cortex. Transverse section. Scale 100 µm.

Vertebrata nigra

(Hudson) Díaz-Tapia & Maggs

Twisted Siphon Weed

Appearance: Bush-like thalli that consist of several upright axes from a basal system of matted prostrate branches. Thalli are a clear red colour and up to 10 cm in height. Branches on all sides, but relatively few in the lower part of the alga. In the upper part, branchlets form dense fascicles adpressed to the main branch. The alga becomes almost black when dry.

Structure: The segments consist of 10-13 periaxial cells, straight or spirally twisted round the axial cell. The segments are 1-2 (-3) times as long as wide. Trichoblasts frequent or sparse, the scar cells characteristically large. Apices with trichoblasts are curved in an S-shape. No cortex. Primary branches arise in the axil of a trichoblast. Secondary branches arise from scar cells or are endogenous from central axial cells. Branches in the small fascicles develop as secondary branches in the axil of a primary branch. The prostrate branches attach by rhizoids cut off from periaxial cells with a cross wall. The upright branches develop as endogenous branches from the prostrate branches or from the lower part of older upright branches.

Reproduction: Antheridial branchlets are approximately cylindrical and without sterile cells at the apex. They develop as one or both of the branches in the first dichotomy of trichoblasts. Gonimocarps are spherical. The pericarp has angular cells in rows that decrease in size towards the opening. The tetrasporangia form spiral series in the branches of the fascicles.

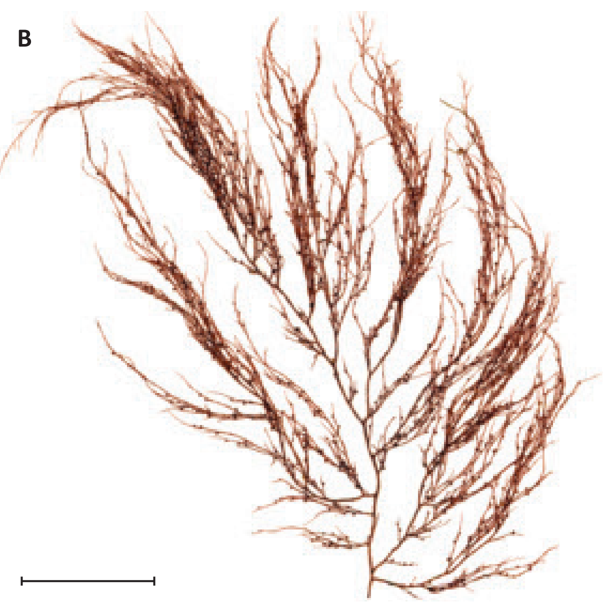
Seasonal variation: Collected in May-November. Antheridia recorded in July, mature gonimocarps and tetrasporangia in June-August. It is likely that the spores germinate during summer and over winter as small thalli, according to Rosenvinge (1923-24).

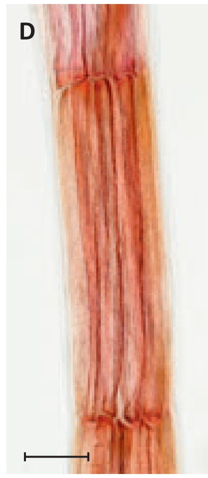
Habitat: On bivalve shells and pebbles, 1-18 m depth.

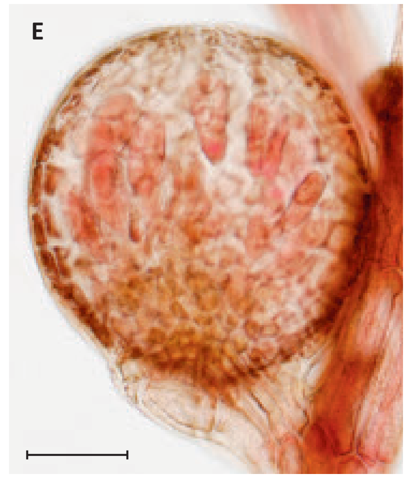
References: Díaz-Tapia et al. (2017), Kapraun & Rueness (1983, *Polysiphonia nigra*), Maggs & Hommersand (1993, *P. nigra*), Rosenvinge (1923-24, *P. atrorubescens*).

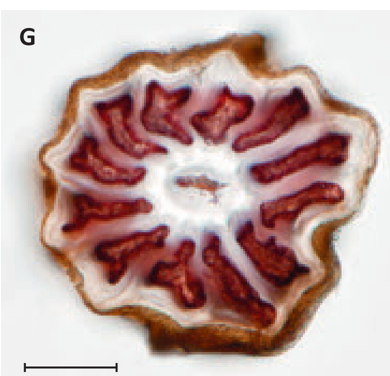
A

B









C: *Vertebrata nigra*. Apex of tetrasporophyte, fascicle of S-shaped curved branches. Scale 100 µm. C-H: Rehydrated herbarium material.

D: *Vertebrata nigra*. Segment without cortex with 10-12 periaxial cells, 5 of them are visible from the outside. Scale 100 µm.

E: *Vertebrata nigra*. Spherical gonimocarp. Scale 100 µm.

F-G: *Vertebrata nigra*. Branches with 10 and 12 periaxial cells respectively, no cortex, transverse sections. Outer part of the southern harbour jetty, sheltered side, Hirsholm, 1 m, 22.8.1976. Scale 50 µm.

H. *Vertebrata nigra*. Tetrahedrally divided tetrasporangia (arrow) in spirally twisted series. Scale 100 µm.

A: *Vertebrata nigra*. Several ascending branches from a matted base. Branchlets in fascicles in the upper part of the alga. Scale 2 cm. A, C, H: On bivalve shell, Skiveren, 0.5 m, 14.6.1981.

B: *Vertebrata nigra*. Female gametophyte with gonimocarps. Scale 2 cm. B, D, E: On bivalve shell, Tversted Strand, 0.5 m, 2.7.1980. Leg.: Aa. Kristiansen.

Tribe: Pterosiphonieae

Symphyocladiella parasitica

(Hudson) D.Bustamante, B.Y.Won, S.C.Lindstrom & T.O.Cho

Recent synonym: *Symphyocladia parasitica* (Hudson) Savoie & G.W.Saunders

Parasitic Winged Weed

Appearance: The uprights are feather-like, branched, dark red to almost black and up to 2-4 cm in height. The distinct main branches are repeatedly branched a few times and have distichous regularly alternating branches. The uprights arise from prostrate branches, which may be the only part of the alga present.

Structure: Uniaxial syntagma with segments of 7-8 periaxial cells without cortex. The branches arise from every second segment. Trichoblasts occur only on gametophytes with reproductive structures. Prostrate branches constructed similarly to the upright branches. Rhizoids with attachment pads arise from the periaxial cells separated from them with a cross wall.

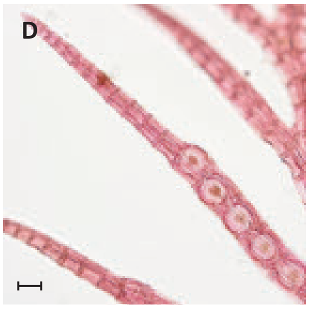
Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Tetrasporangia are the only reproductive structure recorded on the alga from Danish waters. They are tetrahedrally divided and form spiral series in the upper branches with a single sporangium per segment.

Seasonal variation: Few collections from Danish waters, from June-August with tetrasporangia. Probably perennial like the alga from the Swedish West coast (Kylin 1944).

A: *Symphyocladiella parasitica.* Well-developed feather-like specimens. Herthas Flak, collected by dredge, 10.8.1968. Leg.: H. Nielsen. Scale 2 cm.

B: *Symphyocladiella parasitica.* Complanate apex with alternating branches from every second segment. Scale 200 µm. B, D: Tønneberg Banke, 15 m, 10.6.1990.

C: *Symphyocladiella parasitica.* Prostrate branch, rhizoids cut off from periaxial cells with a cross wall. Læsø Trindel, 18 m, 3.6.1993. Scale 100 µm.



D: *Symphyocladiella parasitica.* Young branch with tetrasporangia in a series. Scale 50 µm.

Habitat: On stones and boulders and epiphytic on haptera of Forest Kelp (*Laminaria hyperborea*). Collected on stone reefs in the Northern and Eastern Kattegat, 8-23 m depth.

References: Bustamante et al. 2019, Kylin (1944, *Pterosiphonia parasitica*), Maggs & Hommersand (1993, *P. parasitica*), Rueness (1977, *P. parasitica*), Savoie & Saunders (2016, *Symphyocladia parasitica*), Suneson (1940, *P. parasitica*).

Tribe: Rhodomeleae

Harveyella mirabilis

(Reinsch) F.Schmitz & Reinke

Wolf's Parasitic Ball

Appearance: Small hemispherical to irregularly clumpy parasites, approximately 1 mm across. They are light rose or virtually colourless.

Structure: Syntagma of radiating filaments that arise from narrow filaments growing between the cells of the host. The radiating filaments form a medulla of large cells surrounded by a cortex of small cells. There are no plastids in the cells.

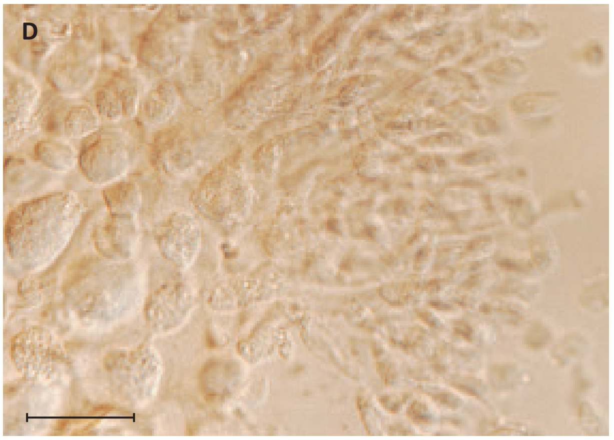
Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Antheridia, in series, form from surface cells. Gonimoblasts initiated as small branch systems embedded in the thallus. Only a single gonimoblast matures and occupies most of the alga. Tetrasporophytes have cruciate tetrasporangia, 15-20 µm in width and 15-45 µm in height, embedded between the surface cells.

Seasonal variation: Collected all year. Antheridia recorded in January-February, July, September-

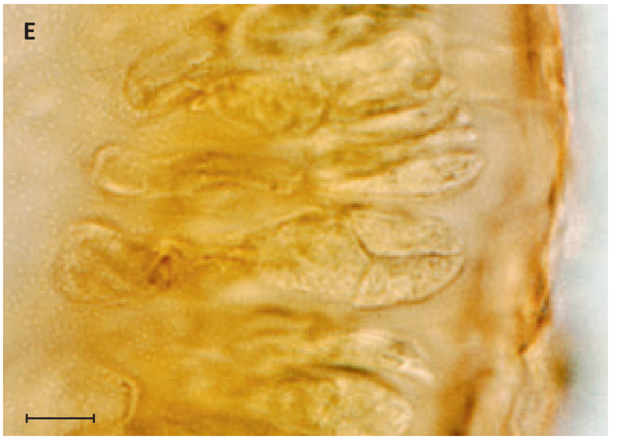
A: *Harveyella mirabilis*. Dark protuberances on Straggly Bush Weed (*Rhodomela confervoides*). Scale 200 µm. A B: Schultz's Grund, 8 m, 9.5.2000.

B: *Harveyella mirabilis*. Parasite and host in transverse section. Scale 100 µm.

C: *Harveyella mirabilis*. Antheridia in series from surface cells and released spermatia. Herthas Flak, 13 m, 2.2.1996. Scale 20 µm.



D: *Harveyella mirabilis.* Gonimoblast, consists of a small branch system embedded among host cells, preparation slightly pressed. Hatter Barn, 9 m, 18.9.1993. Scale 50 µm.



E: *Harveyella mirabilis.* Tetrasporangia between surface cells. Vejrø, 7 m, 26.3.1992. Scale 10 µm.

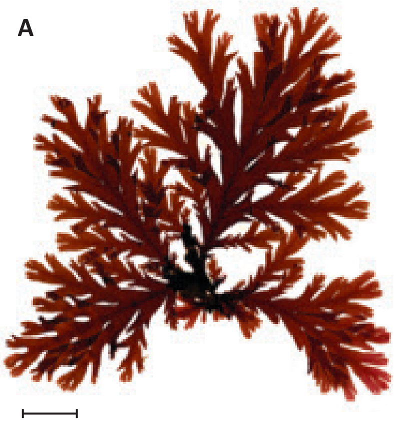
October, gonimoblasts in September, December-January and tetrasporangia in March-August and October.
Habitat: Parasitic on Straggly Bush Weed (*Rhodomela confervoides*) and Northern Tooth Weed (*Odonthalia dentata*), 4-26 m depth.
References: Goff & Cole (1973, 1975), Irvine (1983), Kylin (1944), Rosenvinge (1931), Zuccarello et al. (2004).

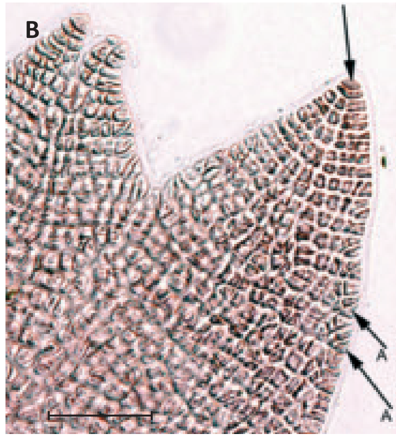
Odonthalia dentata

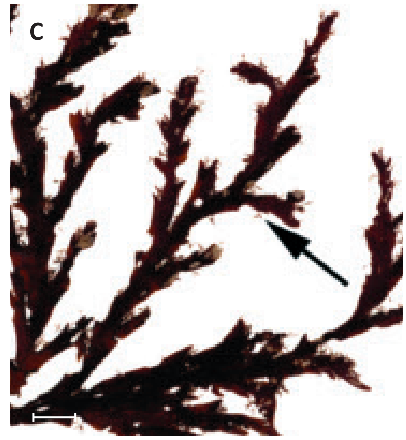
(Linnaeus) Lyngbye

Northern Tooth Weed

Appearance: Bush-like thalli in one plane, up to 20 cm in height, one or several uprights arise from a compact, conical disc-shaped base. They are tough, dark red-brown in colour except young branches which are soft and light red. The branching is distichous with irregularly scattered branches. The branches are ribbon-shaped with coarsely indented margins and are in one plane or with a broad, slightly raised midrib, lightly extending over the flat part of the branches. The basal 0.1-1 cm of the fronds are terete.
Structure: Uniaxial syntagma with 4 periaxial cells, 2 of which divide longitudinally early on in development to give the appearance of 6 periaxial cells. The periaxial cells are transversely divided and as more cells divide, the blade becomes segmented. A segment consists of part of a periaxial cell and cells cut off from it. The segments are visible at the apex of the thallus. Each segment has an apical cell in the lower outer corner. In time, several layers of small cortical cells cover the whole thallus. The indented margin forms as small lateral branches following division of an original apical cell. There are no trichoblasts.
Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. The reproductive structures, 1-2 mm in height, develop in small branchlets from the margin of the blades. Antheridia form a dense cover of small cells, but are not recorded in specimens from Danish waters. Gonimocarps are sessile on alternating minor branches on the fertile branchlets. They are ovoid to spherical with a pericarp of several cell layers. Tetrahedrally divided tetrasporangia are in pairs per segment in the distal part of the fertile branchlets.
Seasonal variation: Perennial overwintering individuals with young blades collected in January-June. Gonimocarps recorded in December-April and tetrasporangia in January-March.
Habitat: On boulders and pebbles and as epiphyte. Collected by divers, 3-31 m depth.







A: *Odonthalia dentata*. Thallus in one plane with coarsely indented margin. Scale 2 cm. A, D: Herthas Flak, 12 m, 30.5.1992.

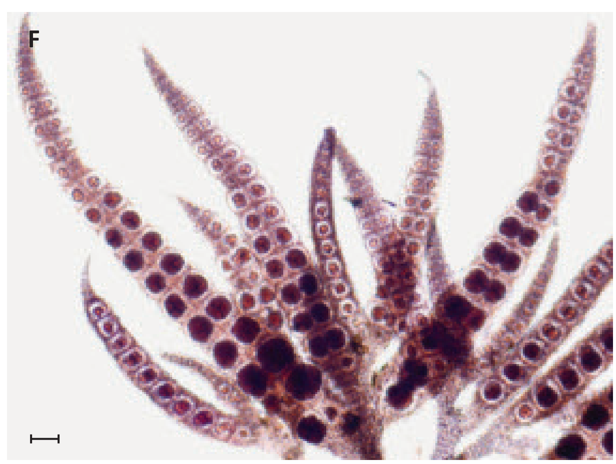
B: *Odonthalia dentata*. Uniaxial syntagma, apical cell (upper arrow) and segments with a small triangular apical cell in the lower corner of each segment (lower arrows). Læsø Trindel, 8 m, 31.5.1992. Scale 50 µm.

C: *Odonthalia dentata*. Tetrasporophyte with fertile branchlets (arrow). Tønneberg Banke, 13.5 m, 16.1.1997. Scale 2 cm.

D: *Odonthalia dentata*. Older dark alga with light red young blades. Scale 2 cm.

E: *Odonthalia dentata*. Gonimocarps on alternating branchlets. Hirsholm, drift, 27.12.1985. Scale 200 µm.

F: *Odonthalia dentata*. Fertile branchlets with paired tetrasporangia in each segment. Fornæs Fyr, drift, 4.2.2016. Scale 100 µm.



Resembles: Young *O. dentata* may be confused with *Membranoptera alata* but recognised by the triangular apical cell at the lower outer corner of each segment while the equivalent cell is in the upper corner in *M. alata*. Furthermore, the midrib is conspicuous in *M. alata* but absent or faint in *O. dentata*. The apex of *M. alata* is often pseudodichotomously branched with slightly curved branches.

References: Falkenberg (1901), Kylin (1944), Maggs & Hommersand (1993), Rosenvinge (1923-24).

Rhodomela

Straggly Bush Weed, Straggly Tail Weed

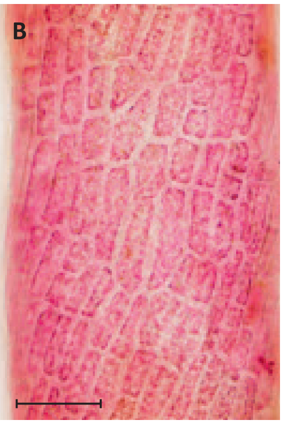
Appearance: Much branched red-brown bush-like thalli, up to 26 cm in height, with a single or several upright main branches from a disc-shaped base. There are conspicuous main branches with several orders of scattered branches on all sides, of which many are short and recurved. The branches of Straggly Bush Weed (*Rhodomela* sp.) in the Northern Kattegat are relatively stiff and bristle-like, resembling a bottlebrush when taken out of the water. It is characteristic that the branches end in a millimetre-long divided tuft of branches. The morphology changes with season and futhermore, becomes slender towards the Baltic Sea.

Structure: The branches consist of segments with (5-) 6 (-7) periaxial cells. The periaxial cells are as high as the axial cells when they form, but soon undergo transverse divisions into 2-3 smaller cells. Longitudinal divisions initiate a medulla of several layers around the central axial cells. The surface consists of a cortex of small angular elongated cells. Trichoblasts are in a spiral at the apex occurring singly from each segment. They consist of uniseriate, colourless cylindrical cells and are pseudodichotomously branched. The trichoblasts are numerous in spring when the alga grows rapidly, and they contribute to the soft appearance at that time of year. Primary branches replace trichoblasts.

Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Antheridia cover the antheridial branchlets as a confluent layer of small colourless cells. Gonimocarps are ovoid to spherical. Tetrasporangia tetrahedrally divided, occur in pairs per segment separated by small sterile cells.

Resembles: Purple Claw Weed (*Cystoclonium purpureum*) may look similar when the twisted branch apices are absent, but it has awl-like branches that attenuate towards a single apical cell, and the surface consists of rounded cells which appear pointed when viewed with a magnifying glass. In Straggly Bush Weed, (*Rhodomela* sp.) the periaxial cells develop at the apex so it is not pointed, and the cortex consists of elongated, rectangular cells.

A: *Rhodomela* sp. Apex with many pseudodichotomously branched trichoblasts. Primary branches replace trichoblasts. Periaxial cells soon transversely divided (arrow). Herthas Flak, 18 m, 9.6.1991. Scale 50 µm.



B: *Rhodomela* sp. Cortex of elongate angular cells with many disc-shaped plastids. Broen, 14 m, 10.9.1991. Scale 50 µm.

Comment: Some authors mention that three species occur in the North Atlantic while others consider them forms of *R. confervoides*. Rosenvinge (1923-24) referred *Rhodomela* from Danish waters to a single species as *R. subfusca* (Woodward) C.Agardh including five forms: the typical f. *genuina* and in addition, f. *lycopodioides*, f. *virgata* (which are considered separate species here), f. *tenuior* and f. *abyssicola*. The forma f. *lycopodioides* was considered to be a separate species by Kjellman (1883), Rueness (1977), and Maggs & Hommersand (1993) as *Rhodomela lycopodioides* (Linnaeus) C.Agardh. This is characterised by a few main branches with many dense short branches. This form fits the Danish name ulvehaletang [Wolf's Tail Weed], but it is known from Danish waters by only a single individual in the algal herbarium, Natural History Museum of Denmark, from an older collection obtained by dredge in Skagerrak. However, this species is common in Iceland and the Faroe Islands.

Rhodomela subfusca f. *tenuior* (C.Agardh) Svedelius and *R. subfusca* f. *abyssicola* Rosenvinge are very tiny forms in the Baltic Sea, the latter from deep water at Bornholm.

References: Falkenberg (1901), Kjellman (1883), Kornmann & Sahling (1977), Kylin (1944, *R. subfusca, R. virgata*), Maggs & Hommersand (1993), Rietema (1995), Rosenvinge (1923-24, *R. subfusca*), Rueness (1977), Svedelius (1901).

Rhodomela confervoides

(Hudson) P.C.Silva

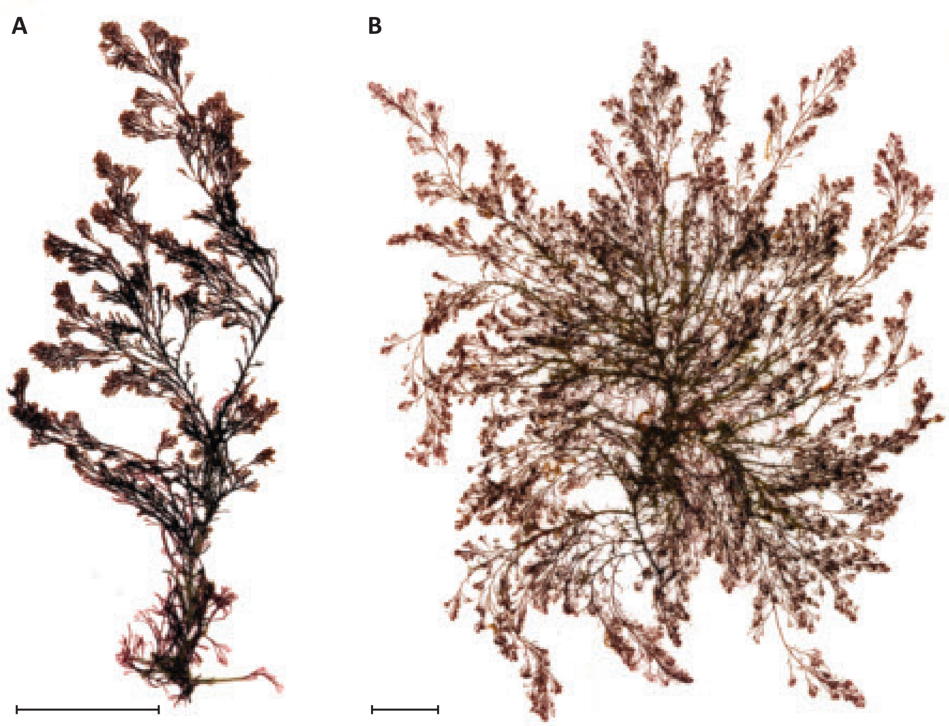
Straggly Bush Weed

Appearance: Much and repeatedly branched red-brown bush-like thalli with conspicuous main branches.

Structure: Well-developed branches have several layers of small cortical cells and an abrupt change to much larger medullary cells, visible in transverse sections.

Reproduction: Reproductive structures develop in the apex of vegetative branches.

Seasonal variation: Perennial; growth begins in January-February from overwintering thalli. In March-



A: *Rhodomela confervoides*. Female gametophyte. Scale 2 cm. A, F-G, I: Klokkegrund, 3.5 m, 6.3.1997.

B: *Rhodomela confervoides*. Much branched large bush-like thallus, new growth in apical part of branches. Vejrø, 11 m, 26.3.1992.

C

C: *Rhodomela confervoides*. Spring alga with soft apices. Vejrø, 13 m, 9.4.1989. Scale 2 cm.

D

D: *Rhodomela confervoides*. Slender alga. Davids Banke, Bornholm, 17 m, 17.6.2009. Leg.: C. Darling. Scale 2 cm.

E

E: *Rhodomela confervoides*. Summer alga with bristle branches. Briseis Flak, 8.5 m, 8.6.1989. Scale 2 cm.

F

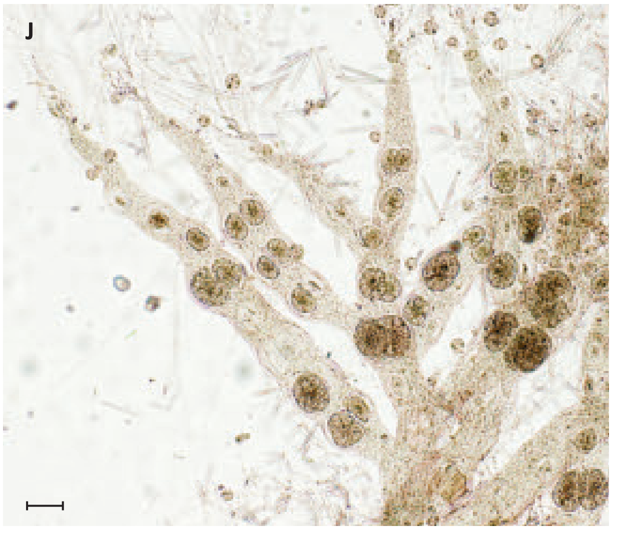
F: *Rhodomela confervoides*. Central axial cell, 6 periaxial cells surrounded by relatively large cells and abrupt change to several layers of small cortical cells. Scale 100 µm.

June new, soft branches are present. In the summer the alga has the stiff bottle-brush appearance, best developed on the alga in the Northern Kattegat. Antheridia recorded in January-May, gonimocarps in January-June and tetrasporangia in January-June and September.

G: *Rhodomela confervoides.* Apex covered by colourless antheridia. Scale 100 µm.

H: *Rhodomela confervoides.* Apex with young and mature gonimocarps. Scale 100 µm. H, J: Schultz's Grund, 8 m, 9.5.2000.

I: *Rhodomela confervoides.* Apex with young gonimocarps, several with trichogyne (arrow). Scale 100 µm.



J: *Rhodomela confervoides.* Paired tetrasporangia per segment in the youngest branches. Scale 100 µm.

Habitat: On stones and epiphytic on perennial red algae, on Serrated Wrack (*Fucus serratus*) and Oar Weed (*Laminaria digitata*). Collected by divers, 0.5-23 m depth.

Comment: Culture studies by Rietema (1995) showed a physiological adaptation to growth under different conditions, such as salinity, where the alga becomes genetically modified.

Rhodomela virgata

Kjellman

Appearance: Coarse, red-brown bush-like alga with conspicuous main branches and branches on all sides.
Structure: Well-developed branches gradually increase in cell size from the surface towards the medulla of large cells, seen in transverse section.
Seasonal variation: Perennial, in winter the main branches appear denuded with the branches almost gone, except for branchlets with reproductive structures. In spring, growth recommences both from the base and the overwintering main branches. Antheridia recorded in January, gonimocarps in January-February and tetrasporangia in January.
Comment: Described by Kjellman (1883) and accepted as a separate species by Kylin (1944) and Kornmann & Sahling (1977) but considered a form of *R. confervoides* by Rosenvinge (1923-24 as *R. subfusca*), Rueness (1977), Maggs & Hommersand (1993).

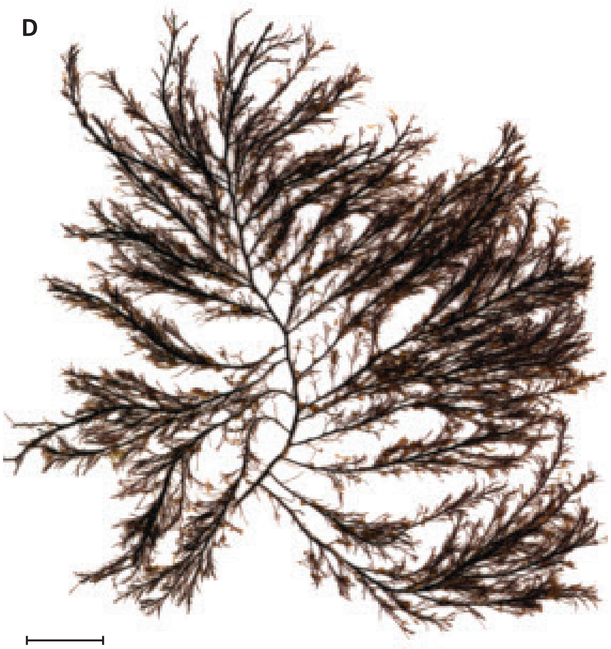
B

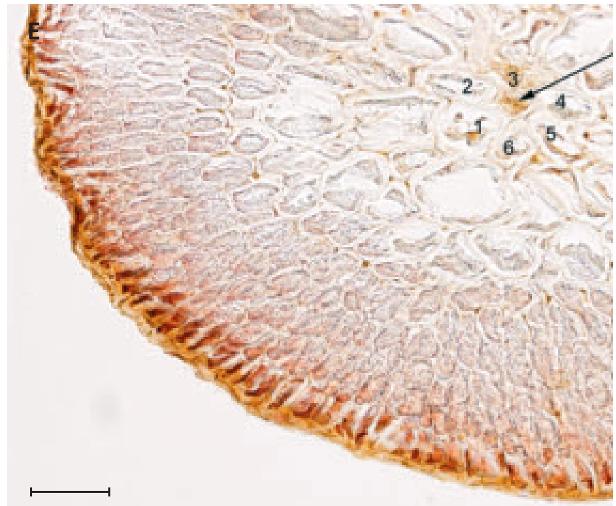
B: *Rhodomela virgata*. Young branches on old main branches and from the base. Kims Top, 19 m, 1.6.1992. Scale 2 cm.

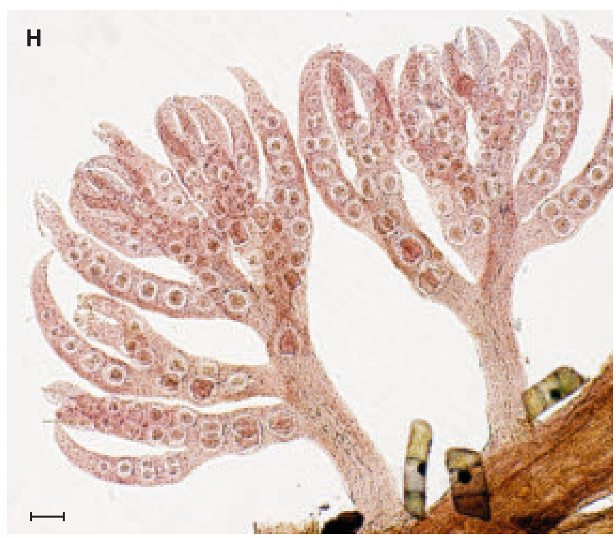
A: *Rhodomela virgata*. Tetrasporophyte in winter. Emaciated main branches with fertile branchlets (arrow). Kims Top, 19 m, 15.1.1997. Scale 2 cm.

C

C: *Rhodomela virgata*. Summer alga with coarse bristle-like branches. Scale 2 cm. C, E: Kims Top, 18 m, 25.8.1993.







D: *Rhodomela virgata*. Coarse summer alga. Herthas Flak, 13 m, 21.8.1991. Scale 2 cm.

E: *Rhodomela virgata*. Central axial cell (arrow) surrounded by 6 periaxial cells (1-6) and medullary cells, gradually smaller in size towards the cortex, transverse section. Scale 100 µm.

F: *Rhodomela virgata*. Fertile branchlets covered by antheridia. Scale 100 µm. F-H: Kims Top, 21.5 m, 15.1.1997.

G: *Rhodomela virgata*. Fertile branchlets with gonimoblasts. Scale 100 µm.

H: *Rhodomela virgata*. Fertile branchlets with pairwise tetrasporangia in each segment. Scale 100 µm.

Family: Wrangeliaceae · Tribe: Compsothamnieae

Compsothamnion thuioides

(Smith) F. Schmitz

Alternate Bush Shrublet

Appearance: Delicate pink bushy alga up to 2-3 cm in height. The branches are complanate and several arise together from prostrate filaments.

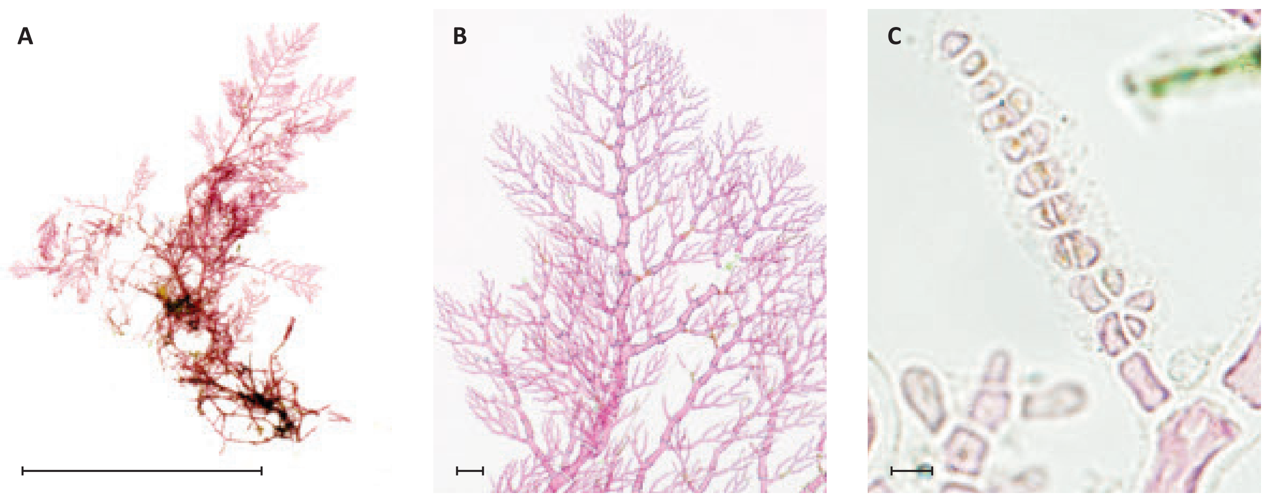
Structure: The uprights consist of uniseriate filaments without cortex. They are regularly repeatedly branched in one plane. The branches are distichous and regularly alternating with a single branch from each cell of the main axis. Branchlets arise from the branches in the same pattern with the first branchlet on the adaxial side of the branch. The cells are cylindrical except those of the main axis which may be slightly constricted above the middle part. There are many irregular disc-shaped plastids per cell. From the main axis long narrow sparsely branched filaments arise at irregular intervals, and probably act as runners.

Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Antheridial branchlets are elongate club-shaped on a stalk of 1-2 cells on the distal branchlets. They were observed on individuals which also had tetrasporangia. Female reproductive structures are not recorded on the alga from Danish waters. Tetrahedrally divided tetrasporangia are apical on stalks of 1-3 cells on the youngest branchlets. Sporangia with eight spores (octosporangia) also observed on the alga with tetrasporangia.

Seasonal variation: Only collected in August with antheridial branchlets, tetra- and octosporangia.

Habitat: Epiphytic on other algae on stone reefs, 14.5-21.5 m depth.

References: Maggs & Hommersand (1993).



A: *Compsothamnion thuioides*. Scattered complanate branches. Kims Top, 21.5 m, 26.8.1993. Scale 1 cm.

B: *Compsothamnion thuioides*. Apex with repeated regularly alternating branches. Kims Top, 18 m, 25.8.1993. Scale 100 μm.

C: *Compsothamnion thuioides*. Antheridial branchlet. Scale 10 μm. C, D: Herthas Flak, 18 m, 28.8.1993.

D: *Compsothamnion thuioides*. Tetrahedrally divided tetrasporangium (left arrow) and octosporangium (right arrow). Scale 20 μm

Tribe: Griffithsieae

Griffithsia

Mrs Griffiths's Weeds

Delicate pink thalli of upright, repeatedly pseudodichotomously divided branches, which consist of large uniseriate cells that are visible to the naked eye, with no cortex. The upright branches arise from slender, prostrate matted filaments. Growth is apical from a rounded apical cell. The cylindrical cells are constricted at the crosswalls and contain many disc-shaped plastids. The alga attaches to the substratum by rhizoids that originate from the lower cells of the upright branches. The life history comprises isomorphic gametophytes and tetrasporophyte. The reproductive structures develop from the distal end of cells in the upper part of the alga and appear as if they form whorls around the crosswalls. Tetrasporangia are tetrahedrally divided.

References: Maggs & Hommersand (1993).

Griffithsia corallinoides

(Linnaeus) Trevisan

Mrs Griffiths's Coral Weed

Appearance: Branches equally long, up to 2-3 cm in height, and attach to the substratum by narrow rhizoids from which several upright branches arise.

Structure: Pseudodichomous branching occurs every 1-3 cells. The cells are up to 100-200 µm in width and 4-6 times as long as wide with rounded ends. The filaments are constricted at the crosswalls. Oldest cells are obpyriform with the distal end broader than the base. The youngest cells are relatively short and the apical cell approximately spherical.

Reproduction: Reproductive structures have not been observed in the alga from Danish waters. In the British Isles, antheridia form on tiny branchlets in a whorl around the distal end of young cells. Gonimoblasts occur individually, and have several lobes surrounded by incurved filaments (involucral branches). Tetrasporangia form a whorl at crosswalls next to the apex and are surrounded by small, curved branches.

Seasonal variation: Only a single collection from Danish waters, August.

Habitat: On boulders, 22 m depth.

Comment: The individuals of this species become 10-15 cm in height at the Swedish West coast, with records of female gametophytes and tetrasporophytes.

References: Kylin 1944.

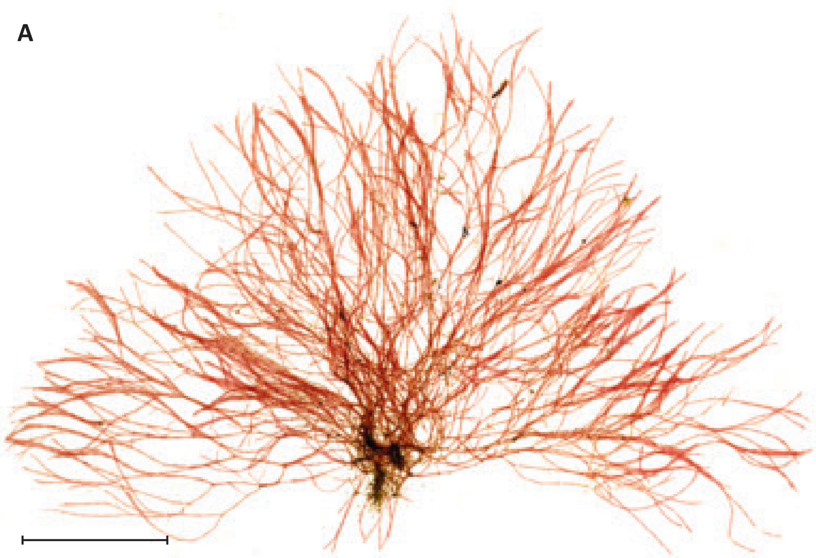
A: *Griffithsia corallinoides.* Regularly dichotomously branched specimens with large cells (arrow). Kims Top, 22 m, 26.8.1993. Scale 1 cm.

Griffithsia devoniensis

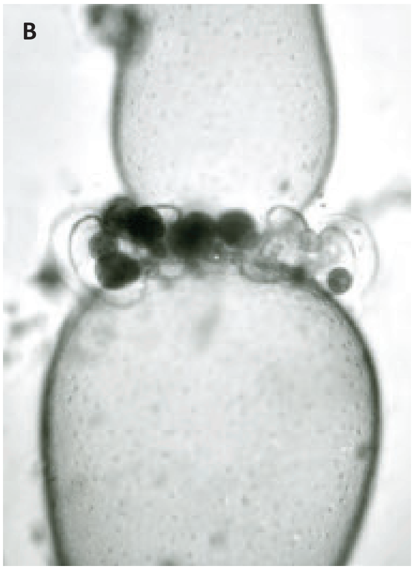
Harvey
Mrs Griffiths's Devon Weed

Appearance: Thalli of uniseriate pseudodichotomously branched filaments, which might be matted together. They are fragile and up to 5-10 cm in height.
Structure: Branching starts a few cells below the round apical cell. The cells are cylindrical, only slightly rounded and constricted at the crosswalls. The lower cells are c. 300 µm in width and 4.5-8 times as long as wide and apical cells are c. 18 µm in width. Several multicellular rhizoids originate from the upper part of the basal cells.
Reproduction: Tetrasporangia develop in clusters on small branchlets which form whorls at the crosswalls together with incurved cells. Tetrasporangia are the only reproductive structures observed on the alga in Danish waters. In the British Isles, antheridia on small branchlets form whorls around the crosswalls. Gonimoblasts consist of 3 lobes surrounded by a few unicellular incurved filaments.
Seasonal variation: Collected in July-August, tetrasporangia recorded in August.
Habitat: On mussel shells and small stones, 0.5-5 m depth.
Resembles: Mrs Griffiths's Little Flower (*Halurus flosculosus*) looks similar but has stiff branches without constrictions at crosswalls and pointed apical cells, and 3-4 branches may occur at branching points.
References: Christensen 1947.

A: *Griffithsia devoniensis*. Regularly dichotomously branched with large elongate cells. The bay between Ørding and Sillerslev, Mors, drift, 30.7.1945. Leg.: T. Christensen. Scale 2 cm.



B: *Griffithsia devoniensis*. Tetrasporangia with incurved cells in a whorl surrounding a crosswall. Jegind Tap, Kaas Bredning, 2-5 m, 20.8.1974. Leg.: H. Bak and L. Mathiesen.



Halurus flosculosus

(J.Ellis) Maggs & Hommersand

Mrs Griffiths's Little Flower

Appearance: Dark rose thalli of slender, relatively stiff pseudodichotomous branches up to 15 cm in height. Several upright branches arise from narrow matted filaments attached to the substratum.

Structure: The uniseriate branches are pseudodichotomously branched, but 3-4 branches may arise at some of the branching points. Growth is apical from a pointed apical cell. Branching starts a few cells below the apical cell with branches arising from each cell or at intervals of four cells. The cells are cylindrical or slightly broader at the top, 350-400 µm in width and 3.5-6 times as long as wide. The walls are relatively thick without constrictions at the crosswalls. There is no cortex. Branched multicellular rhizoids arise from the basal cells and contribute to the attachment of the alga.

Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Reproductive structures develop on special curved branchlets and form whorls on short branches next to the apex. No record of gametophytes in Danish waters. Tetrahedrally divided tetrasporangia are sessile on the adaxial side of incurved branchlets.

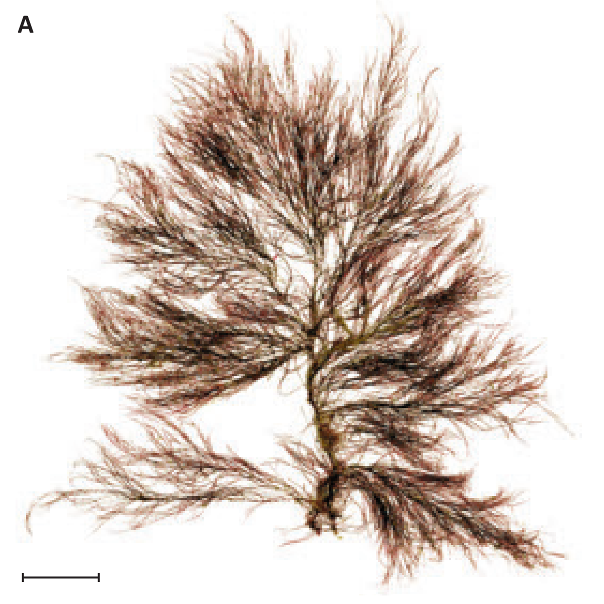
Seasonal variation: Collected in August with tetrasporangia.

Habitat: On boulders, 16 m depth.

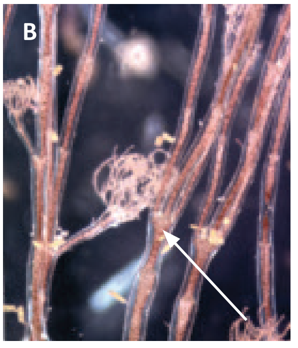
Resembles: Mrs Griffiths's Devon Weed (*Griffithsia devoniensis*) looks similar but has soft branches constricted at crosswalls and rounded apical cells.

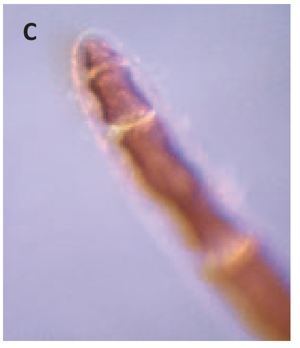
Comment: Rare in Danish waters, only collected once (Stone reef investigations of Det Marine Fagdatacenter, 2011).

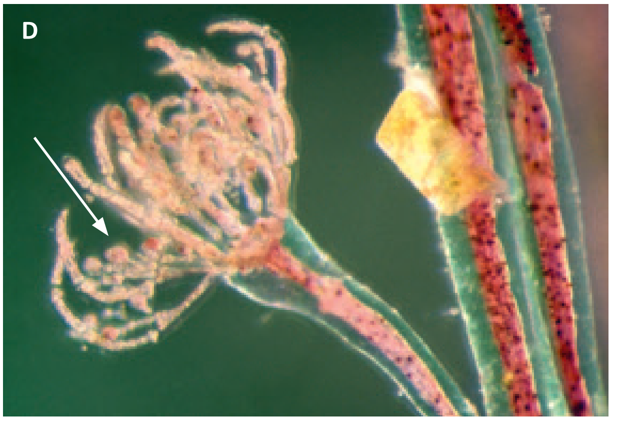
References: Maggs & Hommersand (1993).



A: *Halurus flosculosus*. Bushy alga with straight, pseudodichotomous branches. Scale 2 cm. A-D: Kims Top, 16 m, 17.8.2011.







B: *Halurus flosculosus*. Tetrasporophyte, tetrasporangial branches in whorls on short branchlets. Branching point with 3 branches (arrow). B-D: Photo by S. Lundsteen.

C: *Halurus flosculosus*. Apex with conical apical cell.

D: *Halurus flosculosus*. Small branch with whorl of tetrasporangial branchlets (arrow).

Tribe: Ptiloteae

Plumaria plumosa

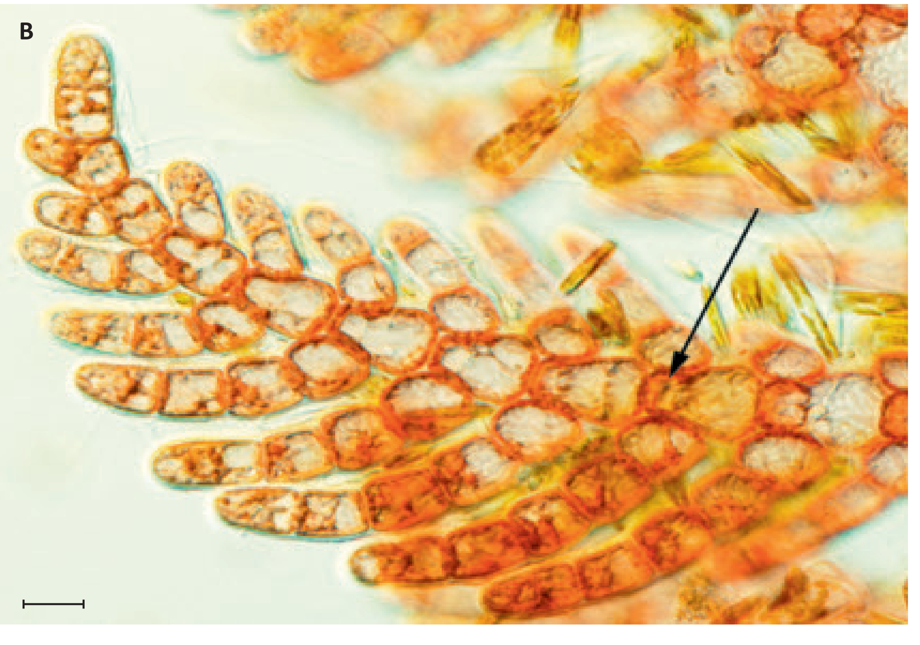
(Hudson) Kuntze

Soft Feather Weed

Appearance: Several uprights arise from a disc-shaped base, they are dark wine-red or brownish red and up to 8 cm in heigh. Branches repeatedly branched in one plane.

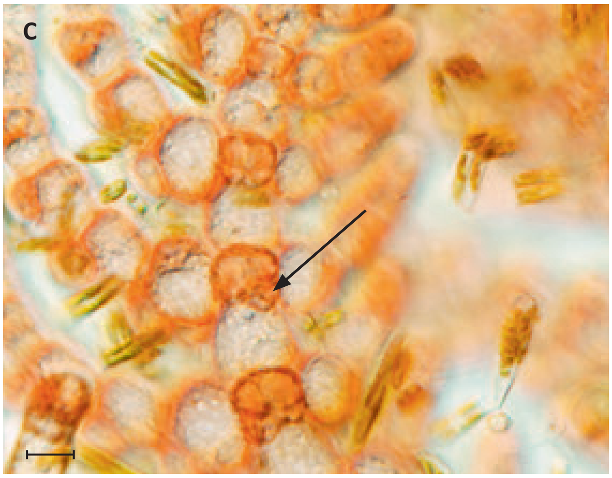
Structure: Uniaxial syntagma with pyriform central axial cells. Opposite branches from each of the central axial cells arise immediately below the apical cell. Further down the branch, opposite cells are cut off between the opposite branches. These cells are the initiation of a small-celled cortex, which is extended further by cell divisions in the lower cells of the branches. There is no cortex at the apex or in the youngest parts of branches. The cortex eventually becomes multilayered and consists of small, rounded cells with plastids. In the lower part of the main axis there are narrow downward-growing filaments between the central axial cells and the outer cortical cells. The branches are distichous with a short branch opposite a longer branch, which alternate irregularly at inter-

A: *Plumaria plumosa*. Dark red complanate alga. Northern harbour jetty, Frederikshavn, 0.5 m, 21.6.1988. Scale 2 cm.



B: *Plumaria plumosa*. Apex, pyriform central axial cells with opposite branches from each cell. The first cortical cell (arrow) between the opposite branches formed several segments below the apical cell. Scale 20 µm. B, C: The head of the southern harbour jetty, Hirsholm, 0.5 m, 14.4.2015.

C: *Plumaria plumosa*. Initiation of cortex from the cells between opposite branches (arrow). Scale 20 µm.



vals of 2-3 segments. The branches curve upwards and grow above the main axis. Some of the longest branches develop into new main axes at irregular intervals. The vegetative cells contain ribbon-shaped plastids. Red algal hairs are sometimes present, apical on small branches. The disc-shaped base consists of tangled filaments.

Reproduction: Isomorphic dioecious gametophytes, tetrasporophyte and individuals with parasporangia. A single tetrasporangium was observed in an older investigation, otherwise paraspores are the only known reproduction in algae from Danish waters. The parasporangia form dark clumps of cells at the apex of small branches.

Seasonal variation: Perennial, thalli are worn away in winter and recommence growth in spring. Parasporangia recorded all year except spring, most frequent in summer.

Habitat: On boulders, at shallow water in the shade between the boulders, and in deeper water also epiphytic. In the Northern Kattegat collected by divers, 0.5-13.5 m depth. In other districts the collections are few and scattered, 6-17 m depth.

Comment: Individuals with parasporangia are triploid and have a more northern distribution than sexual individuals (Drew, 1939).

References: Drew (1939, *P. elegans*), Maggs & Hommersand (1993), Rosenvinge (1923-24, *P. elegans*).

D: *Plumaria plumosa*. Parasporangium. Per Nilen, 6 m, 27.8.2013. Scale 20 µm.

Ptilota gunneri

P.C.Silva, Maggs & L.M.Irvine

Feathered Wing Weed

Appearance: Feather-shaped alga, relatively stiff, dark red, up to 15 cm in heigh. Several uprights arise from a disc-shaped base.

Structure: Uniaxial syntagma, the cortex originates just below the apical cell and becomes multi-layered. Further down the thallus, there are many thin, downward-growing, filaments between the central axial cells and the cortex. The thallus is complanate, and the main axes have distichous opposite, regularly alternating long and short branches, which arise from every second cell of the central axis. On each branch cell there are short opposite branchlets, which become corticated. The branches curve upwards and overtop the main axis. Some of the longer branches grow out to new main axes at irregular intervals. The disc-shaped base consists of narrow filaments.

Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte, reproductive structures develop at the apex of the short opposite branches. Antheridial branchlets terminate in a series of 6-8 axial cells on which small colourless spherical antheridia in distichous series form a cluster. Gonimoblasts spherical and surrounded by small involucral branchlets. Tetrahedrally-divided tetrasporangia form clusters on small, in part uniseriate, branchlets.

Seasonal variation: Perennial, slightly worn away in winter. In spring, new branches arise in continuation of the older thallus or as new branches from the base of branchlets. Antheridia recorded in May and August, carpogonia in June, mature gonimoblasts and tetrasporangia in June-September.

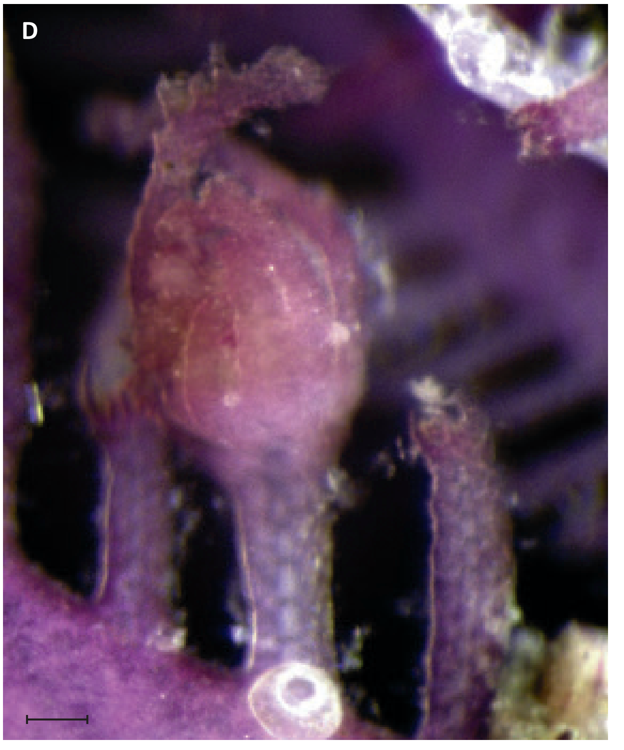
Habitat: On stipes of Oar Weed (*Laminaria digitata*) and Forest Kelp, (*L. hyperborea*) and on boulders, 11-15 m depth in Skagerrak, collected by divers in the Northern Kattegat, 11-21 m depth, and drift in the Northern part of the Sound.

References: Maggs & Hommersand (1993), Rosenvinge (1923-24, *P. plumosa*).

A: *Ptilota gunneri*. Complanate dark red alga with distichous branches. Kims Top, 14.5 m, 4.2.1996. Scale 2 cm.

B: *Ptilota gunneri*. Apex, main axis with regularly alternating long and short opposite branches that arise from every second axial cell, incurved and growth above the apical cell (arrow). Store Middelgrund, 20.5 m, 9.6.1993. Scale 50 µm.

C: *Ptilota gunneri.* Antheridial branchlet with spherical antheridia (arrow). Kims Top, 19 m, 9.8.1995. Scale 10 µm.



D: *Ptilota gunneri.* Short branchlet with apical gonimoblast surrounded by involucral branchlets. Kims Top, 15 m, 28.8.2013. Scale 100 µm. Photo by S. Lundsteen.

Tribe: Spermothamnieae

Spermothamnion repens

(Dillwyn) Magnus

Creeping Bush Weed

Appearance: Prostrate filaments from which scattered, upright narrow branches arise, so the alga appears as a tuft or a velvet-like cover, 0.1-2 cm in height. The species also occurs as drifting spherical tufts, 3-5 cm in diameter and light red in colour.

Structure: The branches are uniseriate without cortex. Branches occur on all sides and are scattered or opposite and often arise with a perpendicular angle to the main axis and at variable distances. The cells are cylindrical, 30-42 µm in width and 4-5 times as long as wide. Prostrate filaments attach to the substratum with unicellular attachment pads, which are plate-shaped and divided into several lobes.

Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Antheridial branchlets, appear as small cones and are apical on short branches. Gonimoblasts develop into spherical cell clusters, surrounded by 3-4 (-8) few-celled unbranched filaments from the cell below (involucral branches). Tetrahedrally divided tetrasporangia occur individually on a stalk-cell or in small clusters that develop after division of the stalk-cell, and a new sporangium develops apically on the new stalk-cell. Antheridial branchlets and tetrasporangia typically occur on the same individual, occasionally also with gonimoblasts.

Seasonal variation: Perennial, most of the thallus decays in autumn and overwinters as prostrate filaments from where new uprights arise in spring. In late summer drifting tufts resembling powder-puffs are frequent in shallow water.

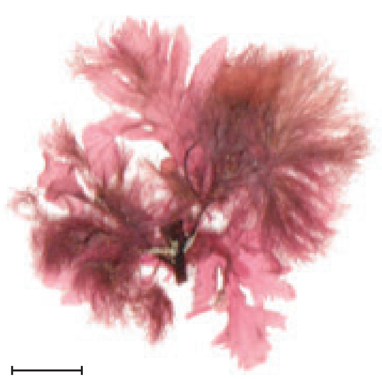
Habitat: Epiphytic on larger algae, 0.5-25 m depth and collected by dredge in older collections at 31 m depth in the North Sea.

Resembles: The *Trailliella*-phase of *Bonnemaisonia hamifera*, looks similar but has gland cells. The cells of Creeping Bush Weed (*S. repens*) are 4-5 times as long as wide, and the attachment pads are unicellular, while the *Trailliella*-phase of *B. hamifera* has relatively short cells, never with opposite branches and multicellular attachment pads.

References: Kylin (1944), Maggs & Hommersand (1993), Rosenvinge (1923-24).

A

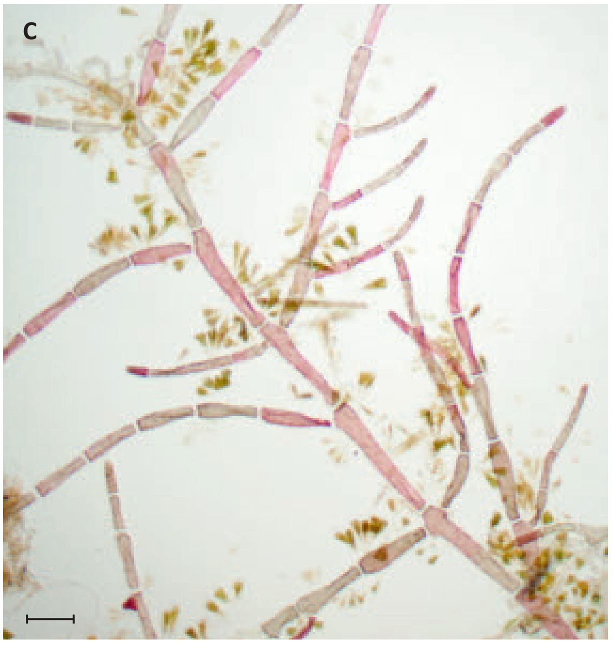
B



A: *Spermothamnion repens*. Creeping on Clawed Fork Weed (*Furcellaria lumbricalis*) (arrow) with other epiphytic red algae: Purple Claw Weed (*Cystoclonium purpureum*), Soft Feather Weed (*Plumaria plumosa*) and Sea Oak (*Phycodrys rubens*). Per Nilen, 11 m, 6.6.1989. Scale 2 cm.

B: *Spermothamnion repens*. Larger tufts with Sea Oak (*Phycodrys rubens*). North of Gilbjerg Hoved, 8.5 m, 30.5.1989. Scale 1 cm.

C



C: *Spermothamnion repens*. Scattered and opposite vegetative branches of long cylindrical cells. Brown epiphytic diatoms. Tangen, 7.5 m, 15.9.1996. Scale 100 µm.

D

D: *Spermothamnion repens*. Unicellular attachment pad (arrow) from prostrate filament. Tønneberg Banke, 14.5 m, 20.8.1994. Scale 20 µm.

E: *Spermothamnion repens*. Antheridial branchlet. Store Middelgrund, 11 m, 25.8.1993. Scale 10 µm.

F: *Spermothamnion repens*. Carpogonium (right arrow) with trichogyne and attached antheridia (left arrow). Scale 10 µm. F, H: Læsø Trindel, 8 m, 26.8.1993.

G: *Spermothamnion repens*. Gonimoblast with few involucral branches (arrow). Tønneberg Banke, 13 m, 20.8.1991. Scale 20 µm.

H: *Spermothamnion repens*. Tetrahedrally-divided tetrasporangia. Scale 20 µm.

Order: Gigartinales · Family: Calosiphoniaceae

Schmitzia neapolitana

(Berthold) P.C.Silva

Stringy Jelly Weed

Appearance: Upright thallus is pink gelatinous soft and very smooth, up to 3-5 (-11) cm in height. Terete branches occur on all sides, repeatedly branched with scattered branches, which are 0.5-1 mm in diameter at the base. The life history comprises a crustose phase (see comment).

Structure: Uniaxial syntagma. A few cells below the apical cell the axial cells are surrounded by 3 (-4) radiating filaments. These filaments are repeatedly branched, although restricted in growth and held together in a common jelly-like slimy wall substance and consist of uniseriate cylindrical cells with several disc- to short ribbon-shaped plastids. From the lower cells of the radiating filaments, narrow downward-growing filaments arise which cover the axial cells.

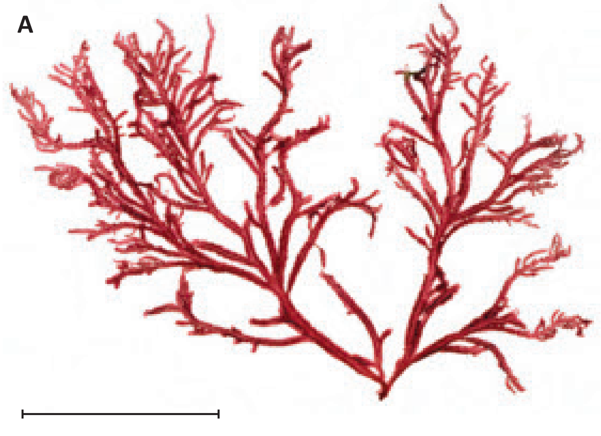
Reproduction: Upright phase of isomorphic dioecious gametophytes. Antheridia form in whorls round the upper cells of the radiating filaments at the surface of the thallus. Spherical gonimoblasts develop at the inner part of the radiating filaments.

Seasonal variation: Collected with antheridia and gonimoblasts in August.

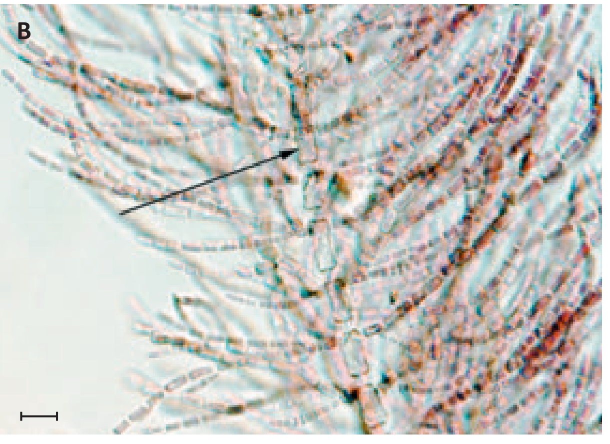
Habitat: On small stones and calcified crustose red algae, 14.5-20.5 m depth.

Comment: The heteromorphic life history with upright gametophytes and a crustose tetrasporophyte were noticed for *S. hiscockiana* Maggs & Guiry in a study of the species from Ireland (Hiscock & Maggs, 1984 and Maggs & Guiry, 1985). The crust consisted of upright narrow and thick filaments, which in surface view appeared as small and large cells. Among the narrow filaments were apical obliquely cruciately divided tetrasporangia. Similar crust-forming tetrasporophytes were collected in Danish waters at the same localities and depth where the upright Stringy Jelly Weed (*S. neapolitana*) was found. These crusts probably represent the tetrasporophyte of this species. They consist of dense unbranched filaments that arise from a basal layer of radiating filaments without pit connections or cell fusions. Apical obliquely cruciately divided tetrasporangia occurred between cells of narrow filaments, recorded in April.

References: Hiscock & Maggs (1984), Karlsson et al. (1992), Maggs & Guiry (1985).

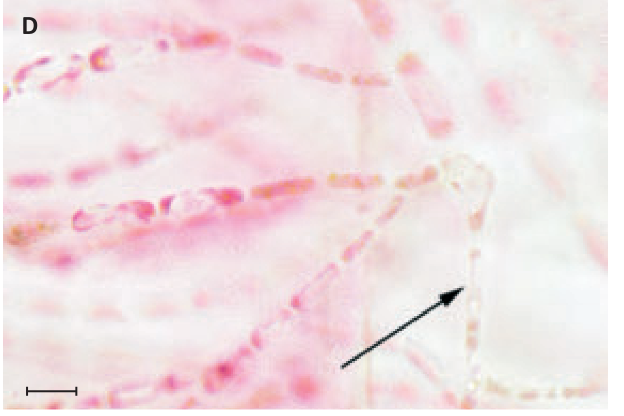


A: *Schmitzia neapolitana.* Pink, repeatedly branched alga of terete branches. A, D-E: Herthas Flak, 20.5 m, 28.8.1993. Scale 2 cm.



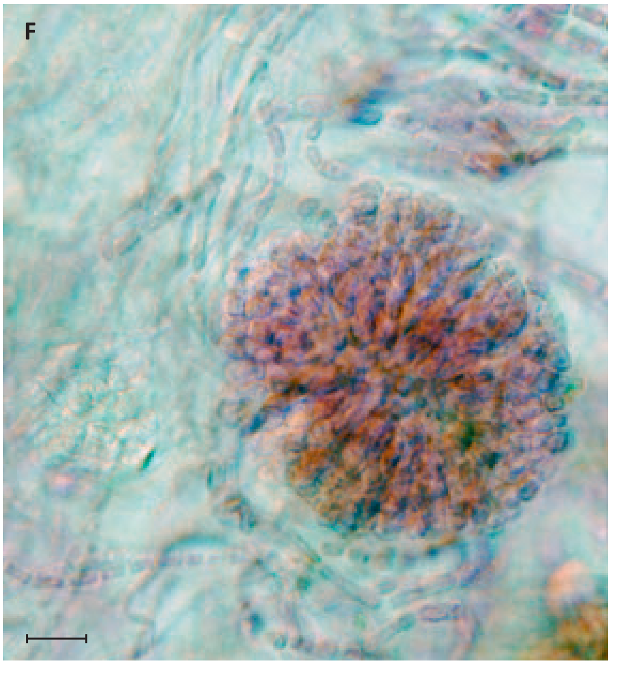
B: *Schmitzia neapolitana.* Central axial cell (arrow) with radiating filaments. B-C: Tønneberg Banke, 10 m, 27.8.1993. Scale 20 µm.

C: *Schmitzia neapolitana*. Apex of uniaxial syntagma, central axial cells surrounded by whorls of branched filaments. Scale 50 µm.

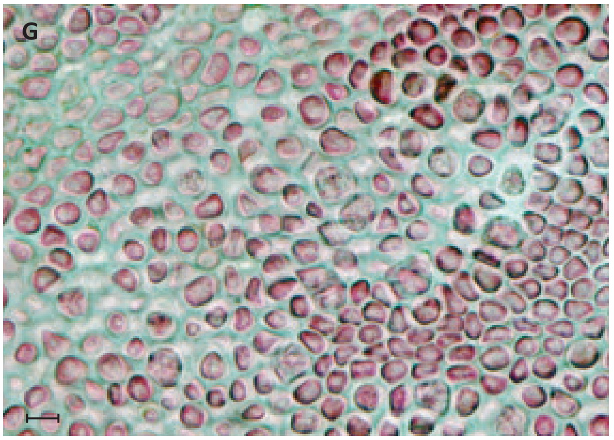


D: *Schmitzia neapolitana*. Downward-growing narrow filament (arrow) from the basal cell of one of the radiating filaments. Scale 10 µm.

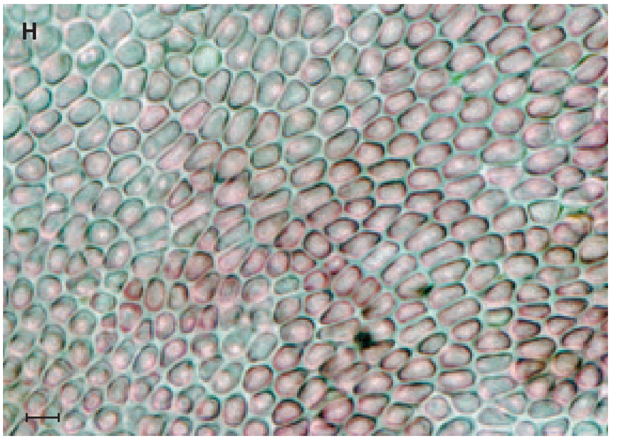
E: *Schmitzia neapolitana*. Antheridia (arrow) at the apex of radiating filaments. Scale 10 µm.



F: *Schmitzia neapolitana*. Spherical gonimoblast between filaments. Tønneberg Banke, 15 m, 27.8.1993. Scale 20 µm.

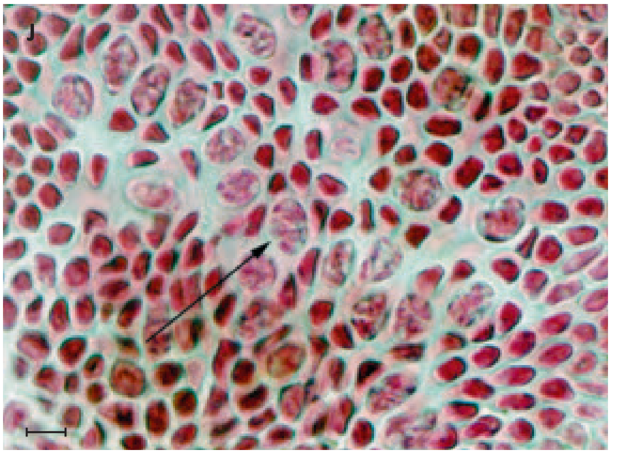


G: *Schmitzia neapolitana*. Crustose alga, small and large cells in surface view. Scale 10 µm. G-J: Probably the tetrasporophyte. Læsø Trindel, 17 m, 11.4.1991.



H: *Schmitzia neapolitana,* Basal layer, no pit connections or cell fusions. Scale 10 µm.

I: *Schmitzia neapolitana*. Upright filaments. Scale 10 µm.



J: *Schmitzia neapolitana*. Tetrasporangium (arrow) between the upright filaments in surface view. Scale 10 µm.

Family: Cruoriaceae

Cruoria pellita

(Lyngbye) Fries

Soft Crust Weed

Appearance: Extensive dark red crusts, soft to touch, with a velvet-like sheen on the surface. They may become up to 12 cm in diameter and 0.1-0.5 cm in thickness.

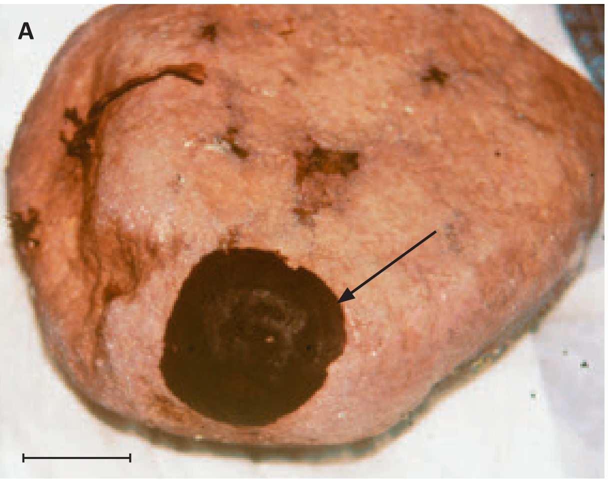
Structure: A basal cell layer of radiating filaments with dense ascending unbranched or sparsely branched uniseriate filaments. Upright filaments are held together by a gelatinous wall substance and are easily separated by application of slight pressure. Filaments decrease in thickness from the base towards the apex, and this reduction in size is largest at the base while the filaments may be of an even thickness in the upper part. The lowest cells are almost barrel-shaped, 12.5-14 µm in width, and towards the top become cylindrical, (6-) 7.5-9 (-11) µm in width. Apical cells are square-ended or rounded. The upper cells have an oblique cap-shaped plastid in the upper end. Short filaments may arise from the underside of the basal layer and grow downwards or along the substratum and form a dense matted layer.

Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Reproductive structures are lateral on the upright filaments. Antheridia are stick-shaped and form small clusters in the upper end of the filaments. Mature gonimoblasts appear as large dark spindle-shaped cell-clumps between the upright filaments. The tetrasporangia are spindle-shaped and zonate, 45-60 µm in width and 250-283 µm in height.

Seasonal variation: Perennial. Gonimoblasts recorded in January-February and tetrasporangia in January-March, May and August-September.

Habitat: On stone and pebbles, common on shells of Horse Mussel (*Modiolus modiolus*), Blue Mussel (*Mytilus edulis*) and stipes of Forest Kelp (*Laminaria hyperborea*), rarer on Serrated Wrack (*Fucus serratus*) and Brown Sea Oak (*Halidrys siliquosa*). Collected by divers, 1-24.5 m depth and by dredging to 30 m depth.

Resembles: Hennedy's Dark Red Crust (*Haemescharia hennedyi*) appears similar but has upright filaments of an even thickness, and upper cells 4-6 µm in width,

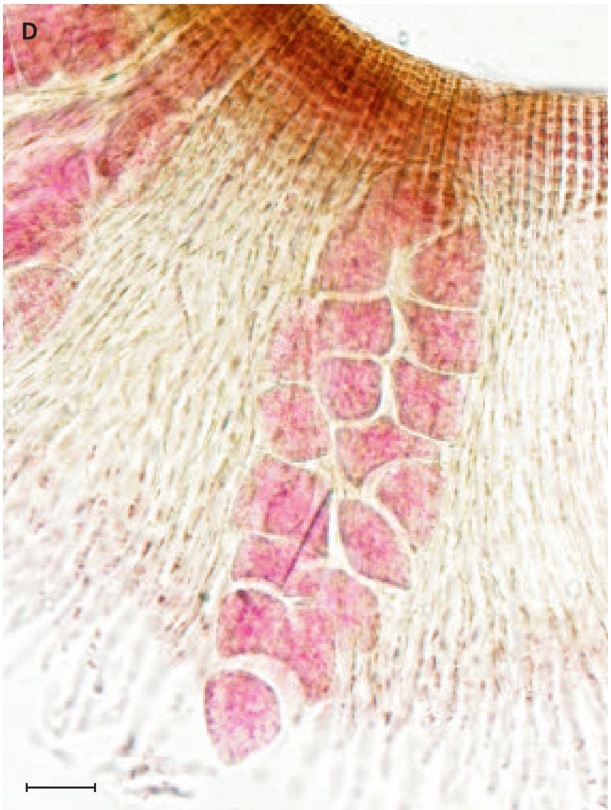


A: *Cruoria pellita*. Dark red crust (arrow) on rock with Common Shore Paint Weed (*Phymatolithon lenormandii*). Scale 2 cm. A, B: Jessens Grund, 8 m, 7.3.1997.

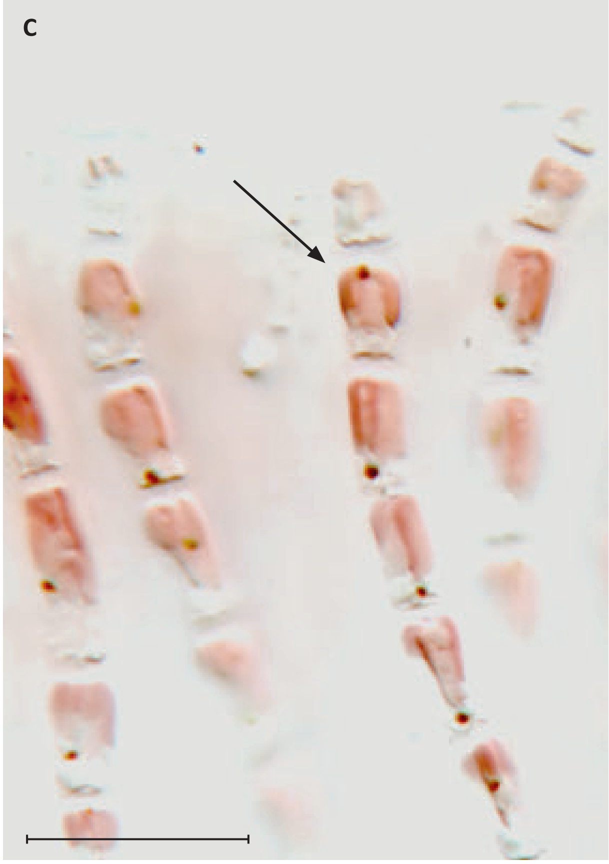
B: *Cruoria pellita*. Basal layer (arrow) of matted filaments with long ascending filaments and short downward-growing filaments. Scale 50 µm.

cruciate tetrasporangia are intercalary in series within the upright filaments. While the filaments decrease in size in Soft Crust Weed (*Cruoria pellita*), it has large zonate tetrasporangia. In the area close to the distribution border in the Baltic Sea the filaments of Soft Crust Weed (*C. pellita*) are slender and it is difficult to distinguish between the two species without the presence of reproductive structures.

References: Maggs & Guiry (1989), Rosenvinge (1917).



D: *Cruoria pellita*. Gonimoblast of large dark red cell clumps between upright filaments. Slightly pressed. Herthas Flak, 13 m, 2.2.1996. Scale 50 µm.



C: *Cruoria pellita*. Distal part of upright filaments, apical cells with cap-shaped plastid (arrow). Store Middelgrund, 18 m, 20.8.2015. Scale 20 µm. Photo by S. Lundsteen.

E: *Cruoria pellita*. Zonate tetrasporangium (arrow) between upright filaments whose cells clearly diminish from base to top. Bolsaks, 8 m, 5.3.1997. Scale 50 µm.

Family: Cystocloniaceae

Cystoclonium purpureum

(Hudson) Batters

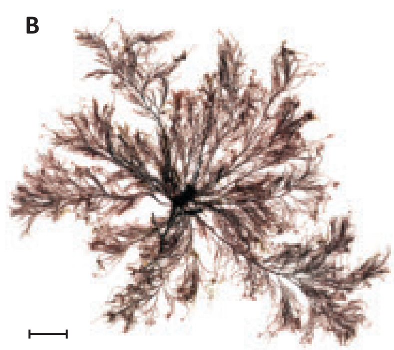
Purple Claw Weed

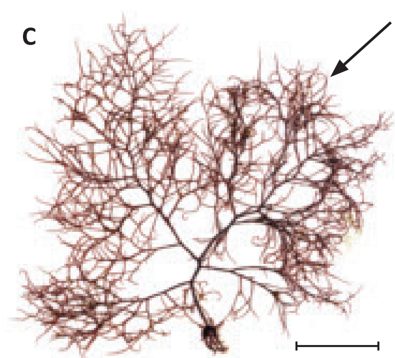
Appearance: Bush-like alga of terete branches with a very distinct main axis, up to 2 mm in diameter. Thallus soft light red-brown, and up to 50 cm in height in the North Sea, Skagerrak and the Northern Kattegat. Branches on all sides, are scattered and repeatedly branched. The main axis arises from an attachment disc, which is later camouflaged by sparsely branched downward-curved pointed branches. If in contact with the substratum these may form small attachment pads. The thickness of the upright branches tapers gradually towards the apex into a pointed top. In some individuals, the tips of branches are spirally twisted (tendrils) or terminate in short branches with attachment pads. In shallow water on exposed shores, such as the outside of harbour jetties, the lower part of the main axis is frequently without branches and these have no tendrils. In deeper water the main axis is narrow and the thallus becomes matted together by many tendrils. In the inner districts the alga is only up to 20 cm in height, and often small and thin. In the brackish water districts in the Belt Sea and the Baltic Sea the alga is tiny, with the main axis and other branches of equal thickness.

Structure: Uniaxial syntagma with the central axis terminating in a small apical cell cut off by an oblique crosswall. From the central axial cells a few periaxial cells are cut off. Branched filaments arise from the periaxial cells and form a medulla and towards the surface a compact, multilayered cortex. Between the medullary cells there are many tiny filaments so older individuals have a densely matted medulla. The inner part of the cortex consists of ovoid cells with a gradual transition to the outer layers of small rounded densely connected assimilating cells, 5-7.5 µm in diameter in surface view.

Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Antheridia form colourless patches, developing from surface cells of the branches. Gonimoblasts develop in the medulla and appear as knots in the branches. Zonate tetrasporangia occur in the cortex of slightly thickened branches.

Seasonal variation: Perennial with well-developed thalli in May-September. The upright part of older





A: *Cystoclonium purpureum*. Distinct main axis, many branches some of which terminate in tendrils (arrow). At the base, short downward-curving branches. Hvidstens Rev, Hirsholmene, 4.5 m, 1.9.1988. Scale 2 cm.

B: *Cystoclonium purpureum*. Epiphytic with many tendrils on Brown Sea Oak (*Halidrys siliquosa*). North of the jetty, Nordre Rønner, Læsø, 0.5 m, 24.5.2005. Scale 2 cm.

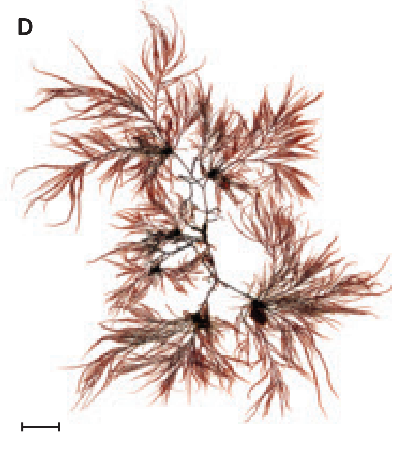
C: *Cystoclonium purpureum*. Tiny alga with small tendrils (arrow). Sønderborg bugt, 3-5 m, 3.6.1983. Leg.: L. Mathiesen & M. Laursen. Scale 2 cm.

individuals decays in late summer and early autumn, and only the basal branches survive the winter. Growth resumes from these basal branches the following spring in February-April, with more uprights from the same base. Spore production takes place in June-September. The spores germinate and develop into uprights, a few centimetres in height. These overwinter as juvenile stages that recommence growth in spring.

Habitat: On stone and boulders in the upper part of the sublittoral, frequent in the Northern Kattegat and the Samsø area. At greater depth epiphytic on larger algae. Common on Brown Sea Oak (*Halidrys siliquosa*), which in the summer may be completely matted together with large much branched Purple Claw Weed (*C. purpureum*).

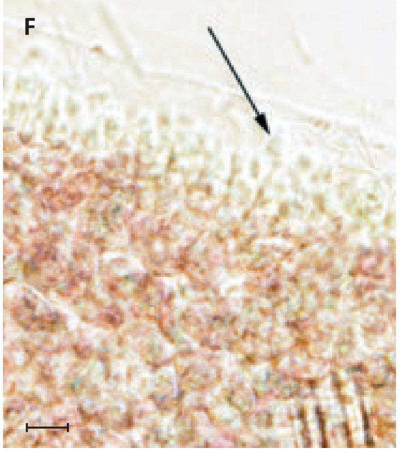
Resembles: Straggly Bush Weed (*Rhodomela confervoides*), may look similar but does not have pointed apices and the cortex consists of large angular cells.

References: Dixon & Irvine (1977), Rosenvinge (1931), Thrainsson & Hommersand (2012).

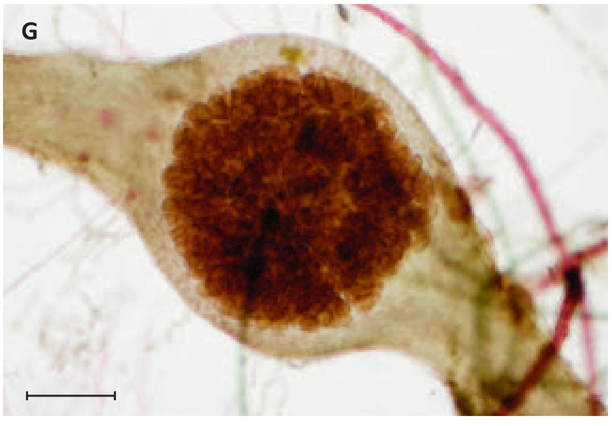


D: *Cystoclonium purpureum*. Growth in spring, resumed from overwintering basal branches. Several individuals on Black Scour Weed (*Ahnfeltia plicata*). Hirsholm, drift, 19.3.1982. Scale 2 cm.

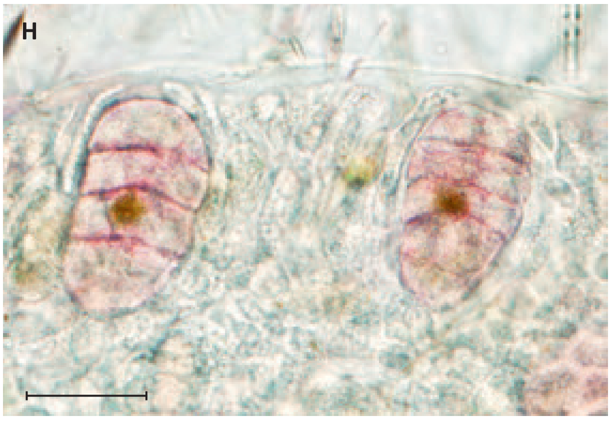
E: *Cystoclonium purpureum*. Uniaxial syntagma, apical cell cut off by an oblique wall. Torup Flak, 6 m, 25.7.1994. Scale 10 µm.



F: *Cystoclonium purpureum*. Antheridia from surface cells (arrow). Mosel-grund Syd, 7 m, 2.8.1994. Scale 10 µm.



G: *Cystoclonium purpureum*. Spherical gonimoblast, forming a knot of dark cells in a branch. Torup Flak, 11 m, 25.7.1994. Scale 200 µm.



H: *Cystoclonium purpureum*. Zonate tetrasporangia between cortical cells. Schultz's Grund, 7.4 m, 30.8.2013. Scale 50 µm.

Rhodophyllis divaricata

(Stackhouse) Papenfuss

Leafy Rose Weed

Appearance: Small fan-shaped membranous fronds, pink to clear red. Blades forked or split into several lobes. Most are less than 1 cm but a few up to 3 cm in height. They attach to the substratum by a small basal disc.

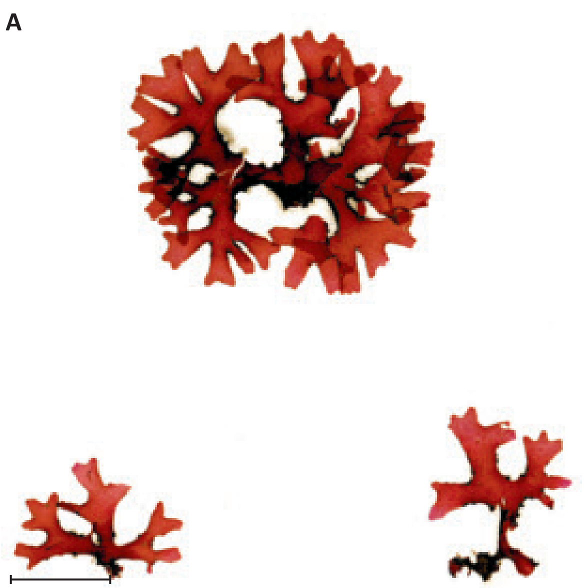
Structure: The thin syntagmatic thallus consists of three layers, in the middle a medulla of tiny filaments, branched as a net and covered by a monostromatic cortex on both sides. The cortex consists of rounded cells with a border of small cells along the edges of the blade. Growth is diffuse and also occurs from one or more apical cells in the upper part of the thallus. Apical cells have oblique walls. Cells contain many disc-shaped plastids.

Reproduction: Isomorphic monoecious gametophyte and tetrasporophyte. Antheridia develop from groups of cortical cells, where 4 antheridia mother cells are cut off from each cell. Mature gonimocarps are spherical and develop on the flat side of the blade or close to the edge. Zonate tetrasporangia develop from scattered surface cells in the youngest part of the blade.

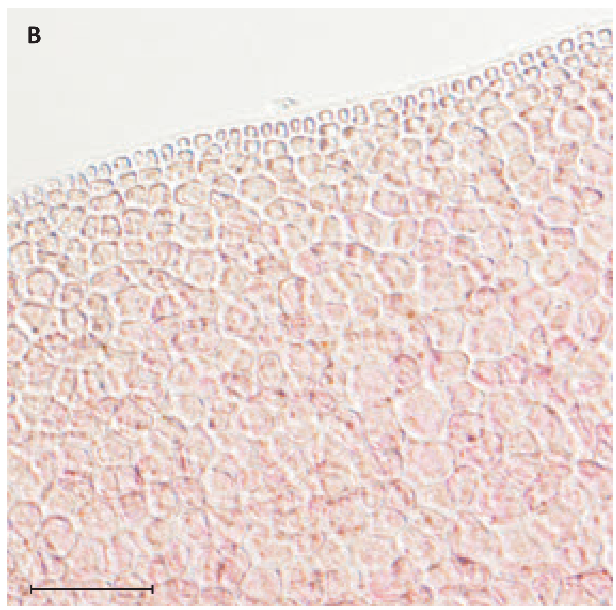
Seasonal variation: Collected in January, February, May-September. Antheridia recorded in August, gonimocarps and tetrasporangia in August-September.

Habitat: On solid substratum, hydroids and other algae, 10-26 m depth.

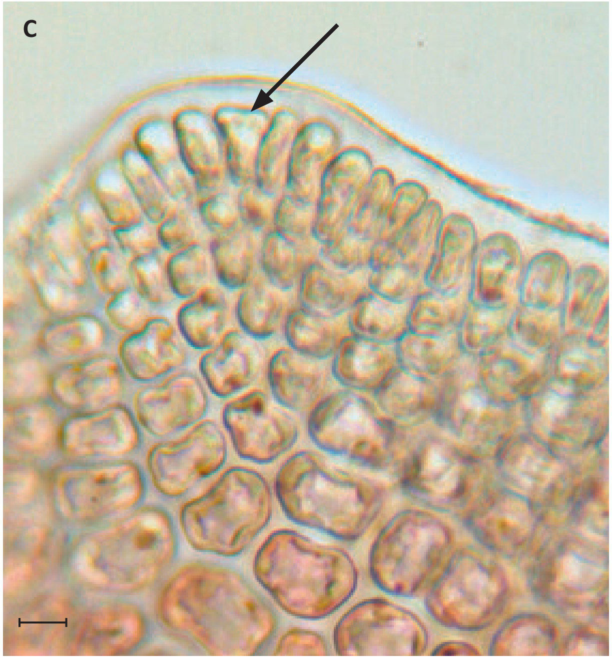
References: Dixon & Irvine 1977, Rosenvinge 1931 (*Rhodophyllis bifida*).



A: *Rhodophyllis divaricata*. Membranous dichotomous split blades. Kims Top, 18 m, 25.8.1993. Scale 2 cm.



B: *Rhodophyllis divaricata*. Rounded surface cells with border of small cells at the edge. Scale 50 µm. B-D, F: Tønneberg Banke, 13 m, 27.8.2013.



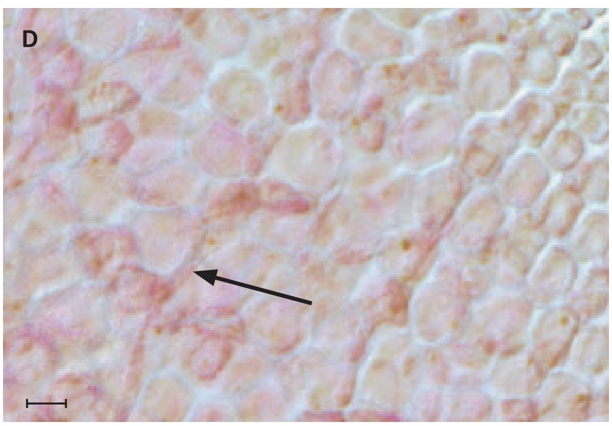
C: *Rhodophyllis divaricata*. Apical cell with oblique walls (arrow). Scale 10 µm. Photo by S. Lundsteen.

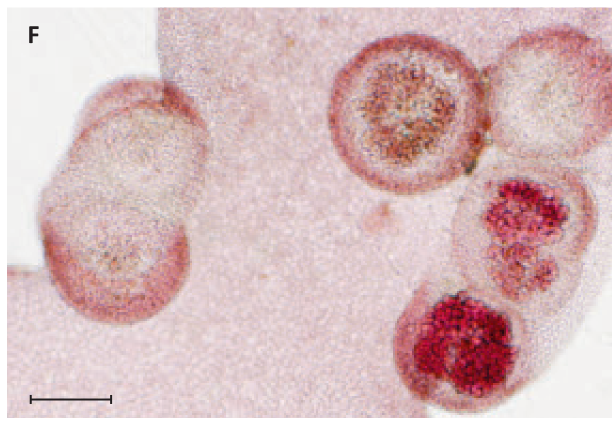
D: *Rhodophyllis divaricata*. Medulla of tiny filaments (arrow). Optical transverse section. Scale 10 µm.

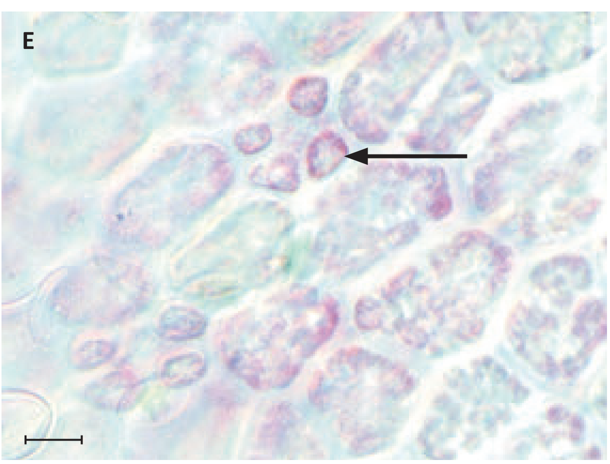
E: *Rhodophyllis divaricata*. Antheridia mother cells (arrow); from vegetative cells. Tønneberg Banke, 15 m, 20.8.1991. Scale 10 µm.

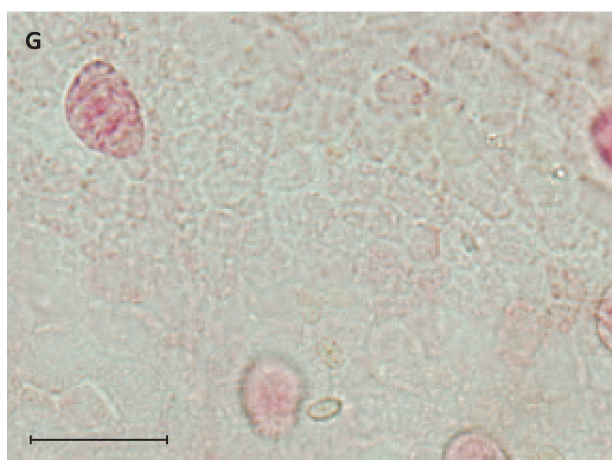
F: *Rhodophyllis divaricata*. Spherical young and mature gonimocarps with dark red gonimoblasts. Scale 200 µm.

G: *Rhodophyllis divaricata*. Zonate tetrasporangia. Tønneberg Banke, 15 m, 12.8.1990. Scale 10 µm.









Family: Dumontiaceae

Dilsea carnosa

(Schmidel) Kuntze

Red Rags

Appearance: Thick dark spatula-shaped red blades with an entire margin, expanding from a narrow basal stipe. Blades are commonly 15-30 cm in length but may become up to a square metre on stone reefs in the Northern Kattegat. Red Rags (*D. carnosa*) is thus the largest red alga in Danish waters. The blades are veinless and opaque. They are brittle, and the oldest blades often split in several irregularly elongate lobes. Several blades of different age and size arise from a disc-shaped base.

Structure: The outer part of the cortex consists of radiating filaments of small, rounded cells, c. 5 µm in diameter in surface view. The inner part of the cortex consists of relatively large irregular cells which covers a medulla of longitudinal thick-walled filaments matted together by narrow filaments.

Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Antheridia form from surface cells in pale sori in the youngest part of the thallus but are not recorded on thalli in Danish waters. Gonimoblasts occur scattered in the inner part of the cortex. Cruciate tetrasporangia develop in the inner part of the cortex and remain embedded. Spores are released by decay of the blade.

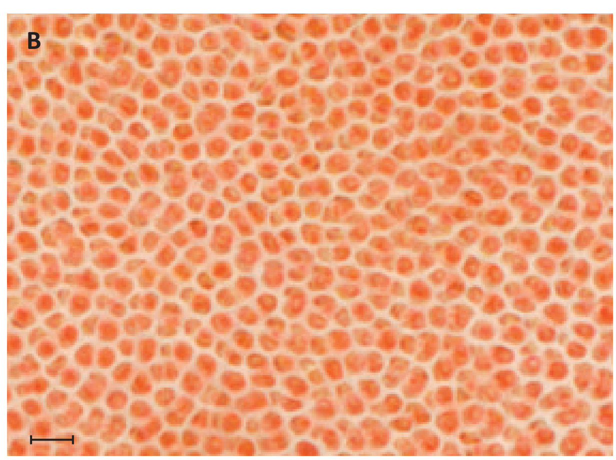
Seasonal variation: Perennial with reproductive structures in winter. Mature gonimoblasts recorded in March and mature tetrasporangia in February-April.

Habitat: On solid substratum on stone reefs. Collected by divers, 4-21 m depth and by dredge to 30 m depth.

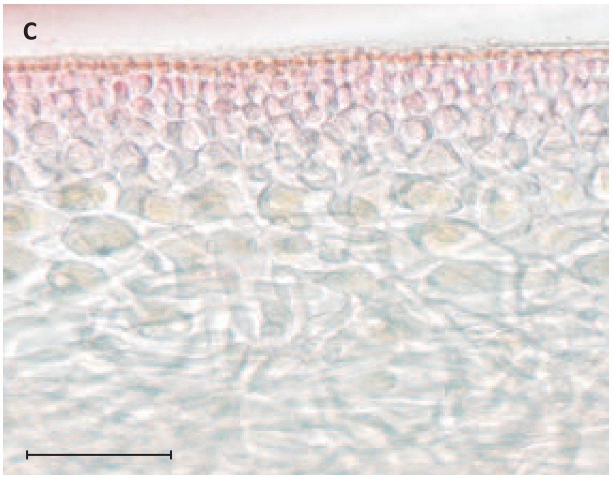
Resembles: The young blades in particular are reminiscent of Dulse (*Palmaria palmata*), but this species is transparent, does not have a filamentous medulla, and has larger surface cells, 8-15 µm in diameter, whereas they are only 5 µm in Red Rags (*D. carnosa*).

References: Irvine (1983), Rosenvinge (1917, *D. edulis*).

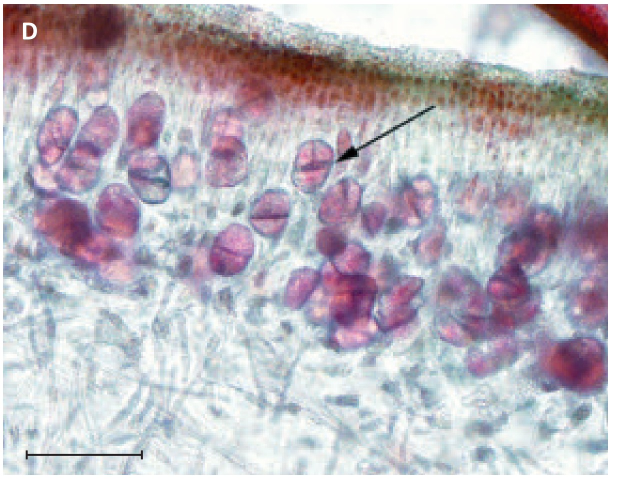
A: *Dilsea carnosa*. Spatula-shaped blades of different age and size, from disc-shaped base. Hirsholm, drift, 21.10.1979. Scale 2 cm.



B: *Dilsea carnosa*. Surface of small, rounded cells. Læsø Trindel, 4 m, 26.8.1993. Scale 10 µm.



C: *Dilsea carnosa*. Small, rounded surface cells and filamentous medulla, transverse section. Lønstrup, Rødgrund, 8 m, 26.8.2013. Scale 50 µm.



D: *Dilsea carnosa*. Cruciate tetrasporangia (arrow) within the cortex. Fornæs Fyr, drift, 3.2.2016. Scale 100 µm.

Dumontia contorta

(S.G.Gmelin) Ruprecht

Dumont's Tubular Weed

Appearance: Upright thallus of sparsely branched terete or slightly flattened branches that grow from a crustose base. Main axis relatively short, with scattered branches on all sides. Branches mainly unbranched and grow above the apex of the main branch. The thallus is commonly 10-20 cm in length, but may be up to 70 cm. The thallus is smooth with a fleshy consistency. Branches are even in thickness, 0.5-10 mm in width and slightly constricted at the base. Young individuals have terete branches which attenuate into a pointed tip. Branches in mature individuals are evenly thick and are in part hollow or flattened and decaying in the upper part. They may appear enlarged and irregularly twisted. The thallus is dark brownish red in shaded localities while it is bright flesh coloured when exposed to the sun, decaying apices are yellow-green. The crustose part of the thallus appears as shiny wine-red spots, millimetres in size before the development of uprights.

Structure: Young thalli grow up from the crustose part as a multiaxial syntagma, but the apical part becomes uniaxial after branching several times. At branching points a single or rarely a few of the central filaments of the multiaxial syntagma curve out and become the central filament of the branch. This results in fewer central filaments in the main axis and eventually there is only a single central filament left with one apical cell. It is characteristic that the apical cell is cut off by a transverse wall. From cells of the central filaments small, rounded cells are cut off and divide to form a cortex of small cells, each with several disc-shaped plastids. Longitudinal growth implies stretching of cells in the middle filaments which in older parts of the thallus are plaited together by very narrow filaments.

The crustose thallus is compact, consisting of a monostromatic basal layer with ascending filaments, 8-10.5 µm in width and with rounded apical cells. Young uprights arise from the crust as a bundle of filaments, initially embedded in the crust. Patches of flat cells are formed on the crust immediately before the uprights appear.

Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Antheridia are small pale cells developing from surface cells. Carpogonia develop from the inner cortical cells. Following fertilization, connecting filaments link to many cells which then form gonimoblasts, embedded in the thallus just below the surface. Tetrasporophytes have cruciate tetrasporangia embedded among the surface cells, they are dark red and give the branches a pointed appearance. Both carpospores and tetraspores are released from the branches when the upper part decays.

Seasonal variation: Young thalli, a few centimetres in height appear from late August and into autumn. Well-developed thalli occur in winter and spring. Mature gonimoblasts and tetrasporangia occur in spring and early summer after which the alga decays and upright individuals are not visible in July to early August. The upright thallus is thus annual while the crusts occur all year and are probably perennial.

Habitat: Common at sheltered shallow water localities on small stones and bivalve shells, 0.5-3 m depth. At stone reefs in areas with gravel seabeds, recorded to 16.5 m depth.

Comment: The seasonality of the upright thallus in Tuborg Havn is illustrated by Kristiansen (1972).

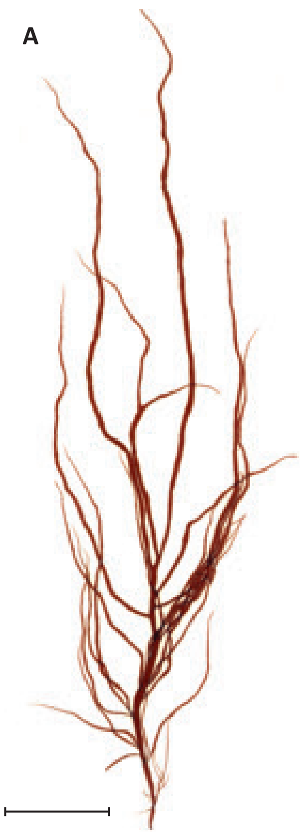
Resembles: Young upright thalli are reminiscent of young Purple Claw Weed (*Cystoclonium purpureum*) but the apical cell of these is cut off by an oblique wall. The crustose thalli are reminiscent of Peyssonnel's Brick-red Crust (*Peyssonnelia dubyi*), but this is brick-red and the upright filaments consist of angular cells.

References: Irvine (1983), Kristiansen (1972), Rosenvinge (1917, *D. incrassata*), Wilce & Davis (1984), Wærn (1961).

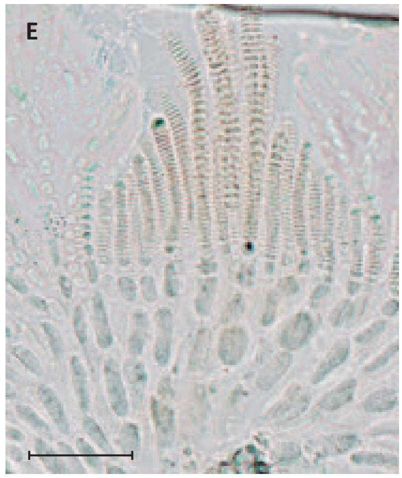
A: *Dumontia contorta*. Young thallus with pointed branches. Bramsnæs, Isefjord, 1 m, 15.1.1995. Leg.: L. Højlund. Scale 2 cm.

B: *Dumontia contorta*. Older fertile thallus with decaying apices. Nordre Rønner, Læsø, 0.5 m, 24.5.2005. Scale 2 cm.

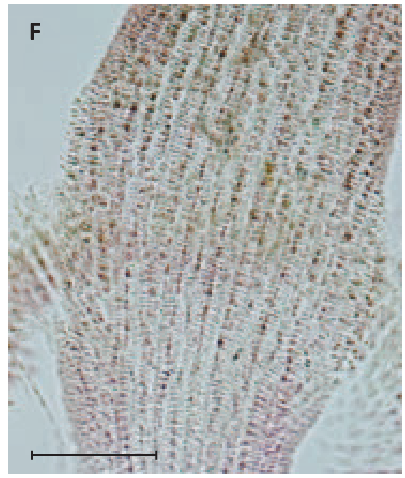
C: *Dumontia contorta*. Crustose thallus of dense ascending filaments, longitudinal section. Scale 50 µm. C, F-H: Schultz's Grund, 7 m, 18.1.1997.



D: *Dumontia contorta.* Crust with initiation of upright, several filaments of short cells. Lillegrund, Mejl Flak, August 2002. Photo green light by S. Lundsteen.



E: *Dumontia contorta.* Upright of several filaments which breaks through the crust. Sæløen, Isefjord, 7.9.1990. Scale 50 µm.



F: *Dumontia contorta.* Lower multiaxial part of a young upright from the crust. Scale 50 µm.

G: *Dumontia contorta.* Apex with a single apical cell cut off by a transverse wall. Scale 10 µm.

H: *Dumontia contorta.* Branching point, a single one of the axial filaments in the main axis curves out (arrow) and becomes the central axis of the branch. Scale 50 µm.

Family: Furcellariaceae

Furcellaria lumbricalis

(Hudson) J.V.Lamouroux

Clawed Fork Weed

Appearance: Bush-like fronds of terete, dichotomously divided branches in narrow dichotomies. At the base there are small downward-growing branches (haptera). Cartilaginous in texture with branches, 0.5-2 mm in width and slightly pointed at the apex. Thalli up to up to 28 cm in height in the Northern Kattegat, whereas in the inner Danish waters they are smaller, only up to 10 cm in height at Bornholm. The colour varies from very dark red-brown to almost black when the alga grows in shaded localities, to yellow-brown with greenish apices in shallow water exposed to the sun. After drying, the alga becomes very dark to almost black. Clawed Fork Weed (*F. lumbricalis*) is able to grow in loose stands where it has short- and secondary branches and the overall shape of the alga becomes spherical.

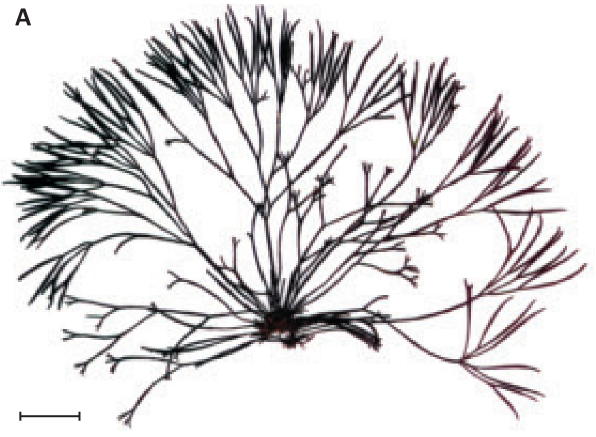
Structure: Multiaxial syntagma, with many apical cells of parallel filaments at the apex. In the middle of the thallus there is a medulla of longitudinal filaments of thick-walled long cells, which are plaited together by narrow filaments in a transverse direction. The cortex consists of radiating filaments of elongate ellipsoid to cylindrical cells, of which the outer cells form the surface of small assimilating cells in 1-2 layers.

Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Reproductive structures develop in the apical parts of young branches which increase slightly in width. The fertile male gametophytes have pale yellow apices, where antheridia develop from surface cells. Gonimoblasts develop from the inner cortical cells and appear in the transition area between the cortex and medulla as dark spherical cell clumps. Zonate tetrasporangia are embedded among cortical cells.

Seasonal variation: Perennial, grows all year but most growth is in the spring. Reproductive structures develop in late summer and autumn and are mature in December-March. Carpogonia recorded in August.

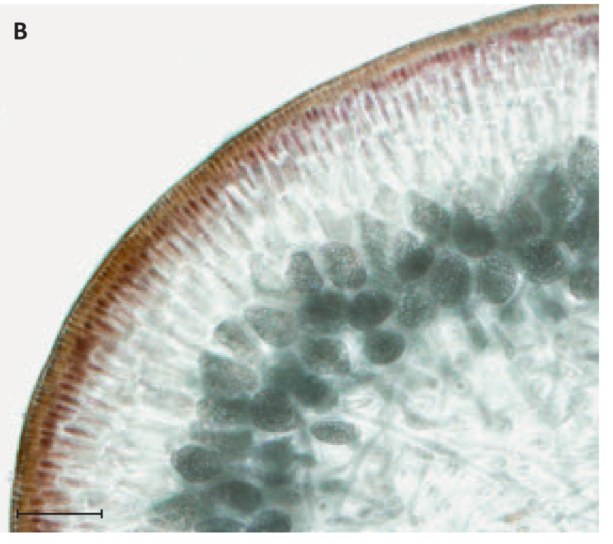
Habitat: On solid substratum, collected by divers, 0.5-18 m depth. In older collections by dredge to 40 m depth.

A



A: *Furcellaria lumbricalis*. Terete dichotomously branched frond with short haptera at base. Hirsholm, 0.5 m, 3.7.1991. Scale 2 cm.

B



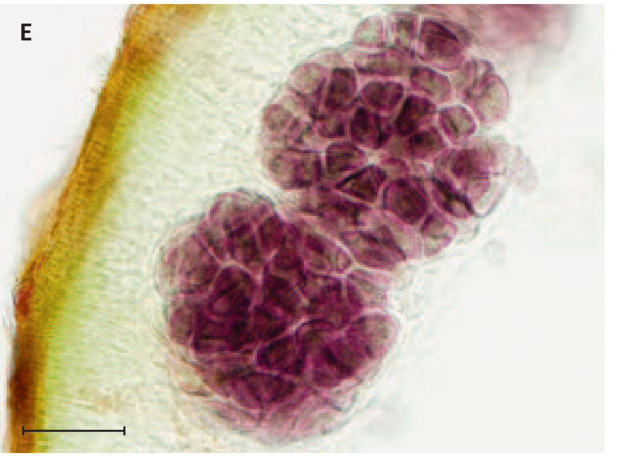
B: *Furcellaria lumbricalis*. Vegetative branch, medulla of thick-walled filaments, plaited together by narrow filaments, a layer of large cells with red algal starch. Cortex of radiating filaments with a surface of small assimilating cells. Part of transverse section. Lønstrup, Rødgrund, 8 m, 26.8.2013. Leg.: M.B. Rasmussen. Scale 100 µm.

Resembles: Discoid Fork Weed (*Polyides rotunda*), looks similar but has a basal attachment disc, rounded axils, obtuse apices and is brownish red in colour.

Comment: During World War II, commercial exploitation of Clawed Fork Weed (*F. lumbricalis*) began from Danish waters for the production of "danagar" or furcellaran, extracted from the cell walls. Furcellaran has a thickening effect and is used in the food industry. The production was based on loose individuals. Unfortunately, the crop was not monitored, and collected to such an extent that it almost became extinct. Production of furcellaran is no longer profitable in Denmark and the factory producing it stopped in 2008.

References: Austin (1960), Kristiansen (2014), Lund (1969, *F. fastigiata*), Lund & Christensen (1969), Rosenvinge (1917, *F. fastigiata*).

C: *Furcellaria lumbricalis*. Male gametophyte with pale apices. The beach at Holmbæk outflow, Vesterø Havn, Læsø, drift, 15.3.2006. Scale 2 cm.



E: *Furcellaria lumbricalis*. Apex of female gametophyte with gonimoblasts. Transverse section. Briseis Flak, 6 m, 18.1.1997. Scale 100 µm.

D: *Furcellaria lumbricalis*. Surface covered by colourless antheridia and released spermatia (arrow). Transverse section. Beach north of Vesterø Havn, Læsø, drift, 2.4.2013. Scale 20 µm.

F: *Furcellaria lumbricalis*. Apex of tetrasporophyte with zonate tetrasporangia. Transverse section. Hirsholm, drift, 27.12.1985. Scale 100 µm.

Halarachnion ligulatum

(Woodward) Kützing

Sea Spider Weed

Appearance: Gametophyte phase an upright thallus irregularly dichotomously branched with flat branches and frequently with secondary branches. It is soft, membranous, and transparent red, up to 10 cm height. Branches gradually taper in width towards the apex. The narrow lower part resembles a stipe with a crustose base. The tetrasporophyte phase of the life history is a thin pink crust and was previously considered a separate species, *Cruoria rosea* (P.Crouan & H.Crouan) P.Crouan & H.Crouan.

Structure: Multiaxial syntagma with few axial filaments in a gelatinous wall substance. The cortex of 2-3 cell layers consists of rounded to slightly angular cells, 5-12 µm in diameter in surface view. The medulla is traversed by narrow filaments that arise from cells just below the cortex and fix to cortical cells in the opposite side of the thallus.

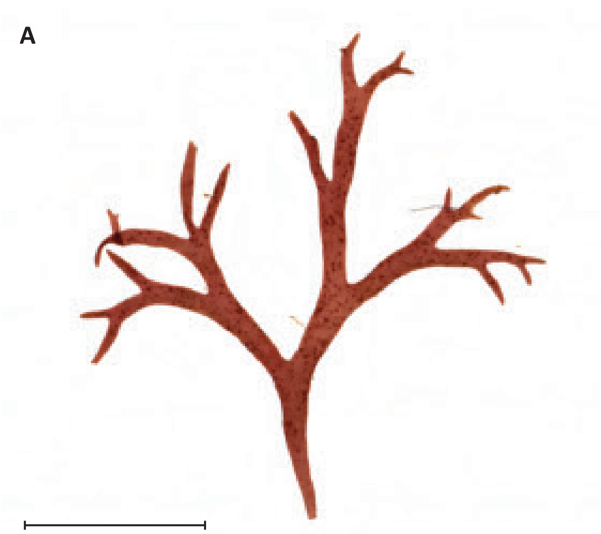
The crustose phase has a monostromatic basal layer with upright, loosely connected, short filaments of 3-6 cells. Large upright gland cells replace some of the upright filaments. Gland cells are 7-13 µm in width and 3-6 times as long as wide. Crusts are soft and the filaments easily separate by application of slight pressure. There are no cell fusions or pit connections.

Reproduction: The upright gametophytes are monoecious. Antheridia are scattered on the branches, forming by divisions of surface cells. Gonimoblasts are spherical and develop in the outer part of the medulla. Zonate tetrasporangia in the crusts are lateral on the lower cells of the upright filaments or apical on short filaments of only 1-2 cells.

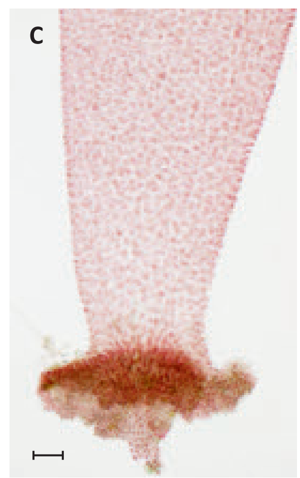
Seasonal variation: Upright thalli collected in February and May-September. Antheridia recorded in July-August and gonimoblasts in August-September. The crusts collected in January-February and April-August. Tetrasporangia recorded in January-February and June.

Habitat: On solid substratum at stone reefs, 10-20 m depth.

References: Knauss & Hommersand (1989), Maggs & Guiry (1989), Rosenvinge (1917).

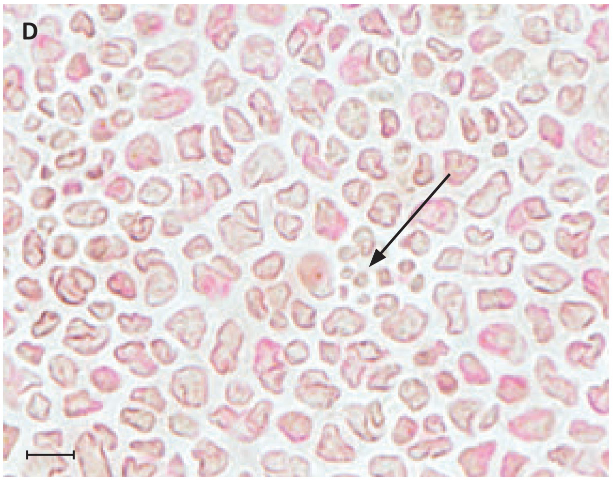


A: *Halarachnion ligulatum*. Irregularly dichotomously branched upright alga. Boblerev, Herthas Flak, 20 m, 16.8.2004. Scale 2 cm.

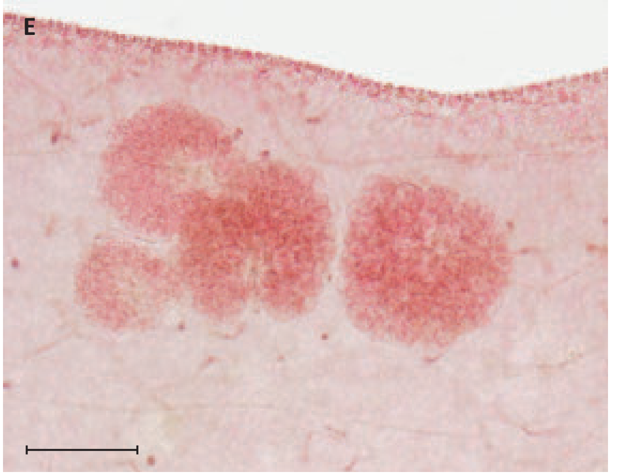


B: *Halarachnion ligulatum*. Apex, middle filaments visible through the cortex of rounded cells. Scale 50 µm. B-C: Kims Top, 14.5 m, 5.6.1993.

C: *Halarachnion ligulatum*. Lower part of upright thallus, which arise from a disc-shaped base. Scale 50 µm.



D: *Halarachnion ligulatum*. Antheridia from scattered surface cells (arrow). Scale 10 µm. D-E: Kims Top, 14.5 m, 9.8.1995.



E: *Halarachnion ligulatum*. Gonimoblasts in the outer part of the medulla. Optical longitudinal section, also showing middle filaments and cortex of small cells. Scale 100 µm.

F: *Halarachnion ligulatum*. Part of crustose alga, monostromatic basal layer with loosely connected upright filaments and large gland cell (arrow). Scale 20 µm. F-G: Herthas Flak, 18 m, 12.6.1990.

G: *Halarachnion ligulatum*. Crustose tetrasporophyte with zonate tetrasporangium (arrow). Scale 20 µm.

Family: Gigartinaceae

Chondrus crispus

Stackhouse

Irish Moss

Appearance: Individual upright fronds are fan-shaped, repeatedly dichotomously divided, flat from the base and up to 15-17 cm in height. Several and up to 20-30 fronds arise from a crustose base. Thallus is compact and cartilaginous with a smooth surface. The colour varies from dark brownish red in shaded localities to yellow-green at shallow water exposed to the sun. Some individuals (gametophytes) have bluish iridescent under water. Morphological variation encompasses wide as well as narrow fronds, which can be completely flat or very undulate. The widest and largest specimens in Danish waters were collected at the shores of Skagerrak. Very curly, approximately spherical thalli occur in shallow water at sheltered localities, while those with narrow, relatively long frond sections grow in deeper water. Morphological variation is described as different forms, of which several occur in Danish waters, including f. *incurvatus* (Lyngbye) Rosenvinge.

Structure: Multiaxial syntagma, with a medulla of filaments with very thick walls, plaited together by narrow filaments. The cortex consists of radiating filaments of small assimilating cells, decreasing in size towards the surface.

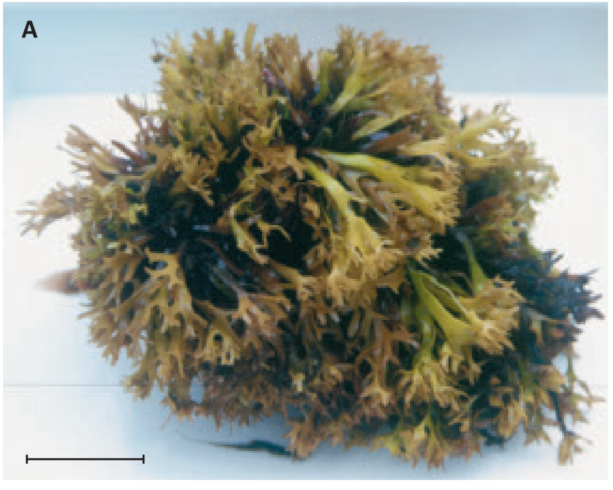
Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Antheridia form colourless patches on the surface of the apices of young lobes. Gonimoblasts develop on the surface of the fronds, forming approximately circular, slightly thickened dark spots, up to 2 mm in width. In the tetrasporophyte, cruciate tetrasporangia also occur as thickened dark spots, but they have an irregular outline.

Habitat: On stone and boulders, 0-18 m depth. In older collections by dredge to 20 m depth.

Seasonal variation: The basal crust is perennial. Older fronds are regularly detached and replaced by young fronds from the same base. Reproductive structures recorded in March-October.

Resembles: Curly thalli may be reminiscent of Grape Pip Weed (*Mastocarpus stellatus*), but this has chan-

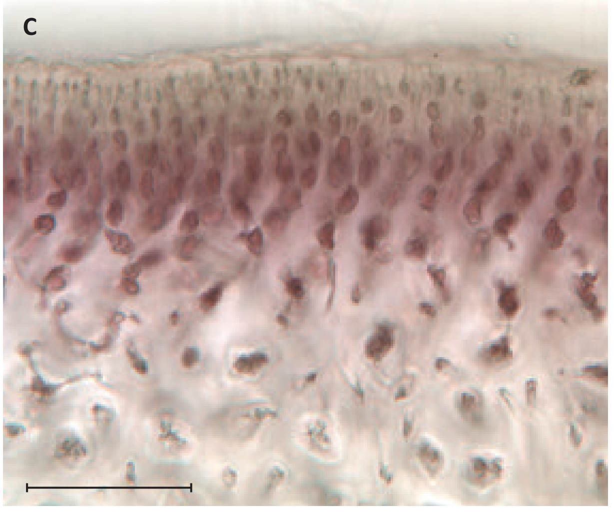
A



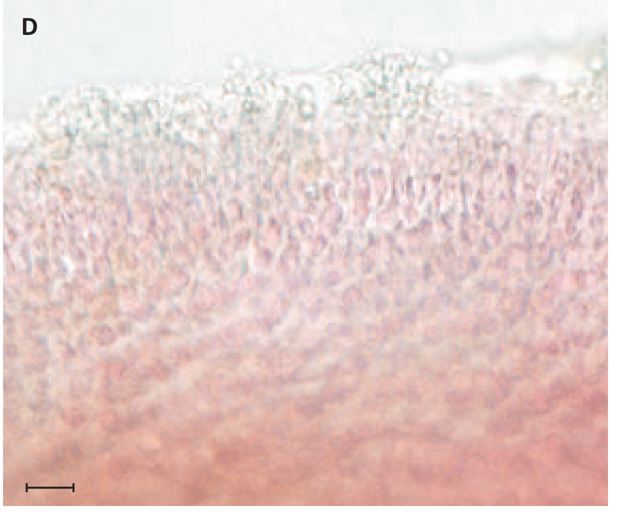
A: *Chondrus crispus*. Yellow-green fronds covering a stone the size of a hand. Shallow water exposed to sun, Hirsholm, 0.5 m, 11.7.2003.

B

B: *Chondrus crispus*. Many dark red, narrow fronds from a crustose base. They are dichotomously divided, and in part covered by calcified red algal crusts and hydroids. Tønneberg Banke, 15 m, 12.8.1990. Scale 2 cm.

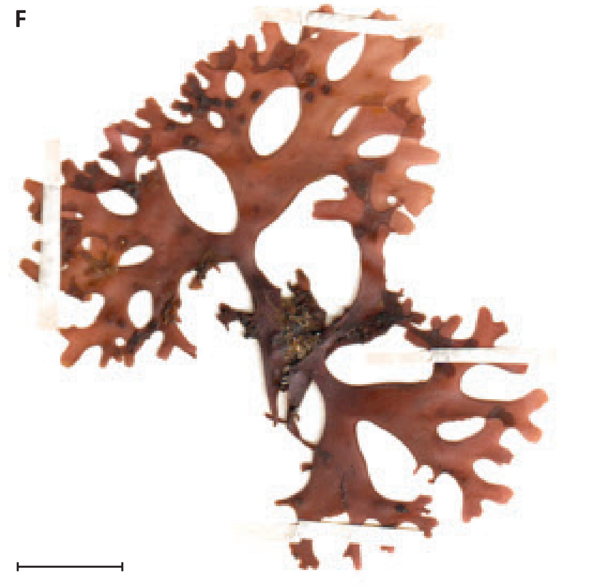


C: *Chondrus crispus*. Medulla of pale cells with thick walls plaited together by narrow filaments. Cortical filaments of small assimilating cells. Transverse section. Schultz's Grund, 7.5 m, 30.8.2013. Scale 50 µm.



D: *Chondrus crispus*. Male gametophyte with pale antheridia. Transverse section of apex. Scale 10 µm. D-E: Exposed side of breakwater near the ferry berth, Vesterø Havn, Læsø, 0.5 m, 2.7.2008.

E: *Chondrus crispus*. Male gametophyte with pale apices. Scale 2 cm.

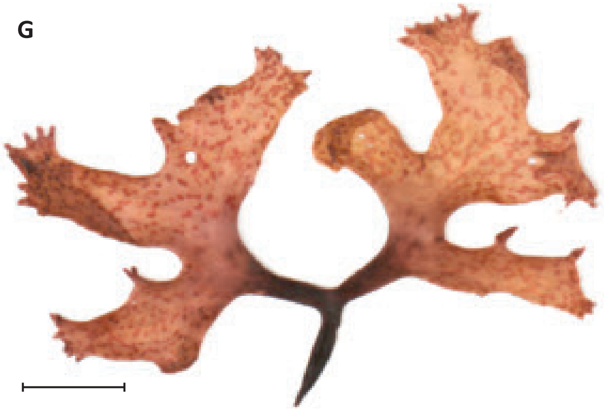


F: *Chondrus crispus*. Female gametophyte with dark round spots of cystocarps. Draget, Nissum Bredning, 0.5 m, 8.4.1971. Scale 2 cm.

nelled fronds and some have papillae on the surface of the fronds.

Comment: Carrageenan is extracted from the cell walls and used commercially in the food industry (E 407). In private households it is used when making jam, by addition of "Melatin", a well-known product in Denmark in which carrageenan is a main ingredient. Irish Moss (*C. crispus*) can be used directly in the kitchen, as carragenan is extracted by boiling. Milk boiled with Irish Moss (*C. crispus*) gets a pudding-like consistency when cooled down. Kappa-carrageenan is extracted from the gametophytes and lambda-carrageenan from the tetrasporophytes. The two products do not have the same gelling force, so it is useful to be able to separate them in an easy way. Examinations showed that only the lambda-carrageenan producing gametophyte phase is iridescent (Fournet et al., 1993).

References: Dixon & Irvine (1977), Fournet et al. (1993), Kylin (1944), Rosenvinge (1931), Rueness (1977).



G: *Chondrus crispus*. Tetrasporophyte with irregular spots of tetrasporangia. Deget, Frederikshavn, 0.5 m, 21.6.1978. Scale 2 cm.

H: *Chondrus crispus*. Cruciate tetrasporangia. Deget, Frederikshavn, 0.5 m, 19.6.1979. Scale 10 µm.

I: *Chondrus crispus* f. *incurvatus*. Fronds with narrow sections. Skarø, The archipelago south of Funen, 1 m, 19.8.1993. Leg.: N. Rask. Scale 2 cm.

Family: Gloiosiphoniaceae

Gloiosiphonia capillaris

(Hudson) Carmichael in Berkeley

Sticky Tube Weed

Appearance: Upright red-brown bush-like alga, very smooth and soft, up to 3-10 (-17) cm in height. There is a distinct main axis with repeatedly branched scattered branches on all sides. The main axis may be up to 3 mm in width and become hollow with time. Branches are constricted at the base. Young thalli have dense branches and appear almost tousled. Older thalli have lost many branches giving the main axis a plucked appearance. One or several upright thalli arise from a small attachment disc. Older individuals may have short prostrate branches at the base, from which new uprights may arise. The life history is heteromorphic with upright gametophytes and a crustose tetrasporophyte.

Structure: The uprights are a uniaxial syntagma. They have a central axis of long cylindrical cells, from each of which arise four radiating filaments that are repeatedly dichotomously branched. The dimensions of the cells decrease towards the surface where the cells become confluent and form a cortex of small approximately isodiametric cells. The innermost cell of the radiating filaments is relatively long, and a hollow tube develops around the central axis. In the lower parts, narrow downward-growing filaments form a medulla around the central axis.

The crustose phase is 3 mm in width with a basal layer of radiating filaments from which dense upright filaments arise. The cells of the basal layer are 6-9 µm

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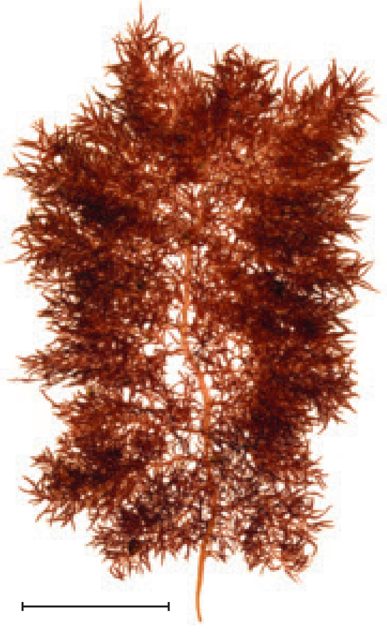
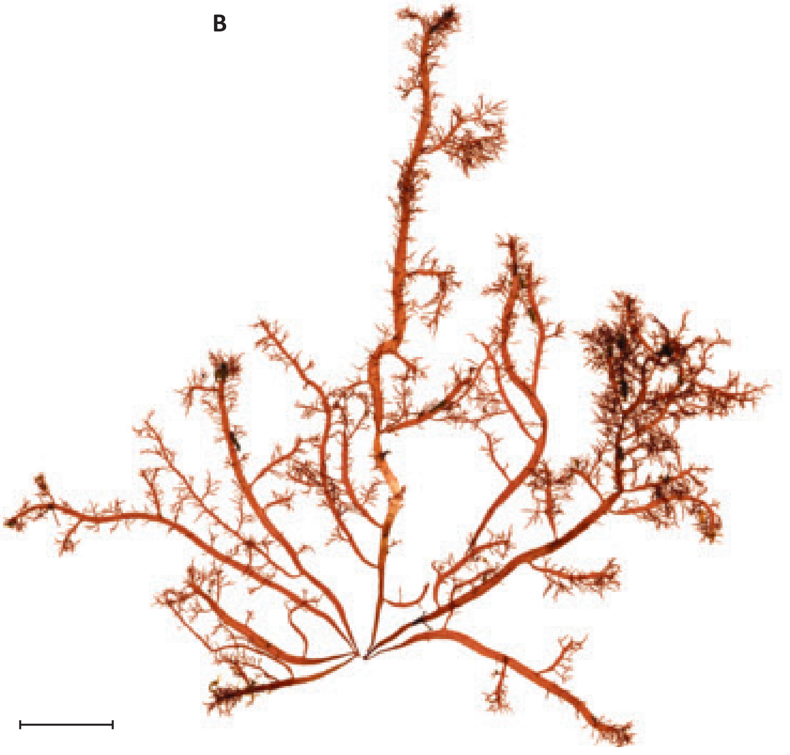
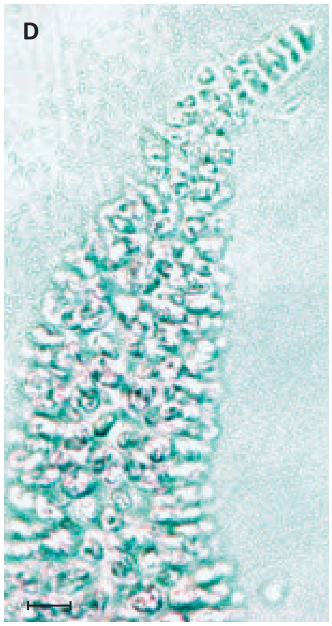


A: *Gloiosiphonia capillaris*. Distinct main axis and dense branches, much branched on all sides. Hirsholm, drift, 23.7.1986. Scale 2 cm.

B

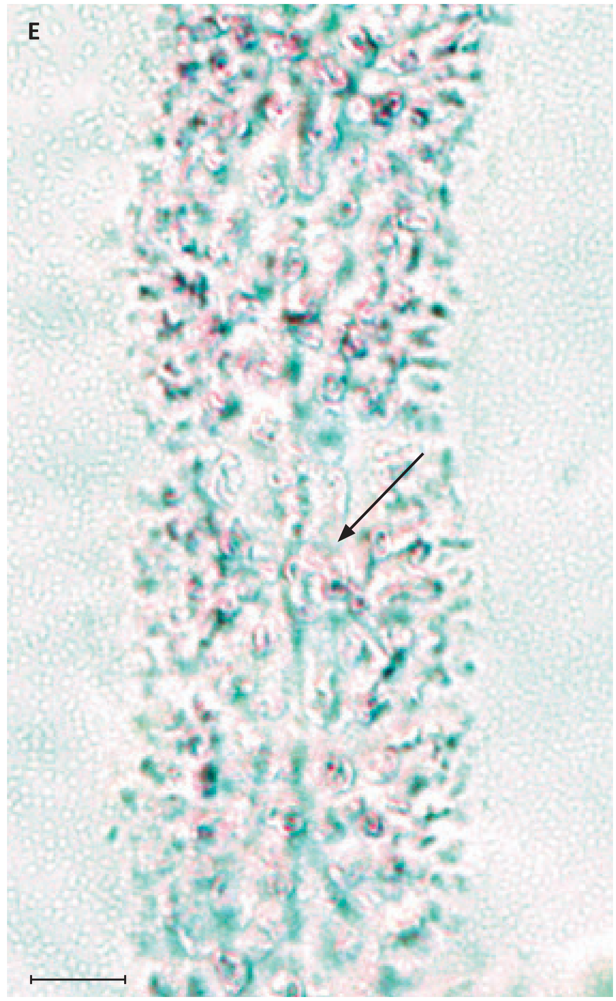


B: *Gloiosiphonia capillaris*. Older 'emaciated' alga, several uprights from the same base. Tile works, Helligsø, 0.5 m, 3.9.1993. Leg.: T. Christensen. Scale 2 cm.

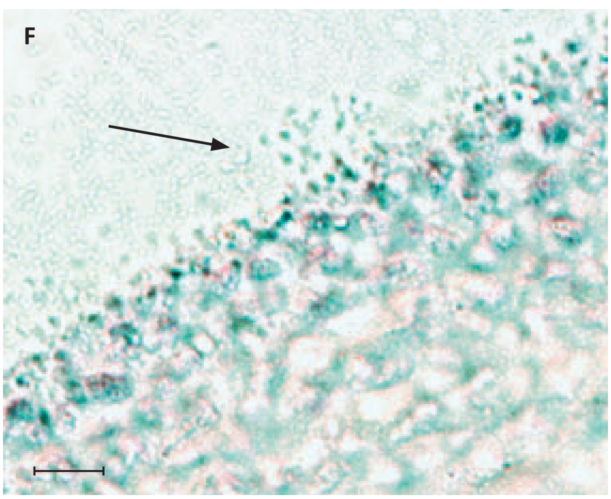


C: *Gloiosiphonia capillaris*. Branch with constricted base. Scale 100 µm. C-F: Kølpen, Hirsholmene, 3 m, 16.6.1997.

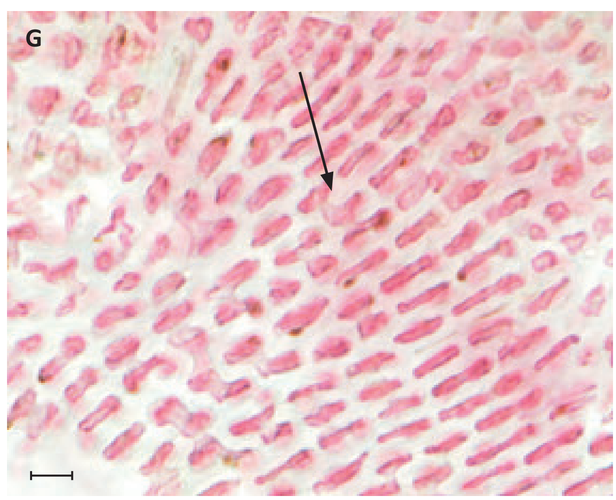
D: *Gloiosiphonia capillaris*. Apex of uniaxial syntagma, apical cell and surface of small cells. Scale 10 µm.



E: *Gloiosiphonia capillaris*. Central axis with whorls of filaments (arrow), optical longitudinal section. Scale 20 µm.



F: *Gloiosiphonia capillaris*. Antheridia from surface cells and released spermatia (arrow). Scale 20 µm.



G: *Gloiosiphonia capillaris*. Basal layer of crust with cell fusions (arrow). Scale 10 µm. G-I: Tangen, 7 m, 15.9.1996.

in width and 4-9 µm in length and cell fusions are frequent. The upright filaments consist of 4-7 cells of an even thickness and apical red algal hairs may occur. Each cell contains a plate-shaped plastid. The crusts are probably identical with *Cruoriopsis danica* Rosenvinge, which is described from Danish waters (see comments).

Reproduction: The upright gametophytes are isomorphic, monoecious or dioecious. Antheridia develop from the outer cortical cells and appear as small colourless cells at the surface. Gonimoblasts develop between the cortical cells. In the crustose tetrasporophyte, tetrasporangia develop from apical cells of the filaments. The tetrasporangia are obliquely cruciately divided, 14-18 µm in width and 23-30 µm in length at maturity. The germinating spores grow into new tetrasporophytes, or gametophytes, so there is an irregular change of generations (Maggs, 1988).

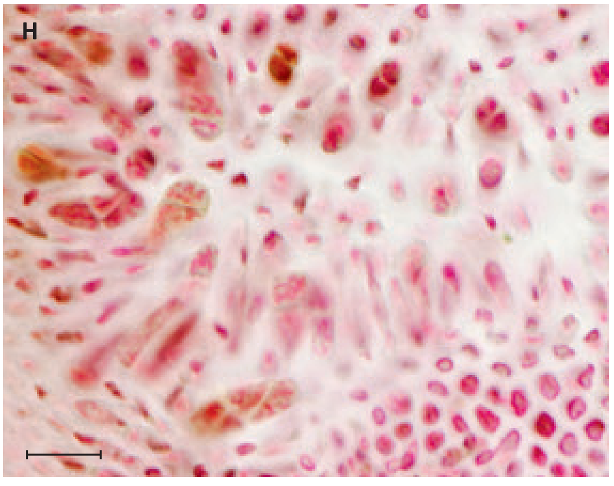
Habitat: On gravel and small stones, upright algae collected at 0.5-5 m depth. The crustose phase collected at 7 m depth, and as *C. danica* by Rosenvinge in the Limfjord, 1-2 m depth and at Middelfart, 15-19 m depth.

Seasonal variation: Upright phase collected in May-September. Antheridia recorded in June, mature gonimoblasts in July and tetrasporangia in May and August-September.

Resembles: The crustose phase is reminiscent of Plain Red Crust (*Rhodophysema elegans*), which also has a basal layer with cell fusions, but in this species the cells are long (1.5-3 times as long as wide), and paraphyses occur between the tetrasporangia in patches on the surface of the crust.

Comment: Culture studies of Sticky Tube Weed (*G. capillaris*) from Nova Scotia, Canada, showed that the life history comprised a crustose tetrasporophyte, identified as *Cruoriopsis hauckii* Batters, later confirmed by studies of the algae from Scotland. When Rosenvinge described *Cruoriopsis danica*, he expressed a possible identity with *C. hauckii*. Unfortunately, he was misled by comparison with material send by Batters. The material studied by Batters when he described *C. hauckii*, was heterogenous, and the slide preparations Rosenvinge received from Batters, were not *C. hauckii* according to Irvine & Farnham (1983, p. 35). Therefore *C. danica* is probably a synonym of *C. hauckii,* and thus representing the tetrasporophyte of *G. capillaris.*

References: Bird et al. (1991), Edelstein (1970), Edelstein & McLachlan (1971), Irvine & Farnham (1983), Maggs (1988), Oltmanns (1904), Rosenvinge (1917, *G. capillaris* and *C. danica*).



H: *Gloiosiphonia capillaris*. Crust with tetrasporangia, surface view. Scale 20 µm.

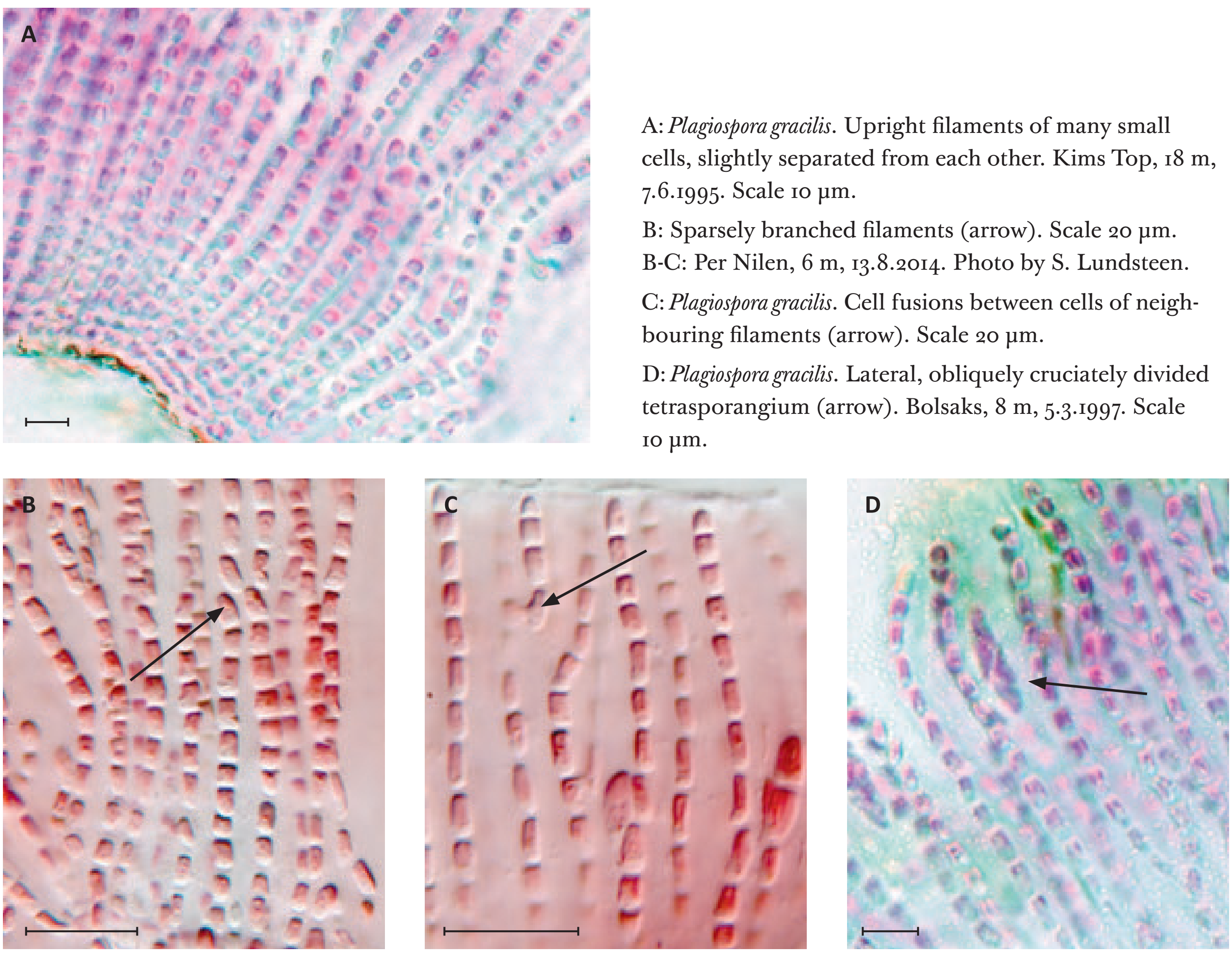
I: *Gloiosiphonia capillaris.* Crust of upright filaments with apical tetrasporangia (arrow). Scale 10 µm.

Plagiospora gracilis

Kuckuck

Graceful Spindle Spore Crust

Appearance: Small, compact, smooth, and slightly oily dark purple crusts, up to 1.5 cm in diameter and closely adpressed to the substratum.
Structure: Upright filaments, which form the main part of the crusts, are held together by a gelatinous substance and easily slide away from each other by application of slight pressure. Filaments are of a uniform thickness and consist of up to 30 small cells, 4.5-5.5 µm in width and as long as wide. Cell fusions occur between cells of neighbouring filaments but are difficult to observe. There is an inconspicuous basal layer of 1-2 cells, but it may appear as if the filaments are growing individually (without a basal layer).
Reproduction: Tetrasporangia are the only known reproductive structures. They are spindle-shaped, 6-9 µm wide and 17-22 µm in length, oblique cruciate and occur laterally on intercalary cells in the upper part of the crusts.
Seasonal variation: Probably perennial but only collected in January-August. Tetrasporangia recorded in January-April, June and August.
Habitat: On rocks and gravel, 4-20 m depth.
References: Irvine (1983), Maggs & Saunders (2016), Rosenvinge (1917, *Cruoriopsis gracilis*).



A: *Plagiospora gracilis*. Upright filaments of many small cells, slightly separated from each other. Kims Top, 18 m, 7.6.1995. Scale 10 µm.

B: Sparsely branched filaments (arrow). Scale 20 µm.
B-C: Per Nilen, 6 m, 13.8.2014. Photo by S. Lundsteen.

C: *Plagiospora gracilis*. Cell fusions between cells of neighbouring filaments (arrow). Scale 20 µm.

D: *Plagiospora gracilis*. Lateral, obliquely cruciately divided tetrasporangium (arrow). Bolsaks, 8 m, 5.3.1997. Scale 10 µm.

Family: Haemeschariaceae

Haemescharia hennedyi

(Harvey) K.L.Vinogradova & Yacovleva

Hennedy's Dark Red Crust

Appearance: Soft fleshy dark bordeaux-red crusts, 1-3 mm in thickness and up to 3 cm in diameter. Surface smooth with a velvet-like sheen.

Structure: A monostromatic basal layer of confluent prostrate filaments from which arise both long upright filaments and downward-growing, few-celled unbranched filament. The upright filaments are sparsely branched and loosely connected in a gelatinous wall substance. They slide from each other by application of slight pressure. They are uniform in thickness, only slightly and gradual decreasing in width from base to apex and 4-6 µm in width in the upper part. Cells cylindrical or rounded at the ends, 2-3 times as long as wide. The apical cells are small and pointed. Each of the cells contains a plate-shaped plastid in the upper end. There are no cell fusions or secondary pit connections.

Reproduction: Isomorphic monoecious gametophytes and tetrasporophyte. Antheridia rod-shaped, developing in small lateral branchlets in the upper part of the upright filaments, but seldom observed in material from Danish waters. Gonimoblasts appear as spindle-shaped dark cell clumps among the filaments. The cruciate tetrasporangia develop from vegetative cells in the upper part of filaments and form necklace-like rows of 4-7 sporangia, intercalary in filaments terminating with few vegetative cells.

Seasonal variation: Perennial, antheridia recorded in

A: *Haemescharia hennedyi*. Basal layer with ascending filaments gradually and slightly narrower towards the pointed apical cells. Preparation pressed, so filaments are slightly separated. Scale 20 µm. A, C: Store Middelgrund, 12.5 m, 12.8.2015. Photo by S. Lundsteen.

B: *Haemescharia hennedyi*. Dark red patch on one end of the stone. West coast of Nordre Rønner, Læsø, 4 m, 19.8.2005.

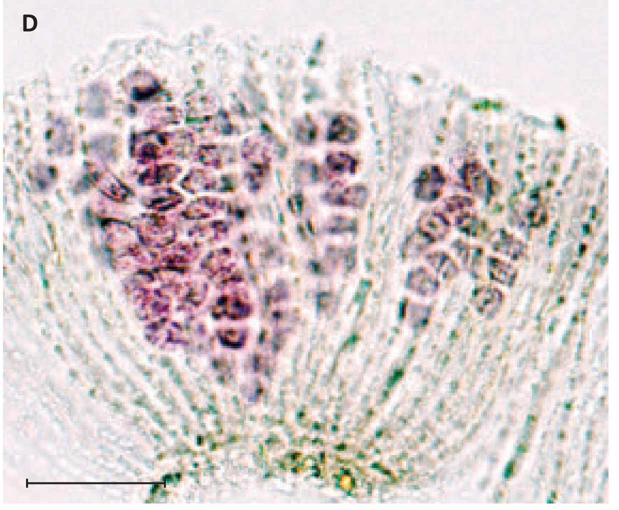
July-August, mature gonimoblasts in January-June, young tetrasporangia in September and mature tetrasporangia in January-July.

Habitat: On boulders and small stones, on Horse Mussel (*Modiolus modiolus*) and Edible Periwinkle (*Littorina littorea*) and on stipes of Forest Kelp (*Laminaria hyperborea*), 2-23 m depth.

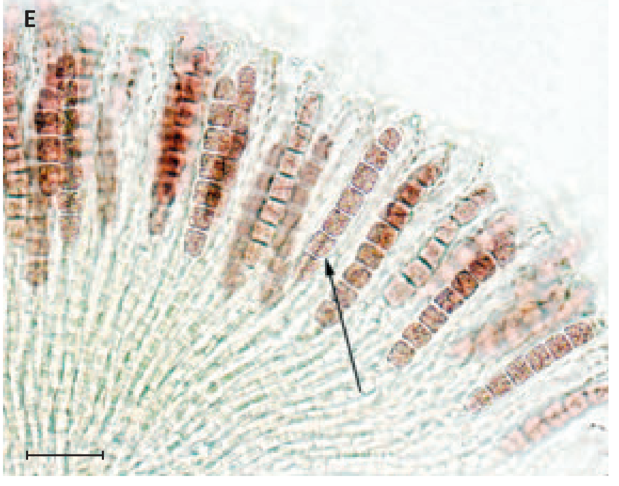
Resembles: Soft Crust Weed (*Cruoria pellita*) appears similar but the upright filaments have larger cells decreasing markedly from the lower to the upper part, where cells are, 6-11 µm in width. Hennedy's Dark Red Crust (*H. hennedyi*) has filaments of even thickness from base to apex and upper cells 4-6 µm in width. Tetrasporangia zonate, individual and large in Soft Crust Weed (*C. pellita*), whereas they are cruciate, small and intercalary in series in Hennedy's Dark Red Crust (*H. hennedyi*).

References: Rosenvinge (1917, *Petrocelis hennedyi*), Wilce & Maggs (1989).

C: *Haemescharia hennedyi*. Basal layer with ascending filaments and short downward-growing filaments. Scale 20 µm. Photo by S. Lundsteen.



D: *Haemescharia hennedyi*. Gonimoblasts of dark cells between the upright filaments. Lysegrund, 10.5 m, 10.1.1997. Scale 50 µm.



E: *Haemescharia hennedyi*. Intercalary series of cruciate tetrasporangia (arrow). Store Middelgrund, 14.5 m, 14.1.1997. Scale 50 µm.

Family: Kallymeniaceae

Euthora cristata

(C.Agardh) J.Agardh

Crested Spermwell

Appearance: The complanate, pink to wine-red fronds are fan-shaped, up to 1-3.5 cm in height. The fronds consist of narrow lobes, which are irregularly dichotomously divided or frequently unilateral in a manner resembling a cock's comb. Fronds are compact to cartilaginous and arise from a disc-shaped base.

Structure: Syntagma that grows from a single apical cell which is cut off by an oblique wall. The medulla consists of large colourless cells, 30-48 µm in width. The cortex is of one to two cell layers of small cells, 3-7.5 µm in width.

Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Reproductive structures form in the youngest parts of the blades. Antheridia develop from surface cells but not recorded in material from Danish waters. Gonimocarps are spherical and occur at or near the margin of the fronds. Tetrasporangia are obliquely cruciate divided and embedded in the cortex.

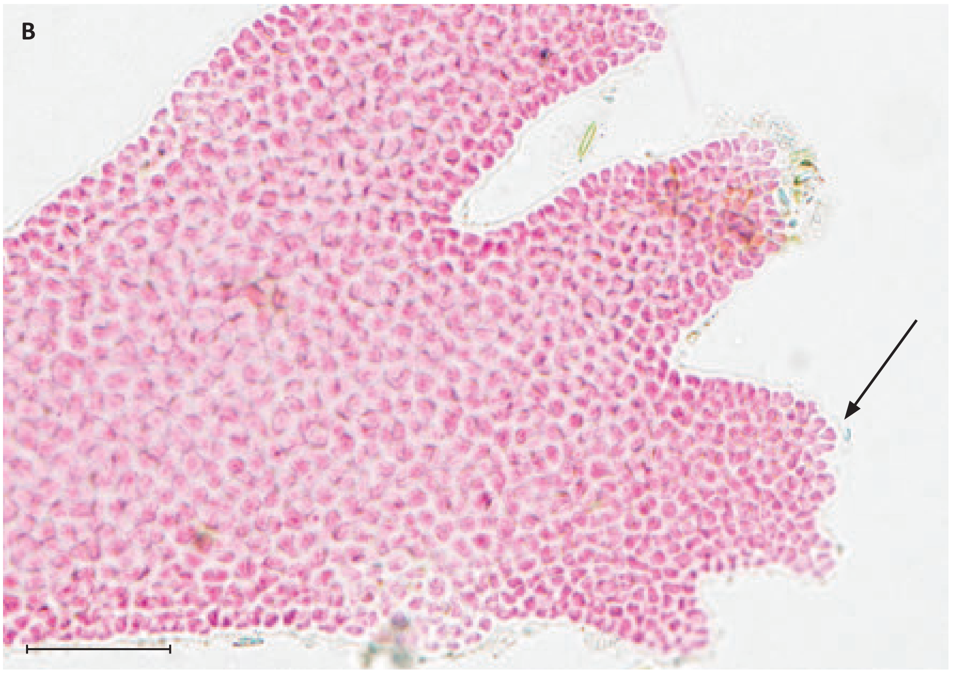
Seasonal variation: Collected in January-February as microscopic upright thalli from the base and as larger thalli in May-August. Gonimocarps recorded in May-August and tetrasporangia in June.

Habitat: On solid substratum, hydroids and coarse algae such as Stalked Leaf Bearer (*Phyllophora pseudoceranoides*), Sea Beech (*Delesseria sanguinea*) and stipes of Forest Kelp (*Laminaria hyperborea*), 11-23 m depth.

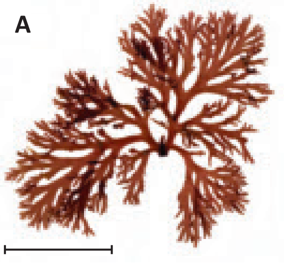
Resembles: Specimens with unilateral branches may resemble Lyngbye's Cock's Comb (*Plocamium lyngbyanum*) but in this species the unilateral branching is carried through and particularly noticeable at the apex.

References: Clarkston & Saunders (2010), Hooper & South (1974, *Callophyllis cristata*), Irvine & Farnham (1983, *C. cristata*), Rosenvinge (1931, *C. cristata*).

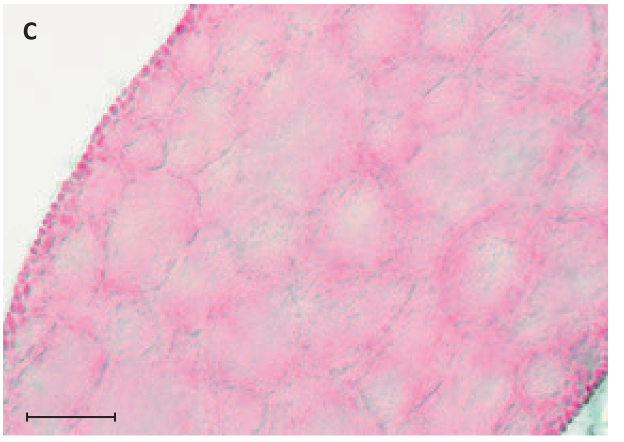
B: *Euthora cristata*. Apex, apical cells with oblique walls (arrow). Kims Top, 14.5 m, 4.2.1996. Scale 50 µm.



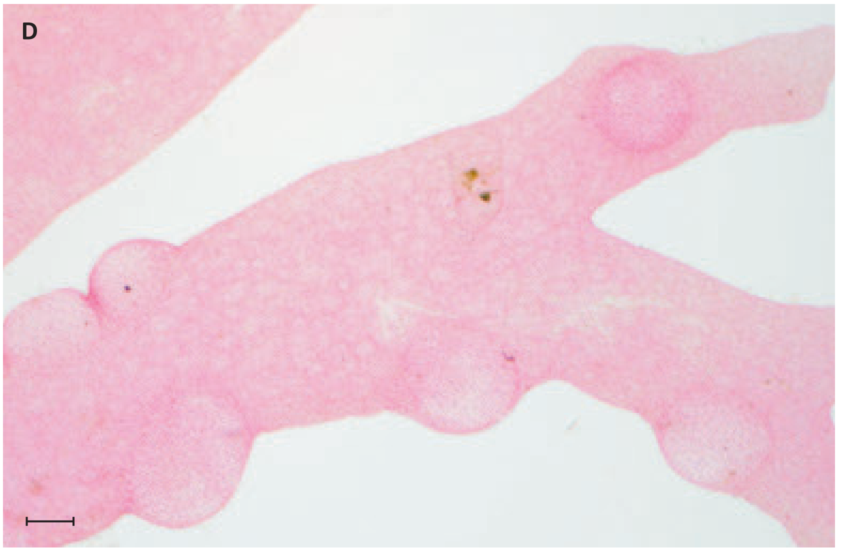
A: *Euthora cristata*. Complanate frond with narrow lobes. Kims Top, 14.5 m, 5.6.1993. Scale 1 cm.

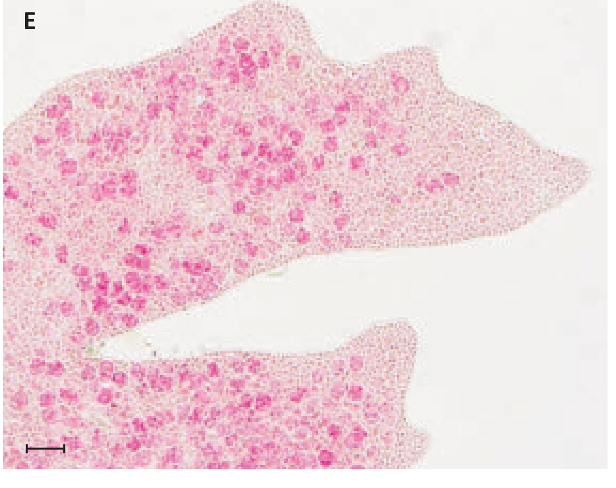


C: *Euthora cristata*. Medulla of large pale cells surrounded by monostromatic cortex of small, coloured cells. Optical longitudinal section. Scale 50 µm. C-D: Munkegrunde, 13 m, 4.8.1994.

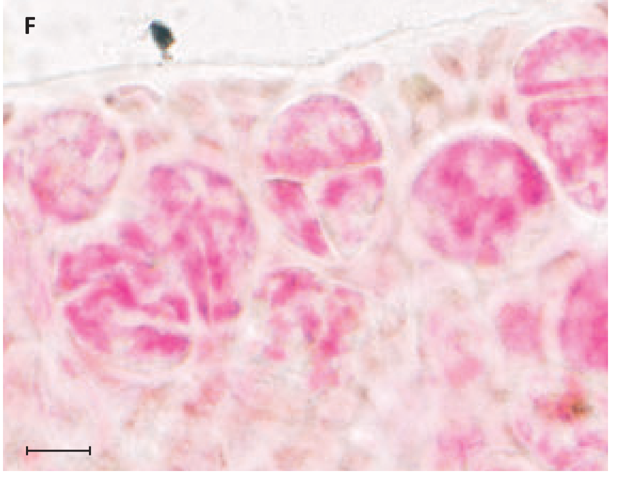


D: *Euthora cristata*. Female gametophyte with gonimocarps. Scale 200 µm.





E: *Euthora cristata*. Tetrasporophyte with scattered tetrasporangia in cortex. Scale 50 µm. E-F: Store Middelgrund, 20 m, 9.6.1993.



F: *Euthora cristata*. Cruciate tetrasporangia. Scale 10 µm.

Metacallophyllis laciniata

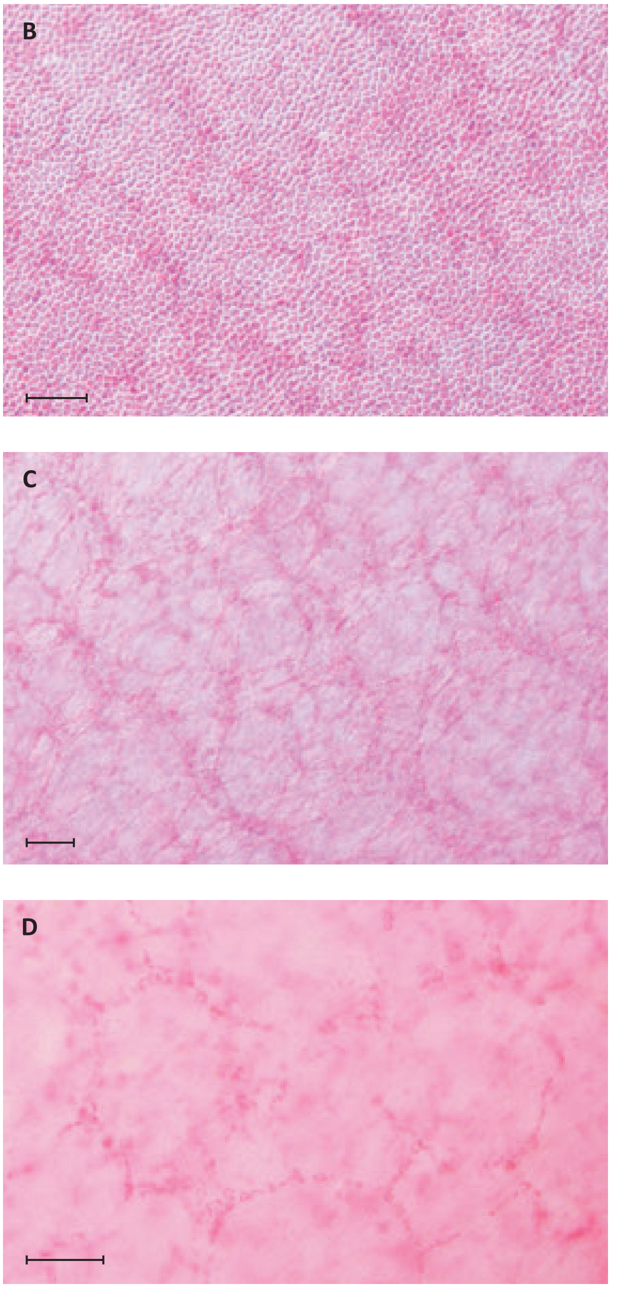
(Hudson) A.Vergés & L.Le Gall

Recent synonym: *Callophyllis laciniata* (Hudson) Kützing

Beautiful Fan Weed

Appearance: Complanate, fan-shaped, dark red-brown blades on a short stipe and with a leather-like consistency. The blade is repeatedly forked or irregularly divided in wide ribbon-shaped lobes which are rounded at the top. The specimen collected in Danish waters was 3 cm in height but in the North Atlantic the species can be up to 15-25 cm in height.
Structure: Multiaxial syntagma, with a medulla of large rounded colourless cells, 70-200 µm in width, and in between narrow irregularly scattered branched filaments of small cells. The cortex consists of a few layers of small cells, 4-6.5 µm in width.
Seasonal variation: Collected in February.
Habitat: Epiphytic on Stalked Leaf Bearer (*Phyllophora pseudoceranoides*), 19 m depth.
Resembles: May be reminiscent of wide fronds of Stalked Leaf Bearer (*Phyllophora pseudoceranoides*) without stipe but it has a medulla of large cells without narrow filaments.
Comment: Only a single, vegetative individual collected in Danish waters. The species is more frequent in the North Atlantic, for instance in the Faroe Islands.
References: Irvine & Farnham (1983, *Callophyllis laciniata*), Saunders et al. (2017).

A: *Metacallophyllis laciniata*. Fan-shaped red-brown blade (arrow) epiphytic on Stalked Leaf Bearer (*Phyllophora pseudoceranoides*). Scale 2 cm. A-D: Kims Top, 19 m, 4.2.1996.



B: *Metacallophyllis laciniata*. Cortex of small cells. Scale 50 µm.

C: *Metacallophyllis laciniata*. Medulla of large, rounded cells and branched filaments of small cells. C-D: Optical transverse section at different levels. Scale 50 µm.

D: *Metacallophyllis laciniata*. In the middle of the medulla, branched filaments of small cells around large cells. Scale 50 µm.

Family: Phyllophoraceae

Coccotylus hartzii

(Rosenvinge) L.Le Gall & G.W.Saunders

Wedge Red Leaf Parasite

Appearance: Irregularly finger-like to spherical knots on individuals of Lobed Leaf Bearer (*Coccotylus brodiei*) and Short Leaf Bearer (*C. truncatus*). The faded light red colour of the species varies from slightly yellow to greenish red. It is up to 5 mm in diameter with short dense branches up to 1 mm in width. It is common for several individuals to occur scattered on the same host specimen.

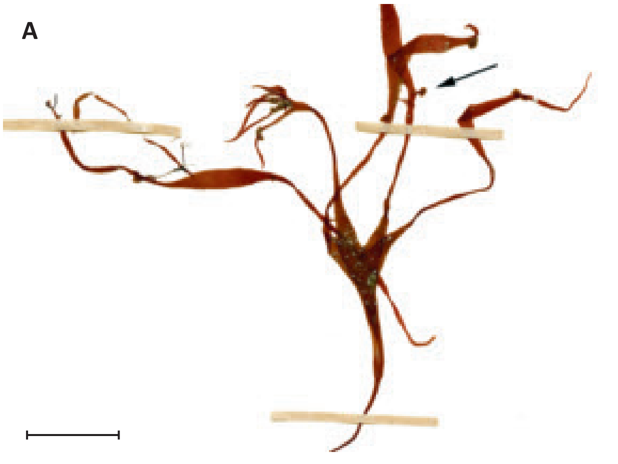
Structure: Multiaxial syntagma, which has a medulla of large cells surrounded by a cortex of dense radiating rows of small cells, 4-5 µm in diameter in surface view. Within the host, branched filaments grow between the medulla and cortical cells, pit connections occur with cells of the host.

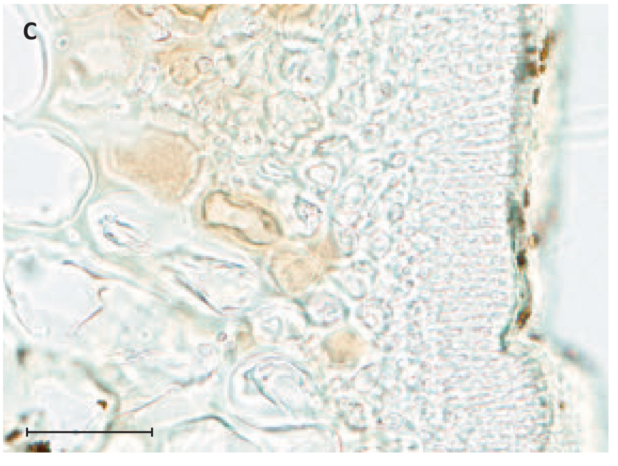
Reproduction: Monoecious gametophytes and a reduced tetrasporophyte, which develops on the female gametophyte. Antheridia develop in cavities which have opening pores to the surface, 3 µm in width. Cruciate tetrasporangia form series in approximately spherical branches (nemathecia) on the surface.

Seasonal variation: Recorded all year, with nemathecia in March-July.

Habitat: Parasite on Lobed Leaf Bearer (*C. brodiei*) and Short Leaf Bearer (*C. truncatus*).

References: Dixon & Irvine (1977, *Ceratocolax hartzii*), Le Gall & Saunders (2010b), Rosenvinge (1931, *C. hartzii*).





A: *Coccotylus hartzii*. Small clustered alga (arrow) on Lobed Leaf Bearer (*C. brodiei*). Romsø Sund, 8 m, 19.5.1900. Leg.: C. Ostenfeld. Scale 2 cm.

B: *Coccotylus hartzii*. Clustered alga the size of a pin-head with small bright outgrowths. Schultz's Grund, 8 m, 23.8.2014. Photo by S. Lundsteen.

C: *Coccotylus hartzii*. Medulla of large cells and cortex of dense filaments of small cells. Revfisk, Hatter Barn, 10 m, 21.10.2014. Scale 50 µm.

Identification key to *Coccotylus brodiei* and *C. truncatus*

1a.	Blades on stipes from all parts of the alga even the upper part of old fronds. Characteristic forked blades with pointed lobes, but the blades may have a regular margin or split into three or more lobes	*C. brodiei*
1b.	Blades on stipes only on the lower part of the alga. Blades are regularly forked with rounded lobes that typically become ribbon-shaped. Initiation of young blades occurs from the edge of older blades without formation of stipes	*C. truncatus*

Coccotylus brodiei

(Turner) Kützing

Lobed Leaf Bearer

Appearance: Cartilaginous fronds of triangular blades on terete, relatively long and frequently branched stipes. One or more uprights from a basal disc. Thalli are commonly c. 15 cm in height but may be up to 33 cm in the Belt Sea, whereas they only grow to a few centimetres in the Baltic Sea at Bornholm. The thallus is reddish brown, young parts bright while older parts are dark. New blades with a stipe occur from all parts of the alga. They commonly arise from the edge of the blades, typically from the upper edge of older blades, rarely from the flat side of blades. Stipes, sometimes have complanate parts, but these are probably remnants of an eroded blade from which a new blade on a stipe continued to grow. The typical blade has a narrow triangular base with a gradual transition to a wide upper part, which is forked with two pointed lobes. Although there is a great variation in the shape of the blades, some have three or more lobes, and these might be elongated with a rounded apex. Ribbon-shaped lobes are asymmetrical with curved edges. Elongate oval undivided blades are frequent in brackish water localities with some currents. Blades of different shapes are common in single individuals.

Structure: The cortex consists of 1-3 cell layers with surface cells, 2-5 µm in diameter in surface view. The medulla consists of relatively large cells decreasing in size towards the surface.

Reproduction: Isomorphic male and female gameto-

A

A: *Coccotylus brodiei*. Long terete stipes with apical blades, several times forked with pointed lobes. Vejrø, 15 m, 1.9.1993. Scale 2 cm.

B

B: *Coccotylus brodiei*. Both elongate oval and triangular forked blades. Nemathecium at arrow. Nakkebølle Fjord, 4-6 m, 20.8.2015. Leg.: N. Holmboe. Scale 2 cm.

phytes. Antheridia develop in small pale pointed apices of the blades. In female gametophytes spherical branchlets (nemathecia) develop on the upper edge of blades or on the stipes of small blades. They contain radiating branched filaments, which are closely packed with intercalary rows of cruciate tetrasporangia, up to 2.5 mm in diameter at maturity. The nemathecia are reduced tetrasporophytes which develop directely on the female gametophyte (Rosenvinge, 1929). Dioecious specimens are most frequent in Danish waters, individuals with both antheridia and nemathecia have rarely been observed.

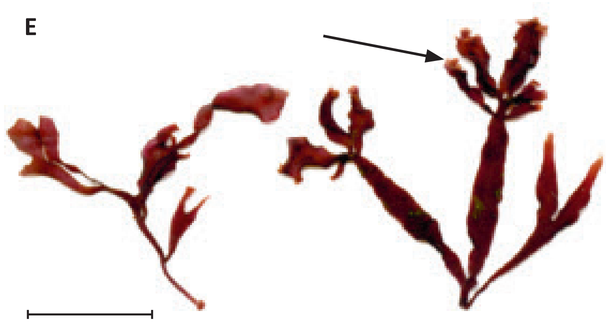
Seasonal variation: Perennial, antheridia recorded in May-June and nemathecia in May-August and November.

Habitat: On small stones and boulders, occasionally recorded as epiphytic, collected by divers, 1-21 m depth.

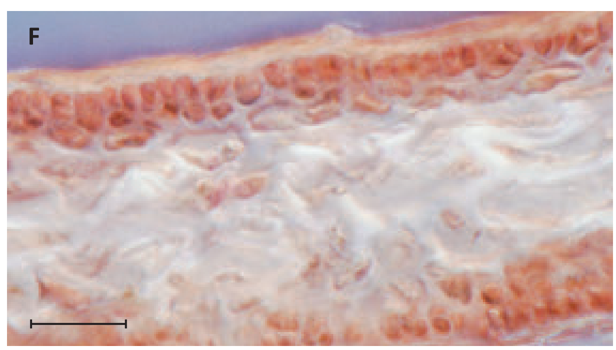
Resembles: Stalked Leaf Bearer (*Phyllophora pseudoceranoides*) may look similar when it occurs with a short stipe and a reduced blade. The two species are best distinguished from each other by the different reproductive structures. The colour is also different and best seen in transparent light. It is useful in distinguishing vegetative thalli, and is bluish red in Stalked Leaf Bearer (*P. pseudoceranoides*) and reddish brown in Lobed Leaf Bearer (*C. brodiei*) and Short Leaf Bearer (*C. truncatus*). Very young individuals may be confused with Sandy Leaf Bearer (*P. crispa*) and Dulse (*Palmaria palmata*), both of which have an abrupt transition between large medullary cells and a small-celled cortex, while the transition is gradual in Lobed Leaf Bearer

C. *Coccotylus brodiei*. Several generations of stipes and narrow blades. Vejrø, 13 m, 9.4.1989. Scale 2 cm.

D: *Coccotylus brodiei*. Several generations of branches, both relatively wide and narrow blades and small apical branches as in f. *stellata*. With nemathecium (arrow). Sæløen, Isefjord, 5 m, 31.8.1989. Scale 2 cm.



E: *Coccotylus brodiei*. Tiny specimen from the Baltic Sea. Antheridia in pale apices of the blades (arrow). Christiansø, Bornholm, 7 m, 16.6.2009. Leg.: C. Darling. Scale 1 cm.



F: *Coccotylus brodiei*. Large medullary cells with a gradual transition to the cortex of 1 or 2 layers of small cells. Bølshavn, Bornholm, 8 m, 21.6.1994. Scale 20 µm.

(*C. brodiei*) and Short Leaf Bearer (*C. truncatus*). Furthermore, the relatively large medullary cells of Dulse (*P. palmata*) are visible throughout the thin cortex when examined microscopically.

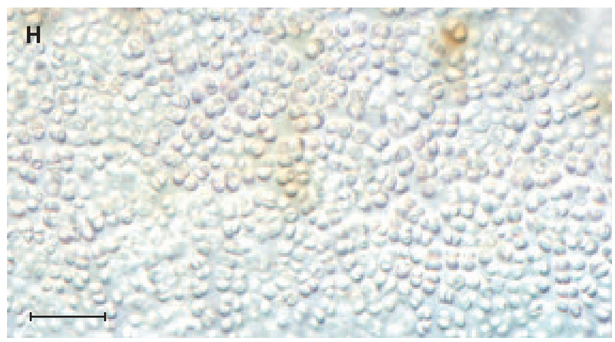
Comment: Previously, Lobed Leaf Bearer (*C. brodiei*) and Short Leaf Bearer (*C. truncatus*) were considered to be morphological variations within a single species. Genetic investigations of Canadian algae (Le Gall & Saunders, 2010b) showed them to be two independent species.

An examination of the large collection of Danish herbarium material in the Natural History Museum of Denmark showed the morphology to agree with the two different Canadian species. Rosenvinge (1931) described two growth forms within Lobed Leaf Bearer (*C. brodiei*, as *Phyllophora brodiaei*) but because of a gradual transition in morphology he did not consider them to be individual species. Several unattached forms were distinguished by Rosenvinge (1931), one of them, as *Phyllophora brodiaei* f. *stellata,* has very narrow blades. These forms probably belong in Lobed Leaf Bearer (*C. brodiei*).

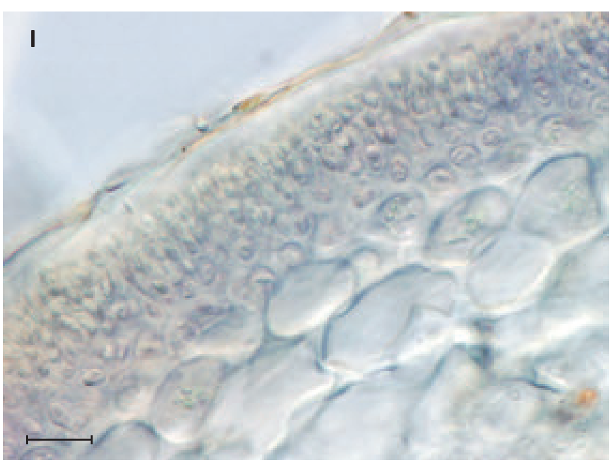
Wedge Red Leaf Parasite (*C. hartzii*) occurs both on Lobed Leaf Bearer (*C. brodiei*) and Short Leaf Bearer (*C. truncatus*). It may be scattered on the surface or at the edge of the blades as small light red bulb-shaped or branched protrusions up to 5 mm in diameter.

References: Dixon & Irvine (1977, *Phyllophora truncata*), Le Gall & Saunders (2010b), Kristiansen (2014), Lundsteen & Nielsen (2015), Newroth (1971a, b, *P. truncata f. brodiaei*), Newroth & Taylor (1971, *P. truncata* f. *brodiei*), Rosenvinge (1929, 1931, both *C. brodiei* and *C. truncatus* as *P. brodiaei*).

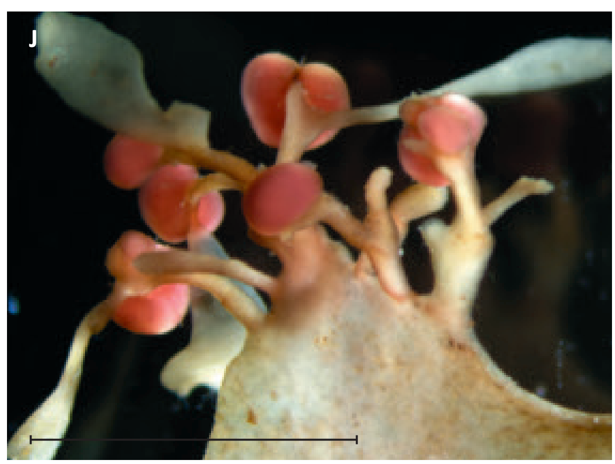
G: *Coccotylus brodiei*. Part of male gametophyte with antheridia in pale apices of the blade (arrow). Scale 1 cm. G-I: Northern part of Odense Fjord, 3 m, 12.5.2009. Leg.: N. Holmboe.



H: *Coccotylus brodiei*. Surface with antheridia. Scale 20 µm.



I: *Coccotylus brodiei*. Apical part of blade with antheridia, transverse section. Scale 20 µm.



J: *Coccotylus brodiei*. Part of female gametophyte with spherical nemathecia. Kirkegrund, 8 m, 20.8.2014. Scale 2.5 mm. Photo by S. Lundsteen.

Coccotylus truncatus

(Pallas) M.J.Wynne & J.N.Heine

Short Leaf Bearer

Appearance: Cartilaginous frond of triangular blades, apical on terete, relatively short stipes, reddish brown colour. Thalli ribbon-shaped to 10 cm in length. Young thalli have a single blade which is heart-shaped or elongate oval. Older thalli have forked blades with symmetrical ribbon-shaped sections and rounded apices. The thalli are only slightly branched, and blades on stipes only occur in the lower part of the alga. Yearly growth continues with new blades developing from the upper part of the old ones. New blades do not have a terete stipe but a narrow base which appears like a constriction of the frond. The number of constrictions therefore reflects the age of the individual. New rounded blades sometimes form along the edge of older blades or from the stipe. They have a narrow basal part but lack a terete stipe.

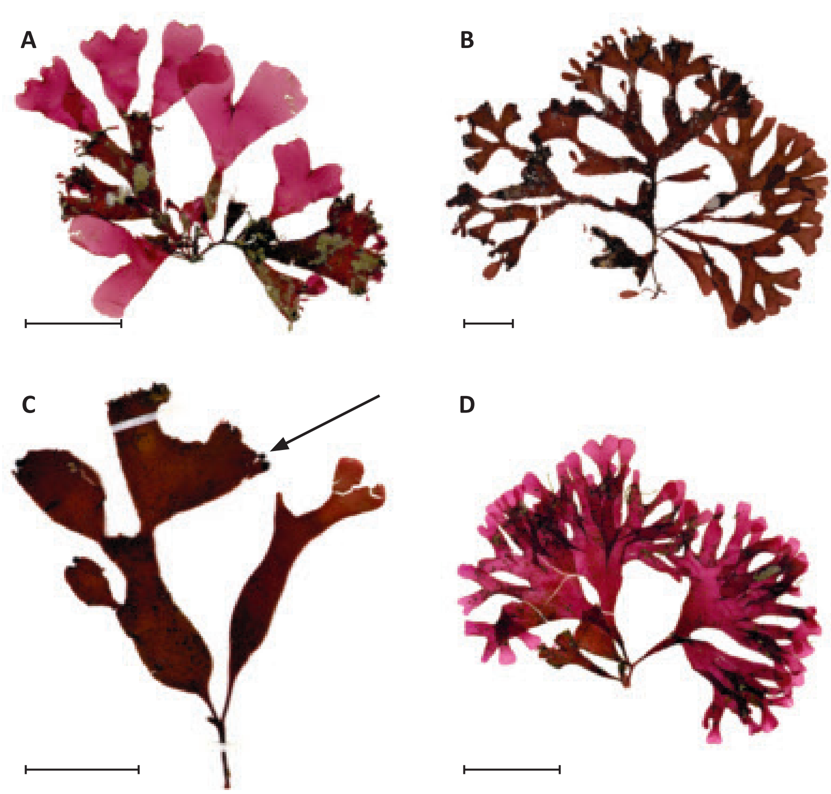
Structure: The cortex consists of 1-3 cell layers with surface cells, 2-5 µm in diameter in surface view. The medulla consists of relatively large cells gradually decreasing in size towards the surface.

Reproduction: Isomorphic male and female gametophytes. Antheridia develop in small pale apices of the blades. In female gametophytes, spherical branchlets (nemathecia) are located near the outer edge of the blades, only up to c. 1 mm in diameter. Nemathecia are reduced tetrasporophytes which develop directely on the female gametophyte (Rosenvinge, 1929). They contain densely packed radiating branched filaments, with intercalary rows of cruciate tetrasporangia. Dioecious individuals are most frequent in Danish waters, and only a single specimen with both antheridia and nemathesia recorded.

Seasonal variation: Perennial, up to 3-4 years old; collected with young blades in February and May-June. Antheridia recorded in June, nemathecia in August-September and February.

Habitat: On boulders and gravel, 9-27 m depth.

Resembles: Stalked Leaf Bearer (*Phyllophora pseudoceranoides*) may look similar. The two species are best dis-



A: *Coccotylus truncatus*. Perennial, with new bright red blades with narrow bases arising from older darker blades. Store Middelgrund, 20 m, 4.6.1989. Scale 2 cm.

B: *Coccotylus truncatus*. Older thallus with several generations of blades. Falske Bolsaks, 15 m, 13.9.1991. Scale 2 cm.

C: *Coccotylus truncatus*. Narrow blades with nemathecium at the edge (arrow). Kims Top, 24.5 m, 4.2.1996. Scale 2 cm.

D: *Coccotylus truncatus*. Atypical wide fan-shaped blades with addition of new blade from the upper edge. Wedelsborg, the Little Belt, 9 m, 25.8.1988. Scale 2 cm.

tinguished from each other by the different reproductive structures. The colour is also different and best seen in transparent light. It is useful in distinguishing vegetative thalli, being bluish red in Stalked Leaf Bearer (*P. pseudoceranoides*) and reddish brown in Short Leaf Bearer (*C. truncatus*). It might also be reminiscent of Sandy Leaf Bearer (*Phyllophora crispa*), as both species have elongate ribbon-shaped blades. It is almost impossible to distinguish young individuals of these two species from each other. Older blades in Sandy Leaf Bearer (*P. crispa*) typically have a pleated edge whereas this is smooth in Short Leaf Bearer (*C. truncatus*). Furthermore, new blades develop from the upper part of the blades in Sandy Leaf Bearer (*P. crispa*), whereas they develop from the edge of the blades in Short Leaf Bearer (*C. truncatus*).

Comment: Separated from Lobed Leaf Bearer (*C. brodiei*) by Le Gall & Saunders (2010b) after genetic studies of Canadian material. Wedge Red Leaf Parasite (*C. hartzii*) may occur scattered on the surface or at the edge of the blades as small light red bulb-shaped or branched protrusions up to 5 mm in diameter.

References: Le Gall & Saunders (2010b), Kristiansen (2014), Lundsteen & Nielsen (2015), Newroth (1971a, b, *P. truncata* f. *truncata*), Newroth & Taylor (1971, *P. truncata* f. *truncata*), Rosenvinge (1929, 1931, both *C. brodiei* and *C. truncatus* as *P. brodiaei*).

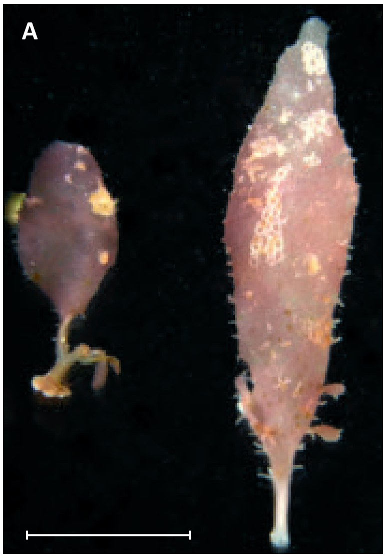
Erythrodermis traillii

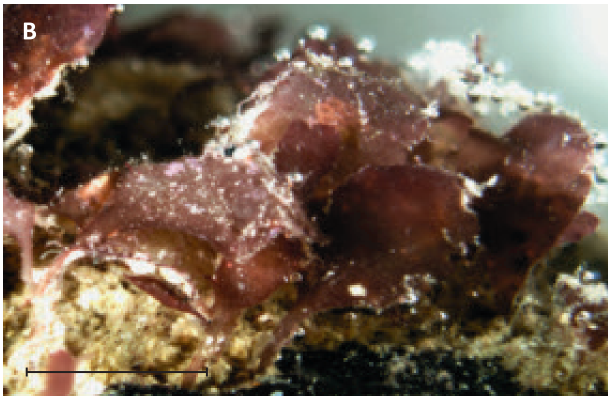
(Holmes ex Batters) Guiry & Garbary

Traill's Leaf Bearer

Appearance: Upright elongate spathulate, reddish brown, compact blades on a short stipe, up to 1-2 cm in height and 3.5 mm in width. The stipe is 0.5-1 mm in length, seldom with a single branch and has a small basal disc. The blades are unbranched but on rare occasions forked. The margin is regular or sparsely dentate before the formation of reproductive structures. The tetrasporophyte is crustose and consists of small, flat, bright red spots on pebbles. It was previously known as *E. allenii* Batters.

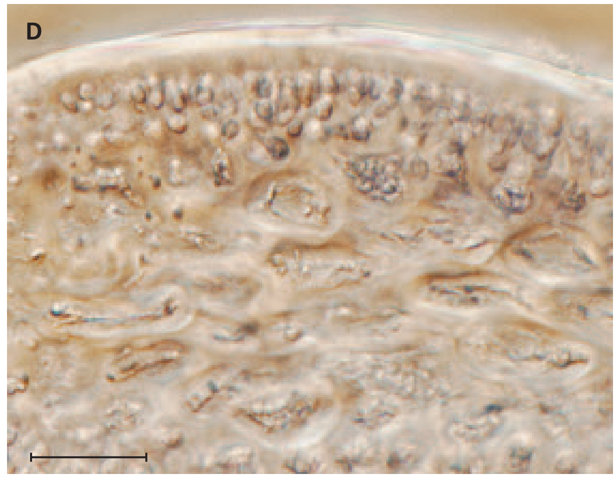
Structure: Uprights are multiaxial syntagma with large medullary cells which become smaller towards the surface. The cortex consists of 2-3 cell layers of small, rounded cells, 2-7 µm in diameter in surface view. The crustose tetrasporophyte consists of upright,

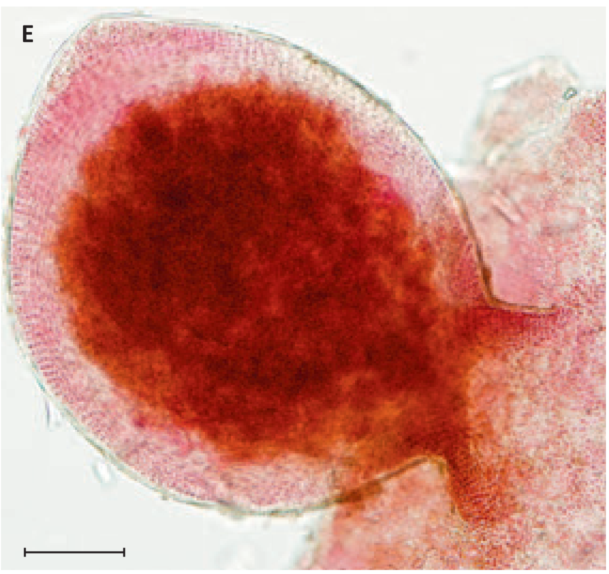


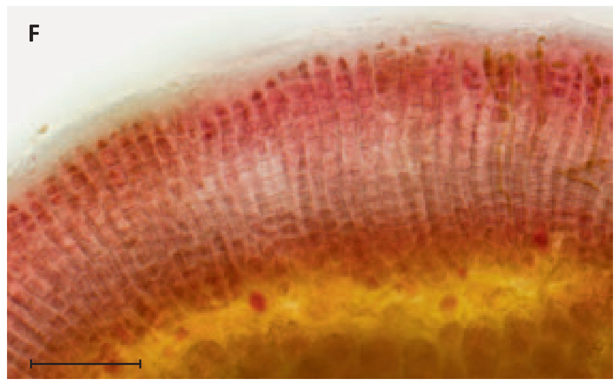


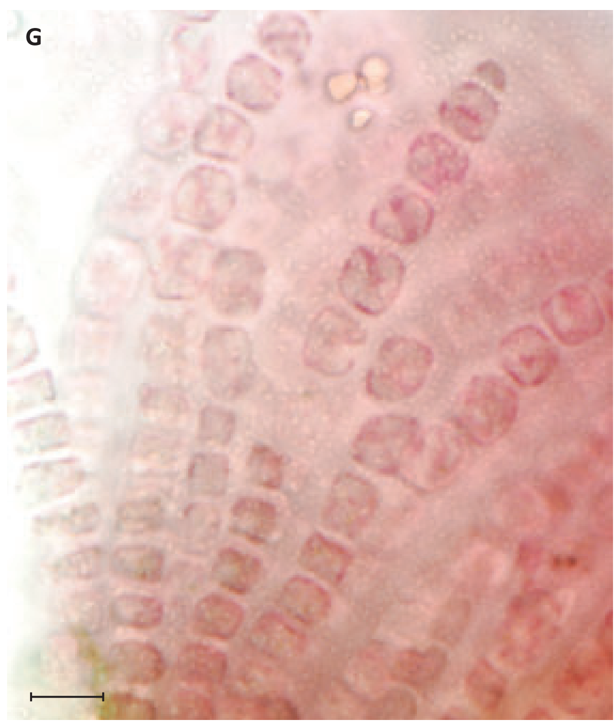
A: *Erythrodermis traillii.* Individual blades from basal discs, one of them with a branched stipe. Rødgrund, Lønstrup, 13 m, 15.8.2014. Scale 5 mm. Photo by S. Lundsteen.

B: *Erythrodermis traillii.* Dense stand of blades. Per Nilen, 11 m, 12.8.2014. Scale 5 mm. Photo by S. Lundsteen.









C: *Erythrodermis traillii*. Male bladelet with colourless antheridia. Scale 100 µm. C-D: Kims Top, 18 m, 28.8.2013.

D: *Erythrodermis traillii*. Surface with antheridia, transverse section. Scale 50 µm.

E: *Erythrodermis traillii*. Bladelet with gonimocarp. Herthas Flak, 10 m, 2.2.1996. Scale 100 µm.

F: *Erythrodermis traillii*. Crustose tetrasporophyte with upright filaments, which have short rows of dark red tetrasporangia, longitudinal section. Scale 50 µm. F-G: Kims Top, 14.5 m, 9.8.1995.

G: *Erythrodermis traillii*. Short rows of cruciate tetrasporangia. Scale 10 µm.

rarely branched filaments arising from a basal layer. The crust is soft and the filaments easily separate from each other by application of slight pressure. The basal layer is monostromatic and secondary pit connections frequent. Cells in the upright filaments are approximately equally as high as wide.

Reproduction: Isomorphic dioecious gametophytes. Reproductive structures occur in millimetre large bladelets on the margin of the blades. Antheridia form in small groups as colourless surface cells in male bladelets. Gonimocarps are approximately spherical bladelets. Tetrasporangia occur in upright filaments that are close together and form slightly raised patches (sori) on the crustose tetrasporophyte. The tetrasporangia are approximately spherical, 5.5-7 µm in diameter, and form 4-5 cells long intercalary rows below the apical cell of the filaments.

Seasonal variation: Probably perennial, upright thalli collected in February, May-August. Reproductive gametophytes recorded in February and August. Crusts with tetrasporangia only observed once, August.

Habitat: On stone reefs, typically on the oblique side of the boulders or on stones at the size of a hand in the outer part of the dense vegetation at a stone reefs. Here Traill's Leaf Bearer (*Erythrodermis traillii*) typically grows in dense stands and the blades form a more or less confluent cover on the rocks. Collected by divers at 7-23 m depth. In older collections by dredge at 31 m depth.

Resembles: Elongate individually occurring blades with entire margin can barely be distinguished from small young unbranched Sandy Leaf Bearer (*Phyllophora crispa*).

References: Dixon & Irvine (1977, *Erythrodermis allenii, Phyllophora traillii*), Maggs (1989, *E. allenii, P. traillii*), Rosenvinge (1931, *P. traillii*).

Fredericqia deveauniensis

Maggs, L.Le Gall, Mineur, Provan & G.W.Saunders

Appearance: Extensive crust with irregular pits in the surface after spore release.

Structure: Upright filaments with several coalescent tissue layers beneath the original basal layer.

Reproduction: Sori of tetrasporangia or bisporangia on the surface of different individuals. Spores germinate and develop into crusts. Upright gametophytes with narrow forked thalli known from other area (Maggs et al., 1992, 2013).

Comment: The crustose phase of this species, was reported from Danish stone reefs in Kattegat, by Maggs et al., 1992 as *Gymnogongrus* sp. and in 2013 as *Fredericqia deveauniensis*.

References: Maggs et al. (1992, *Gymnogongrus* sp., 2013).

Mastocarpus stellatus

(Stackhouse) Guiry

Grape Pip Weed

Appearance: Upright thallus is cartilaginous and consists of irregularly forked blades, dark reddish purple to almost black. The thallus is commonly 2-5 cm in height but may be up to 12 cm. Blades are variable in width, some 1 mm in width and others slightly more than 1 cm in width. Blades are frequently curled and wavy. The outer outline is narrow triangular with a gradual transition to the basal part with a very short stipe. Blades are channelled or slightly inrolled with a slightly thickened margin, best seen in transverse sections of the stipe. There are often papillae on the surface of the blades. The basal disc has several upright blades. The crustose tetrasporophyte is not recorded from Danish waters.

Structure: There is a medulla of filaments with very thick walls. It is surrounded by a cortex of radiating filaments, 7-10 cell layer thick, in which the dimensions of the cells decrease towards the surface.

Reproduction: Culture studies by Guiry & West (1983) showed various life histories. In one of them, there is a direct development from carpospores germinating and developing into the upright morphology as in the previous generation. In another, there is both a crustose tetrasporophyte and an upright gametophyte phase, which might be monoecious or dioecious. The tetrasporophyte was previously considered a separate species, *Petrocelis cruenta* J.Agardh. In Danish water, only individuals with gonimoblasts are observed, these develop in papillae on the blades, the papillae are up to 1 mm in height. Specimens from Hirtshals were included in the culture studies by Guiry & West (1983) and had a direct development from carpospores.

Seasonal variation: Perennial with the largest growth in March-April, when new apices are red. Gonimoblasts recorded in August.

Habitat: On boulders at shallow water.

Comment: Collected by I.P. Jacobsen in the harbour of Thisted, 1869. Later collected at the same locality by Rosenvinge, who also collected the species at Aarhus, 1915 and at Skagen, 1929. T. Christensen found it at Hirtshals, 1972, and it was collected at harbour jetties in Strandby, 1972. It was not observed in Frederikshavn until 1992, where it became a dominant species at the northern harbour jetty from where it

A

A: *Mastocarpus stellatus*. Relatively wide blades with papillae. Exposed side, northern harbour jetty, Frederikshavn, 0.5 m, 6.6.2002. Scale 2 cm.

probably spread to Vesterø havn, Læsø, with collections from there in 2008.

Resembles: Distinguished from Irish Moss (*Chondrus crispus*) by the channelled blades and the papillae on the blades.

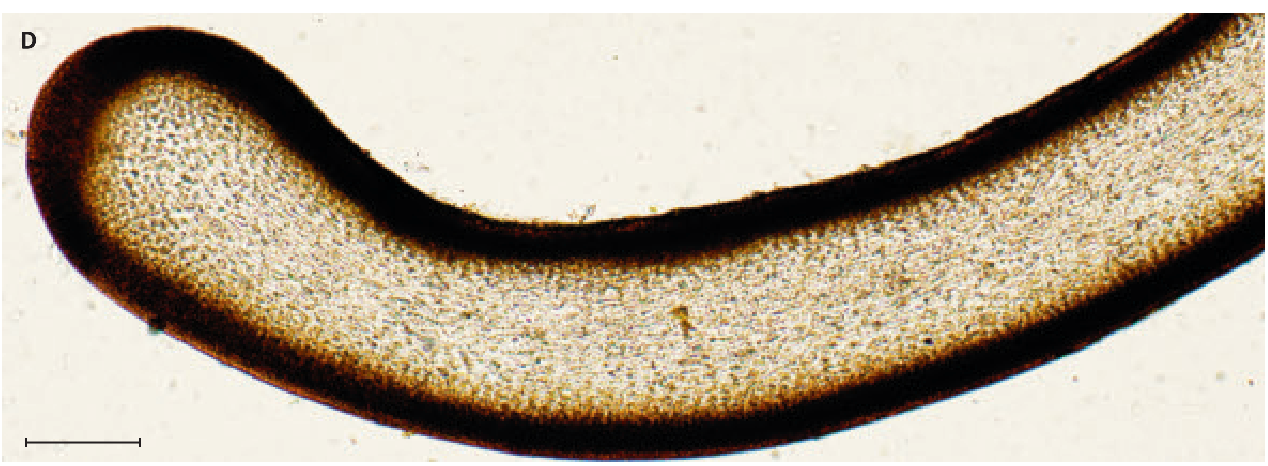
Comment: Known as Irish Moss together with *C. crispus* in Ireland and Scotland. The algae are dried and used in cooking, and to prepare a drink, said to relieve symptoms of colds or influenza.

References: Dixon & Irvine (1977, *Gigartina stellata, Petrocelis cruenta*), Guiry & West (1983, *G. stellata*), Rosenvinge (1931, *G. mamillosa*).

B: *Mastocarpus stellatus.* Single blade with large papillae. Scale 1 cm. B-D: Aarhus, 0.5 m, 22.1.2015. Leg.: K.L. Krabbe. Photo by S. Lundsteen.

C: *Mastocarpus stellatus.* Medulla of filaments with thick walls, cortex of radiating cell rows. Transverse section. Scale 100 µm.

D: *Mastocarpus stellatus.* Channelled blade, transverse section, lower part of blade. Scale 200 µm.



Phyllophora crispa

(Hudson) P.S.Dixon

Sandy Leaf Bearer

Appearance: Upright thalli of ribbon-shaped blades, 5-10 mm in width and up to 20 cm in height, red to bright brick-red colour. Basal disc with a single or several uprights. There are several generations of scattered blades, that may be triangular with very short stipes. Blades entire or bi- to trifurcate in the upper part, with an almost fan-shaped outline. The apices of the blades are rounded or cut off as a straight line. New blades develop on the flat side of the blade typically just below the upper margin. The central part of the blade is the thickest and may resemble a short midrib particularly near the base. Unattached narrow forms occur in the Belt Sea and the western part of the Baltic Sea. The blades of these are up to 0.1-2 mm in width with a dentate and sometimes wavy edge. Such unattached forms were referred to f. *bangii* and f. *tenuior* by Rosenvinge (1931) as formae of *P. epiphylla*.

Structure: Thallus a multiaxial syntagma with large medullary cells covered by a cortex of 2-3 layers of small cells, 2-6.5 µm in diameter in surface view.

Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Antheridia form in small cavities at the surface of spherical extensions which have short stalks. They are scattered on the surface of the blades, particularly near the edges and are c. 0.5 mm in diameter. Gonimocarps are scattered on the blades. At maturity they resemble cauliflowers on short stalks and are 1-2 mm in diameter. Tetrasporangia develop in small flat outgrowths (nemathecia), resembling buttons on stalks scattered on the blades. Cruciate tetrasporangia occur in rows.

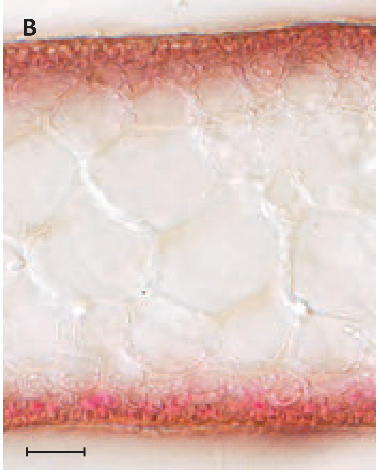
Seasonal variation: Perennial, a single generation of blades probably formed each year, thus thalli with 5-6 generations of blades are 5-6 years old. Antheridia recorded in September, gonimocarps in November-March and nemathecia with tetrasporangia in winter.

Habitat: On rocks and frequent on small stones and gravel, 5-15 m depth.

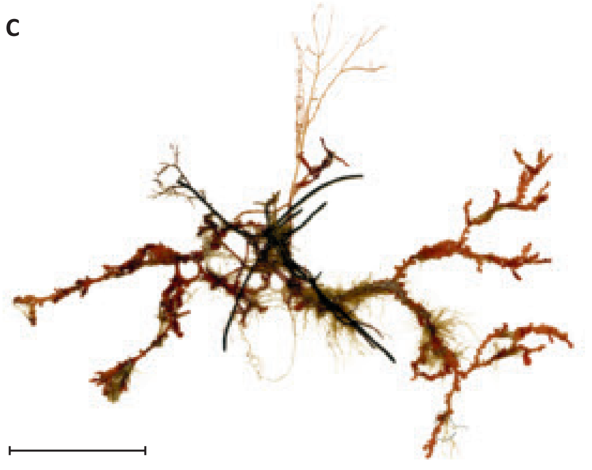
Resembles: It is almost impossible to recognize young unbranched blades from young Short Leaf Bearer (*Coccotylus truncatus*), even if they are unbranched, short ribbon-shaped or forked and fan-shaped. New blades with a short stipe-like base develop on the older blades in Sandy Leaf Bearer (*P. crispa*), while the new blades in Short Leaf Bearer (*C. truncatus*) develop from the edge of older blades without a stipe like base. Young Sandy Leaf Bearer (*P. crispa*) is also reminiscent of Traill's Leaf Bearer (*Erythrodermis traillii*), which can only be distinguished when the blades have a slightly dentate margin.

References: Dixon & Irvine (1977), Rosenvinge (1931, *Phyllophora epiphylla*).

A: *Phyllophora crispa*. Thallus of ribbon-shaped and triangular blades. Herthas Flak, 20 m, 21.8.1991. Scale 2 cm.



B: *Phyllophora crispa*. Large medullary cells decreasing in size towards the cortex of 2-3 layers of small cells. Tønneberg Banke, 14 m, 27.8.2013. Scale 20 µm.



C: *Phyllophora crispa*. Small unattached f. *bangii*. West of Fyns Hoved, 5 m, 8.8.1906. Scale 2 cm. Leg.: Rosenvinge.

Phyllophora pseudoceranoides

(S.G.Gmelin) Newroth & A.R.A.Taylor ex P.S.Dixon & L.M.Irvine

Stalked Leaf Bearer

Appearance: Cartilaginous upright dark bluish red-purple thalli, with fan-shaped blades on terete stipes. The stipes are relatively long and 1-2 mm wide. Several blades frequently arise together from the basal disc. Branching occurs from the stipes or the lower blades. The blades are wide fan-shaped with an obtuse angle (> 90°) at the base and with many lobes. These form by repeated splitting of the blades, becoming narrower towards the top, and typically rounded at the apex. Sometimes the base of the frond is narrow before it fans out. The appearance of the alga differs in different districts. In Skagerrak individuals only grow up to 12 cm in height. In the Belt Sea the blade is narrow, less split and up to 28 cm in height. In the Baltic Sea they are short, slender, and rarely up to 3-5 cm in height.

Structure: Multiaxial syntagma with large medullary cells, decreasing in size towards the surface. The cortex is multilayered, the outer layer consisting of small cells, 2-6 µm in diameter in surface view.

Reproduction: Isomorphic gametophytes and tetrasporophyte. Antheridia develop in small groups in

A: *Phyllophora pseudoceranoides*. Long stipes with repeatedly split fan-shaped blades. The lobes of blades narrower towards the apex. Many epiphytes. Torup Flak, 9 m, 25.7.1994. Scale 2 cm.

B


C

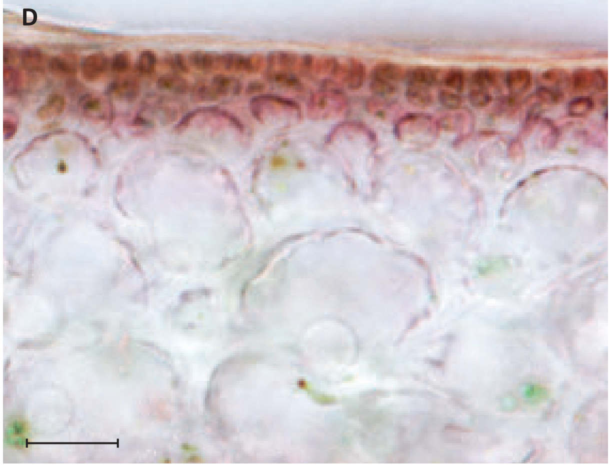

B: *Phyllophora pseudoceranoides.* Both narrow and wide blades. Møns Klint, 17 m, 7.9.2004. Scale 2 cm.

C: *Phyllophora pseudoceranoides.* The stipes are the major part of this small alga. Venegrund, 8 m, 26.9.1992. Scale 2 cm.

the cortex of special bladelets. They are pale and develop at the edge of vegetative blades. Gonimocarps develop into spherical or lemon-shaped outgrowths with short stalks on the stipes or edges of vegetative blades. Gametophytes are typically dioecious, rarely monoecious with both male and female reproductive structures in one individual. Tetrasporangia occur in slightly thickened dark areas (nemathecia) on both sides towards the basal part of blades. Here cruciate tetrasporangia form intercalary necklace-like rows in dense filaments.

Seasonal variation: Perennial, with a new generation of blades each year. Growth stops in winter after which some blades renew growth with further splitting into more lobes while other blades do not grow further. Very young thalli only have a short stipe from the basal disc in the first year and blades do not develop until the following year. New stipes with blades from the apex of the lobes rarely occur. Antheridia recorded in June-October, female reproductive structures initiate development in July, mature gonimoblasts recorded in winter, and still present in March-May. Nemathecia initiate development in June-July and have mature tetrasporangia in December-January (Rosenvinge, 1931).

Habitat: One of the dominant species on stone reefs,

D


D: *Phyllophora pseudoceranoides.* Large medullary cells, decreasing in size towards the cortex of small cells. Transverse section of vegetative blade. Kims Top, 21.5 m, 26.8.1993. Scale 20 µm.

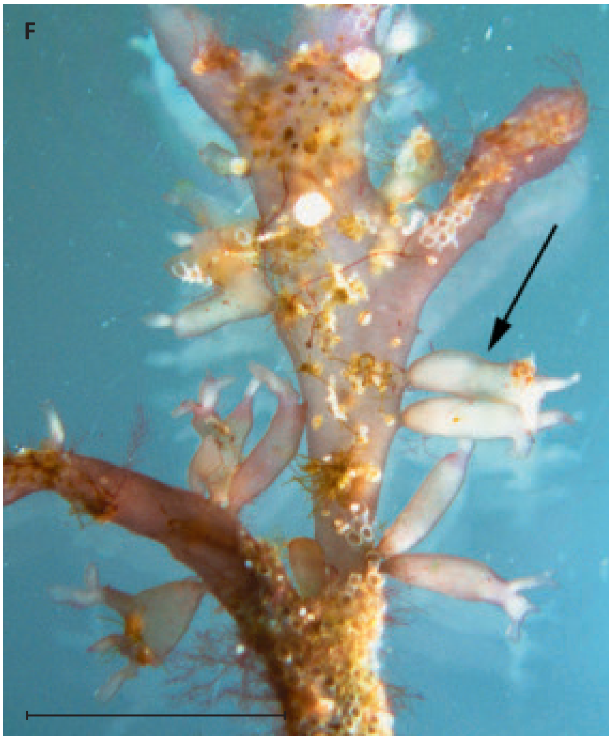
E

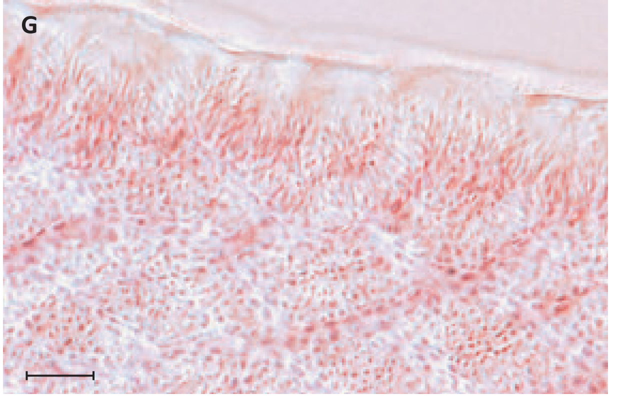

E: *Phyllophora pseudoceranoides.* Wide blades and gonimocarps (arrow). Kims Top, 18.5 m, 15.1.1997. Scale 2 cm.

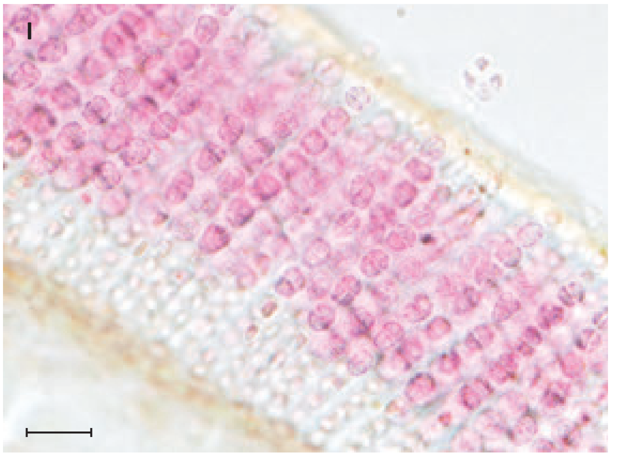
frequent in the lowest layer of a multi-layered seaweed community. On rocks, 0.5-28 m depth.

Resembles: Easily confused with Lobed Leaf Bearer (*Coccotylus brodiei*) and Short Leaf Bearer (*C. truncatus*) but its bluish red-purple colour distinguishes it from the other two species which are brownish red. Furthermore, the long stipes with the wide fan shaped blades and lobes becoming narrower towards the apex are typical for Stalked Leaf Bearer (*P. pseudoceranoides*).

References: Dixon & Irvine (1977), Lundsteen & Nielsen (2015), Rosenvinge (1931, *P. membranifolia*).







F: *Phyllophora pseudoceranoides.* Blade with male bladelets (arrow). Tønneberg Banke, 4.5 m, 13.8.2014. Scale 5 mm. Photo by S. Lundsteen.

G: *Phyllophora pseudoceranoides.* Surface of male bladelet with antheridia. Tønneberg Banke, 10.5 m, 12.8.1990. Scale 20 µm.

H: *Phyllophora pseudoceranoides.* A wide blade and several narrow blades with dark nemathecia (arrows). Kirkegrund, 12 m, 23.8.2015. Scale 2 cm.

I: *Phyllophora pseudoceranoides.* Rows of cruciate tetrasporangia, transverse section of nemathecium. Hirsholm, drift, 27.12.1985. Scale 20 µm.

Family: Polyidaceae

Polyides rotunda

(Hudson) Gaillon

Discoid Fork Weed

Appearance: Bush-like thalli of regularly repeated dichotomously divided terete branches, 1-2 mm wide and up to 18 cm in height. Several upright fronds arise from a basal disc. Cartilaginous with a dark but clearly red colour and with obtuse apices, which might be bright red in colour. Rounded axils give an open appearance, and the alga falls into a fan shape, when taken out of the water and laid down.

Structure: Multiaxial syntagma, with a medulla of colourless filaments surrounded by a well-developed cortex. The medulla consists of longitudinal filaments with thick walls matted together by narrow hyphae-like reversible filaments. The compact cortex consists of dense radiating filaments of ellipsoid cells, gradually decreasing in size to 3-4 layers of small assimilating cells at the surface.

Reproduction: Isomorphic monoecious gametophytes and tetrasporophyte. Sexual reproductive structures develop in warty or longitudinal elongated nemathecia on one side of the youngest parts of branches. Antheridia develop laterally on the filaments which form the nemathecia. Gonimoblasts develop between filaments in the inner part of the nemathecia. Carpogonia have spirally twisted trichogynes. Cruciate tetrasporangia develop between cortical filaments in the youngest parts of the branches which become slightly thickened.

Seasonal variation: Perennial, occurring all year. Antheridia recorded in August-November, gonimoblasts in September-January and mature tetrasporangia in September-October and January-February.

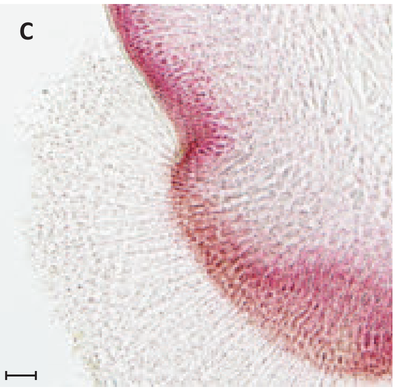
Habitat: Frequent on small stones and gravel, 0.5-17 m depth. In older collections with dredge down to 23.5 m depth.

Resembles: Discoid Fork Weed, (*P. rotunda*) is very reminiscent of Clawed Fork Weed (*Furcellaria lumbricalis*) particularly when the base is absent but is distinguished by its distinctly red colour, the open branching, and the obtuse apices.

References: Bird & McLachlan (1992, *P. rotundus*), Dixon & Irvine (1977, *P. rotundus*), Rosenvinge (1917, *P. rotundus*).

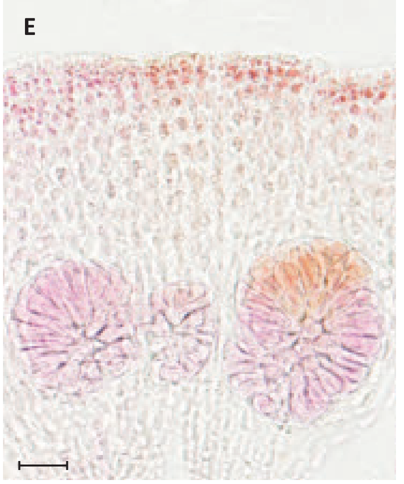
A: *Polyides rotunda*. Terete upright branches, repeatedly dichotomously branched, from a basal disc. Hirsholm, drift, 10.11.1976. Scale 2 cm.

B: *Polyides rotunda*. Medulla of filaments with thick walls, and narrow hyphae-like filaments. Multi-layered cortex of small ellipsoid cells. Part of transverse section. Rødgrund, Lønstrup, 8 m, 26.8.2013. Scale 50 µm.

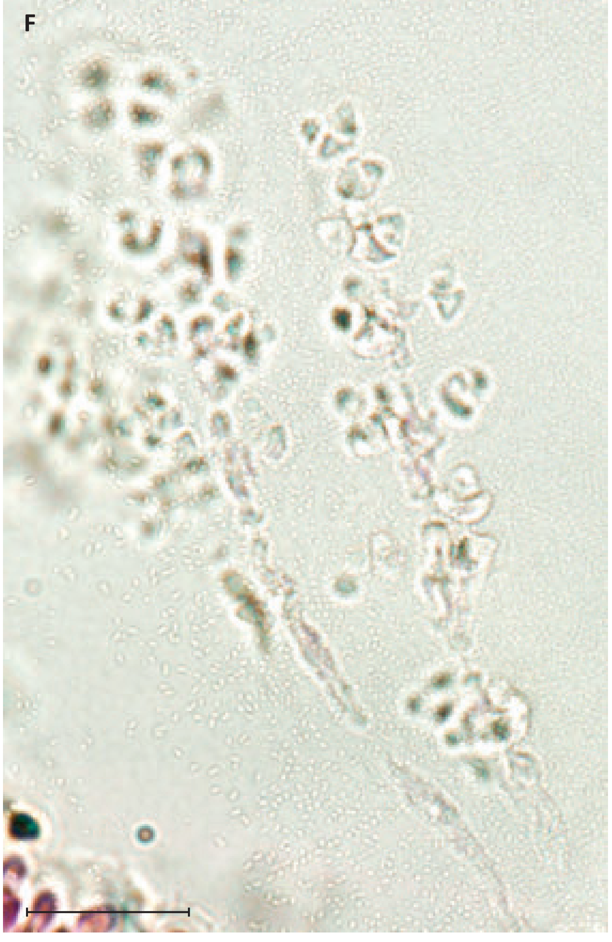


C: *Polyides rotunda.* Male nemathecium, transverse section. Scale 50 µm. C, F: Broen, 9.5 m, 9.9.1991.

D: *Polyides rotunda.* Female nemathecium with young gonimoblasts, transverse section. Middelflak, 8.5 m, 15.9.1991. Scale 100 µm.



E: *Polyides rotunda.* Gonimoblasts in nemathecium. Tisvilde, drift, 11.10.1996. Leg.: S. Wegeberg. Scale 50 µm.



F: *Polyides rotunda.* Filaments with antheridia. Scale 20 µm.

G: *Polyides rotunda.* Cruciate tetrasporangia among cortical filaments, transverse section of thick branch. Hirsholm, drift, 13.2.1981. Scale 50 µm.

Order: Gracilariales · Family: Gracilariaceae

The species in Danish waters have terete branches and are repeatedly branched on all sides. A pseudoparenchyma of large medullary cells covered by a cortex of small cells. The surface is covered by a thick outer wall layer. Branches arise from cortical cells. Isomorphic dioecious gametophytes and tetrasporophyte. Antheridia develop in pits in the cortex (conceptacles) in *Gracilaria* and in patches at the surface of branches in *Gracilariopsis*. In female gametophytes the gonimocarps are small warts on the branches in these genera. The cruciate tetrasporangia occur scattered between the surface cells.

Several species of Gracilariales are used for extraction of agar and are of economic importance. Agar is used as a gelling agent in the food industry and as a stabilizer in growth media used for microbiological research.

References: Christensen (1980), Fredericq & Hommersand (1989a, b), Gurgel et al. (2003), Kylin (1956).

Identification key to species of Gracilariaceae

1a.	Red brown to dark brown branches with a cartilaginous brittle consistency. There is a distinct difference in thickness between different generations of branches	*Gracilaria vermiculophylla*
1b.	Red brown to reddish branches with a leathery elastic consistency, branches of a uniform thickness	2
2a.	Without subcortex and gradual transition from the cortex to the medulla of large cells	*Gracilaria gracilis*
2b.	With subcortex and a distinct transition from the cortex to the medulla of large cells	*Gracilariopsis longissima*

Gracilaria gracilis

(Stackhouse) Steentoft, L.M.Irvine & Farnham

Slender Wart Weed

Appearance: Terete brownish red branches, the alga can be up to 33 cm in height. It is common that several uprights arise from a relatively coarse disc-shaped base. Branches are elastic with a tough leathery consistency with a high tensile strength. Branches are irregularly scattered on all sides and are repeatedly branched 2-3 times and 1-2 mm wide at the base. The lower part of the thallus has dense relatively short branches, and longer branches, frequently of second order, may develop. Young branches are commonly broader than the branches from which they arise. In older thalli, old branches have a constriction at the base. Apices are long pointed and slightly curved. The disc-shaped base typically consists of up to 5-6 amalgamated individual discs.

Structure: The cortex consists of dark pigmented cells in 1-2 cell layers. There is a gradual transition to the large pale cells in the medulla. Cells just below the cortex may be slightly elongated in a radial direction and up to 2-3 times as long as wide.

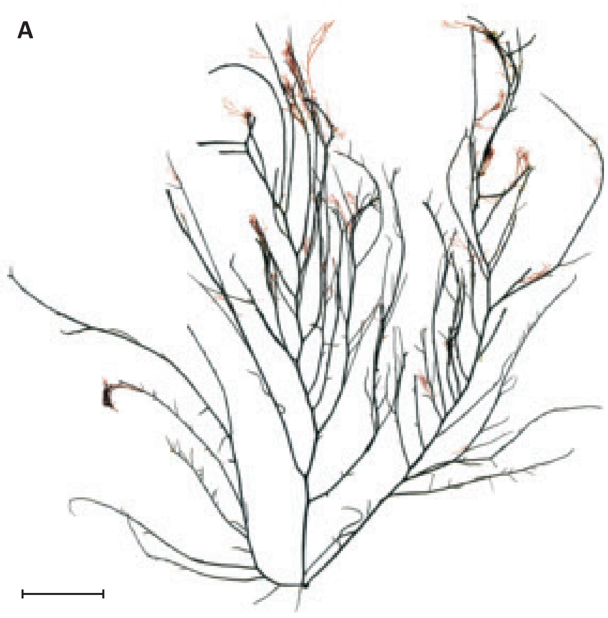
Reproduction: Antheridia form in conceptacles, 50 µm deep with a pore to the surface. Gonimocarps are onion-shaped. Young gonimocarps have a basal constriction at the transition from the branch. Cruciate tetrasporangia occur scattered in the cortex. Branches with antheridia or tetrasporangia are slightly thickened and easily break as opposed to the rest of the thallus.

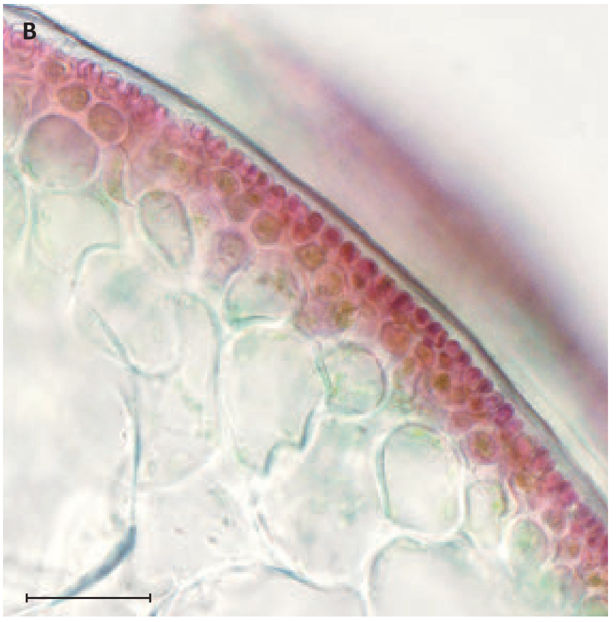
Seasonal variation: Collected in July-August with antheridia, gonimoblasts and tetrasporangia.

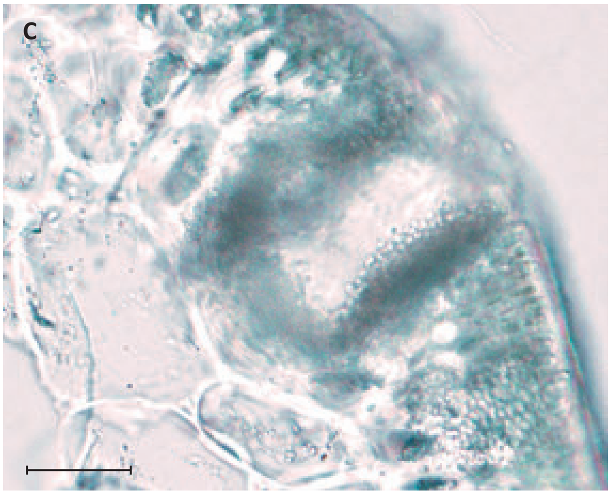
Habitat: On rocks and gravel, 1-6 m depth.

Comment: The identity of drifting algae in Kattegat is uncertain. They are mentioned as *Gracilaria confervoides* f. *tenuissima* by Rosenvinge (1931). Drifting vegetative specimens, observed in large quantities in Haderslev Fjord, 2018 by R. Fredriksen, are probably the same, and identical to Slender Wart Weed (*G. gracilis*).

References: Fredericq & Hommersand (1989a, *Gracilaria verrucosa*), Gurgel & Fredericq (2004), Rosenvinge (1931, *G. confervoides*), Steentoft & Farnham (1997), Steentoft et al. (1995).







A: *Gracilaria gracilis.* Thallus of terete scattered branches on all sides and of a uniform thickness, with small epiphytic *Ceramium* sp. Lovns Bredning, 16.8.2016. Leg.: M. Laursen. Scale 2 cm.

B: *Gracilaria gracilis.* Cortex of 1-2 cell layers, medullary cells gradually increase in size towards the centre, transverse section. Scale 50 µm. B, D-F: Tile works, Helligsø, 3 m, 30.8.2016. Leg.: R. Frederiksen.

C: *Gracilaria gracilis.* Conceptacle with antheridia, transverse section. Holmtange Hage, Løgstør Bredning, 0.8 m, 16.8.2016. Scale 50 µm.

D: *Gracilaria gracilis*. Female gametophyte, gonimocarps form small warts on the branches (arrow). Scale 2 cm.

E: *Gracilaria gracilis*. Branch with gonimocarp, transverse section. Scale 250 µm.

F: *Gracilaria gracilis*. Cruciate tetrasporangia between cortical cells (arrow), transverse section. Scale 50 µm.

G: *Gracilaria confervoides* f. *tenuissima*. Unattached alga with *Cladophora* sp. 600 m outside Nymarke Nakke, Ulvsund, 3 m, 26.4.1930. Scale 2 cm. Leg.: S. Lund.

Gracilaria vermiculophylla

(Ohmi) Papenfuss

Worm Wart Weed or Black Wart Weed

Appearance: Robust red-brown to dark brown alga with terete, cartilaginous branches. Thallus typically 30-40 cm in length, but may be up to 1 m. The uprights arise from a disc-shaped base. Branches are scattered, 1-10 mm wide and 3-4 times repeatedly branched on all sides. There are distinct, coarse main axes and narrower branches, slowly decreasing in thickness towards the pointed apex and constricted at the base.

A: *Gracilaria vermiculophylla.* Female gametophyte with small warts of gonimocarps. 500 m West of the fisher house north of Boller, Dagnæs, Horsens Fjord, 0.5 m, 14.11.2004. Scale 5 cm.

Thalli are brittle and easily snap when lifted out of the water, particularly the larger ones. Pressed specimens adhere poorly to the paper.

Structure: In from the cortex of small cells a subcortex of 2-3 cell layers gradually transitions to the medulla of large, rounded cells.

Reproduction: Antheridia develop on the walls of conceptacles which are 150-200 µm deep with a pore to the surface. Gonimocarps develop in small warts on the branches. The cruciate tetrasporangia are scattered between cortical cells. Asexual reproduction from fragments of the thalli is also frequent.

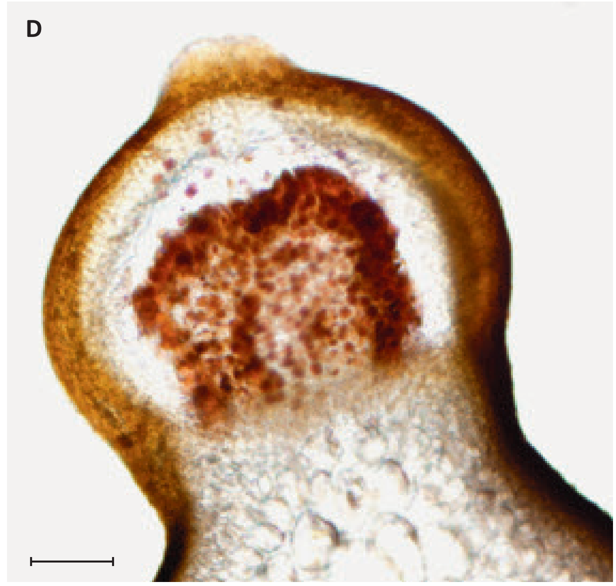
Seasonal variation: Perennial, well-developed thalli collected in February-November. Specimens with reproductive structures collected in March-November.

Habitat: Unattached, kept together by byssus from Blue Mussel (*Mytilus edulis*), or on small stones and bivalve shells at sheltered localities with a seabed of sand and clay, 0-5 m depth.

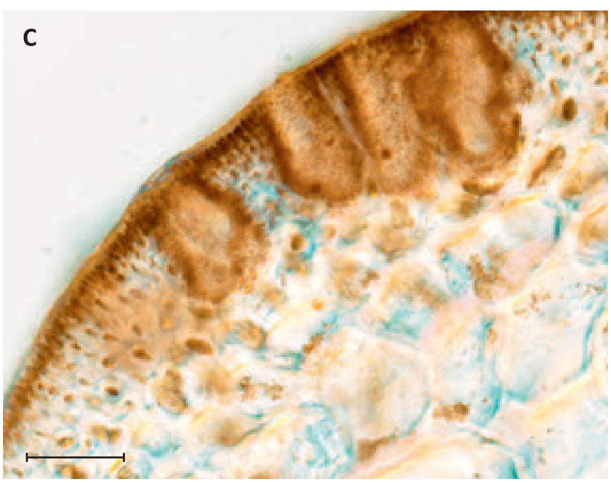
Comment: Invasive species which originates from south-east Asia. The collections in Horsens Fjord, 2003 were the first observations in Danish waters. The dispersal is effective from spores as well as from fragments of the thallus.

References: Gurgel et al. (2018, *Agarophyton vermiculophyllum*), Nyberg (2007), Rueness (2005), Thomsen et al. (2005).

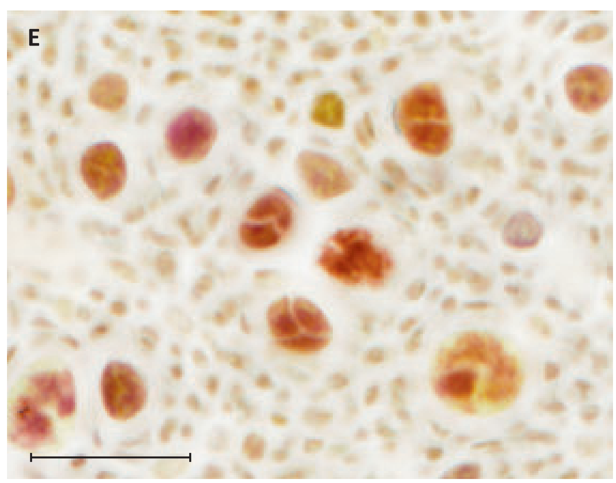
B: *Gracilaria vermiculophylla*. Surface of male gametophyte with conceptacles. Scale 100 µm. B-C: Hvidbjerg, Vejle Fjord, 0.7 m, 26.8.2015. Leg.: R. Frederiksen.



D: *Gracilaria vermiculophylla*. Section through gonimocarp. Sødring, northern side of Randers Fjord, 0.5 m, 27.8.2013. Scale 200 µm. Leg.: N. Sloth.



C: *Gracilaria vermiculophylla*. Conceptacles with antheridia, transverse section of branch. Scale 100 µm.



E: *Gracilaria vermiculophylla*. Scattered cruciate tetrasporangia between surface cells. Outer side of Holtzer Hage, Vejle Fjord, 0.3 m, 16.6.2006. Scale 50 µm. Leg.: Aa. Kristiansen.

Gracilariopsis longissima

(S.G.Gmelin) Steentoft, L.M.Irvine & Farnham

Long Wart Weed

Appearance: Terete reddish brown branches with a tough leathery consistency, 1-2 mm thick at the base. The uprights arise from a thin disc-shaped base. Thalli are up to 45 cm in length, and are densely repeatedly branched with branches on all sides. Branches arise at regular intervals and are of a uniform length in a short growth form. There is also a long growth form where single long branches arise. The apices are straight and taper to a point.

Structure: The cortex consists of 1-2 cell layers of small, pigmented cells. There is a subcortex of 2-3 (-5) cell layers of rounded cells, 3-5 (-8) times as long as wide, slightly increasing in width towards the centre, and distinctly different from the large colourless cells of the medulla.

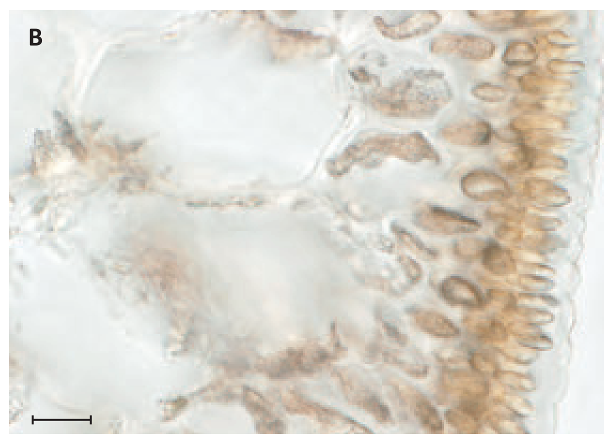
Reproduction: Antheridia form large colourless patches on the surface of the branches. Gonimocarps are rounded warts on the thalli, slightly wider than high and have a central pore, which may have a small ostiole. Cruciate tetrasporangia occur scattered between the cortical cells.

Seasonal variation: Collected in August with gonimocarps.

Habitat: Collected at the exposed head of the southern harbour jetty Hirtshals.

Comment: *Gracilaria gracilis* and *Gracilariopsis longissima* were previously considered variations within a single species, *Gracilaria confervoides* (Linnaeus) Greville or *Gracilaria verrucosa* (Hudson) Papenfuss. The taxonomic status was confirmed by genetic investigations (Gurgel et al., 2003).

References: Gurgel et al. (2003), Steentoft & Farnham (1997), Steentoft et al. (1995).



A: *Gracilariopsis longissima*. Long growth form of female gametophyte with warts of gonimocarps. Scale 2 cm. A, B: The outer end of the pier of concrete blocks, Hirtshals, 2 m, 22.8.1976.

B: *Gracilariopsis longissima*. Cortex of 1-2 cell layers, subcortex of 3-4 cell layers and large medullary cells. Scale 20 µm.

Order: Halymeniales · Family: Halymeniaceae

Grateloupia

Much branched or elongate lanceolate upright fronds which are very smooth with a firm texture. The multiaxial syntagma has a medulla of loosely connected narrow filaments of long pale cells. The cortex consists of radiating few-celled filaments of more or less spherical cells with ellipsoid apical cells approximately two times as long as wide. Isomorphic gametophytes and tetrasporophyte.

Identification key to species of *Grateloupia*

1a.	Frond elongate lanceolate with irregularly lobed projections from the edges of the blade, c. 30 cm in length and 2-4 cm in width	*G. turuturu*
1b.	Frond much branched with distinct main axes, terete or flat 5-10 mm wide and branches on all sides repeatedly branched several times	*G. subpectinata*

Grateloupia subpectinata

Holmes

Grateloup's Fringe Weed

Appearance: Much branched alga, with a distinct, coarse main axis and scattered branches on all sides. Thalli are firm and very smooth, crimson-red and up to 35 cm in height. Branches are long, narrow at the base, taper to a point, and repeatedly branched 1-2 or more times. The main axis is terete with slightly compressed parts or flat up to 5-10 mm wide. The widest part occurs 1-4 cm above a narrow base. Uprights arise from a disc-shaped base.

Structure: Multiaxial syntagma with several apical cells. There is a filamentous medulla and a cortex of radiating filaments, each of which consists of 4-6 small, rounded cells, the outermost ellipsoid with the long axis perpendicular to the surface. In a transitional layer to the medulla the cells are larger, at some distance to each other and appear star-shaped.

Reproduction: Isomorphic gametophytes and tetrasporophyte. Antheridia develop in small groups from the surface cells. Gonimocarps are embedded in the cortex and the outer part of the medulla with a pore to the surface. The cruciate tetrasporangia are embedded in the cortex.

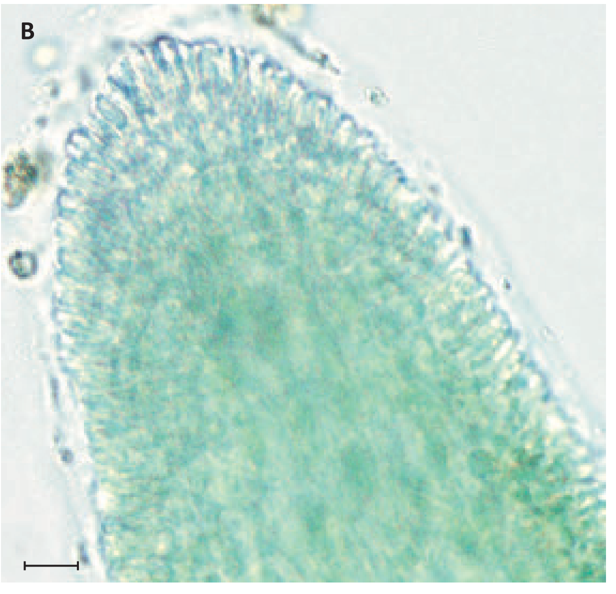
Seasonal variation: Collected in July-September, with gonimocarps in August-September.

Habitat: On rocks, 2.5 m depth.

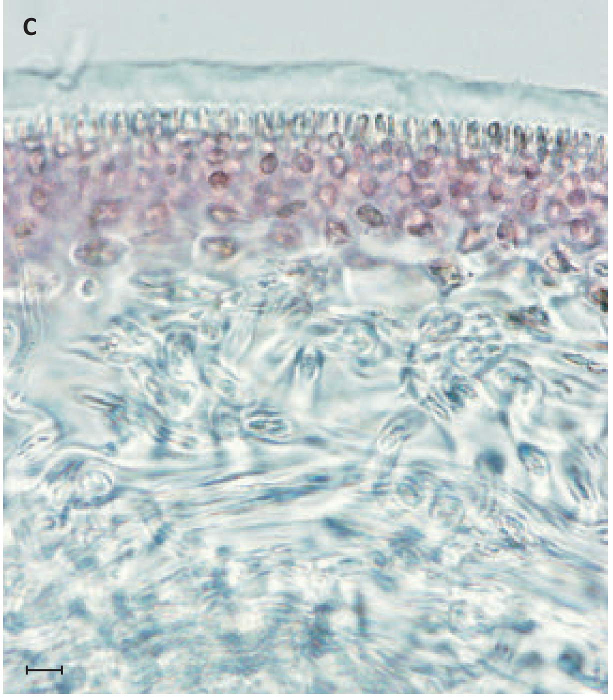
Comment: The first collection in Danish waters was an alga with gonimocarps, 2016. Probably introduced to Europe from Japan by ships or by import of oysters (Guiry in Guiry & Guiry, 2021).

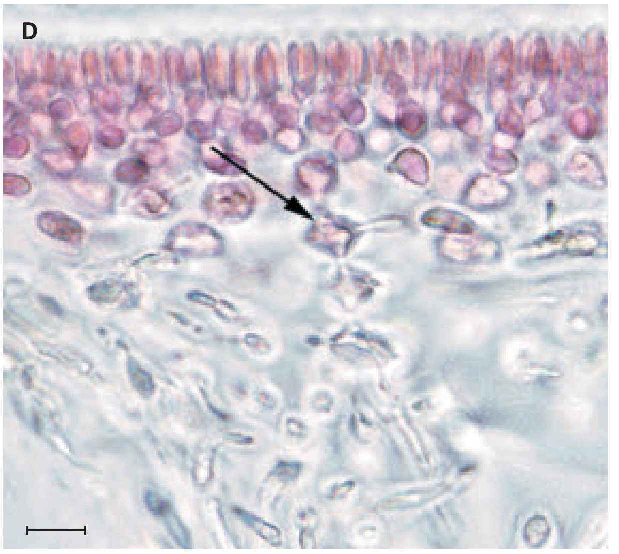
References: Brodie et al. (2016), Guiry in Guiry & Guiry (2021), Irvine & Farnham (1983, *G. filicina* var. *luxurians*), Faye et al. 2004.

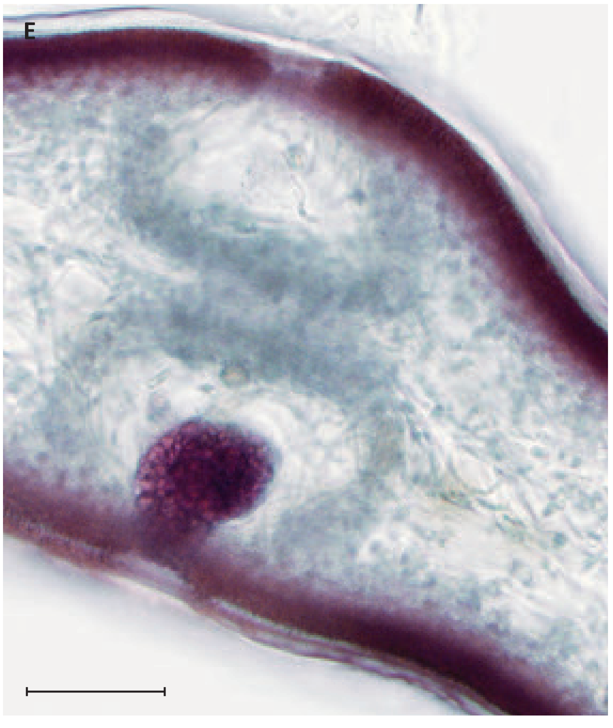
A: *Grateloupia subpectinata*. Distinct main axis and scattered lengthy pointed branches on all sides. Scale 5 cm. A-E: Knud Strand, Sallingsund, 0.4 m, 31.8.2016. Leg.: M. Laursen.



B: *Grateloupia subpectinata*. Apex with several apical cells. Scale 10 µm.







C: *Grateloupia subpectinata*. Medullary filaments and cortex of small cells, transverse section. Scale 10 µm.

D: *Grateloupia subpectinata*. Cortex of few-celled filaments, the outer ones long ellipsoid, and star-shaped cells towards the medulla (arrow), transverse section. Scale 10 µm.

E: *Grateloupia subpectinata*. Gonimocarp embedded in the branch, transverse section. Scale 100 µm.

F: *Grateloupia subpectinata*. Much branched frond, flat main axes. Nykøbing Mors, Østerstrand, 1 m, 5.7.2020. Leg.: P. Schmedes. Scale 2 cm.

Grateloupia turuturu

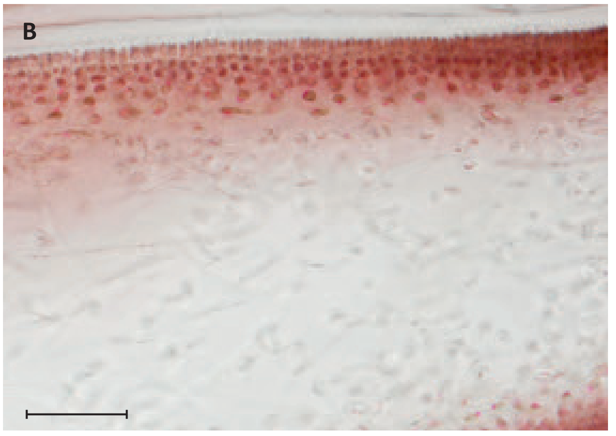
Y.Yamada

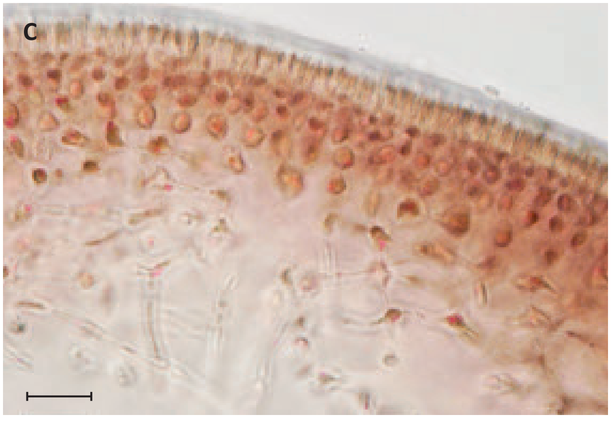
Devil's Tongue Weed

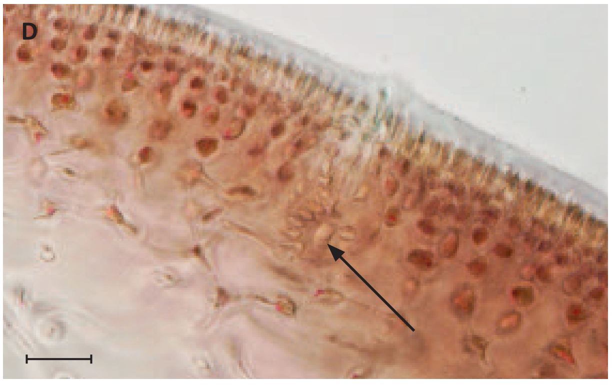
Appearance: Elongate lanceolate blades, c. 30 cm in length and 2-4 cm in width, sometimes with a triangular basal part. British individuals 30-60 (-100) cm in length and 2-20 cm in width (Irvine, 1983). Many proliferations occur irregularly from the edge and surface of the blade. The proliferations have gradually pointed lobes and are slightly undulating so the outline may be reminiscent of a flame. The blades are c. 0.5 mm thick, silky and very smooth with a light red or brownish red colour. One or a few blades arise from a basal disc.

Structure: Multiaxial syntagma with a medulla of loosely connected narrow filaments occurring in all directions. Cortex consists of few-celled filaments of rounded to spherical cells 3-4 µm in diameter with plastids. The outermost cell in each of the cortical filaments is ellipsoid, c. 3 µm in width and 2-3 times as long as wide and covered by a relatively thick outer wall. The medullary filaments are at some distance to each other, have scattered branching points, and consist of long cylindrical cells. Just inside the cortex there are cells which appear star-shaped.

Reproduction: Monoecious gametophytes with







A: *Grateloupia turuturu*. Elongate blade with irregularly projections or new blades from the edge. Female gametophyte, pointed by gonimoblasts. Scale 2 cm. A-D: Tile works, Helligsø, drift, 23.9.2021. Leg: K.L. Krabbe.

B: *Grateloupia turuturu*. Medulla of narrow loosely connected filaments. Cortical filaments of globular cells with an elongate apical cell. Transverse section. Scale 50 µm.

C: *Grateloupia turuturu*. Stellate cells in transition between cortex and medulla. Transverse section. Scale 20 µm.

D: *Grateloupia turuturu*. Young gonimoblast (arrow). Transverse section. Scale 20 µm.

microscopic reproductive structures developing in surface cells (Irvine, 1983). Gonimoblasts occur scattered in the frond and appear as dark pinheads. They are spherical and surrounded by enveloping filaments and have an exit tube to the surface of the blade.
Seasonal variation: Collected in September with gonimoblasts.

Habitat: On rocks, 0.3-0.5 m depth.
Comment: First observation in Danish waters, September 2021. Several fronds occurred in a crop of approximately 5-10 individuals per square metre.
References: Bunker et al. 2020, Guiry in Guiry & Guiry (2021), Irvine 1983 (as *G. doryophora*).

Family: Tsengiaceae

Tsengia bairdii

(Farlow) K.C.Fan & Y.P.Fan
Baird's Worm Weed

Appearance: Tufts of centimetre high uprights. Thallus soft, sparsely, irregularly dichotomously branched and a pink colour. Each of the upright branches arises from a basal disc.
Structure: Multiaxial syntagma, with a compact medulla of filaments with thick walls, held together by narrow filaments. The surface consists of clusters of forked filaments held together by a gelatinous wall material.

Reproduction: Gonimocarps develop from the innermost cortical cells and become approximately spherical. Cruciate tetrasporangia occur both in the basal crust and in upright branches, where they develop between the lower cells of the cortical filaments. Antheridia unknown.
Seasonal variation: Collected in July with carpogonia, gonimocarps and tetrasporangia.
Habitat: On small stones, collected by dredge, 19-15 m depth. Only a single collection from Danish waters.
References: Dixon & Irvine (1977, *Platoma bairdii*), Maggs (1997), Rosenvinge (1917, 1935a, *P. bairdii*).

A: *Tsengia bairdii*. Terete sparsely branched alga. Lyngsodde, the Lilttle Belt, 19-15 m, 23.7.1915. Scale 1 cm. Leg.: Rosenvinge.

Order: Peyssonneliales · Family: Peyssonneliaceae

Peyssonnelia dubyi

P.Crouan & H.Crouan

Peysonnel's Brick-red Crust

Appearance: Compact brick-red crusts up to 1-3 cm wide, (see *Phymatolithon purpureum* figure A). Short radiating, white stripes of calcification are frequently visible through the surface of the crust when examined with the dissection microscope.

Structure: The basal layer has a calcified underside and consists of radiating filaments which grow out into fan-shaped lobes. The margin, therefore, becomes irregular, and the lobes sometimes grow on top of each other. Cells are relatively large, rectangular to irregularly angular. In each cell there are many irregularly-shaped plastids. The crust soon becomes polystromatic and consists of upright, densely packed filaments. The growth of these begins with a single upright cell that is cut off from the basal layer, and from this, 2 or 3 filaments arise that continue the upward growth. The upright filaments repeatedly branched and filaments gradually become narrower towards the top. Upper cells are approximately 10 µm wide and 0.5-2 times as long as wide. Where branches develop in both the basal and the upright filaments, cells are cut off by oblique walls, orientated in opposite directions. The crusts may be of 10 or more cell layers and become overgrown by layers of younger lobes or other algae. From cells in the basal layer short filaments (rhizoids) may grow downwards.

Reproduction: Isomorphic and typically monoecious gametophytes and tetrasporophyte. Reproductive structures develop in slimy spots (nemathecia) on the surface of the crusts. Antheridia develop on special male filaments. Gonimocarps and large cruciate tetrasporangia occur between colourless sterile filaments which form the major part of the nemathecium.

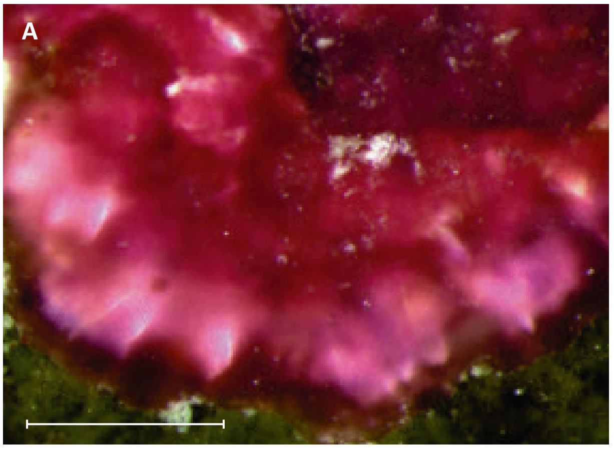
Seasonal variation: Perennial, collected all months except December. Antheridia and gonimoblasts recorded in August, and tetrasporangia in January-March and August.

Habitat: On boulders, small stones and mollusc shells, 2-27 m depth. In older collections by dredge to 30 m depth.

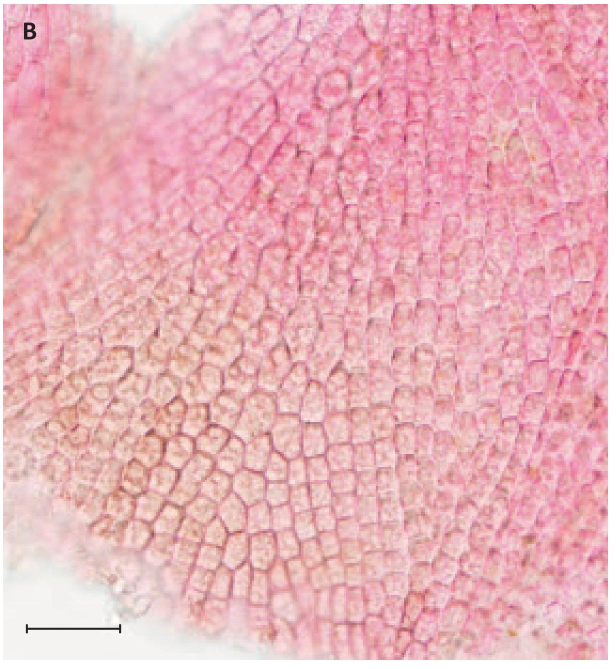
Resembles: Easily recognised from other red algal crusts in Danish waters by the angular cells and oblique walls.

Comment: *Peyssonnelia codana* (Rosenvinge) Denizot is described from Danish waters based on a single collection. It is described as brighter than *P. dubyi*, without calcification and has smaller carpospores. It is reminiscent of *P. dubyi* according to Irvine & Maggs (1983), therefore possibly the same species.

References: Irvine & Maggs (1983), Krayesky et al. (2009), Maggs & Irvine (1983), Rosenvinge (1917, *Cruoriella codana, C. dubyi*).

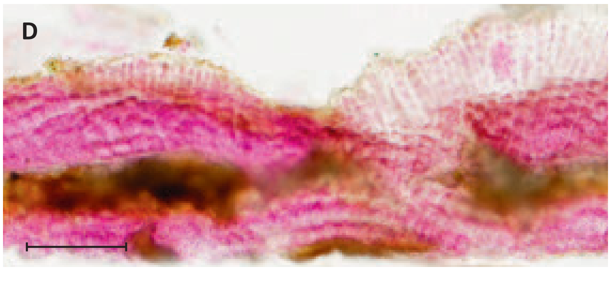


A: *Peyssonnelia dubyi*. Crust with a margin of lobes and white patches of calcification, shining through the crust, visible with dissection microscope. Tønneberg Banke, 14.5 m, 27.8.2013. Scale 1 mm. Photo by S. Lundsteen.

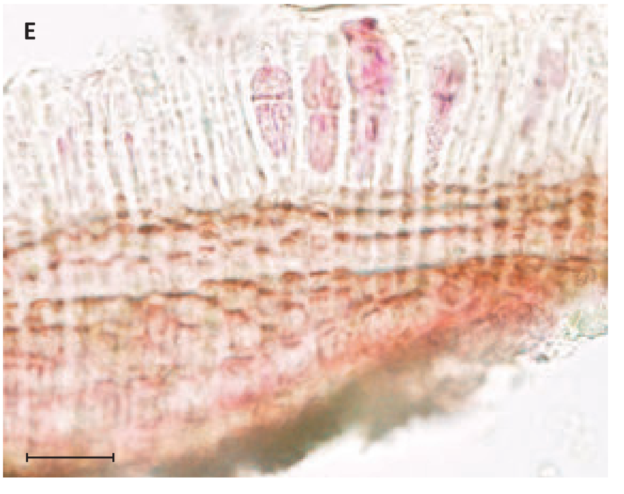


B: *Peyssonnelia dubyi.* Basal layer of radiating filaments. Kims Top, 14.5 m, 17.8.1994. Scale 50 µm.

C: *Peyssonnelia dubyi.* Upright filaments with branching where new cells are cut off by oblique walls. (arrow). Store Middelgrund, 18 m, 20.8.2015. Scale 20 µm. Photo by S. Lundsteen.



D: *Peyssonnelia dubyi.* Overgrown crust of several layers and nemathecia on top of the upper layer. Tile works, Helligsø, 3.5 m, 22.8.2000. Scale 100 µm. Leg.: J. Deding.



E: *Peyssonnelia dubyi.* Nemathecium of uniseriate filaments and cruciate tetrasporangia. Herthas Flak, 20 m, 2.2.1996. Scale 50 µm.

Order: Plocamiales · Family: Plocamiaceae

Plocamium lyngbyanum

Kützing

Lyngbye's Cock's Comb

Appearance: Rose to reddish brown complanate frond with a compact consistency, up to 7.5-10 cm in height. The lower branches are up to 1 mm wide. The main axis has alternating rows of unilateral branches. In each row there are 2-5 branches, the lowest is unbranched and resembles a spine. The youngest series of branches are on the adaxial side of the carrying branch, they are slightly curved and clearly pointed.

Structure: Uniaxial syntagma, with an apical cell which is partitioned transversely by an oblique wall. The axial cells are only visible just below the apical cell. Soon periaxial cells form, divide and develop a cortex of small cells. In older branches there are large medullary cells covered by small cortical cells.

Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Antheridia form a layer of colourless cells on the youngest branches, but they are not observed in the alga from Danish waters. Gonimoblasts are spherical and develop scattered at the margin of the thalli. Tetrasporangia are embedded in two alternating rows in special flat branchlets (stichidia). These have a pair of projecting opposite branches and are apical or replace the outermost branchlets. The tetrasporangia are zonate approximately 60 µm in length.

Seasonal variation: Perennial, collected in January-February and June-October with mature gonimoblasts and tetrasporangia in August.

Habitat: On boulders and epiphytic on Stalked Leaf Bearer (*Phyllophora pseudoceranoides*), Black Siphon Weed (*Vertebrata fucoides*) and stipes of Kelp (*Laminaria* sp.), 14.5-19 m depth. In older collections with dredge to 27 m depth.

A: *Plocamium lyngbyanum*. Complanate alga with unilateral branches. Scale 2 cm. A-B, E: Kims Top, 16 m, 17.8.1994.

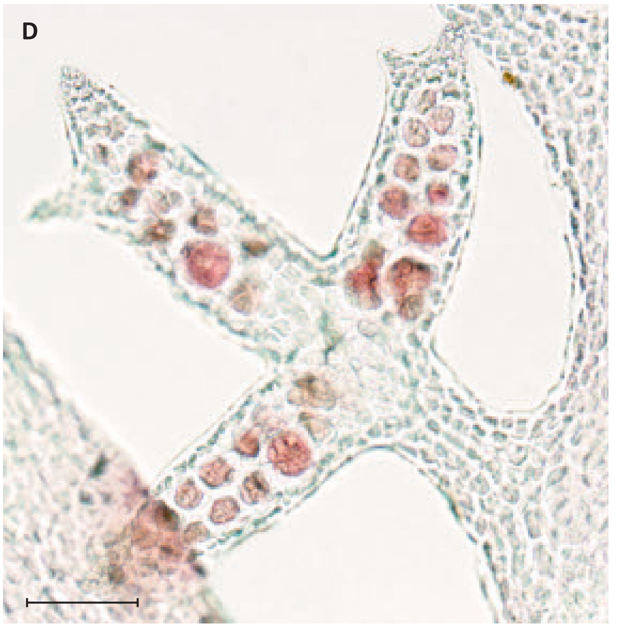
B: *Plocamium lyngbyanum*. Branching, alternating rows of unilateral branches (magnified part of figure A).
Scale 1 cm.

Resembles: The branched stichidia are the most reliable character to distinguish Lyngbye's Cock's Comb (*P. lyngbyanum*) from Cartilaginous Cock's Comb (*P. cartilagineum* (Linnaeus) P.S.Dixon), as this has unbranched stichidia.

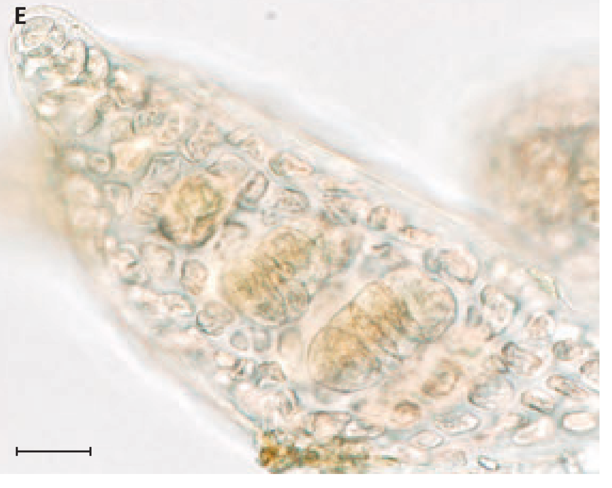
Comment: In the Danish checklists of Christensen et al. (1985) and Nielsen (2005a), *Plocamium* from Danish waters are referred to *P. cartilagineum*. Genetic investigations by Cremades et al. (2011) and Saunders & Lehmkuhl (2005) showed that *P. cartilagineum* as previously understood included several species.

C: *Plocamium lyngbyanum*. Three unilateral branches above a multicellular basal spine. Kims Top, 14.5 m, 4.2.1996. Scale 50 µm.

References: Christensen et al. (1985), Cremades et al. (2011), Nielsen (2005a), Saunders & Lehmkuhl (2005, EUR 1, *P. cartilagineum*), Rosenvinge (1931, *P. coccineum*).



D: *Plocamium lyngbyanum*. Stichidium with tetrasporangia. Rubjerg Knude, Lønstrup, 8 m, 4.8.1904. Scale 100 µm. Leg.: Rosenvinge.



E: *Plocamium lyngbyanum*. Stichidium with zonate tetrasporangia, optical transverse section. Scale 20 µm.

Order: Rhodymeniales · Family: Champiaceae

Chylocladia verticillata

(Lightfoot) Bliding

Juicy Whorl Weed

Appearance: Thalli with relatively thick, hollow terete branches that have constrictions at frequent intervals, up to 26 cm in height. They appear transparent, bright red to flesh coloured or yellow-green. There is a distinct main axis with branches on all sides, scattered, opposite or sometimes in a whorl with branches of unequal length. Branches are repeatedly branched, 0.5-3 mm wide. Branches arise at or slightly above the constrictions. The alga has a small attachment disc at the base.

Structure: Multiaxial syntagma a hollow thallus. There is a medulla of thin, longitudinal filaments that are sparsely branched and have small spherical gland cells. Within the constrictions the cavity is interrupted by separating walls. These consist of a monostromatic cell layer and are connected to the longitudinal filaments. The surface of the fronds consists of two cell layers, one of relatively large cells in part covered with an outer layer of small cells. The outer cell wall is fairly thick.

Reproduction: Isomorphic dioecious gametophytes and tetrasporophyte. Antheridia form in small branch systems which develop from surface cells in whorls around the constrictions of the branches. The gonimocarps form small warts, also around the constrictions of branches. Tetrahedrally divided tetrasporangia are scattered between surface cells in the youngest branches.

Seasonal variation: Well-developed individuals collected in May-October, and young specimens 1 cm in height in March, September and October. Antheridia recorded in August, gonimocarps in July-August and tetrasporangia in August.

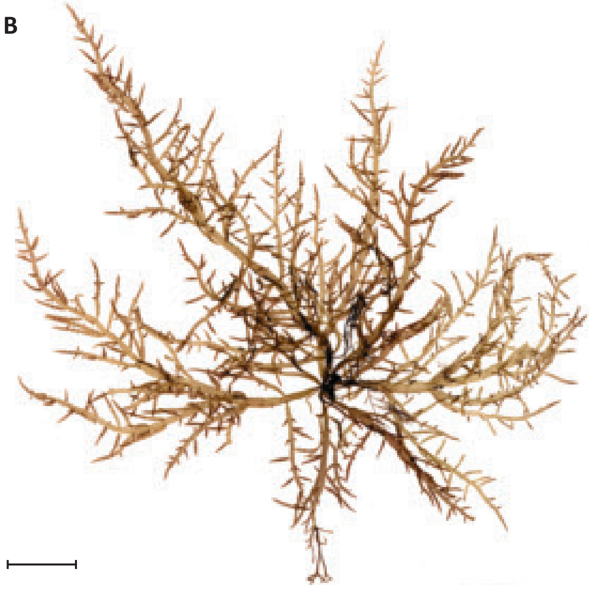
Habitat: On solid substratum and epiphytic on other algae at stone reefs, 1.5-18 m depth.

References: Irvine & Guiry (1983), Rosenvinge (1931, *C. kaliformis*).

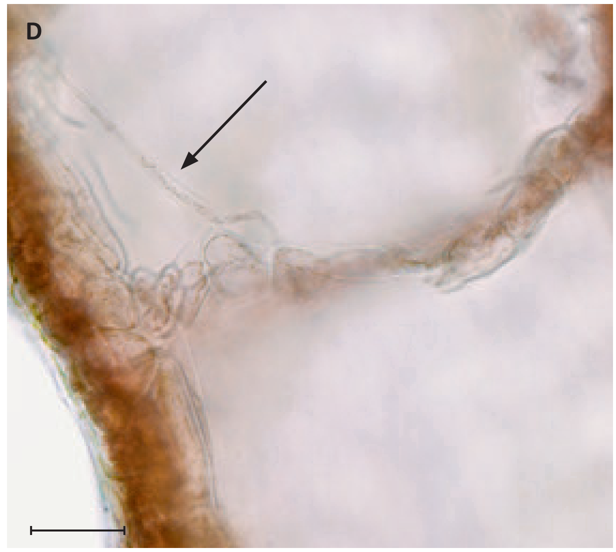
A

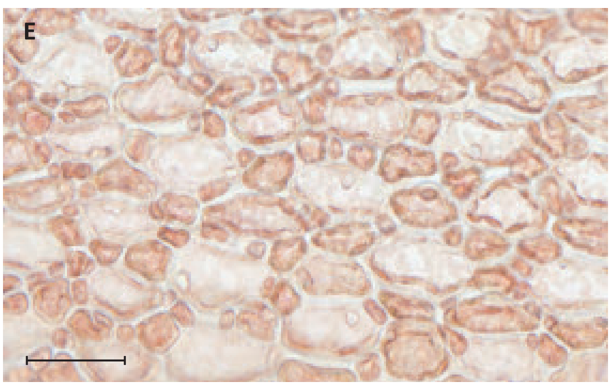
A: *Chylocladia verticillata*. Red female gametophyte, many whorls of branches. Tile works, Helligsø, drift, 12.9.1972. Scale 2 cm.

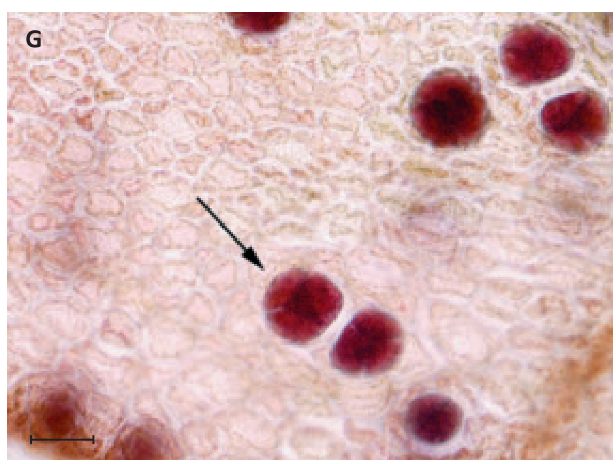
B



B: *Chylocladia verticillata*. Bright, flesh-coloured alga, the apical part of branches dark of tetrasporangia. Outside Hygum Church, Geller Odde, 3.5 m, 23.8.2000. Scale 2 cm.







C: *Chylocladia verticillata*. Apex. Branch with constrictions, longitudinal filaments and separating walls. Optical longitudinal section. Scale 100 µm. C-G: Helligsø, 6 m, 30.8.2016. Leg.: R. Frederiksen.

D: *Chylocladia verticillata*. Monostromatic separating wall connected to the outer wall of the branch and to the longitudinal filaments (arrow). Scale 100 µm.

E: *Chylocladia verticillata*. Surface of large cells in part covered by small cells. Scale 50 µm.

F: *Chylocladia verticillata*. Spherical gonimocarps. Scale 200 µm.

G: *Chylocladia verticillata*. Tetrahedrally divided tetrasporangia (arrow) scattered among surface cells. Scale 50 µm.

Family: Lomentariaceae

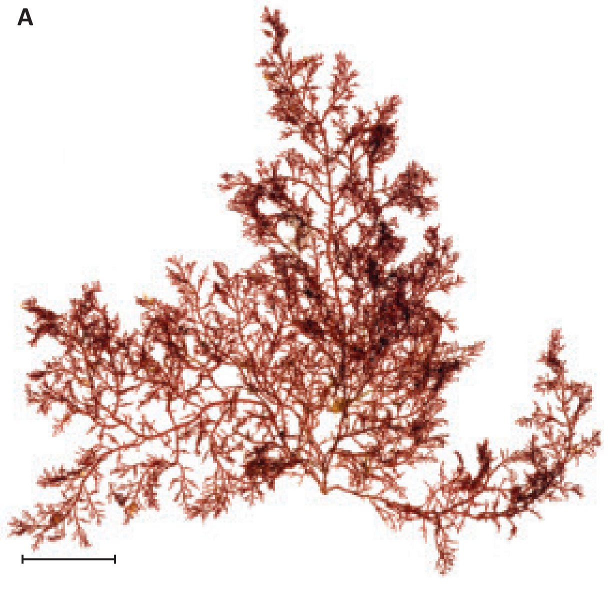
Lomentaria clavellosa

(Lightfoot ex Turner) Gaillon

Club Bead-weed

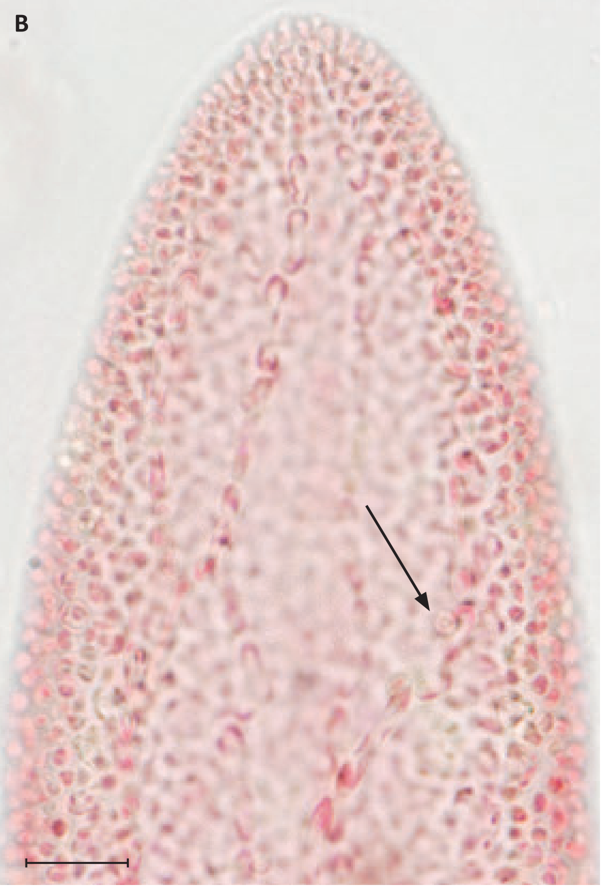
Appearance: Delicate very smooth rose to bright brick-red thalli in part tubular. Mostly 5-10 cm in height, but might be up to 18 cm. There is a distinct main axis, 0.5-1 mm wide, which has a small attachment disc at the base. Branches mainly scattered on all sides, but sometimes opposite and may be distichous so part of the thallus becomes complanate. The branches are terete and hollow but sometimes compressed and frequently with a narrow base.

Structure: Multiaxial syntagma, with a medulla of longitudinal sparsely branched filaments, consisting of narrow cylindrical cells and with small, spherical gland cells. Medullary filaments are close together at the base of the branches, otherwise with a mutual distance. The cortex consists of two cell layers, one layer of large cells in part covered by a layer of small cells.



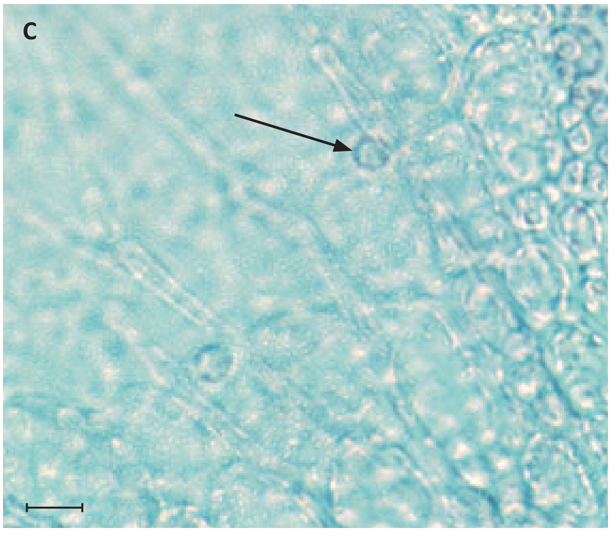
A: *Lomentaria clavellosa*. Distinct main axis with dense branches, repeatedly branched. Herthas Flak, 15 m, 28.8.1993. Scale 2 cm.

Reproduction: Isomorphic gametophytes and tetrasporophyte. Antheridia are pale surface cells in special, irregularly formed branchlets. Gonimoblasts develop in flask-shaped pericarps with a prominent pore. Gametophytes are commonly dioecious, but individuals with both antheridial branchlets and gonimocarps occasionally observed. On the tetrasporophyte tetrahedrally divided tetrasporangia occur in groups, embedded in the cortex in small cavities in the youngest branches.

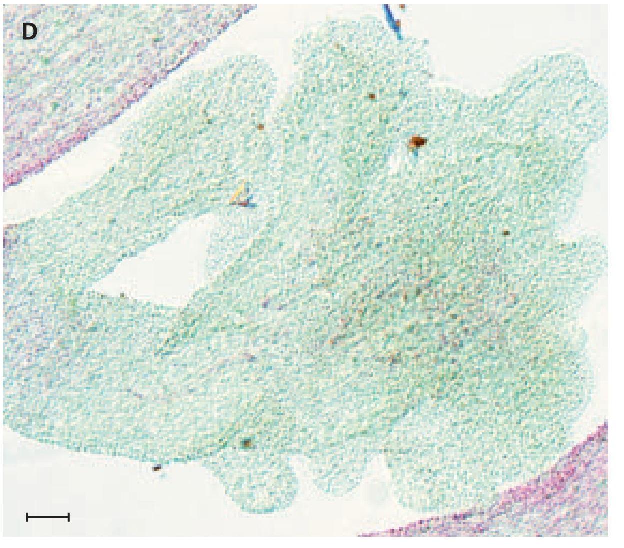


B: *Lomentaria clavellosa*. Apex, several apical cells, medulla of longitudinal filaments with gland cell (arrow) and cortex of small cells. Scale 50 µm. B, D-F: Munkegrunde, 13 m, 4.8.1994.

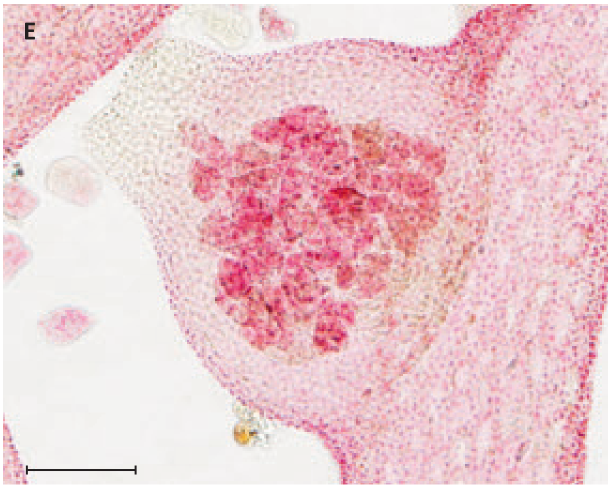
Seasonal variation: A few 2.5 mm in height individuals with basal discs on a hydroid collected in February. Well-developed thalli collected from the end of April to October. Antheridia and tetrasporangia recorded in June-August and gonimocarps in July-August.
Habitat: On solid substratum, on other algae and hydroids at stone reefs, 1.5-22 m depth. In older collections by dredge to 31 m depth.
Resembles: Very small complanate specimens are difficult to distinguish from Orkney Bead-weed (*L. orcadensis*).
References: Irvine & Guiry (1983), Rosenvinge (1931).



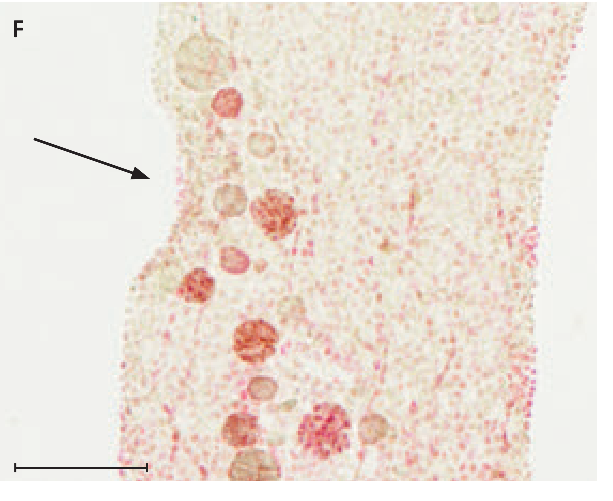
C: *Lomentaria clavellosa.* Medullary filaments of long cylindrical cells with gland cells (arrow), optical longitudinal section. Boblerev, Hirsholm, 7 m, 18.8.2004. Scale 10 µm.



D: *Lomentaria clavellosa.* Male branchlet with antheridia. Scale 100 µm.



E: *Lomentaria clavellosa.* Gonimoblast in pericarp. Scale 100 µm.



F: *Lomentaria clavellosa.* Tetrasporangia in a cavity (arrow). Scale 100 µm.

Lomentaria orcadensis

(Harvey) Collins

Orkney Bead-weed

Appearance: Lanceolate, complanate, rose coloured blades with only a single generation of new blades from the edge of older blades. The alga is mostly a few centimetres in height and 4 mm wide but may be up to 4 cm in height.

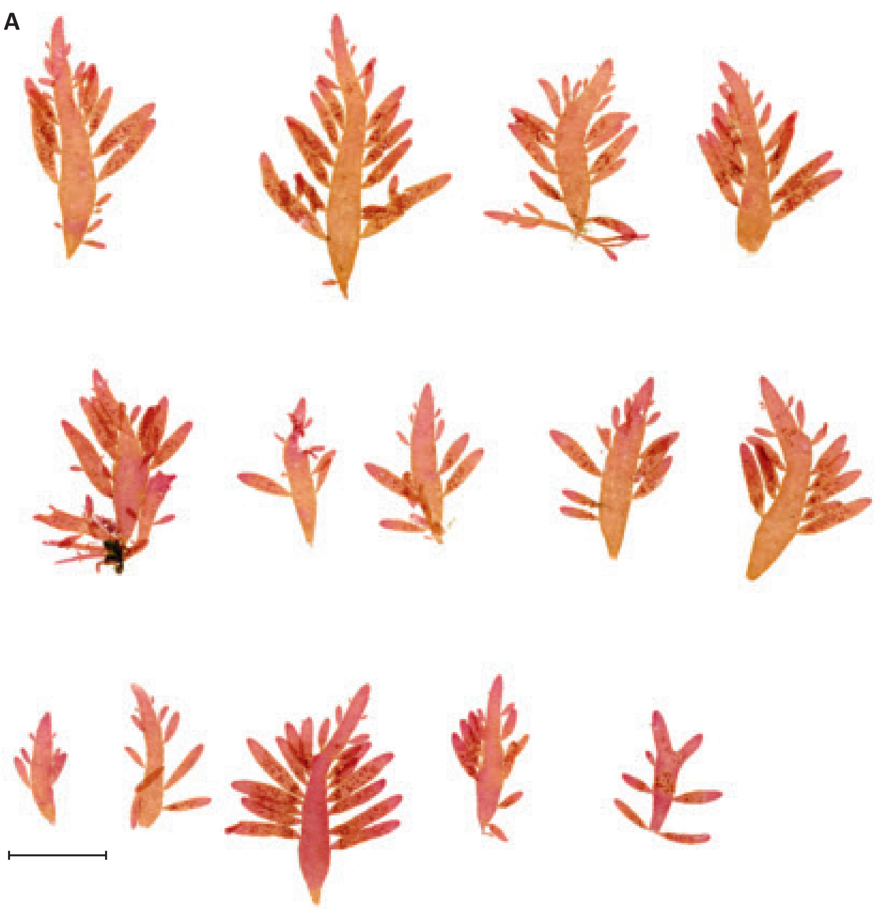
Structure: Multiaxial syntagma, the cortex consists of two cell layers. The outer small cortical cells only in part cover the larger cells below.

Reproduction: Only tetrasporophytes observed in Danish waters. The tetrahedrally divided tetrasporangia are embedded in the cortex in small cavities in the youngest blades.

Seasonal variation: Collected from end of May to end of August. Tetrasporangia recorded in June-August.

Habitat: On solid substratum, other algae and hydroids at stone reefs, 8-22.5 m depth.

References: Irvine & Guiry (1983), Rosenvinge (1931, *L. rosea*), Svedelius (1937, *L. rosea*).



A: *Lomentaria orcadensis*. Lanceolate blades branched from the edge. Dark spots of tetrasporangia in the branches. Nordvest Revet, Græsholmen, Hirsholmene, 4.7.1977. Leg.: H. Nielsen. Scale 1 cm.

Identification key to genera of Rhodophyta – Red algae

In a few cases, identification goes to family, tribe or species

1a.	Upright thallus	2
1b.	Crustose thallus	101
2a.	Not calcified algae	3
2b.	Calcified algae (form air bubbles after addition of acid)	99
3a.	Microscopic alga < 1-2 mm	4
3b.	Larger alga > 1-2 mm	19
4a.	Filamentous thallus	5
4b.	Disc-shaped, wart-like or membranous thallus	15
5a.	Unbranched filaments. Each cell with a stellate plastid	*Erythrotrichia*
5b.	Branched filaments	6
6a.	Grow into calcified material (shells of molluscs and barnacles, calcified worm tubes, and calcified red algae)	Conchocelis
6b.	Does not grow into calcified material	7
7a.	A single plastid pr. cell	8
7b.	Several plastids pr. cell	12
8a.	The plastid, plate-shaped along the cell wall	9
8b.	The plastid, star-shaped and centrally placed	10
9a.	Without pyrenoids. Male gametophyte with androphor, a special long hyalin cell with 2-6 antheridia	*Kylinia*
9b.	With pyrenoids	*Colaconema*
10a.	Cell walls unusual thick (4-8 µm), no pit connections in transverse walls	11
10b.	The cell walls not unusual thick, pit connections between cells (appear like small dark points in the middle of transverse walls), easiest to see in fixed or acid treated material	*Acrochaetium*
11a.	Plastids red	*Stylonema*
11b.	Plastids blue-green	*Chroodactylon*
12a.[7]	Branched filaments in the wall (the tough, chitinous perisarc) of hydroids. Cells cylindrical or with irregular indentations, few ribbon-shaped or irregularly formed plastids per cell	*Rubrointrusa*
12b.	Sparsely branched upright filaments of cylindrical cells	13

13a.	A few long-stretched to spiral-shaped plastids per cell, without pyrenoids	*Grania*
13b.	Many disc-shaped plastids per cell	14
14a.	Basal system, a monostromatic disc	*Meiodiscus*
14b.	Basal system, branched filaments	*Rhodochorton*
15a.(4)	Irregular warts or clumps on other algae	16
15b.	Membranous or disc-shaped	17
16a.	Irregular shape on *Coccotylus*	*Coccotylus hartzii*
16b.	Rounded shape on *Rhodomela*	*Harveyella*
17a.	Upright membrane of small cells, 4-7 µm wide, each with a plastid without pyrenoid. Small monostromatic disc-shaped young algae vault up like bladders which splits open	*Porphyropsis*
17b.	Epiphytic disc	18
18a.	Approximately circular with forked marginal cells	*Sahlingia*
18b.	Irregular with a margin of mutually free short filaments	*Erythrocladia*
19a.(3)	The thallus consists of blades or has sections which look like blades	20
19b.	The thallus does not have flat blade-like sections, branches which are oval in transverse section might occur	41
20a.	The thallus without branches, consists of a rounded or ribbon-shaped blade with regular edges	21
20b.	The thallus with branches	26
21a.	The thallus membranous without veins, mono- or seldom distromatic	22
21b.	The thallus coarser or has veins	23
22a.	Large cells, star-shaped plastids with pyrenoid	Bangiaceae (*Neopyropia*, *Porphyra*, *Pyropia*, *Wildemania*)
22b.	Small cells, 4-7 µm wide, lobed plastids without pyrenoid	*Porphyropsis*
23a.	With coarse veins	*Delesseria*
23b.	Without veins	24
24a.	Oval blade, 1-2 cm in length on a short stipe	*Erythrodermis*
24b.	Mostly larger without stipe, may have a gradual transition to a basal part of the blade appearing like a stipe	25
25a.	Rounded thick blades, easily split or torn apart. The basal part narrow and all blades arise from a basal crust. The thallus dark red, not transparent. Filamentous medulla, surface cells c. 5 µm wide	*Dilsea*
25b.	Blades, oval, ribbon-shaped or triangular. The thallus red and transparent. Medulla of large, rounded cells, surface cells angular, 8-15 µm wide	*Palmaria*

26a.[20]	Elongate lanceolate blade 30-60 μm in length and 2-4 cm in width very smooth with a firm consistency, irregular gradually pointed proliferations from the edge and surface of the blade	*Grateloupia turuturu*
26b.	No proliferations from the edge or surface of blade	27
27a.	The thallus with indented margin	28
27b.	The thallus with regular margin	30
28a.	The blades without veines, coarsely indented margin	*Odonthalia*
28b.	The blades with veines not coarsely indented margin	29
29a.	Sections of the blades equally wide (few mm), main vein distinct, lateral veins only visible through a magnifying glass	*Membranoptera*
29b.	Blades with lobes or irregular dentate margin, lateral veins visible with an unaided eye	*Phycodrys*
30a.	The blades with midribbs or microscopical veins. Young blades arise from the midrib of older blades	31
30b.	The blades without veines	32
31a.	The alga only few centimetres in height with microscopic veins. The oval blades bluish purple	*Apoglossum*
31b.	Larger alga with midribs and veins. Blades lanceolate clear red	*Delesseria*
32a.	The thallus consists of elongate triangular or ribbon-shaped blades, 0.5-1.5 cm in width. The branching occurs from the upper part of the blades which are evenly cut at the bases	*Phyllophora crispa*
32b.	Different	33
33a.	The blades on a terete stipe	34
33b.	Without stipe or with a gradual transition to a stipe looking part in the lowest blade	35
34a.	The blades triangular to wedge-shaped red to brownish red	*Coccotylus brodiei, C. truncatus*
34b.	The blades triangular to fan-shaped. The distal part commonly split in several lobes, which become narrower towards the apex, red to bluish red	*Phyllophora pseudoceranoides*
35a.	Delicate centimetre large alga	36
35b.	Coarser alga	38
36a.	Lanceolate blades, sparsely branched with young blades from the edge of older blades	*Lomentaria orcadensis*
36b.	The outline of the thallus fan-shaped, repeatedly branched	37
37a.	Regularly forked membranous multilayered thallus	*Rhodophyllis*
37b.	Branches unilateral and getting narrower towards the apex	*Euthora*

38a.	Shape of blades oval, triangular, or ribbon-shaped. New blades from the edge of older blades	*Palmaria*
38b.	Outline of blades triangular or fan-shaped. New blades not from the edge of older blades	39
39a.	The lower part of blades, appear commonly like a stipe	40
39b.	The thallus not particularly narrow at base, dark red with a regular surface. Deep water locality	*Callophyllis*
40a.	The thallus with in rolled margins, forked and typically irregularly curved with wart like outgrowth on the frond. Dark red to almost black	*Mastocarpus*
40b.	The blades regularly pseudodichotomous divided. The colour varies from dark red in shaded localities to yellow-green in localities exposed to bright light	*Chondrus*
41a.[(19)]	Unbranched filaments, uni- or multiseriate	42
41b.	Branched thallus	43
42a.	Several centimetres long filaments on boulders in the splash zone	*Bangia*
42b.	0.2-3 cm in length epiphytic filaments, sublittoral, rarely on rocks	*Erythrotrichia*
43a.	Delicate bushes with uniseriate branches, the basal branches might be covered by cortical filaments	44
43b.	Construction more elaborate, branches with several cells, seen in transverse section	56
44a.	Pseudodichotomously branched already from the base	45
44b.	Lateral branched best seen at the base	46
45a.	The thallus soft, the apical cell almost globular, branches constricted at crosswalls	*Griffithsia*
45b.	The thallus stiff, the apical cell conical, branches not constricted at crosswalls	*Halurus*
46a.	With opposite branches	47
46b.	With scattered and no opposite branches	51
47a.	Opposite branches only occasionally. Appears as creeping filaments with upright branches up to a centimetre in height or as a tuft without distinct main axes	*Spermothamnion*
47b.	Most of 1. order branches opposite	48
48a.	Branching mainly in a single plane, the youngest or all parts complanate	49
48b.	Branches in more directions, not complanate	50

49a.	Branches of last order unilateral on the adaxial side of the carrying branch. Gland cells occur and only cover a single vegetative cell. The thalli pink or light red-brown	*Pterothamnion*
49b.	Branches of last order opposite, no gland cells	*Antithamnionella*
50a.	Basal cell of branches short, almost isodiametric. Gland cells on small branches, each covers 2-3 vegetative cells	*Antithamnion*
50b.	Basal cell of branches only slightly shorter than other cells of the branches. Branches of last order may arise from the ad- or the abaxial side of the carrying branch. Gland cells on ordinary branches, each on a single vegetative cell	S*cagelothamnion*
51a.[46]	Uprights arise from creeping filaments with attachment pads, or appear like a tuft without a distinct main axes	52
51b.	The thallus with distinct main axes	53
52a.	Cells short, 1-2.5 times as long as wide. Gland cells apparently outside transverse walls. Only scattered branches	*Bonnemaisonia hamifera* (tetrasporophyte)
52b.	Cells long, 4-5 times as long as wide. No gland cells. Opposite branches occur	*Spermothamnion*
53a.	Branching mainly in a single plane. Each cell in the 1. and 2. orders branches have regularly alternating distichous branches. The algae are pink to bright brownish red	*Compsothamnion*
53b.	Branches on all sides	54
54a.	Vegetative cells with several nuclei	*Callithamnion*
54b.	Vegetative cells with a single nucleus	55
55a.	The upper part of the thallus appears dichotomous branched. Sporangia in rows in special branches	*Seirospora*
55b.	Main axes distinct to the apex, frequently zigzag formed with alternating branches	*Aglaothamnion*
56a.[43]	Thallus segmented, consists of equally shaped groups of cells, best seen in the apical part as the construction may be camouflaged by cortex in older part of the thallus	57
56b.	Thallus not segmented	67
57a.	Each segment consists of an axial cell surrounded by a whorl of smaller cells (cortical band), which covers the axial cells completely or in part	58
57b.	Each segment consists of an axial cell surrounded by a number of equally as high cells (periaxial cells)	59

58a.	The thallus dichotomous branched, occasionally with secondary lateral branches, constructed like the main branches	*Ceramium*
58b.	The thallus lateral branched. The main axes with uniseriate opposite branches	*Atractophora*
59a.	Fine uniseriate dichotomous divided trichoblasts or red branchlets with plastid	60
59b.	With or without colourless trichoblasts in the apical part	62
60a.	Permanent red trichoblasts, 7 periaxial cells, without cortex, tetrasporangia pairwise in ordinary branches in winter	*Vertebrata byssoides*
60b.	Red branchlets near the apex, with cortex, tetrasporangia in special carrot-shaped branchlets	61
61a.	Apical part complanate with distichous branches, 6-8 periaxial cells. In the lower part of the branchlets are the axial cells surrounded by periaxial cells, the apical part is uniseriate with relatively short cells.	*Heterosiphonia*
61b.	Apical part not complanate, with branches on all sides, 4 periaxial cells. Branchlets uniseriate with relatively long cells.	*Dasysiphonia*
62a.	Cortex well-developed, to or almost to the apex	63
62b.	Cortex not to the apex, or not present	65
63a.	Branches without an apical groove	*Rhodomela*
63b.	Branches rounded, with a small apical groove with trichoblasts	64
64a.	Thallus cartilaginous stiff, red-brown or faded to yellow-brown	*Osmundea*
64b.	Thallus soft, light purplish red or pale reddish brown	*Chondria*
65a.	Periaxial cells partitioned by secondary transverse walls (see close to the apex or in young branches). Tetrasporophytes with 2 sporangia per segment (winter fertile)	*Rhodomela*
65b.	Periaxial cells not partitioned by secondary transverse walls. Tetrasporophytes with a single sporangium per segment	66
66a.	Branches on all sides	Polysiphonieae (*Carradoriella*, *Leptosiphonia*, *Melanothamnus*, *Polysiphonia*, *Vertebrata*)
66b.	Branches distichous, complanate frond with regularly alternating branches from every second segment	*Symphyocladiella*
67a.[56]	Thalli with dichotomous branching	68
67b.	Thalli with lateral branches	74
68a.	Thalli soft or very smooth	69
68b.	Thalli with a firm consistency	72

69a.	Branches of an uneven thickness decreasing in width towards the apex. Outline almost like the antler of a deer	*Halarachnion*
69b.	Regularly branched	70
70a.	Thallus hollow, the surface consists of large pale cells and small pigmented cells	*Scinaia*
70b.	Thallus not hollow, the surface consists of uniseriate assimilating filaments.	71
71a.	Medullary filaments not kept together by narrow filaments. Each cell with a stellate plastid. Growth in shallow water.	*Nemalion*
71b.	Medullary filaments kept together by narrow filaments. Deep water locality	*Tsengia*
72a.	Thalli horny stiff, dark almost black. Frequently branched, branches commonly slightly curved, dichotomous as well as lateral branches occur	*Ahnfeltia*
72b.	Branches straight, branching regularly repeated	73
73a.	Thallus dark almost black with acute branch angles. Basal system of short branches (haptera)	*Furcellaria*
73b.	Thallus vine-red with open branch angles. (See the colour in transparent light). Disc-shaped base	*Polyides*
74a.(67)	Branches in a single plane, the thallus or the young parts complanate	75
74b.	Branches on all sides, thallus not complanate	81
75a.	Thallus compact cartilaginous, apex of branches with a small groove	*Osmundea*
75b.	Thallus compact not cartilaginous,	76
76a.	Thallus dark red, almost black	77
76b.	Thallus bright red-rose	78
77a.	Branches of last order without cortex. Axial cells pyriform	*Plumaria*
77b.	Branches of last order with cortex. Opposite branches unequal long	*Ptilota*
78a.	Main axes with unilateral branches (comb-shaped branching)	79
78b.	Main axes with scattered or opposite branches	80
79a.	Much branched, up to approximately 15 cm in height	*Plocamium*
79b.	A few centimetres, the outline fan-shaped	*Euthora*
80a.	Main axes with lateral branches. The youngest branchlets distichous with short cells and a pointed apical cell. Tetrasporangia in special carrot-shaped branchlets	*Heterosiphonia*
80b.	Opposite branches. The lateral branches of unequal length, alternating so the short ones change from right to left	*Bonnemaisonia asparagoides*

81a.[74]	Flat main branches. Thallus very smooth with a firm consistency, much branched with a distinct main axes and lateral branches of several orders, on all sides, and gradually pointed. Multiaxial syntagma	*Grateloupia subpectinata*
81b.	Terete branches	82
82a.	Thallus soft or very smooth	83
82b.	Thallus of a compact consistency	91
83a.	Repeated irregularly dichotomous branching	*Halarachnion*
83b.	Lateral branches	84
84a.	Main axes with many uniseriate branchlets	85
84b.	Main axes without many uniseriate branchlets	86
85a.	Uniseriate branchlets are scattered and pseudodichotomously branched	*Dasya*
85b.	Uniseriate branchlets are in whorls and with opposite branchlets	*Atractophora*
86a.	Multiaxial syntagma	87
86b.	Uniaxial syntagma	90
87a.	Surface of the thallus consists of dense assimilating filaments	88
87b.	Surface of the thallus consists of a cortex of small cells	89
88a.	Thallus much branched, main axis 0.1-3 mm wide. The assimilating filaments consist of small, rounded cells	*Helminthora*
88b.	Thallus sparsely branched; main axis 2-5 mm wide. The assimilating filaments terminate in a club-shaped cell, much larger than other cells	*Helminthocladia*
89a.	Delicate rose algae. Cortex of two cell layers with a layer of large cells only in part covered by minor cells. Medulla of longitudinal running filaments	*Lomentaria clavellosa*
89b.	Large very smooth algae, much branched with distinct main axes and gradually pointed branches in several orders. Cortex of dense cells. Medulla of mated filaments	*Grateloupia subpectinata*
90a.[86]	Thallus much branched on all sides. Branches constricted at base. Central axial cells only visible at the apex, otherwise covered by a confluent cortex of small cells	*Gloiosiphonia*
90b.	Thallus sparsely branched, consists of evenly thick branches. Central axial cells visible at a longer stretch of the branches, surrounded by 3-4 branches in a whorl from each of the axial cells	*Schmitzia*
91a.[82]	Thallus hollow with regular constrictions, inside which the cavity is interrupted by monostromatic separating walls	*Chylocladia*

91b.	Thallus without constrictions and separating walls, with scattered branches	92
92a.	Thallus sparsely branched, brownish red to yellow-green. A relatively short main axis 0.5-10 mm wide, with branches approximately equally as thick, mostly unbranched and longer than the main axes. Young branches with a single apical cell	*Dumontia*
92b.	Much branched or lateral branches shorter than the main axes	93
93a.	Distinct main axes, more robust than the lateral branches	94
93b.	Lateral branches not much different from the main axes	95
94a.	Unbranched downward curved branches at the base of the main axes. Lateral branches gradually pointed and sometimes terminate in spiral twisted tendrils. Well-developed cortex of rounded cells	*Cystoclonium*
94b.	Not special branches at the base, branches terminate in a small tuft of branchlets. Well-developed cortex of angular cells	*Rhodomela*
95a.	Thallus horny stiff, branches slightly curved or bent, dark wine-red to almost black. Both dichotomous and lateral branches	*Ahnfeltia*
95b.	Thallus not horny stiff	96
96a.	Branches pointed	97
96b.	Branches not pointed	98
97a.	Much branched on all sides. Lateral branches frequently terminate in tendrils	*Cystoclonium*
97b.	Sparsely branched almost uniformly thick uprights arise from a crustose base. Medulla of large cells, see transverse section. Gonimoblasts form warts on the branches	Gracilariaceae (*Gracilaria*, *Gracilariopsis*)
98a.	Truncate branches, terminate in a small groove	*Osmundea*
98b.	Terete main axes with lateral branchlets, 1-2 mm in length, and thick of reproductive structures. Winter form	*Delesseria*
99a.(2)	Branched thalli	100
99b.	Small clumps on *Corallina*	*Choreonema*
100a.	Lateral flat branches	*Corallina*
100b.	Pseudodichotomous terete branches	*Jania*
101a. (1)	Crusts without chalk	102
101b.	Calcified crusts (form air bubbles after addition of acid)	Crustose calcified red algae (Corallinaceae)
102a.	Epiphytic on leaves of eelgrass (*Zostera marina*). Polystromatic, basal layer with filaments of rectangular cells with cell fusions. Sori of tetrasporangia and multicellular paraphyses on the surface of the crusts	*Rhodophysema georgei*
102b.	On rock and other solid substratum	103

103a.	Dark red velvet like crust up to 300 µm thick, consists of dense upright filaments, which are easily separated by application of slight pressure	104
103b.	Thin paint-like covers or spots	105
104a.	Basal cells of the upright filaments large, (10-) 12.5-14 µm wide. Cell size decrease towards the surface	*Cruoria*
104b.	Basal cells of the upright filaments small, 5-9 µm wide. Cells only slightly smaller towards the surface	*Haemescharia*
105a.	Thallus brick-red, rhizoids on the underside and therefore loosely attached. Basal layer fan-shaped with upright filaments. At branching points are the first cells cut off by oblique walls, which turn in different directions. Vegetative cells with many plastids	*Peyssonnelia*
105b.	Without rhizoids, densely attached to the substratum	106
106a.	Thallus a compact pseudoparenchyma of relatively small cells, approximately 5 µm wide	107
106b.	Thallus consists of upright filaments, which are easily separated from each other by application of slight pressure	108
107a.	Red crust without cell fusions. Tetrasporangia in grooves (conceptacles)	*Hildenbrandia*
107b.	Bluish purple crust with cell fusions. Tetrasporangia form sori at the surface of the crusts	*Ahnfeltia* (tetrasporophyte)
108a.	Without basal layer	109
108b.	Pseudoparenchymatous basal layer	110
109a.	Upright filaments uniformly thick, 4.5-5.5 µm wide and consists of 25-35 cells. Tetrasporangia lateral on intercalary cells	*Plagiospora*
109b.	Upright filaments consist of a few cells. Tetrasporangia form rows in the upright filaments	*Erythrodermis* (tetrasporophyte)
110a.	Gland cells between few celled upright filaments. Basal layer without cell fusions and secondary pit connections	*Halarachnion* (tetrasporophyte)
110b.	Without gland cells	111
111a.	Several coalescent tissue layers beneath the original basal layer. Sori of tetrasporangia or bisporangia on the surface and irregular pits in the surface after spore release	*Fredericqia* (tetrasporophyte)
111b.	Basal layer with cell fusions, but without secondary pit connections	112
112a.	Paraphyses and cruciate tetrasporangia form sori on the surface of the crust	*Rhodophysema*
112b.	Scattered cruciate tetrasporangia are apical on upright filaments	*Gloiosiphonia* (tetrasporophyte)

Collection localities for Rhodophyta – Red algae

The maps with collection localities of the algae are based on information in the database of the algal herbarium, Natural History Museum of Denmark, which includes records of approximately 60,000 Danish seaweeds.

There is an old tradition in Denmark for collecting attached as well as drift algae, and both are maintained in the algal herbarium. Unfortunately, it is only possible to segregate between these records in some cases. The dots on the maps therefore show where the algae were collected and include both attached and drift algae.

There is a single map for each of the species. For species with a heteromorphic life history, such as species of *Acrochaetium* spp., *Bonnemaisonia asparagoides* and *Gloiosiphonia capillaris*, records of both generations are included in a single map.

There is no map for drift species which have only been collected once. This covers *Aglaothamnion sepositum*, *Callithamnion granulatum* and *Stylonema cornu-cervi*. Nor is there a map for *Jania rubens*, which was recently found.

A map is also missing for the recently introduced *Grateloupia turuturu* and for *Ceramium sungminbooi,* first recorded in Danish waters in 2016, and not recorded in the database.

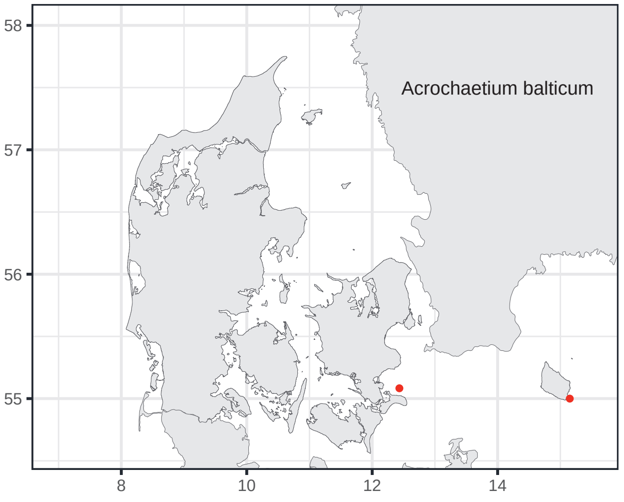
Additional remarks:

Chondria dasyphylla has only been collected attached in the western part of the Limfjord, at Hirtshals and Læsø. The species has been recorded as drift on beaches at Skagerrak and the Northern Kattegat.

Plumaria plumosa, the isolated record northeast of Møn is based on a small drifting individual (Rosenvinge, 1923-24 p. 356).

Polysiphonia stricta, the record outside Møn is based on an older collection by dredge at 27 m depth. The innermost localities towards the Baltic Sea where the species were collected at shallow water are the harbour of Copenhagen and Bagenkop Fiskerihavn, Langeland.

Ptilota gunneri, the collections from Lysegrund and Hesselø are from 1832. The species is only found drift in the Sound.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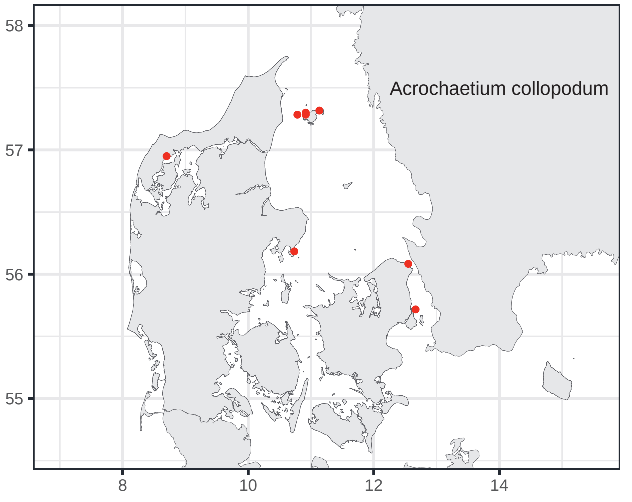
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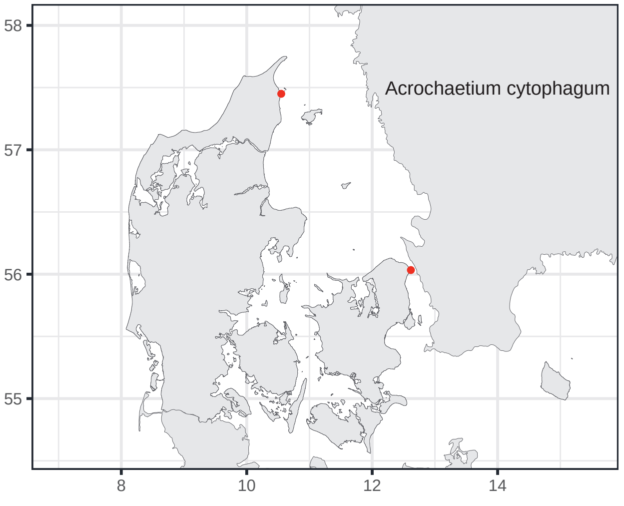
Acrochaetium cytophagum
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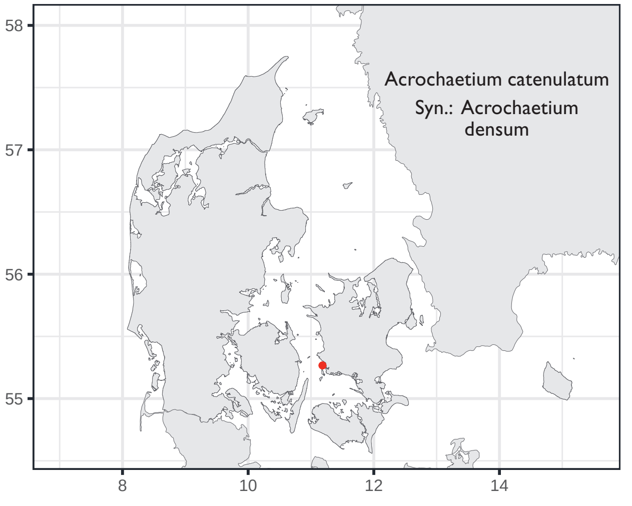
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Syn.: Acrochaetium densum
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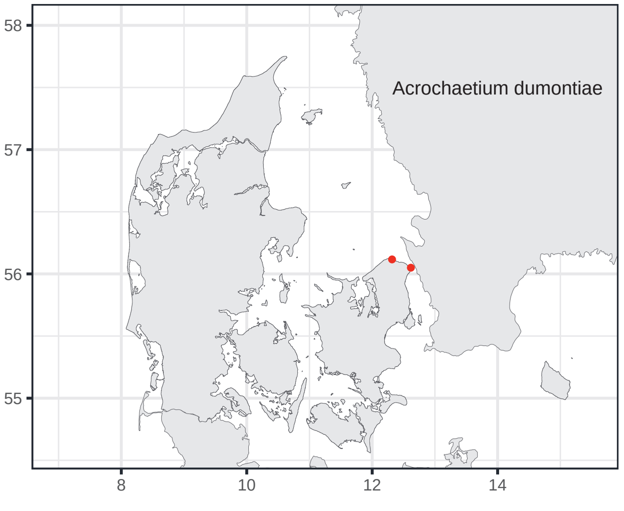
Acrochaetium dumontiae
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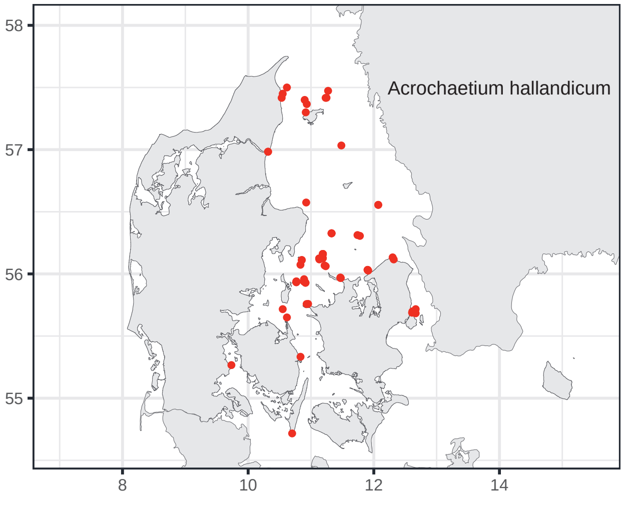
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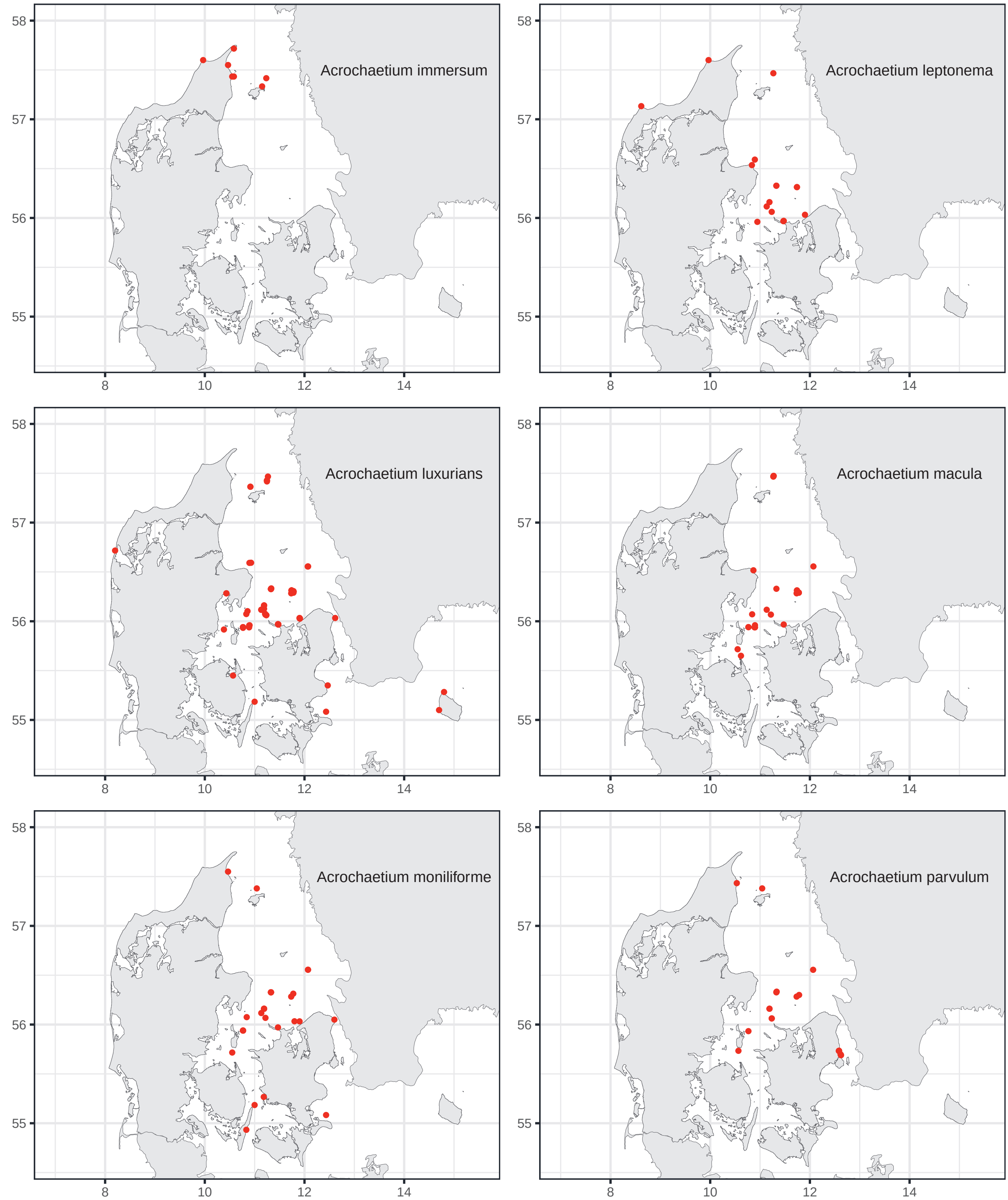
Acrochaetium immersum
Acrochaetium leptonema
Acrochaetium luxurians
Acrochaetium macula
Acrochaetium moniliforme
Acrochaetium parvulum
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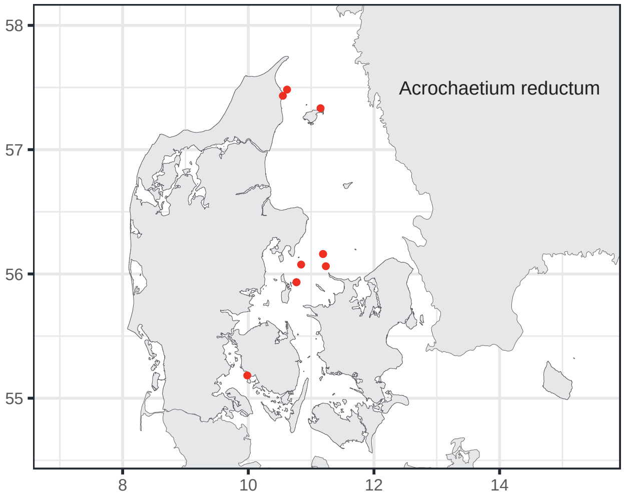
Acrochaetium reductum
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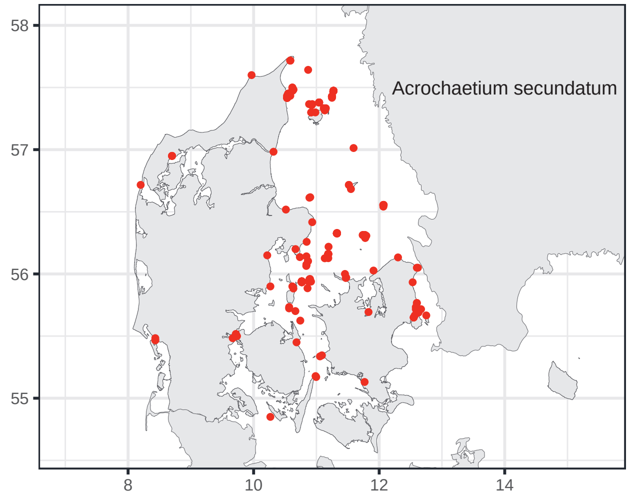
Acrochaetium secundatum
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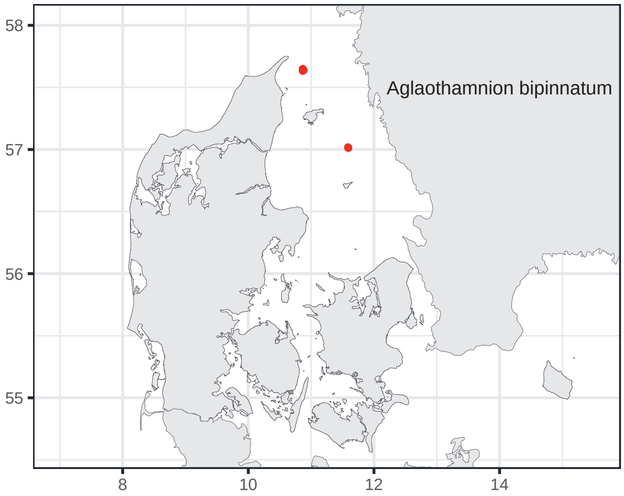
Aglaothamnion bipinnatum
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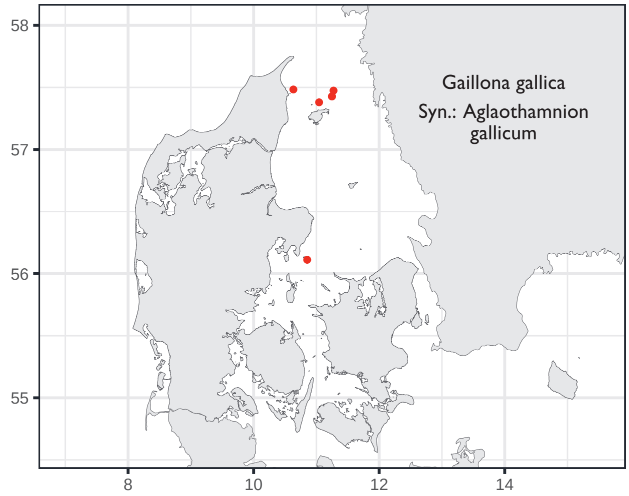
Gaillona gallica
Syn.: Aglaothamnion gallicum
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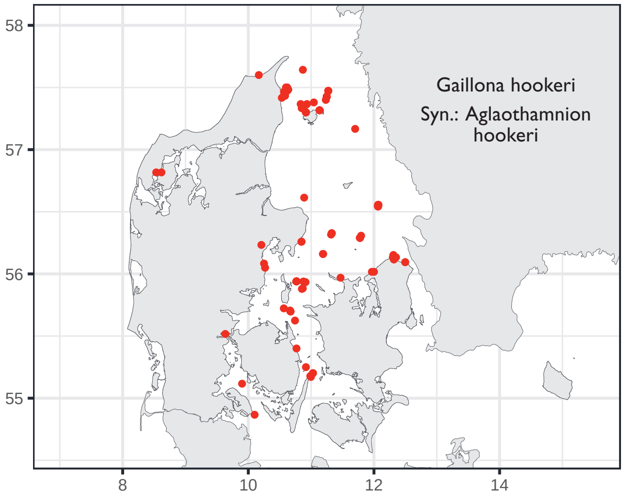
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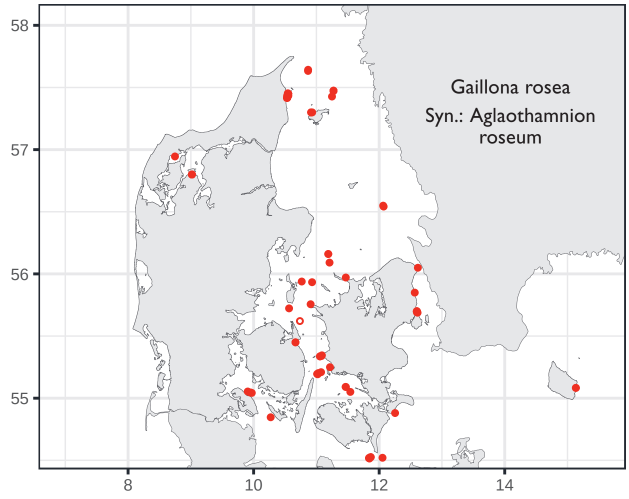
Gaillona rosea
Syn.: Aglaothamnion roseum
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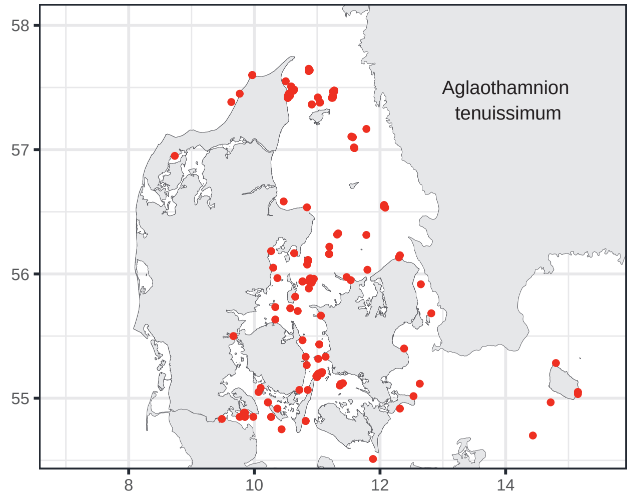
Aglaothamnion
tenuissimum
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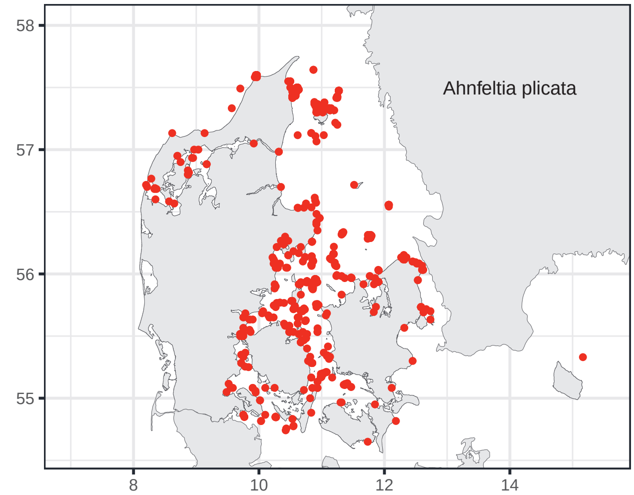
Ahnfeltia plicata
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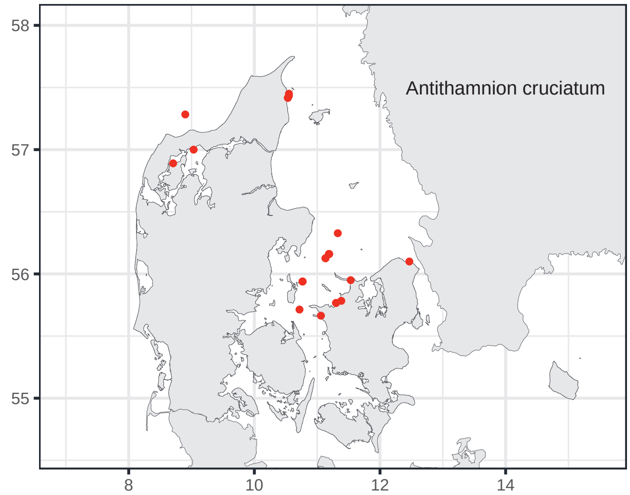
Antithamnion cruciatum
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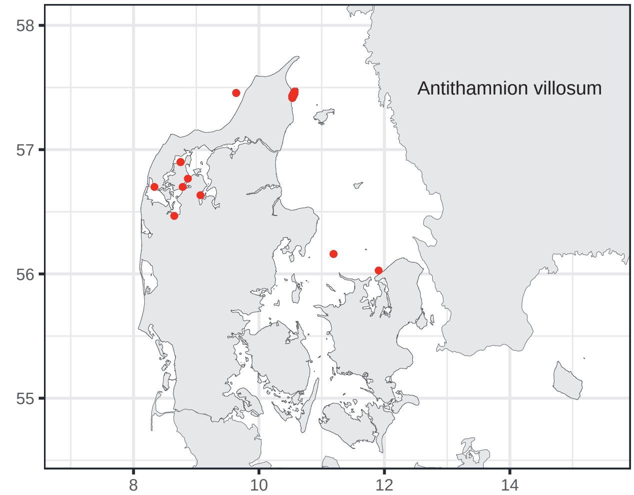
Antithamnion villosum
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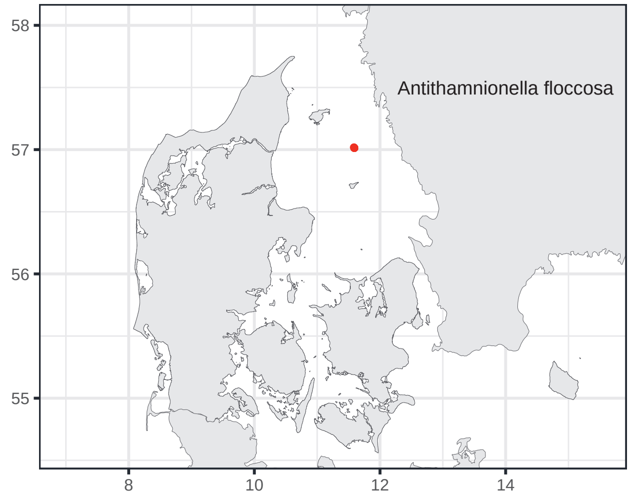
Antithamnionella floccosa
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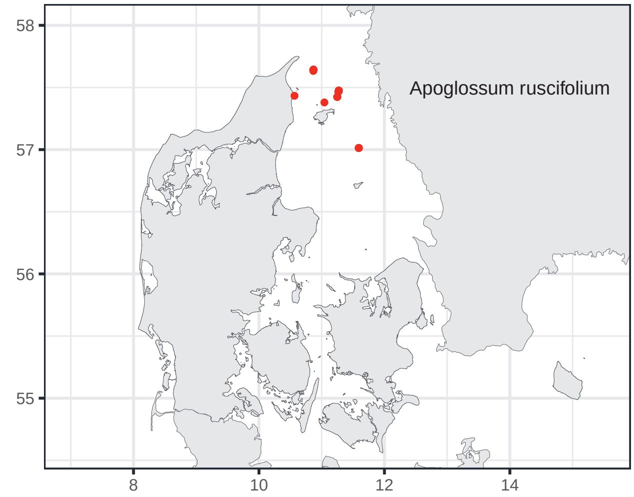
Apoglossum ruscifolium
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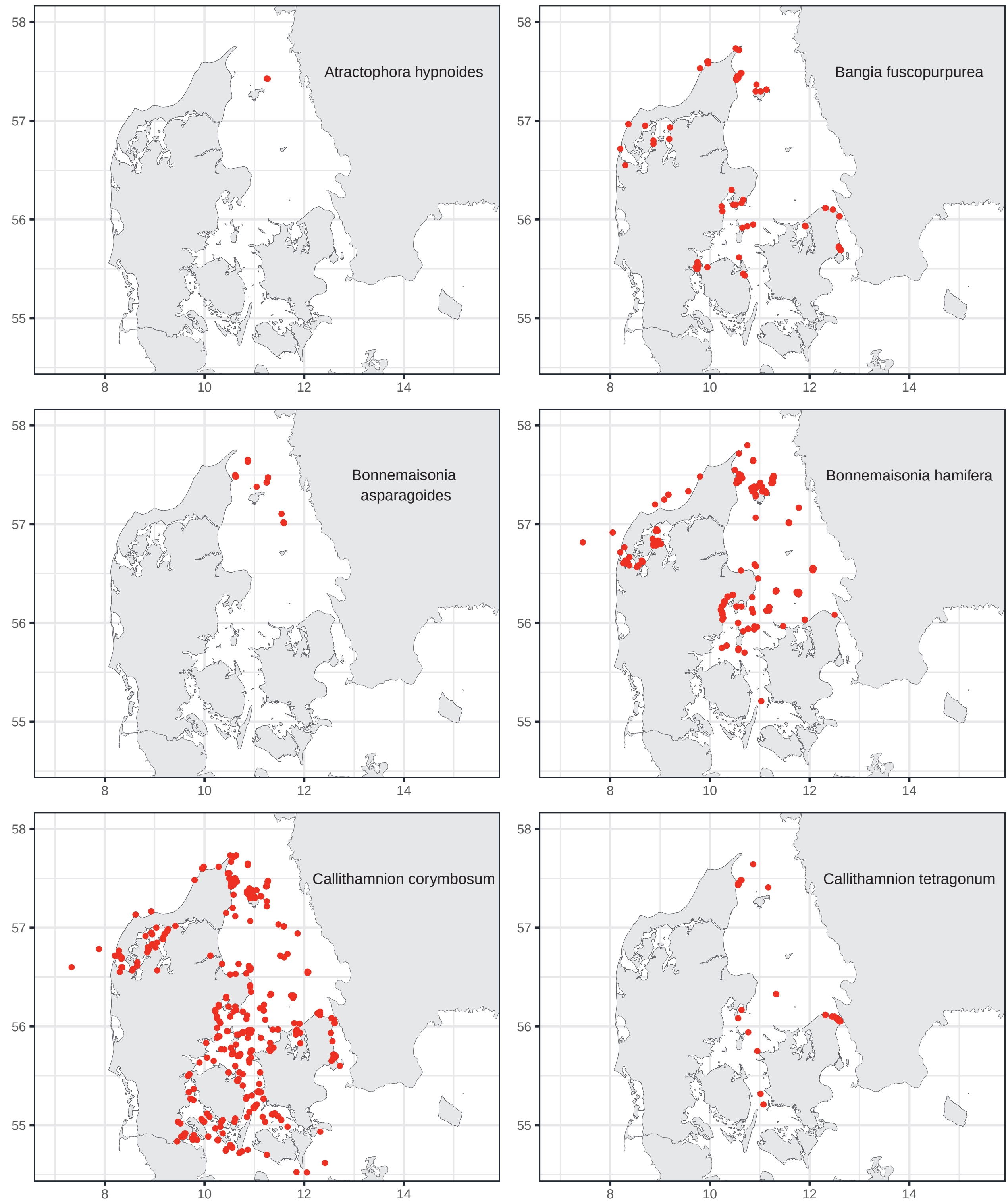
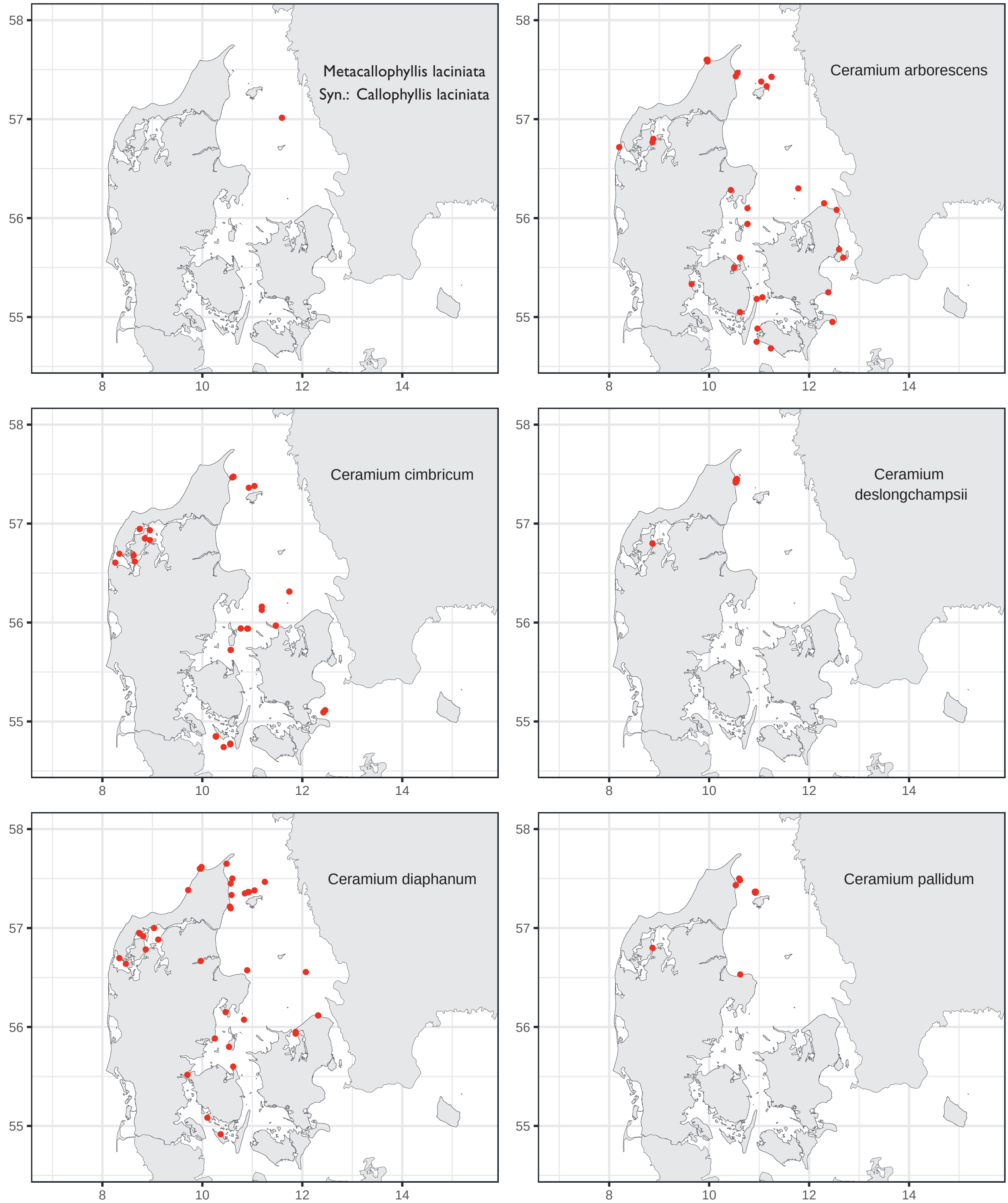
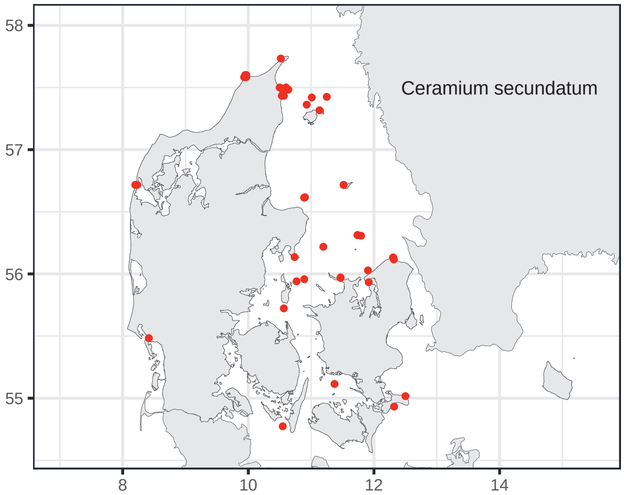

Atractophora hypnoides
Bangia fuscopurpurea
Bonnemaisonia asparagoides
Bonnemaisonia hamifera
Callithamnion corymbosum
Callithamnion tetragonum


Metacallophyllis laciniata
Syn.: Callophyllis laciniata
Ceramium arborescens
Ceramium cimbricum
Ceramium
deslongchampsii
Ceramium diaphanum
Ceramium pallidum


Ceramium secundatum
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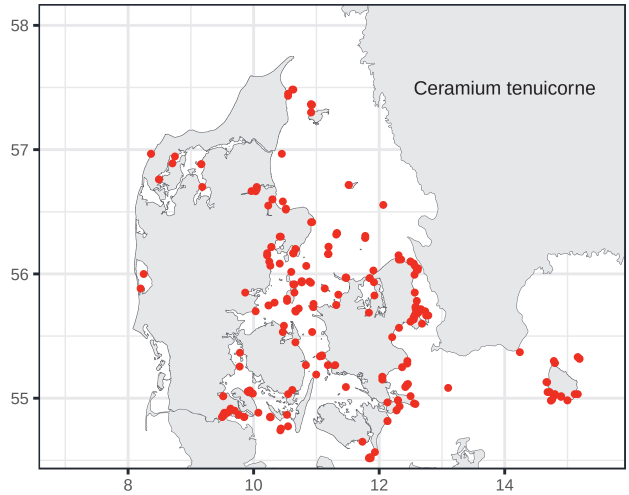
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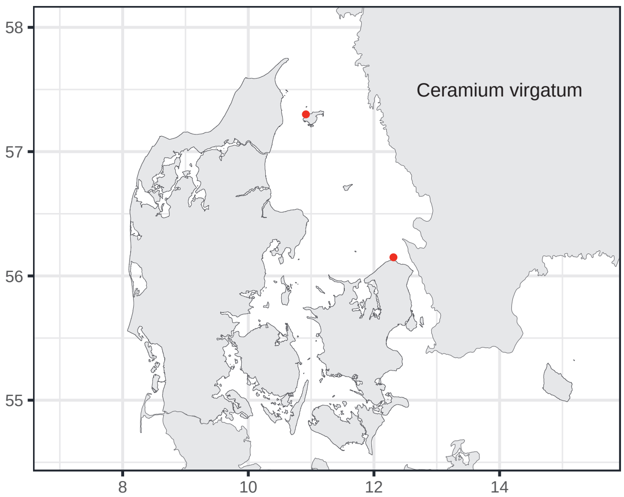
Ceramium virgatum
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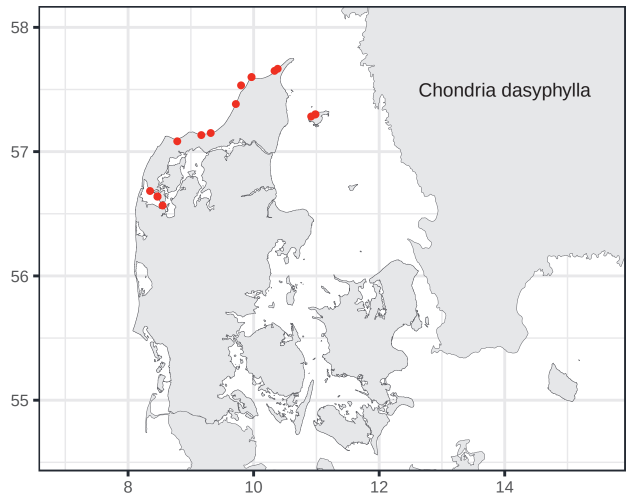
Chondria dasyphylla
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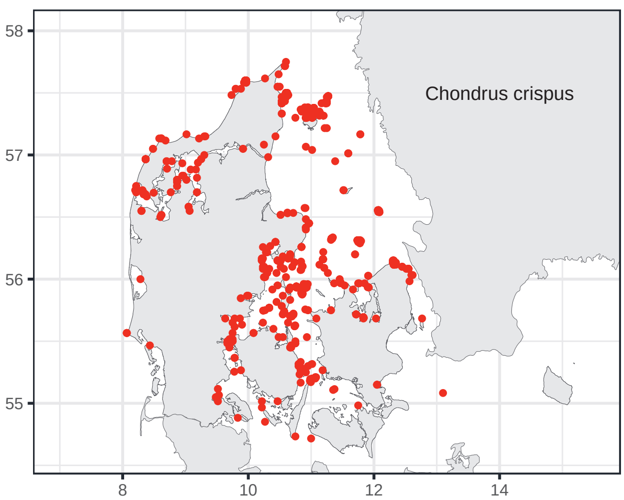
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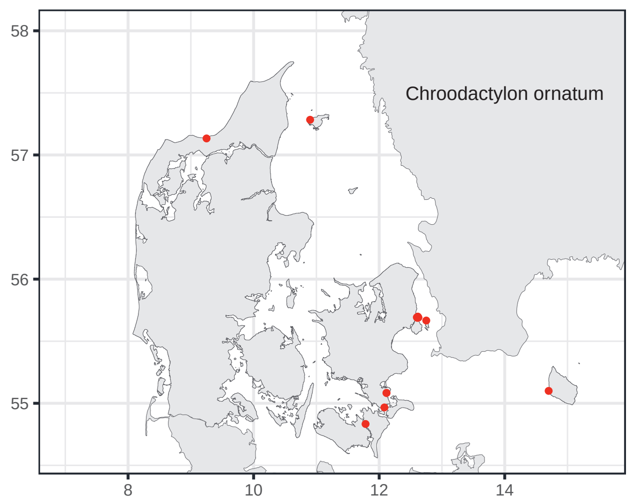
Chroodactylon ornatum
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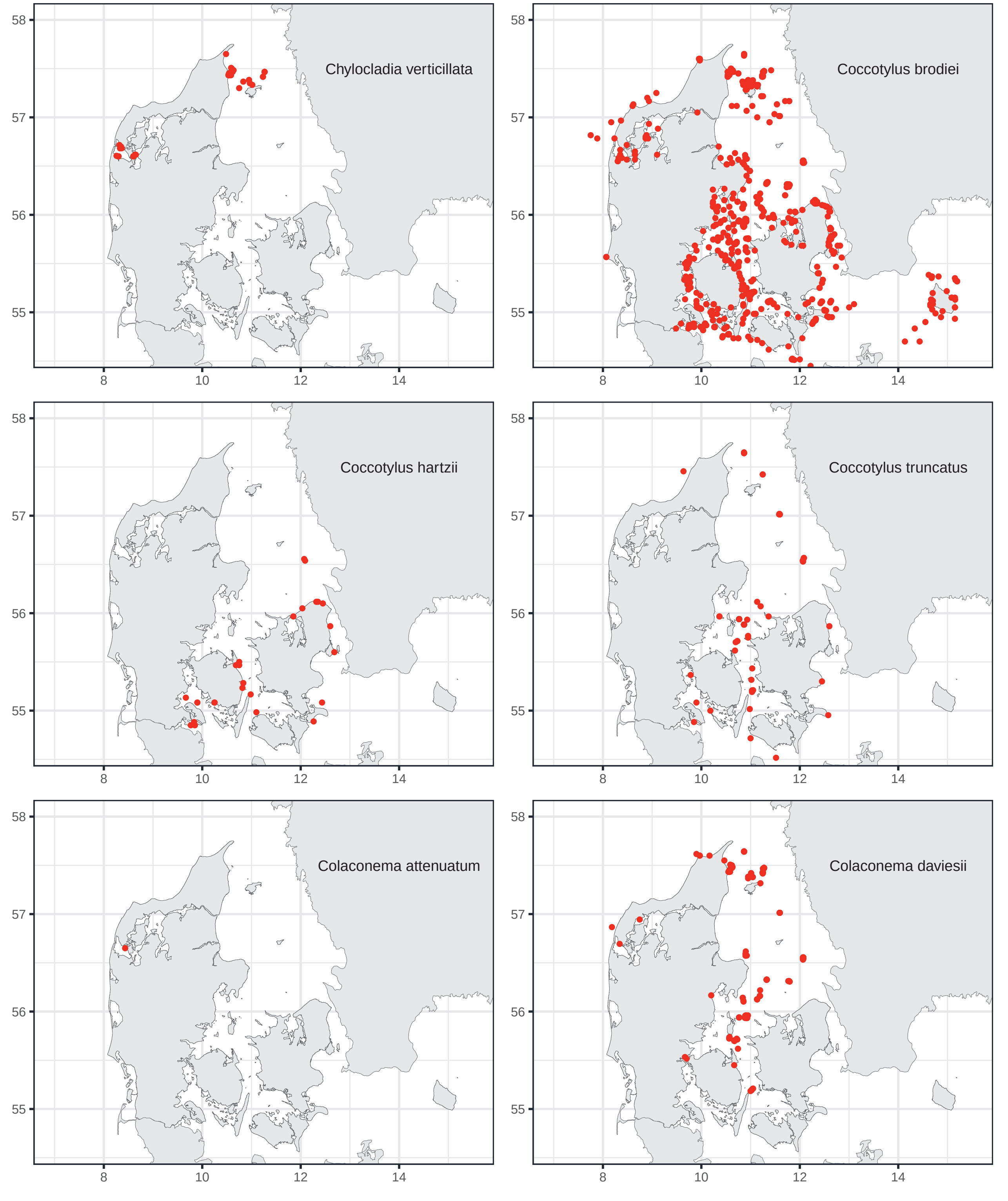
Chylocladia verticillata
Coccotylus brodiei
Coccotylus hartzii
Coccotylus truncatus
Colaconema attenuatum
Colaconema daviesii
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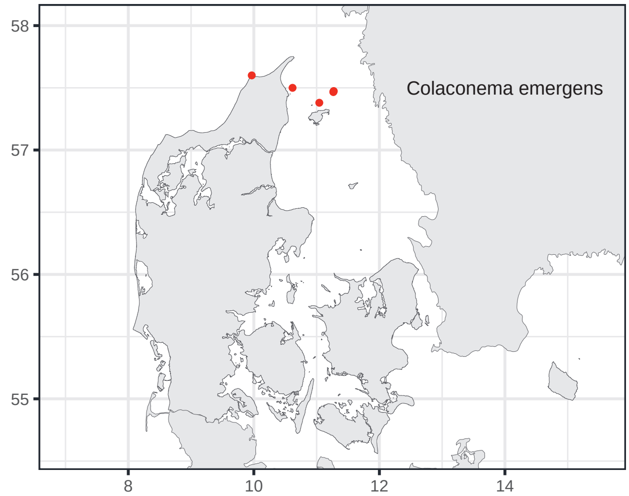
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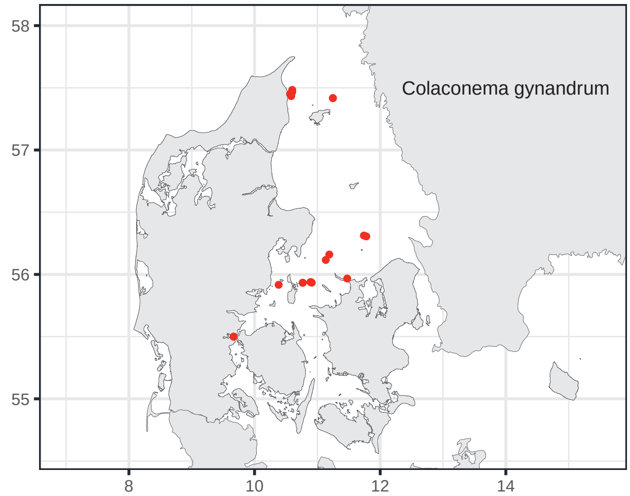
Colaconema gynandrum
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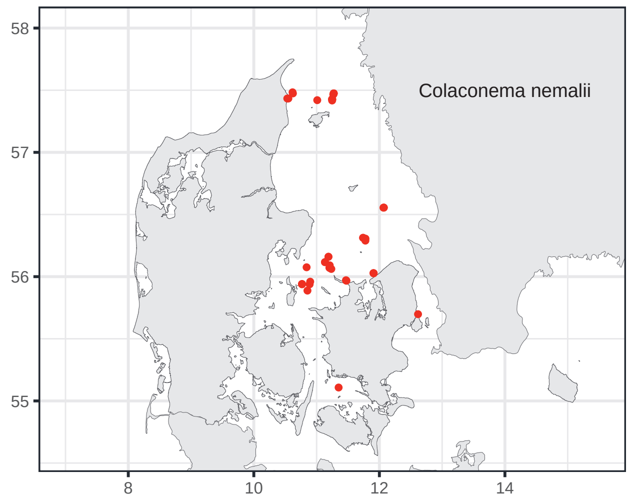
Colaconema nemalii
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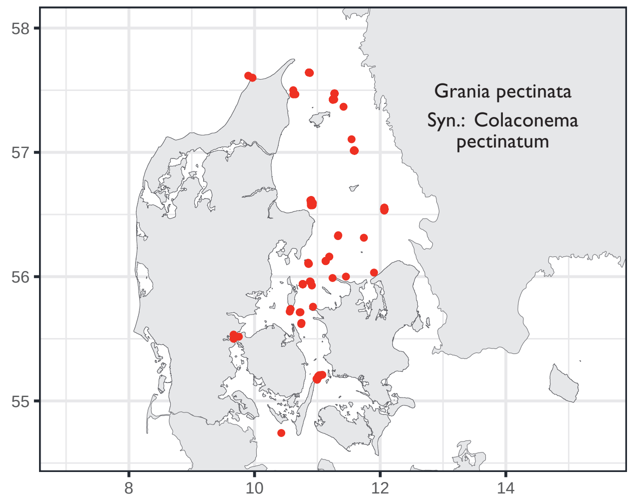
Grania pectinata
Syn.: Colaconema pectinatum
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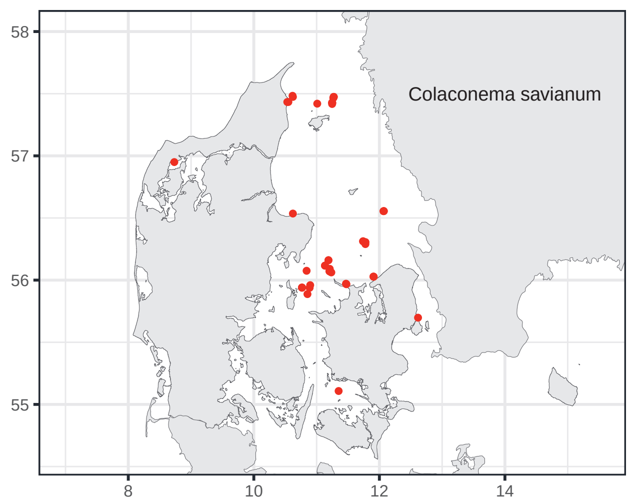
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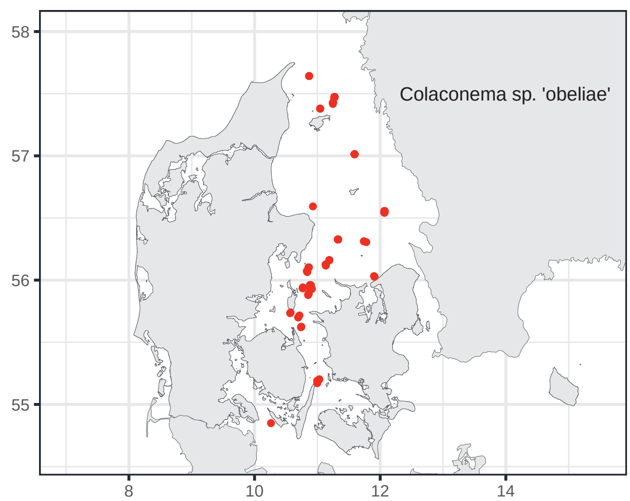
Colaconema sp. 'obeliae'
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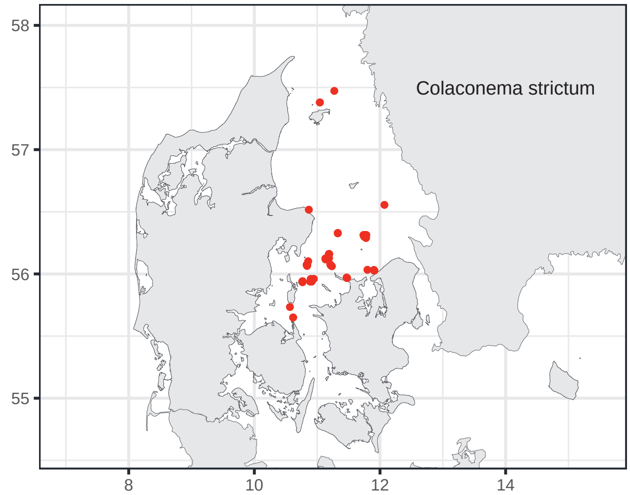
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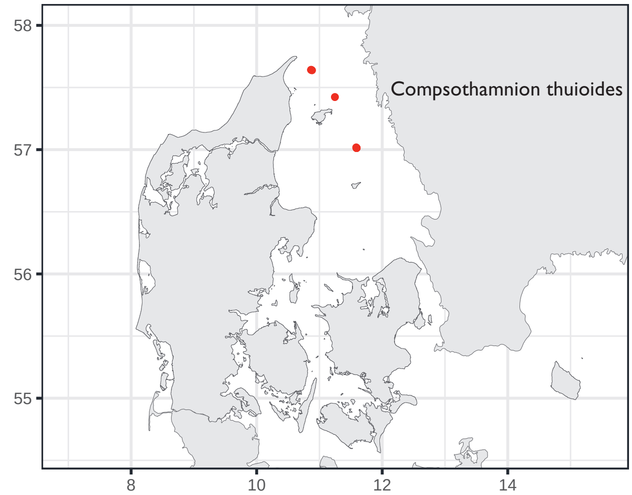
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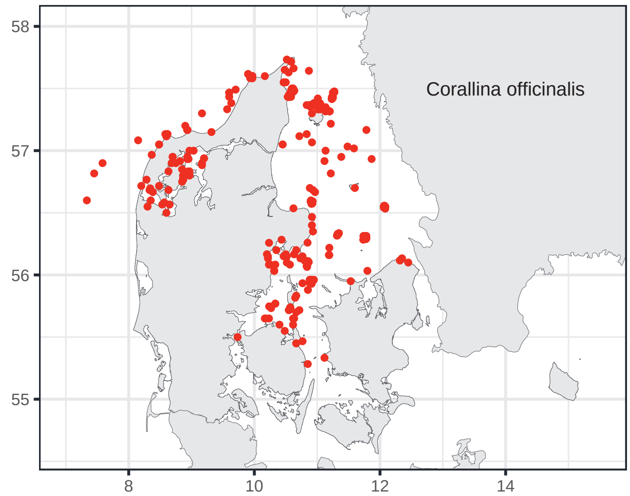
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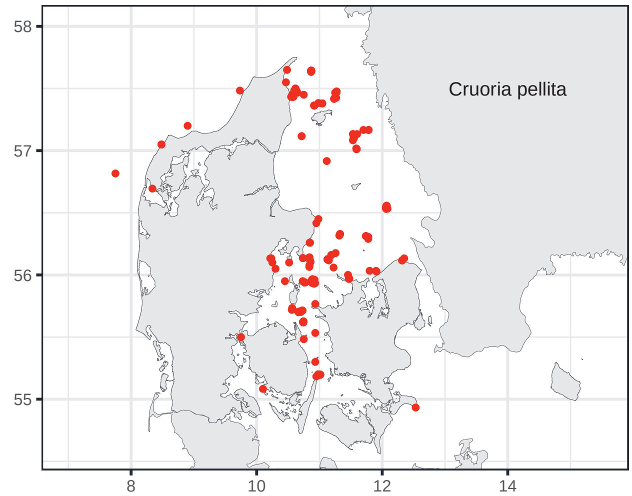
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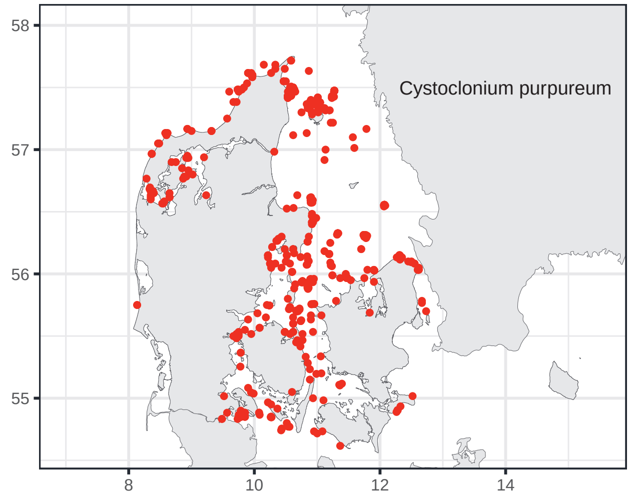
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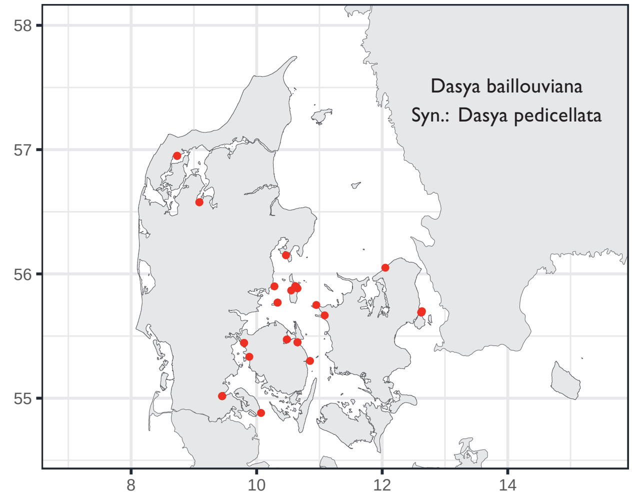
Dasya baillouviana
Syn.: Dasya pedicellata
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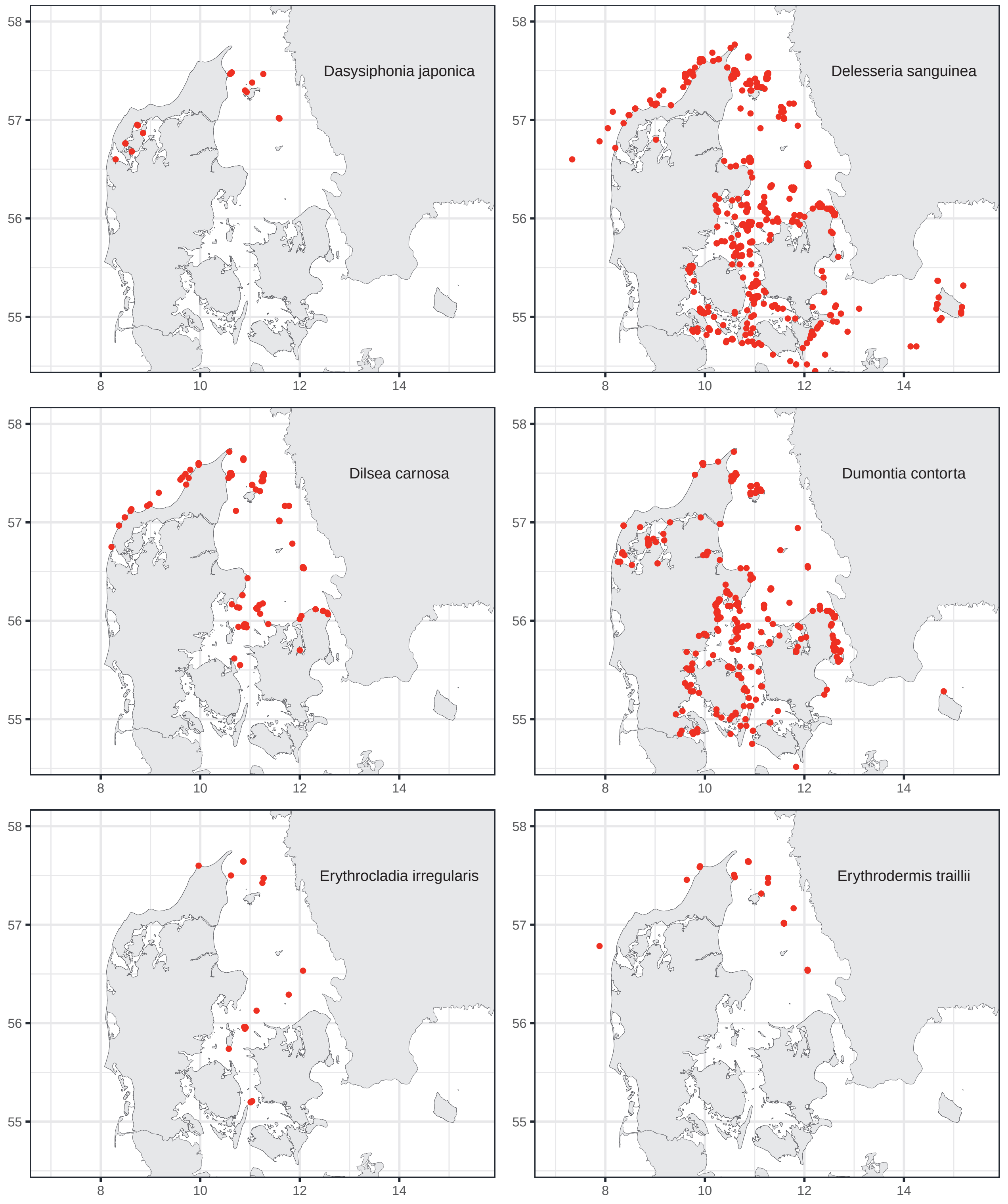
Dasysiphonia japonica
Delesseria sanguinea
Dilsea carnosa
Dumontia contorta
Erythrocladia irregularis
Erythrodermis traillii
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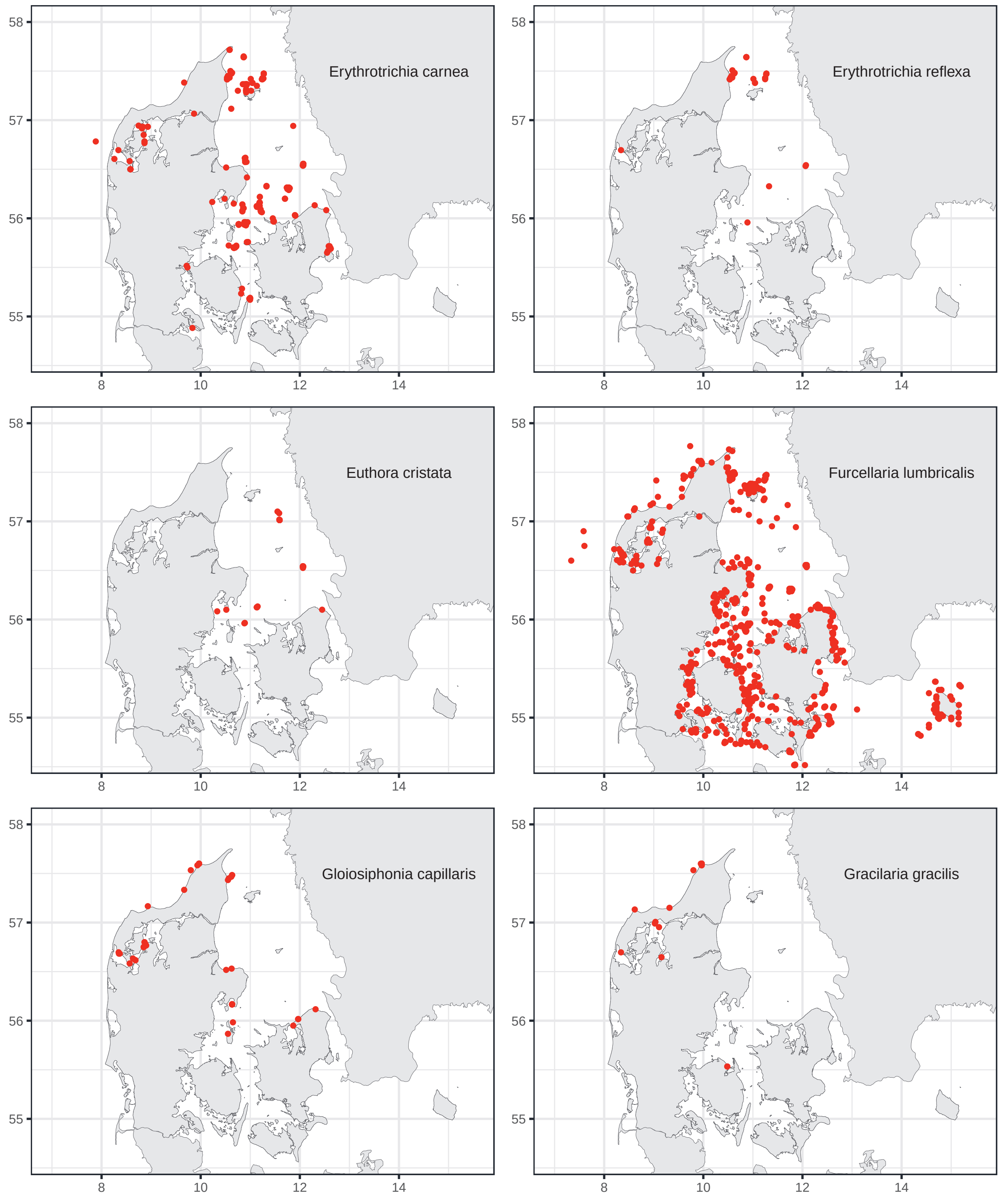
Erythrotrichia carnea
Erythrotrichia reflexa
Euthora cristata
Furcellaria lumbricalis
Gloiosiphonia capillaris
Gracilaria gracilis
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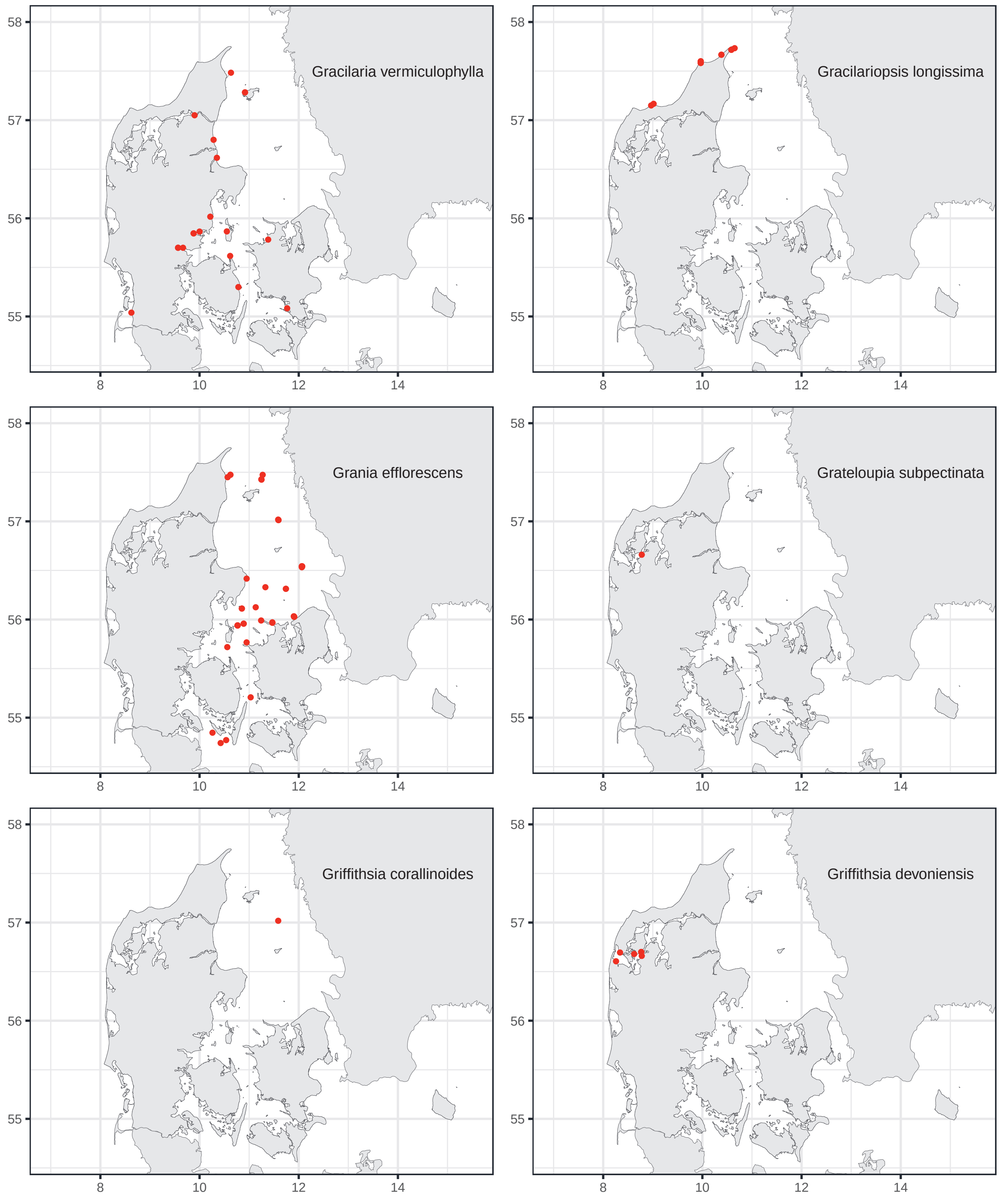
Gracilaria vermiculophylla
Gracilariopsis longissima
Grania efflorescens
Grateloupia subpectinata
Griffithsia corallinoides
Griffithsia devoniensis
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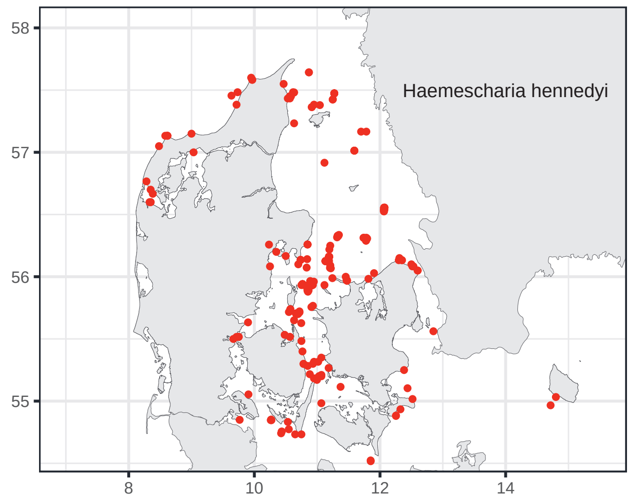
Haemescharia hennedyi
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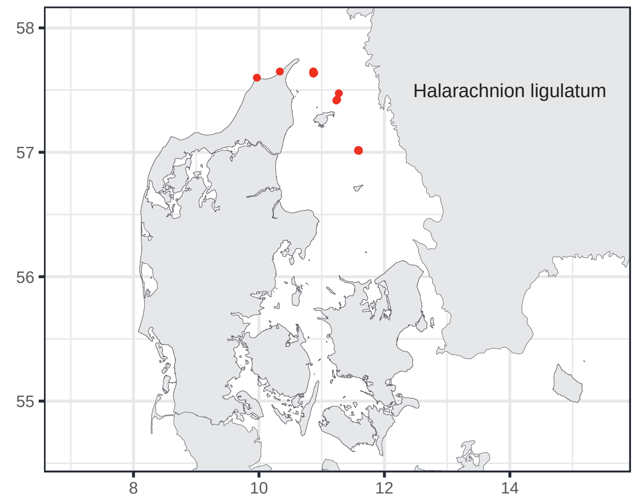
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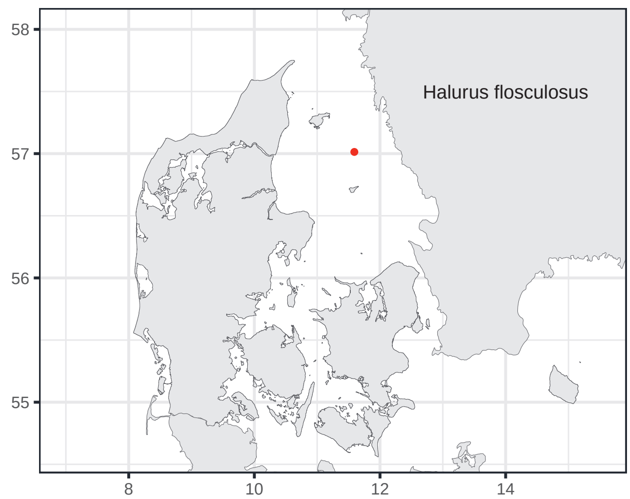
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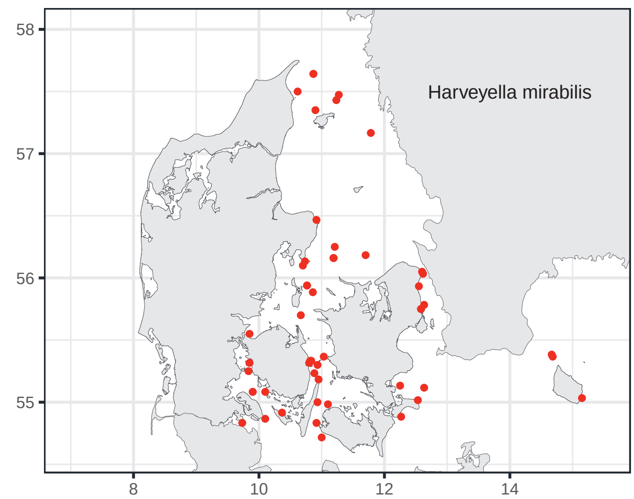
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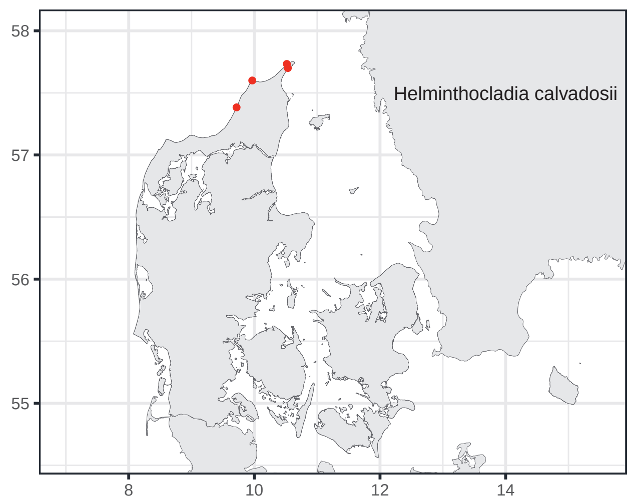
Helminthocladia calvadosii
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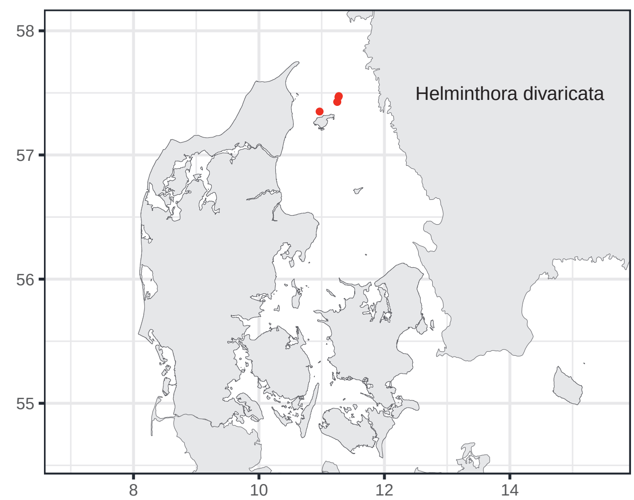
Helminthora divaricata
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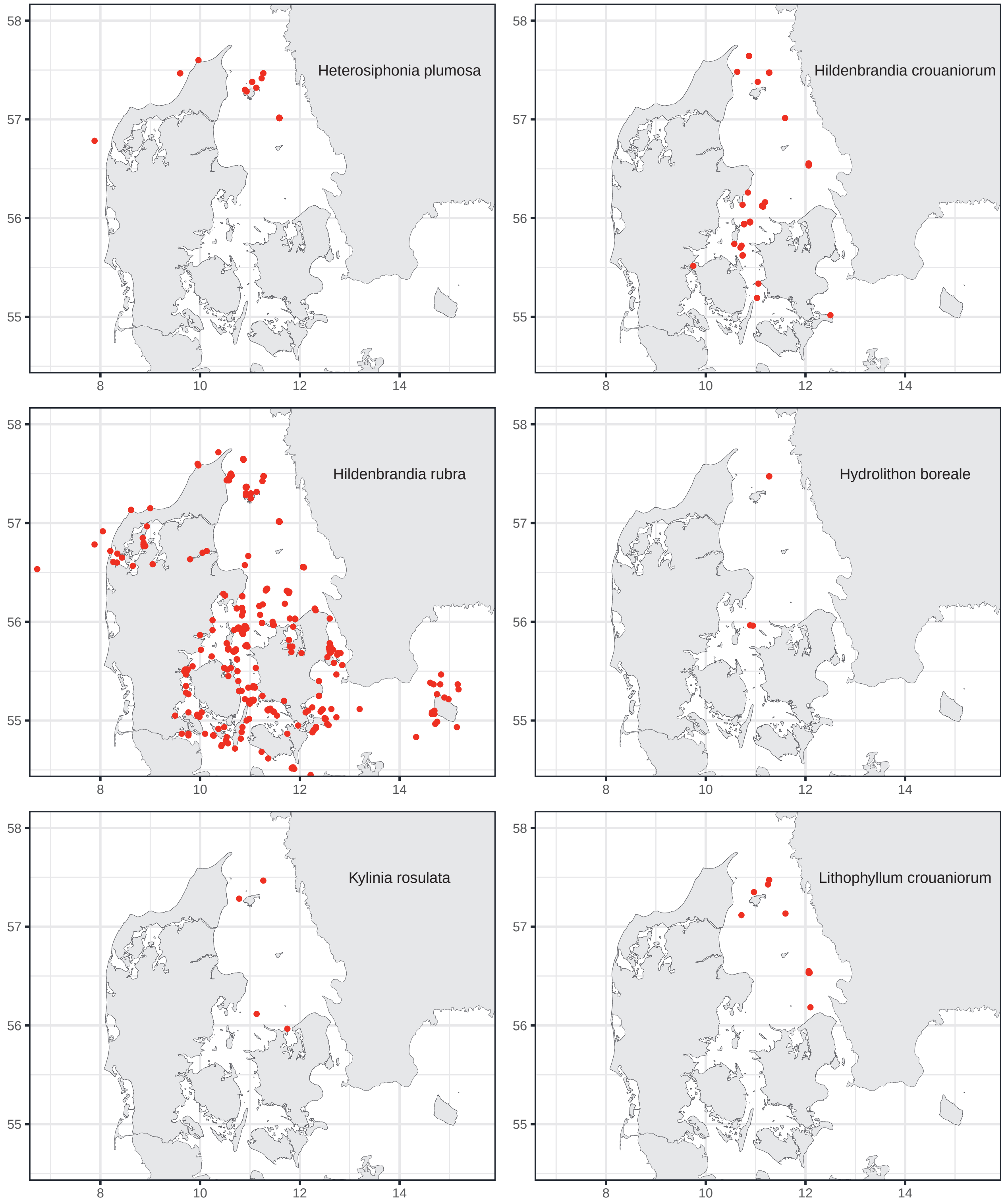
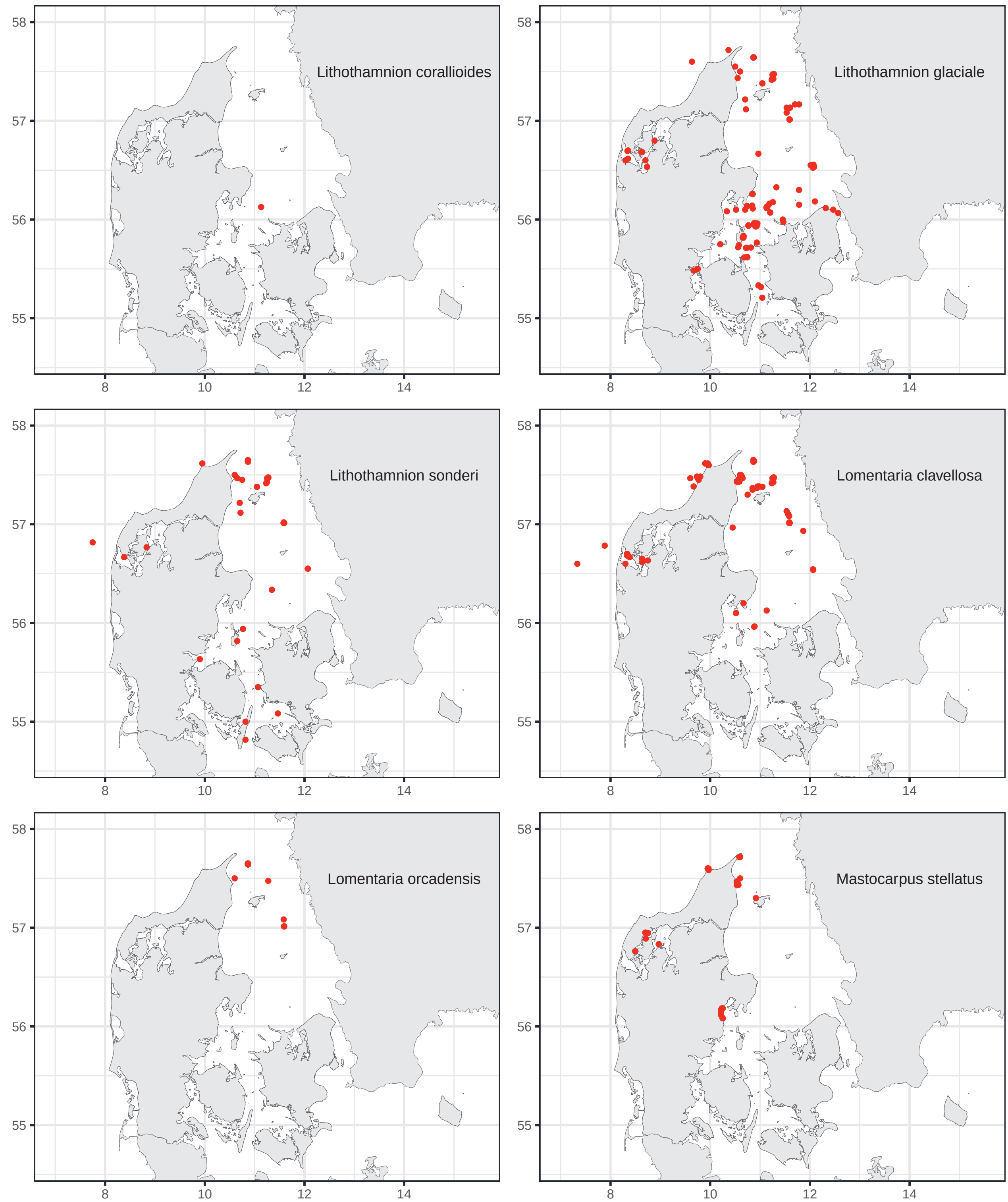

Heterosiphonia plumosa
Hildenbrandia crouaniorum
Hildenbrandia rubra
Hydrolithon boreale
Kylinia rosulata
Lithophyllum crouaniorum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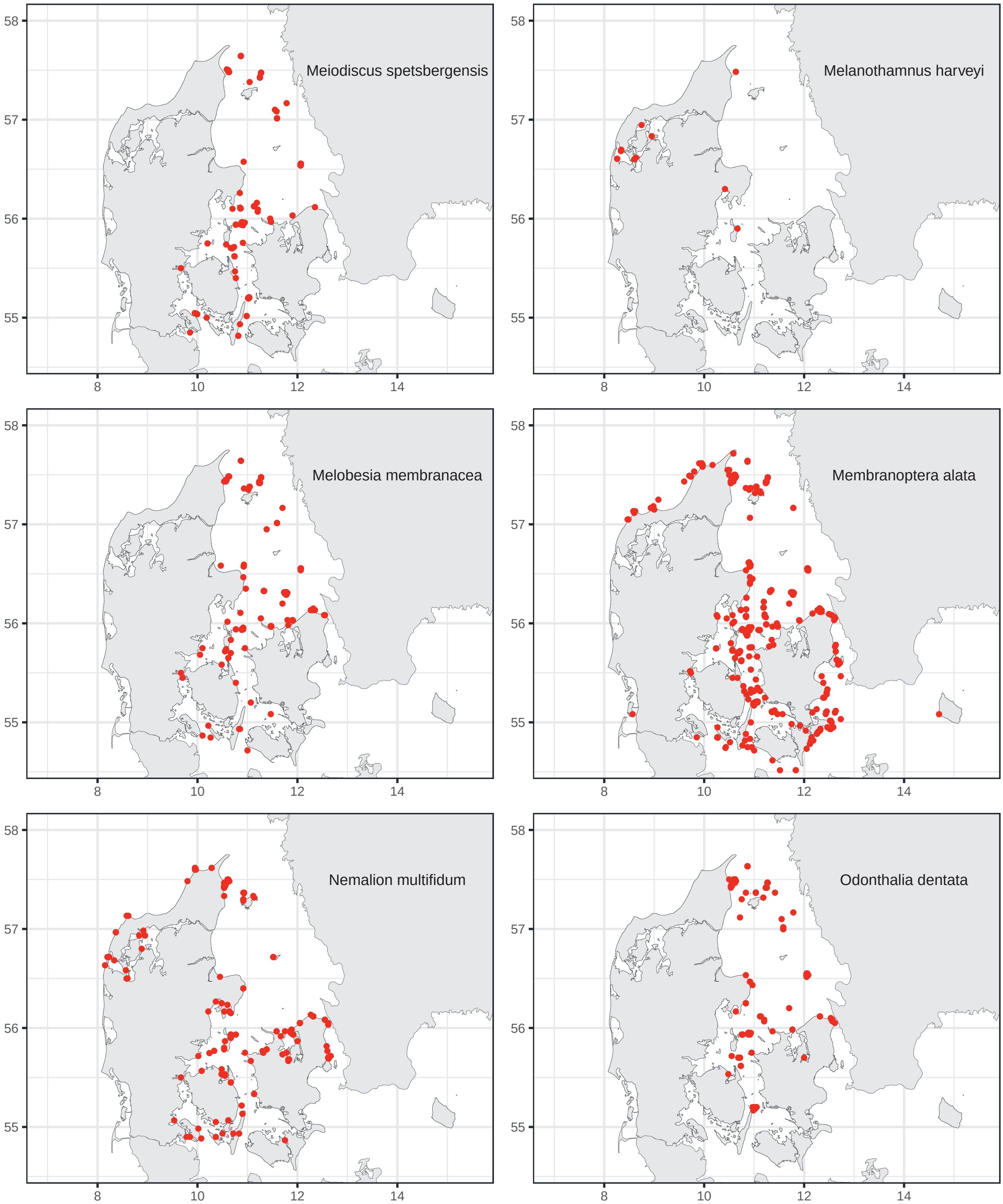
Lithothamnion glaciale
Lithothamnion sonderi
Lomentaria clavellosa
Lomentaria orcadensis
Mastocarpus stellatus


Meiodiscus spetsbergensis
Melanothamnus harveyi
Melobesia membranacea
Membranoptera alata
Nemalion multifidum
Odonthalia dentata
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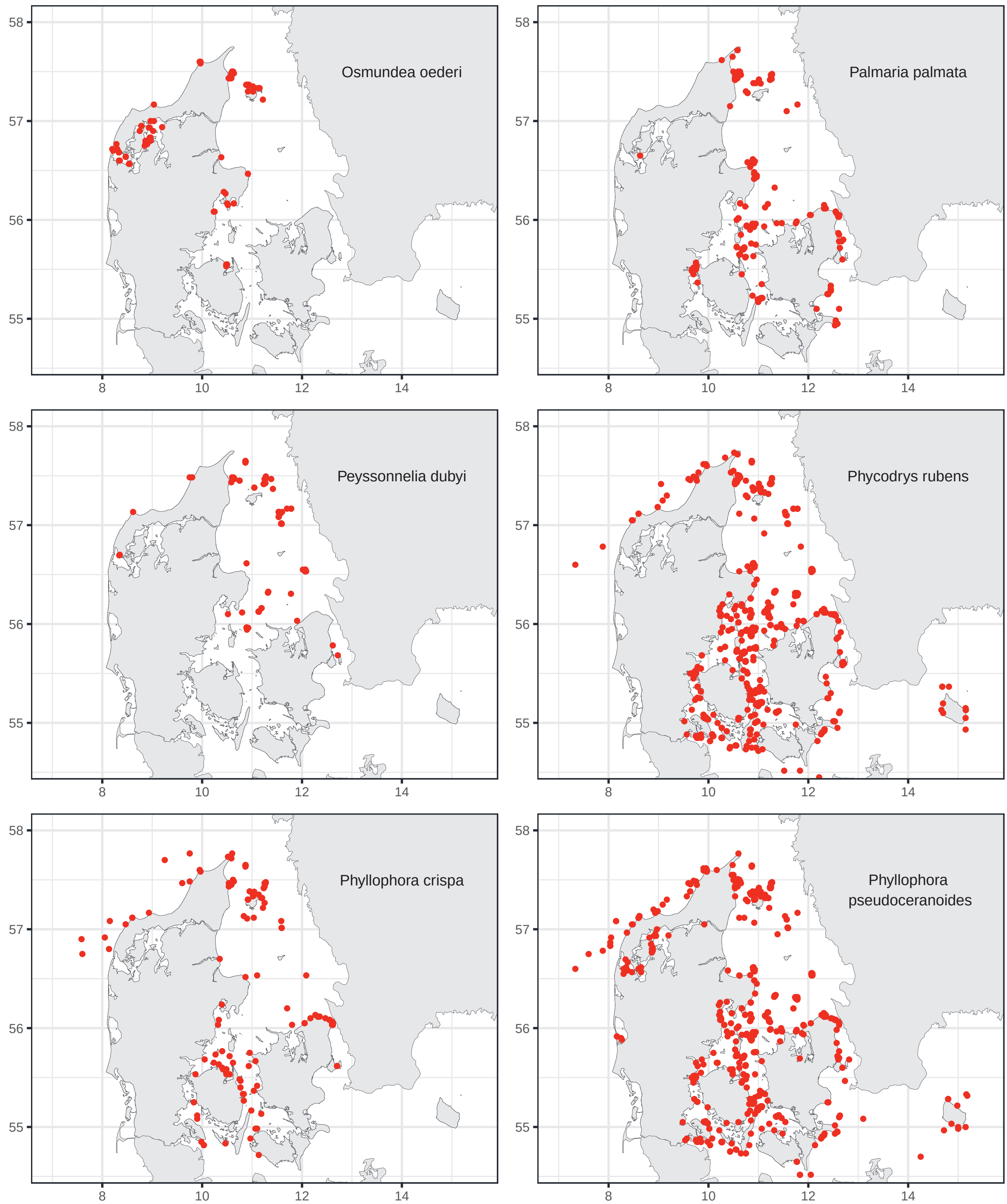
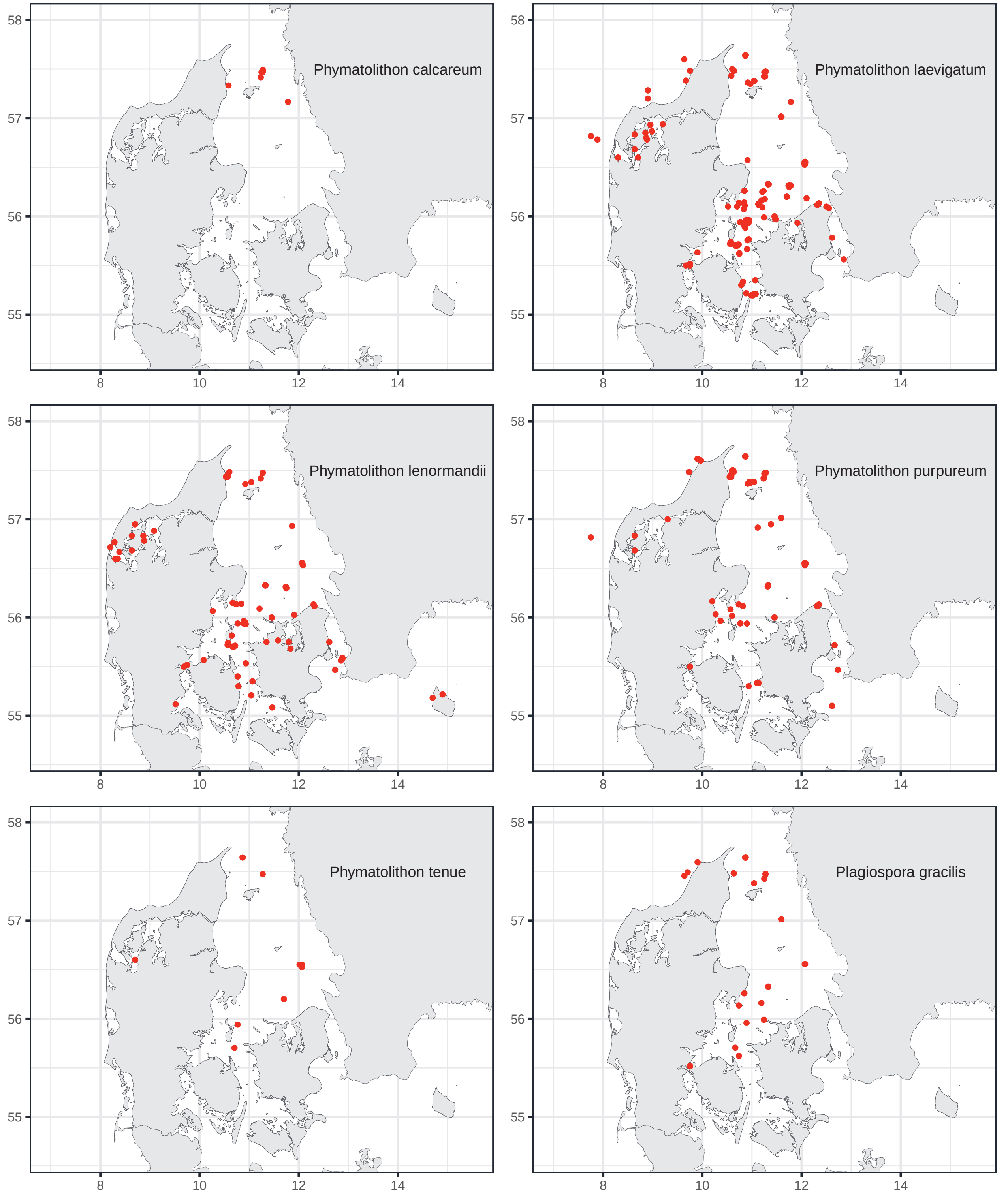
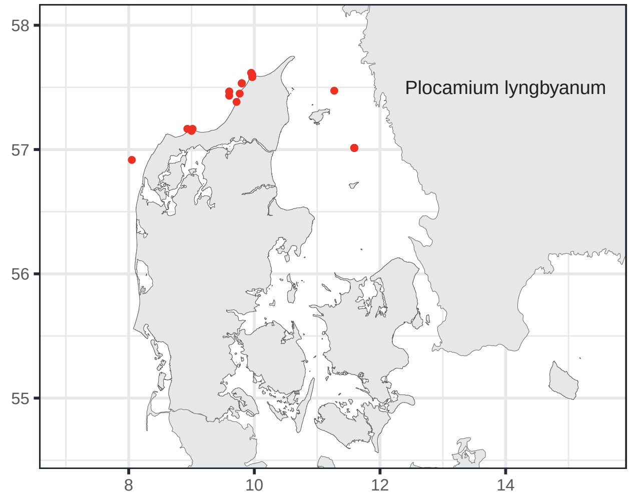

Osmundea oederi
Palmaria palmata
Peyssonnelia dubyi
Phycodrys rubens
Phyllophora crispa
Phyllophora pseudoceranoides


Phymatolithon calcareum
Phymatolithon laevigatum
Phymatolithon lenormandii
Phymatolithon purpureum
Phymatolithon tenue
Plagiospora gracilis


Plocamium lyngbyanum
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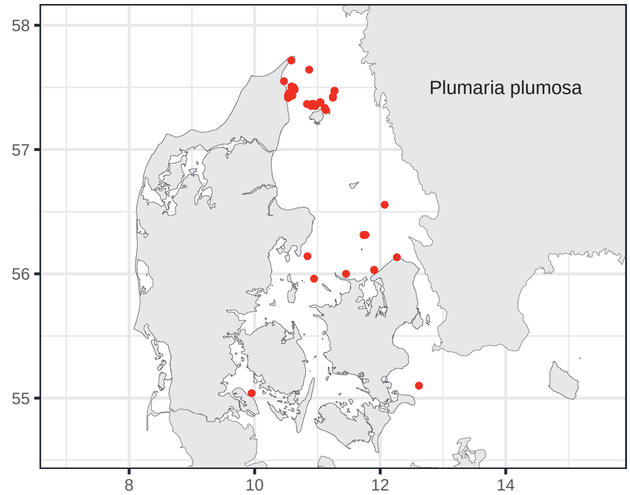
Plumaria plumosa
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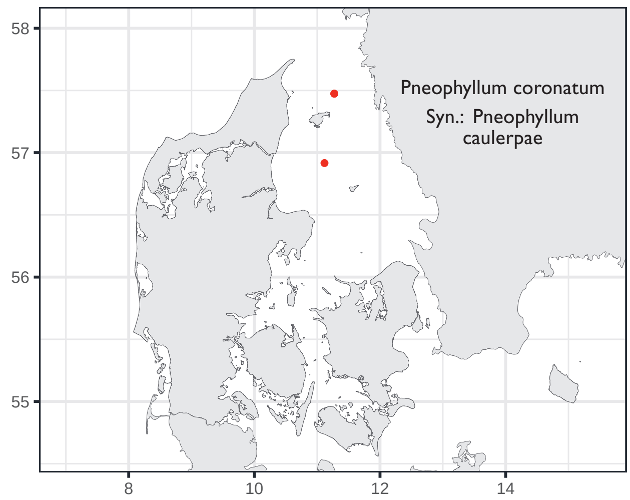
Pneophyllum coronatum
Syn.: Pneophyllum caulerpae
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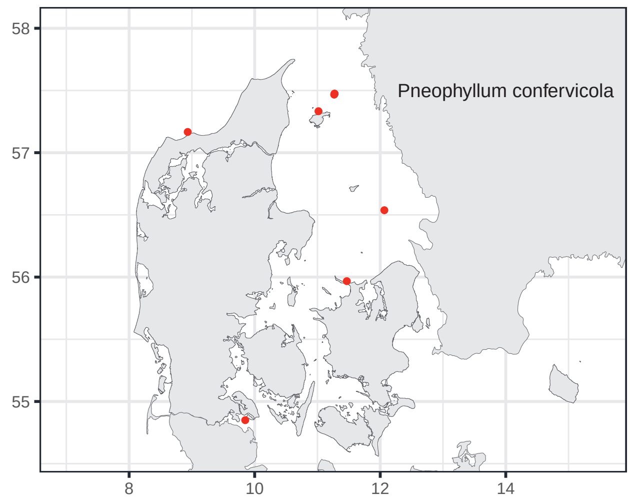
Pneophyllum confervicola
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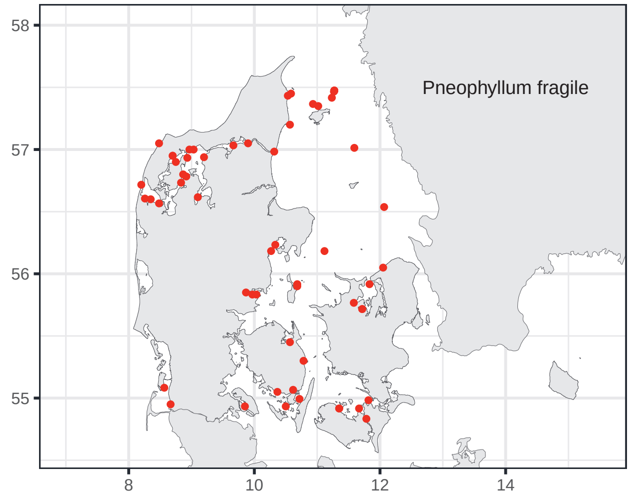
Pneophyllum fragile
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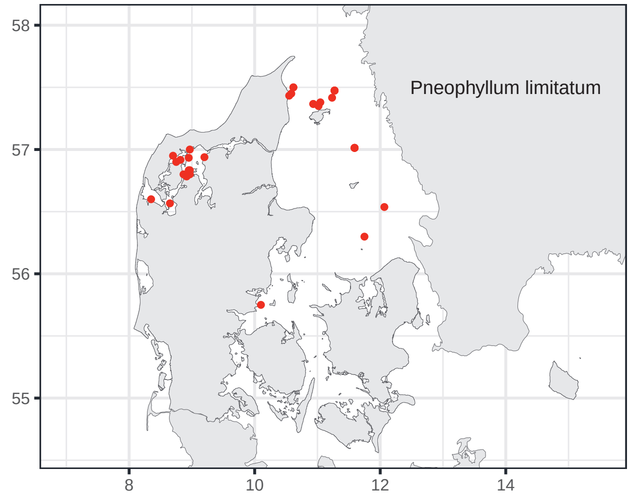
Pneophyllum limitatum
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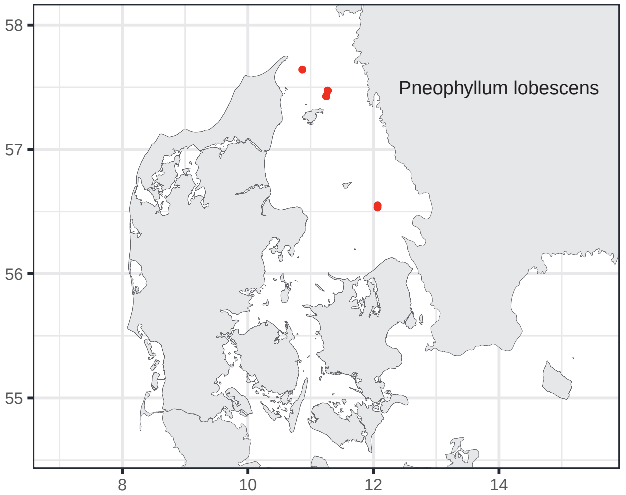
Pneophyllum lobescens
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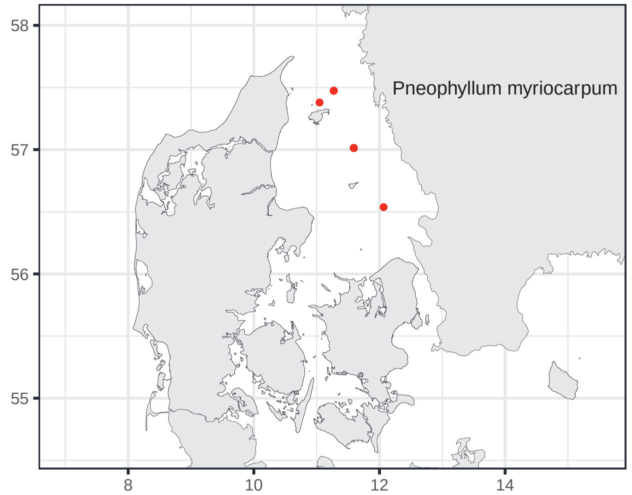
Pneophyllum myriocarpum
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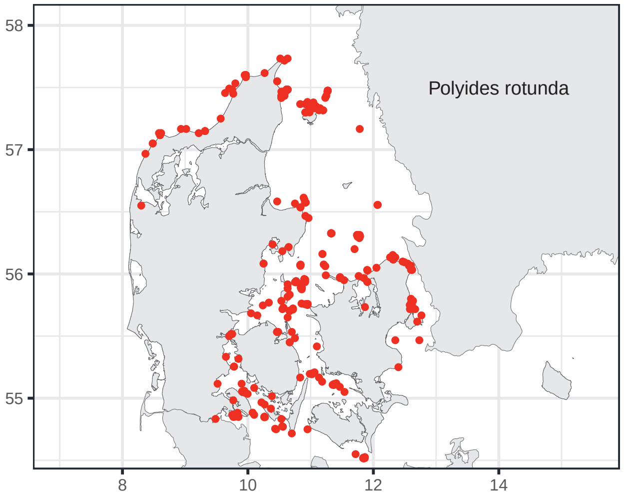
Polyides rotunda
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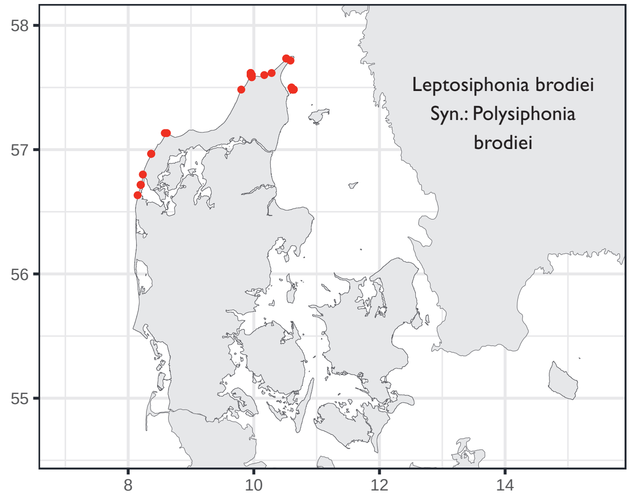
Leptosiphonia brodiei
Syn.: Polysiphonia
brodiei
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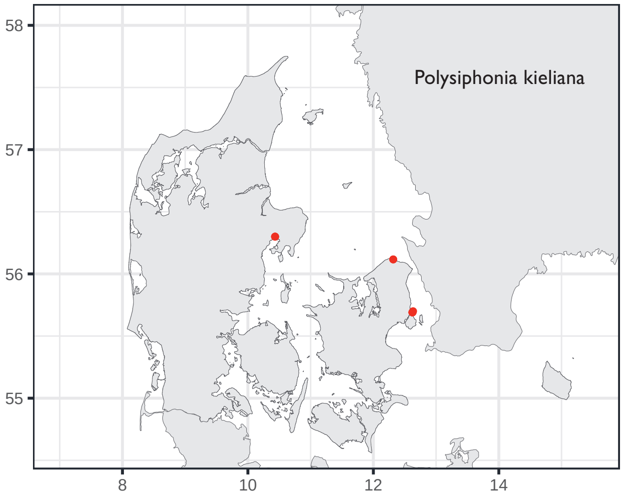
Polysiphonia kieliana
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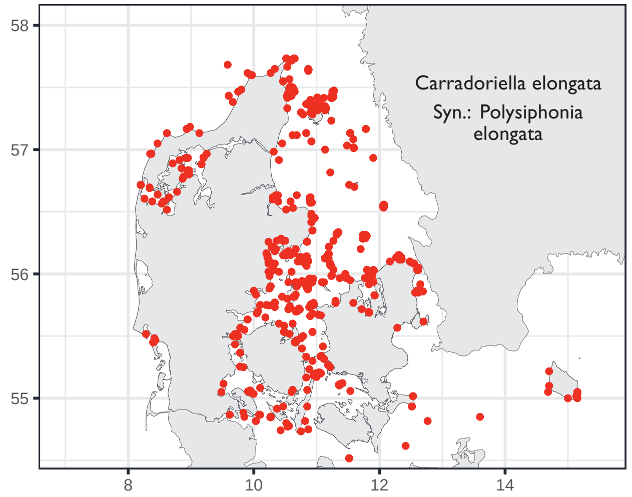
Carradoriella elongata
Syn.: Polysiphonia
elongata
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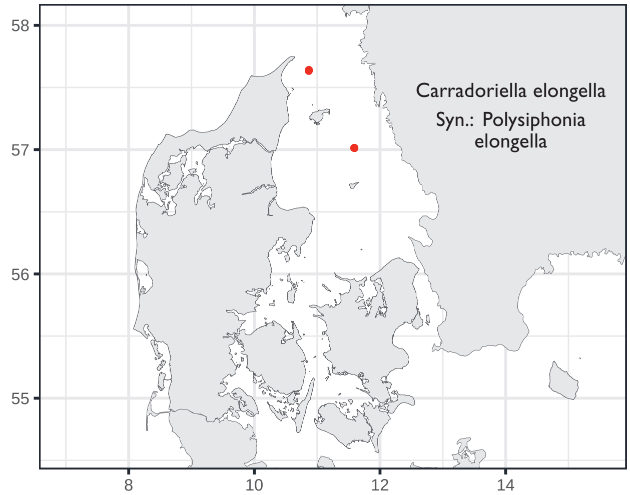
Carradoriella elongella
Syn.: Polysiphonia elongella
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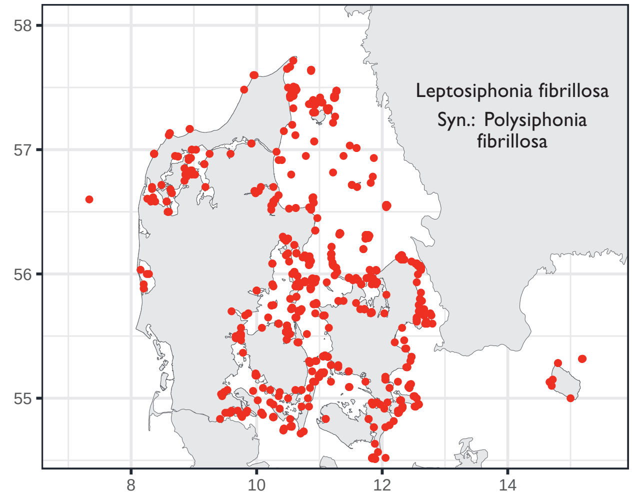
Leptosiphonia fibrillosa
Syn.: Polysiphonia fibrillosa
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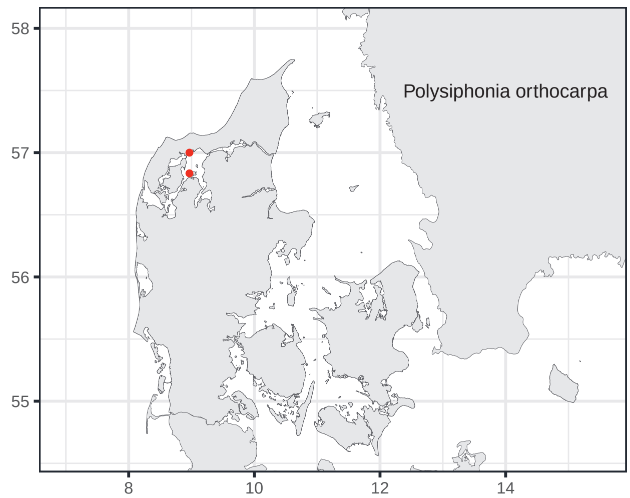
Polysiphonia orthocarpa
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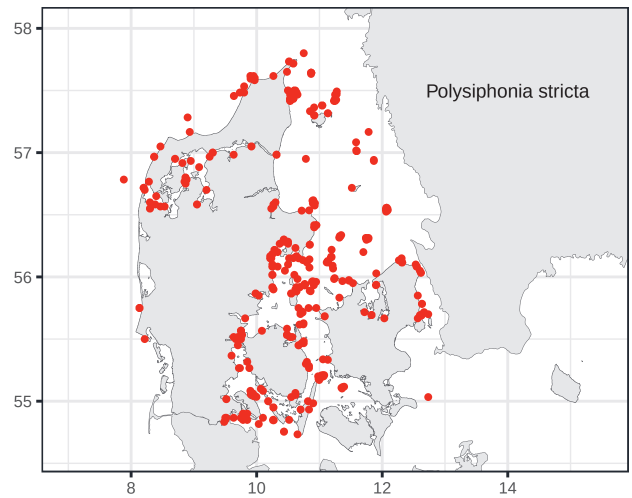
Polysiphonia stricta
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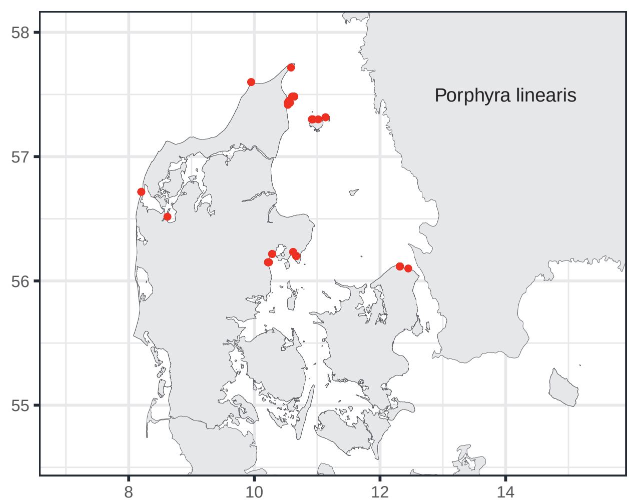
Porphyra linearis
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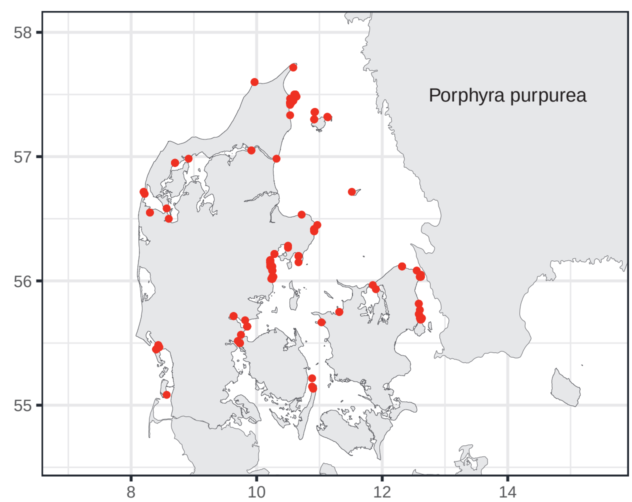
Porphyra purpurea
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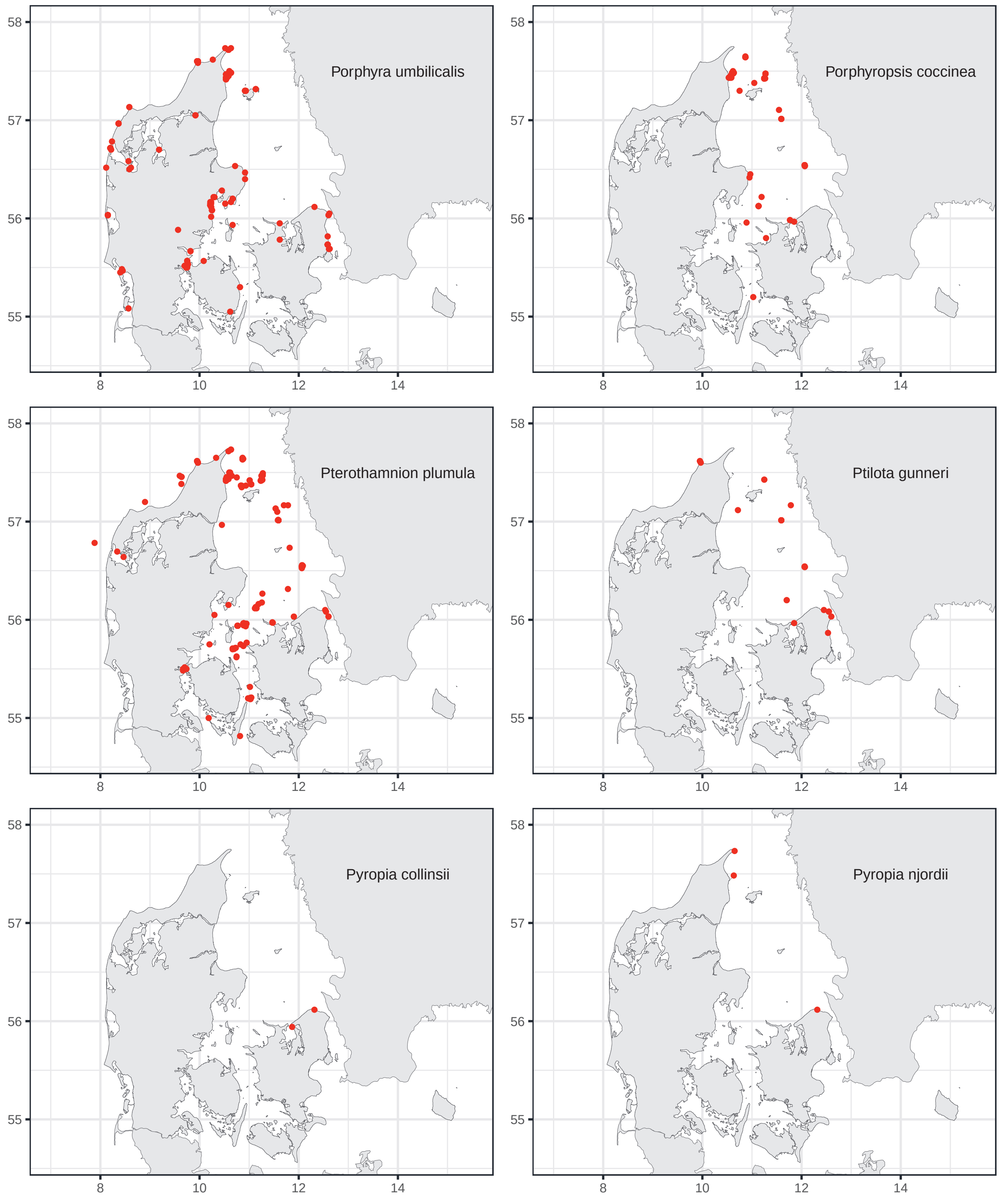
Porphyra umbilicalis
Porphyropsis coccinea
Pterothamnion plumula
Ptilota gunneri
Pyropia collinsii
Pyropia njordii
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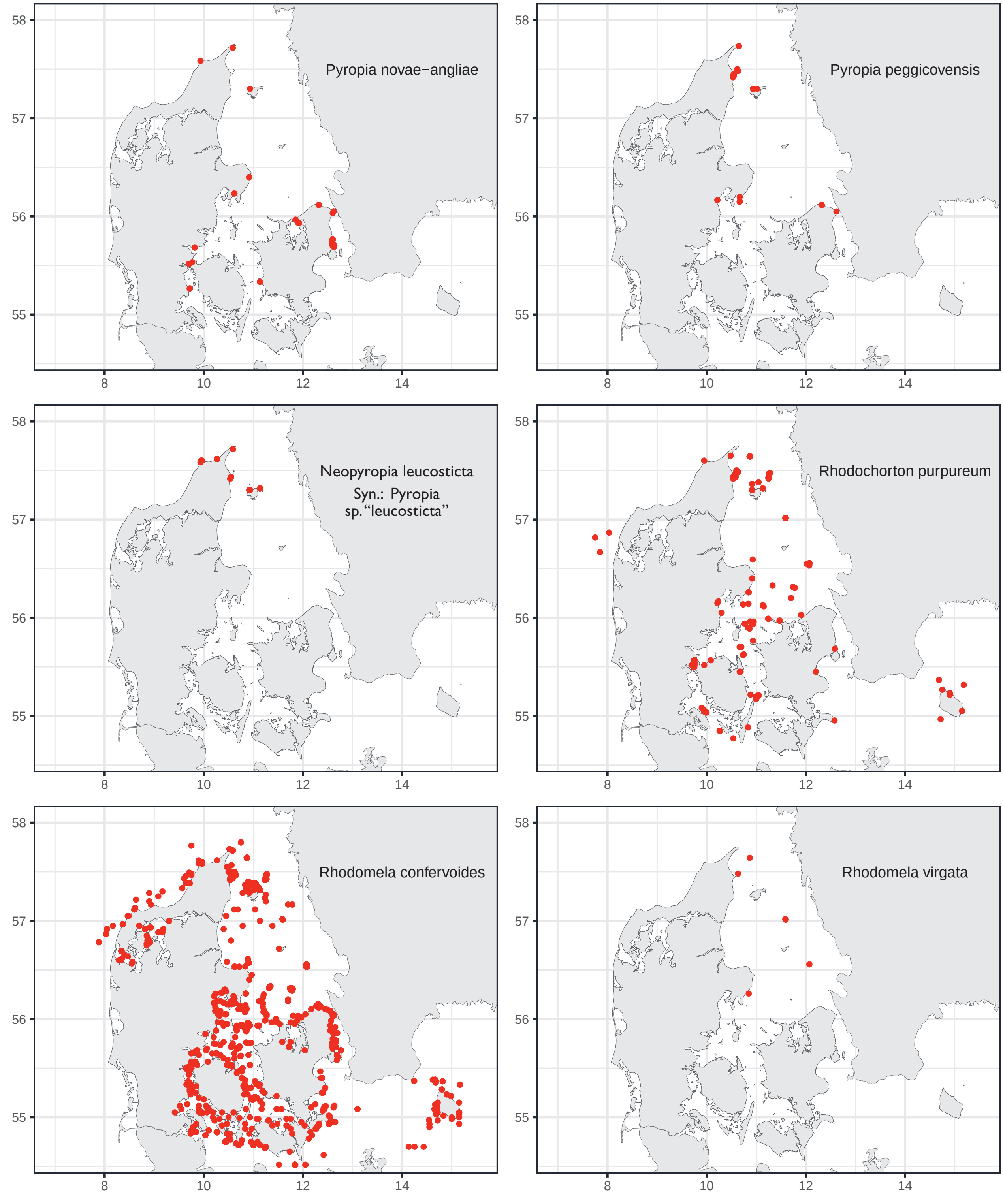
Pyropia novae−angliae
Pyropia peggicovensis
Neopyropia leucosticta
Syn.: Pyropia sp."leucosticta"
Rhodochorton purpureum
Rhodomela confervoides
Rhodomela virgata
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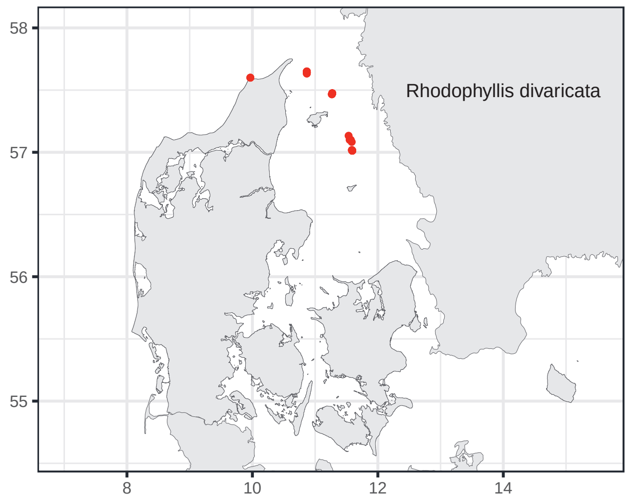
Rhodophyllis divaricata
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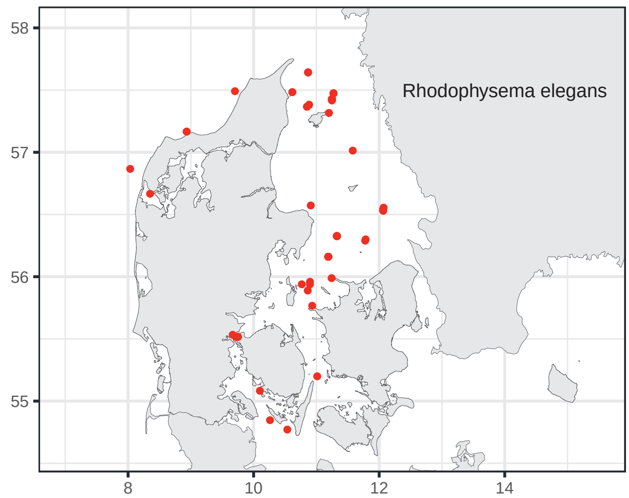
Rhodophysema elegans
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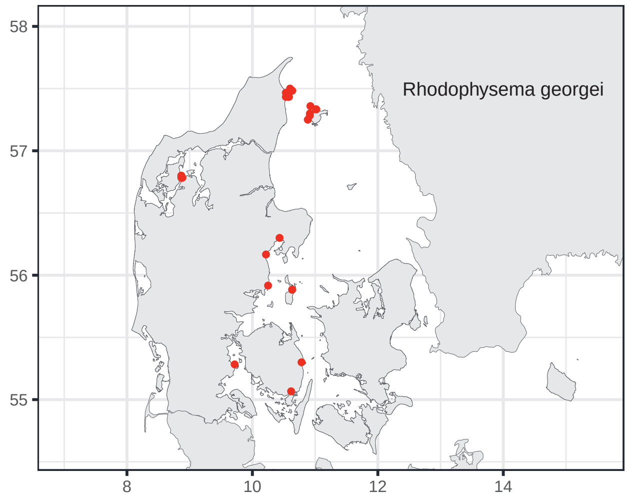
Rhodophysema georgei
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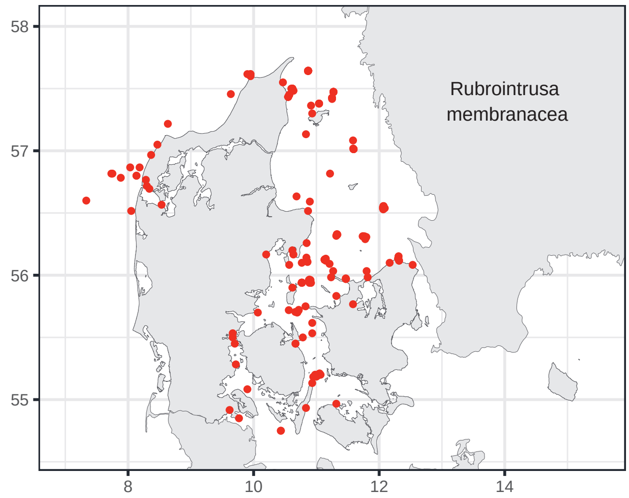
Rubrointrusa
membranacea
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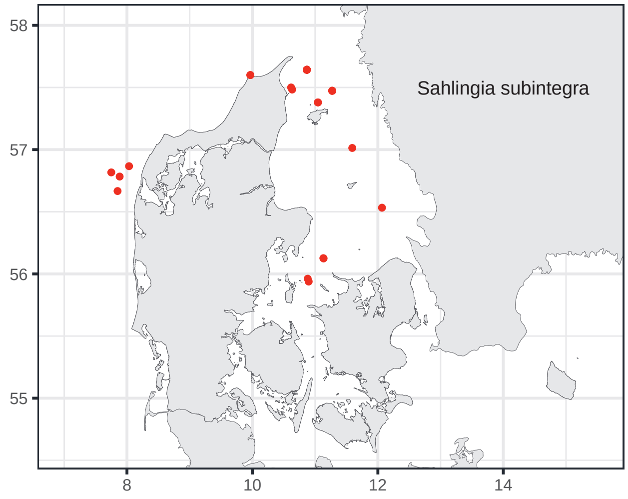
Sahlingia subintegra
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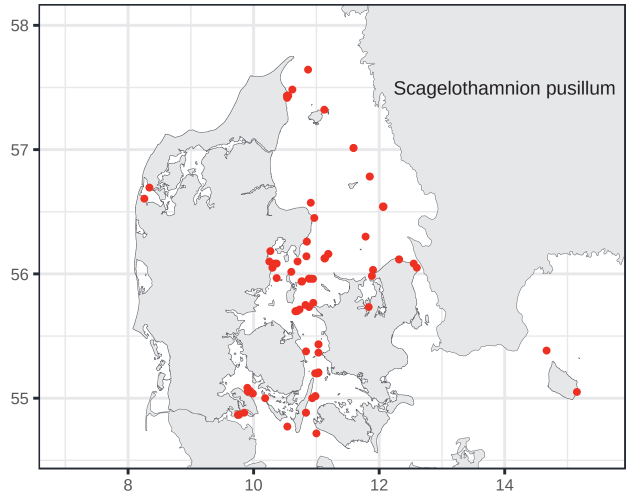
Scagelothamnion pusillum
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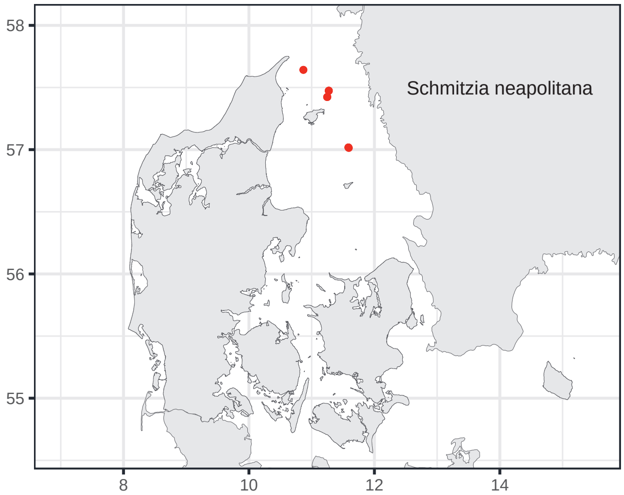
Schmitzia neapolitana
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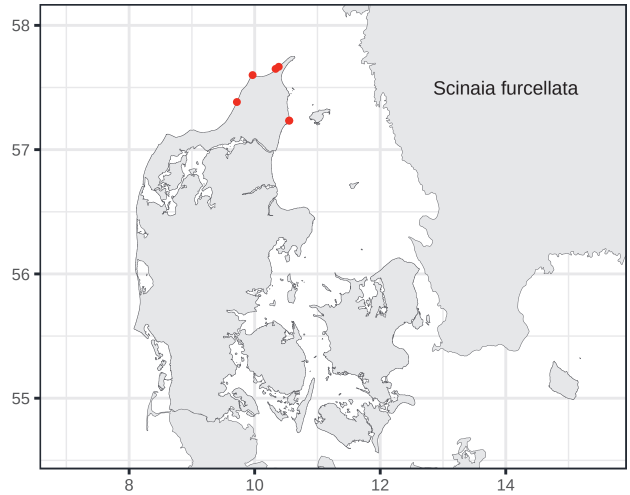
Scinaia furcellata
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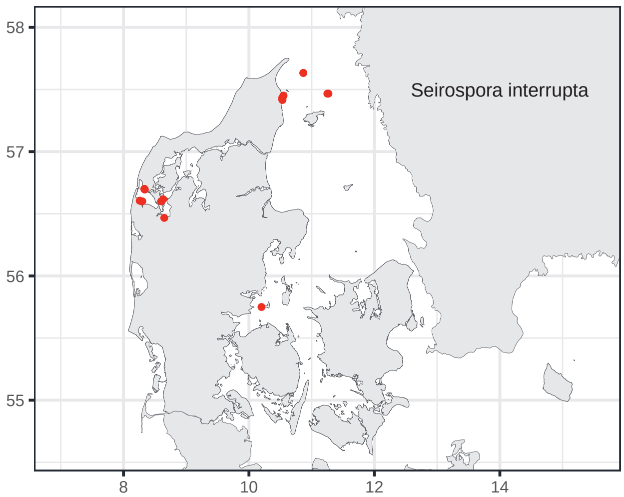
Seirospora interrupta
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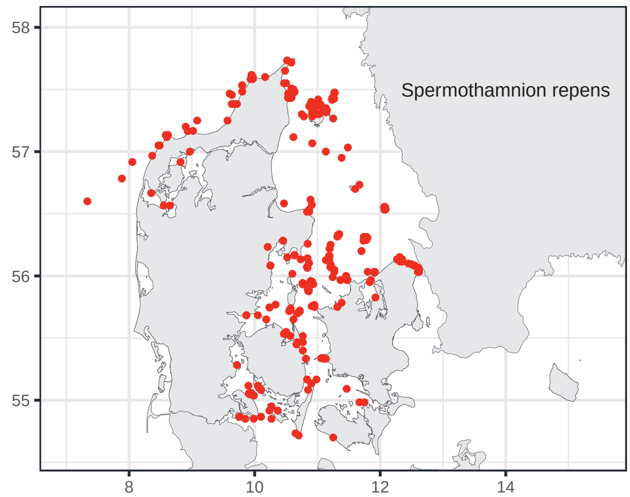
Spermothamnion repens
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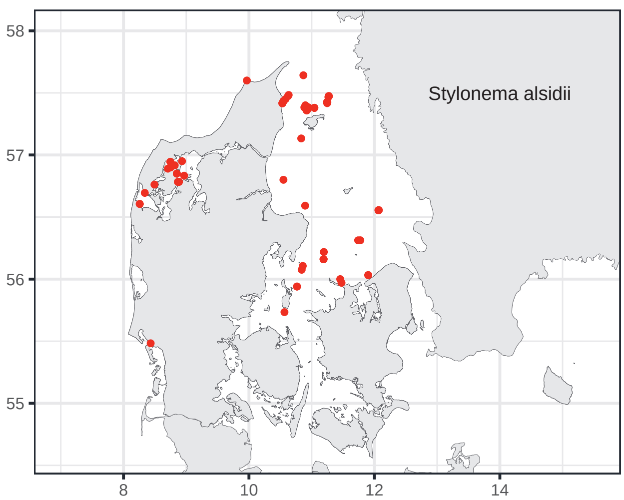
Stylonema alsidii
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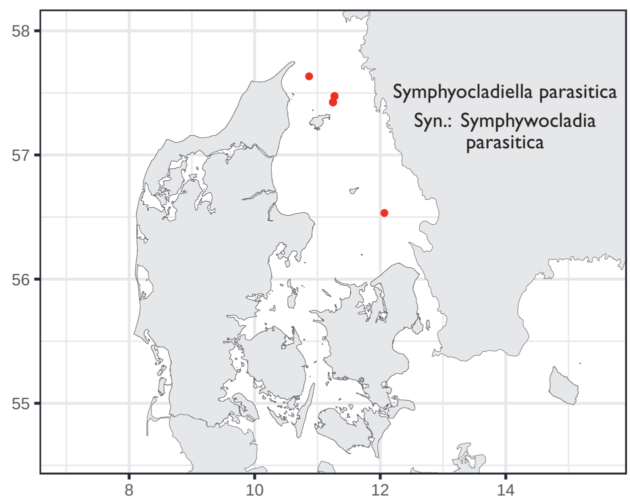
Symphyocladiella parasitica
Syn.: Symphywocladia parasitica
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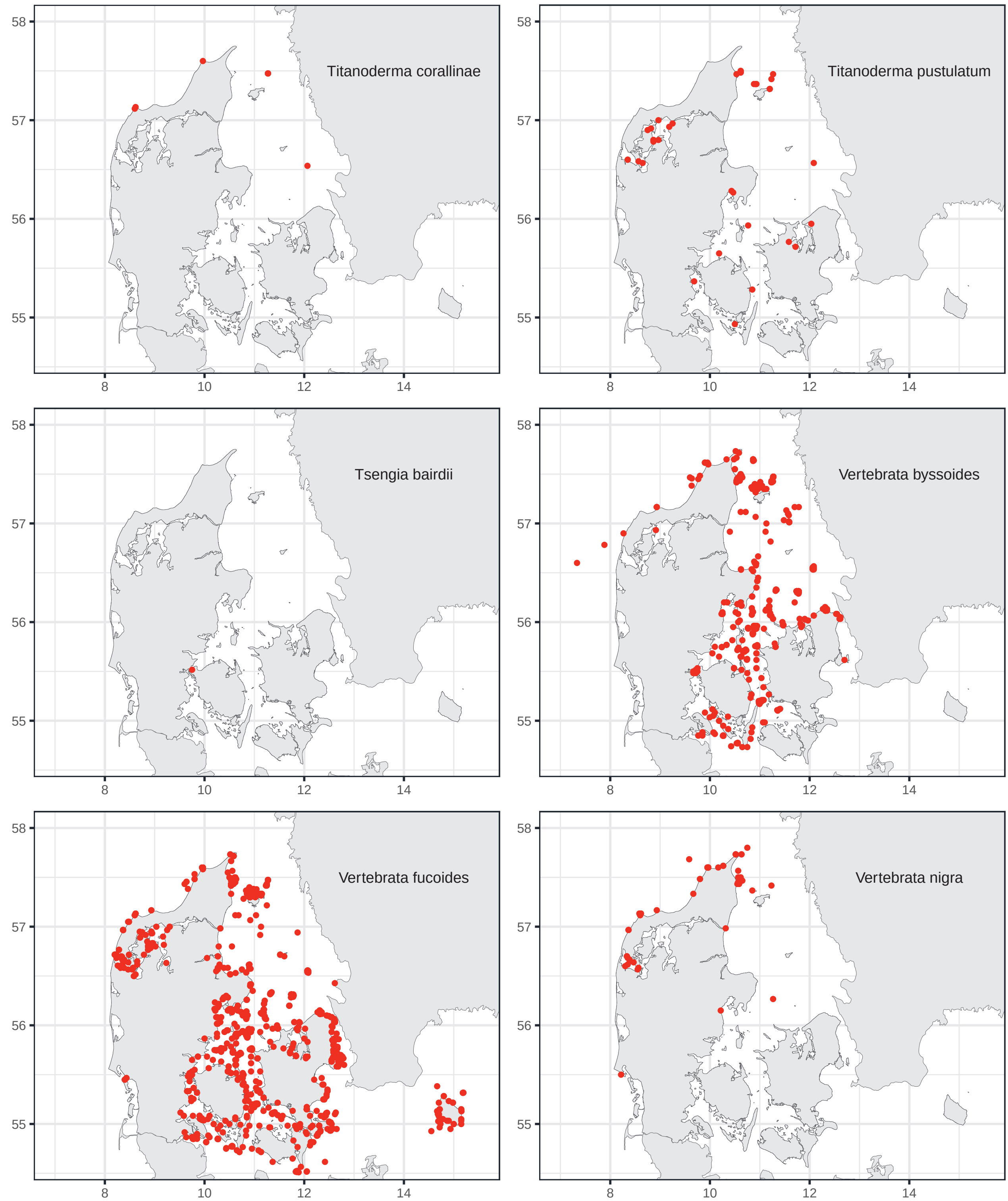
Titanoderma corallinae
Titanoderma pustulatum
Tsengia bairdii
Vertebrata byssoides
Vertebrata fucoides
Vertebrata nigra
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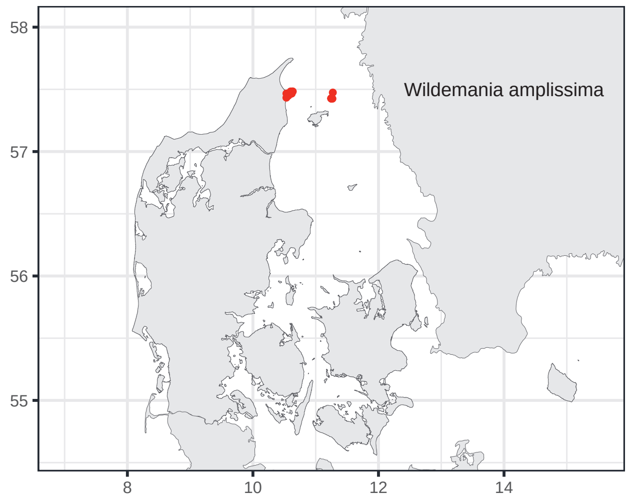
Wildemania amplissima
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Accepted names of species recorded in Danish waters and covered in this book and names of higher rank than species are in **bold letters**. Page numbers in **bold** refer to volume 2.