Neptune's Garden

THE STUNNING LIFE OF MACROALGAE

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Content

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Octopus's Garden
The stunning life of macroalgae

Introduction

The present photographical documentation of algal herbaria is based on a herbarium in the University of Cologne collected by Dr. Karl-Heinz and Dr. Gerlinde Linne von Berg in field excursions to Brittany and the West Mediterranean sea beginning in the end of the 1970ies. Starting with this joint herbarium, Josh Westrich continued with his herbarium studies evaluating the algal herbarium collections of "Botanische Staatssammlung München"; Curator: Dr. Dagmar Triebel. Here especially the herbaria of Dr. Werner Dietrich and Prof. Kurt Adolf Santarius, both Heinrich-Heine University, Düsseldorf, and Prof. Hans Rudolf Jürke Grau, Ludwig Maximilians University of Munich, were photographed. The specimens shown in this book are of great aesthetic value, but also in regard to science: When a new algal species is described, a "type specimen" has to be deposited in a herbarium and scientists have to refer to this "type" when identifying algae. All information about distribution of macroalgae is mainly based on herbaria. Thus we know about invasions of introduced algae and the decrease or loss of species can be monitored by herbaria. Forms and varieties of species can be described, when herbarium specimens from different locations of the world are compared. And last but not least, DNA preparations can be made from herbarium material for sequencing and so also a molecular comparison with the type is possible.

In this book additional information is given about each macroalgal specimen depicted: actual name based on "Algaebase", additional scientific information about life cycles, the geographic distribution, location in vertical profile of the intertidal region, the main features of the three large classes of macroalgae, endosymbiotic origin of algae, industrial use, physiological and morphological adaptations to specific habitats. The pictures and texts are not arranged according to taxonomy, but in connection to the chapters listed in "Content". As a lot of technical terms had to be used, they are explained in the "glossary" at the end of this book. Persons who want to know more about algae may look at the list of literature, which were used to compile the texts.

Desmarestia ligulata

(stackhouse) j.v. lamouroux

Brown algae (Phaeophyceae)

In this collection approximately 200 herbarium specimens are photographed. Herbaria of higher plants are well known and are used to document the occurrence of certain species. Therefore obligatorily a label is added noting the location and date of the collection, the name of the collector and the scientific name of the plant. When the person that identified the plant is not the collector, his/her name is added, too. The herbarium specimen allows other persons to compare it with plants from other parts of the world, to correct the result of determination or to verify morphological variabilities. The very first specimen deposited in a herbarium, normally connected with a formal description of the new species, is called the "type specimen". Authors using this species name have to refer to this type specimen. By comparing different herbaria the worldwide distribution of each species can be investigated. If the morphological variability is high enough, taxa below the species level can be defined. And last but not least with modern methods of DNA analysis small portions of the specimen are sufficient to compare them with probes taken in the field. Algae, especially macroalgae, can also be collected in herbaria. In this collection exclusively macroalgae are shown, most of them from marine localities in Europe, some of them from other parts of the world. The brown alga *Desmarestia ligulata* shown above is found worldwide. The specimen shown has a length of ca. 30 cm.

Desmarestia ligulata

(stackhouse) j.v. lamouroux

Brown algae (Phaeophyceae)

Normally the algae are collected on a field excursion in order to produce herbarium specimens. Therefore typical macroalgae fitting the average of the population in size and habit are taken from the nature. The specimen should cover all characters needed for the identification including the holdfast with which the thallus is attached to the substrate. Also – if possible – reproduction stages should be on the thallus. This can be sporangia or gametangia or in a few cases vegetative propagules. Prior to the drying process the species must be identified using appropriate identification keys (see "literature"). A preliminary label should be added to the herbarium sheet. The algal thallus should be arranged on the sheet in order to show the natural habit in nature. Then the algae are dried in a press: The cell walls of the algae contain sticky substances so they stick by themselves on the paper when drying. Typically the water of the specimen is removed by adding newspapers and exchanging it once a day at least. In order to avoid sticking of the algae to the newspaper, nylon tissue should be draped between the alga and the newspaper. After 5-10 exchanges of drying paper the specimen is ready and a label containing the data needed (see left page) should be sticked on the sheet. The collected algae can be added to an official collection (museum, university etc.). The collector of the two Desmarestia specimens was Prof. Jürke Grau, University of Munich, Botanical Garden. The specimen shown has a length of ca. 30 cm.

Dictyota dichotoma

(Hudson) J.V. Lamouroux

Brown algae (Phaeophyceae)

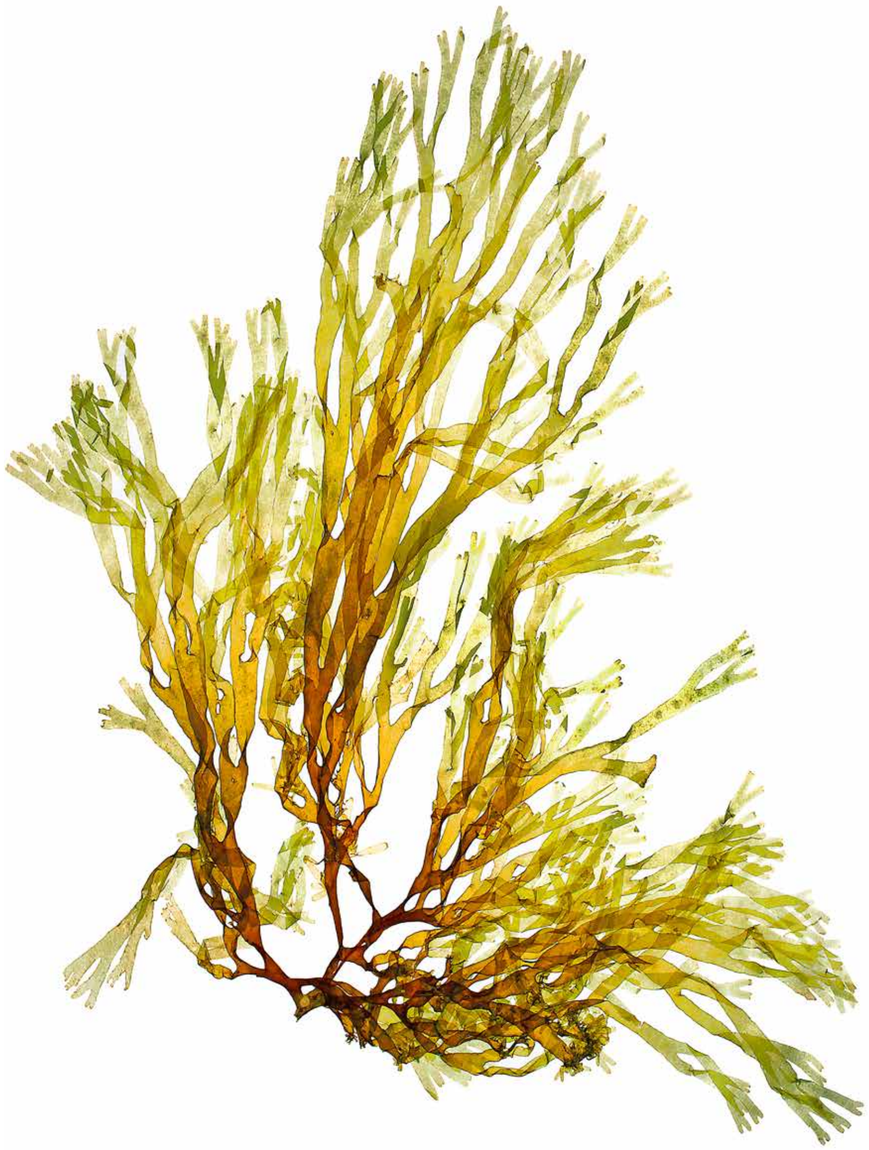
- Approximately 2.5 billion years ago a group of bacteria today called blue-green algae (Cyanobacteria, Cyanophyceae) invented the photosynthesis. Since then the terrestrial atmosphere is containing oxygen. Before the world was dominated by anoxic bacteria for which oxygen was a toxic substance. So the appearance of blue green algae is crucial for the evolution of today´s life. A world with animals, plants and eukaryotic algae we encounter today would not be possible without the invention of the O_2- developing photosynthesis. In the billions of years after this big bang in the evolution of life the stunning diversity of organisms could evolve: The eukaryotic algae, the plants, the fungi and the animals.

- Today the evolution of eukaryotic algae is well known and is connected with endosymbiotic processes: The uptake of a cyanobacterium by a heterotrophic eukaryote followed by domestication of the endosymbiont. The former cyanobacterium was reduced to a photosynthetic organelle called chloroplast in green algae or rhodoplast in red algae. This type of endosymbiosis is known as "primary endocytobiosis".

- In a second step – the so called "secondary endocytobiosis" - a heterotrophic eukaryote took up a eukaryotic alga (a red alga as we now know by phylogenetic analyses). Again the alga taken up was domesticated und reduced to a plastid.

- A lot of major algal groups (such as diatoms and brown algae) evolved from this secondary endocytobiosis.

- *Dictyota dichotoma* shown above belongs to this latter group (secondary endocytobiosis). It is an abundant species in the tidal and subtidal zone in Brittany and the North Atlantic. The specimen has a length of about 20 cm.



Desmarestia ligulata

(Stackhouse) J.V. Lamouroux

Brown algae (Phaeophyceae)

- From a practical point of view one can differentiate between microalgae and macroalgae. Normally microalgae can only be seen with a microscope. A lot of algal groups nearly exclusively contain microalgae.

- The **Gold algae** (Chrysophyceae) are confined to freshwater habitats and comprise flagellated unicellular organisms and colonies.

- The **Cryptophyceae** are flagellated unicellular organisms occurring in the freshwater and in marine habitats. The Cryptophyceae play an important role as a "missing link" in the theory of "secondary endocytobiosis" due to the fact that a rest of the nucleus of the endosymbiotic eukaryote has survived the long timespan of evolution.

- The **Cyanobacteria** are unicellular or filamentous organisms – some of which can also build up macroscopic aggregates.

- The **Diatoms (Bacillariophyceae)** characterized by a shell of silica – are a prominent group of microalgae due to its amazing number of species and the worldwide distribution in all kinds of habitats (marine, freshwater, soils, arctic ice...). The diatoms are responsible for 25 % of oxygen in the atmosphere.

Macroalgae

- Among the numerous groups of algae there are only three in which macroalgae are enclosed:

- The **Green Algae** (Chlorophyta and Streptophyta)
- The **Red Algae** (Rhodophyta)
- The **Brown Algae** (Phaeophyceae)

- *Desmarestia ligulata* has a worldwide distribution and is adapted to cold moderate conditions. Length of the specimen: ca. 20 cm.

Desmarestia ligulata

(Stackhouse) J.V. Lamouroux

Brown algae (Phaeophyceae)

The different species of the genus *Desmarestia* are different in morphology and mode of life. The thallus of *Desmarestia ligulata* is flattened compared to the cylindrical species *D. aculeata* and *D. viridis*, both occurring also in Europe. These three European species reach a length of about 100 cm, but often less than 50 cm. This is in contrast to the *Desmarestia* species in other parts of the world where the thalli reach a length of some meters.

D. ligulata and *D. viridis* have an annual mode of life whereas *D. aculeata* is a perennial macroalga. Interestingly the two annual *Desmarestia* species contain a high concentration of sulphuric acid in their vacuoles – pH-value 1.0 or less. Possibly the algae are so protected from being eaten by sea urchins and snails. There are 25 taxa on the species level and below. Information about the number of species, the validity of names and the worldwide distribution of algal taxa can be obtained from the database "Algaebase": www.algaebase.org/

Compared to *Dictyota dichotoma* all species of *Desmarestia* have a dominant main axis. This is also true for the side branches of first order that are dominant to branches of second order etc. In other brown algal genera, eg *Fucus* and *Dictyota* there are no main axis: When branching, two ramuli of mostly identical value are produced. The orders of brown algae are characterized by their life cycles (explained in chapter 4). It is notable that all *Desmarestia* specimens found in herbaria present only the sporophytic part of the life cycle.

Dictyota dichotoma

(Hudson) J.V. Lamouroux

Brown algae (Phaeophyceae)

Dictyota dichotoma is a species of worldwide distribution. In contrast to Desmarestia the thallus of Dictyota has no main axis. The thallus is growing with an apical cell which from time to time divides anticlinal resulting in two apical cells of the same size. Therefore the resulting branches are completely identical in growth and size. This type of branching is called "dichotomous", a term which is included in the species name. The thallus rarely exceeds the length of 15 cm and the lobes are up to 1.5 cm broad. In microscopical cross-sections the flat thallus is characterized by a small celled brownish photosynthetical layer surrounding a central layer of large mostly colourless cells. The missing of a mid-ridge distinguishes Dictyota from the somewhat similar *Dictyopteris polypodioides*.

The genus *Dictyota contains* 91 species/varieties. Not all of them are dichotomously branched. When one of the two branches is getting more dominant the branching mode is called "anisotomous". The growth with a dominant main axis is called "monopodial".

In some collection sites *Dictyota dichotoma* the population is decreasing e.g. Helgoland. The reason for this is unknown. In comparison the population of other species, e.g. *Codium fragile* is increasing (Kornmann, P. and Sahling, P.-H., 1989).

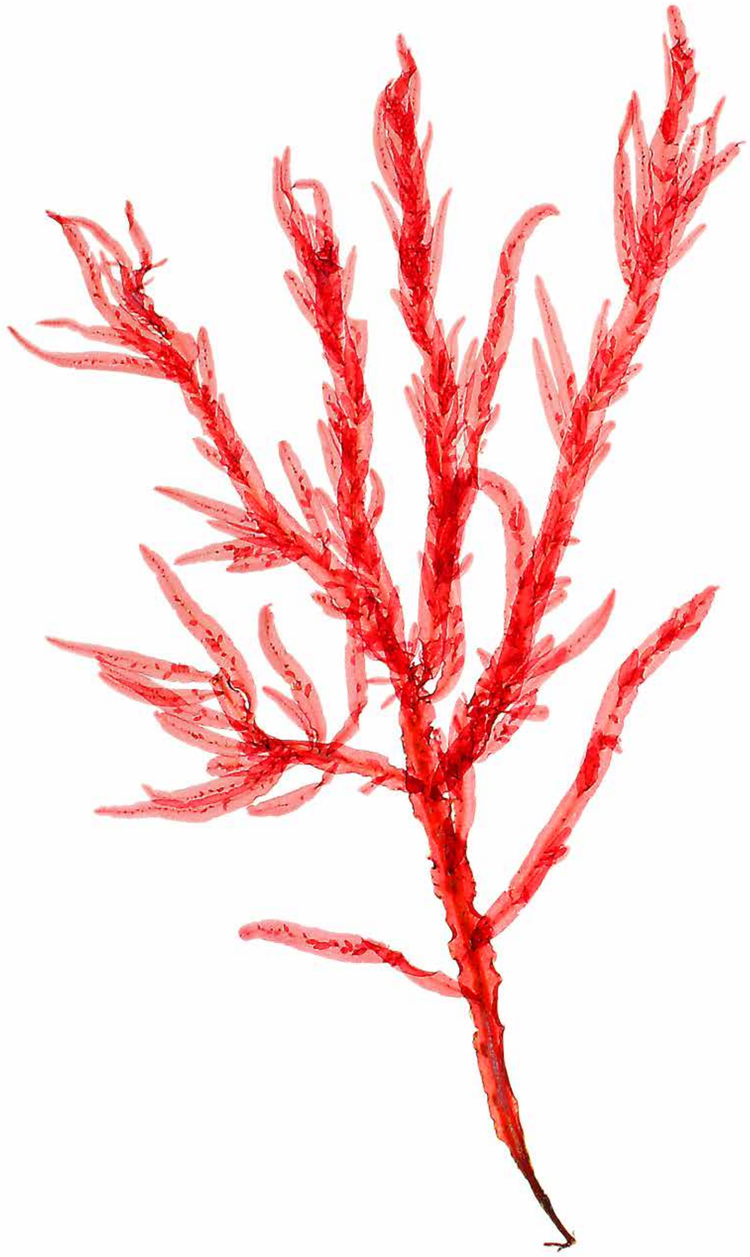
Gastroclonium ovatum

(Hudson) Papenfuss

Red algae (Rhodophyceae)

The definition of the term algae leads to conflicts: Some authors include the Cyanobacteria, because they produce oxygen like the eucaryotic algae, others exclude them, because of the procaryotic organization of the "blue green algae". This distinction would be valid, if the "rest of eucaryotic algae" would build a consistent phylogenetic group. But that is not true. Modern systematics comprise nine more or less distant eucaryotic algal groups: Glaucoplantae, Rhodoplantae, Viridiplantae, Heterokonotphyta, Haptophyta, Cryptophyceae, Dinophyta, Euglenophyceae and Chlorarachniophyta. And they include the Cyanobacteria. Algae are a polyphyletic group which means that the different groups mentioned above are only loosely related to each other, when judged by the evolutionary.

A fitting definition of the algae might be: A lifeform with permanent oxygen producing photosynthesis. The higher plants are excluded although it is well known that they have definitely derived from a special green algal group, the Streptophyte algae. *Gastroclonium ovatum* is one of the numerous red algae (Rhodophyceae) depicted in this book. It is an Atlantic species distributed in both hemispheres. Twelve species of this genus are presently accepted worldwide. The thallus can reach a length of 25 cm.



Hypoglossum hypoglossoides

(Stackhouse) Collins & Hervey

Red algae (Rhodophyceae)

The definition of algae excludes some organisms that contain algae as symbionts, Cyanobacteria as well as eucaryotic algae. The endosymbionts are not reduced to organelles and are capable to live independently from their host. Hosts are the organisms containing the endosymbiotic algae. A lot of such endosymbioses are known. Ciliates like *Paramecium bursaria* and Rhizopoda of the genus *Difflugia* contain the green alga Chlorella as endosymbiont. Most corals in the reefs are not able to live without the Dinoflagellate *Symbiodinium*. The bulk of lichens living on trees and rocks are symbioses of fungi with the green alga and/or Cyanobacteria. The most frequent endosymbiont of homoeomeric lichens is the green alga *Trebouxia*, in the case of heteromeric lichens it is the genus *Nostoc*. Symbiosis with Cyanobacteria is also known in some Bryophytes, the water fern Azolla and in special roots of cycads. In all these cases the endosymbiotic algae are occurring also in free nature.

In *Hypoglossum hypoglossoides* and in all the other eucaryotic algae, the endosymbiont has become dependent on the host. A large portion of the DNA of the ancestral endosymbiotic cyanobacterium has been taken up by the nucleus of the host and the "rhodoplast" is not any more viable in free nature.

Hypoglossum hypoglossoides has a worldwide distribution and is growing on rocks and on algae at the low tidal level and is normally not longer than 10 cm. 30 *Hypoglossum*-species are known worldwide.

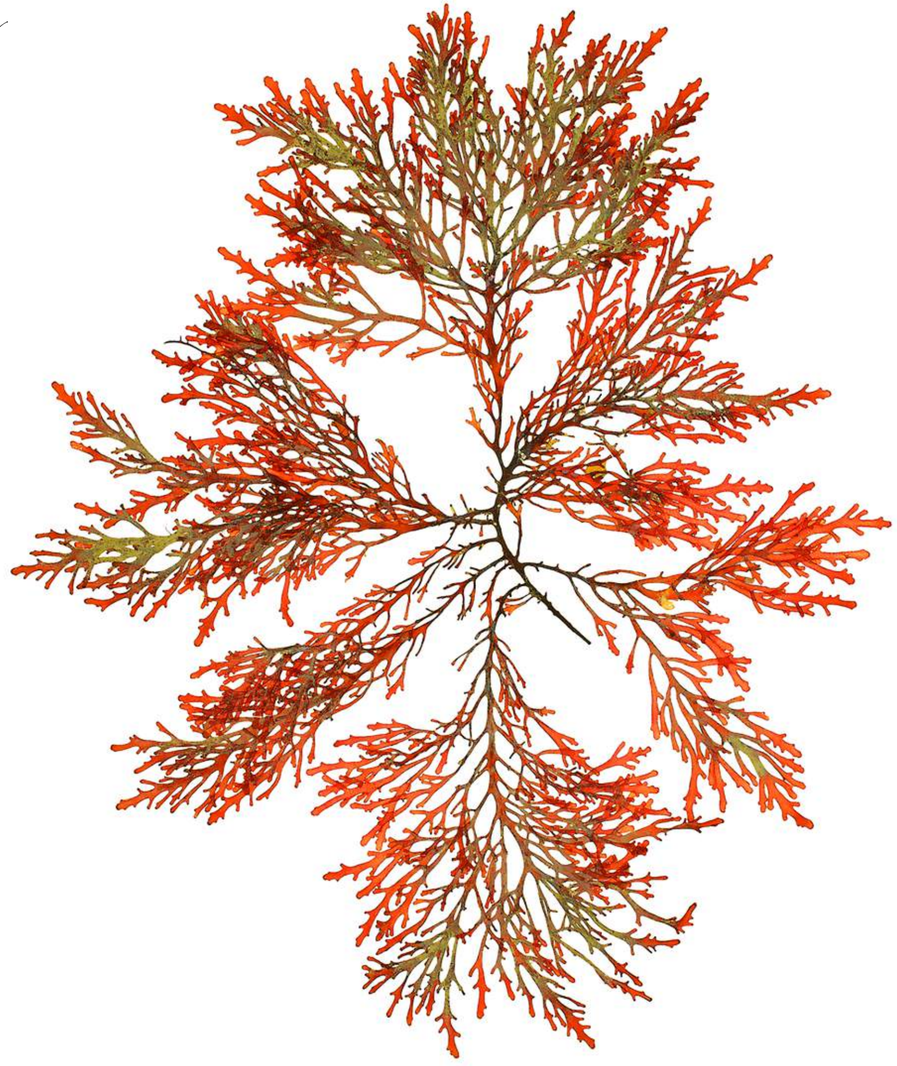
Osmundea pinnatifida

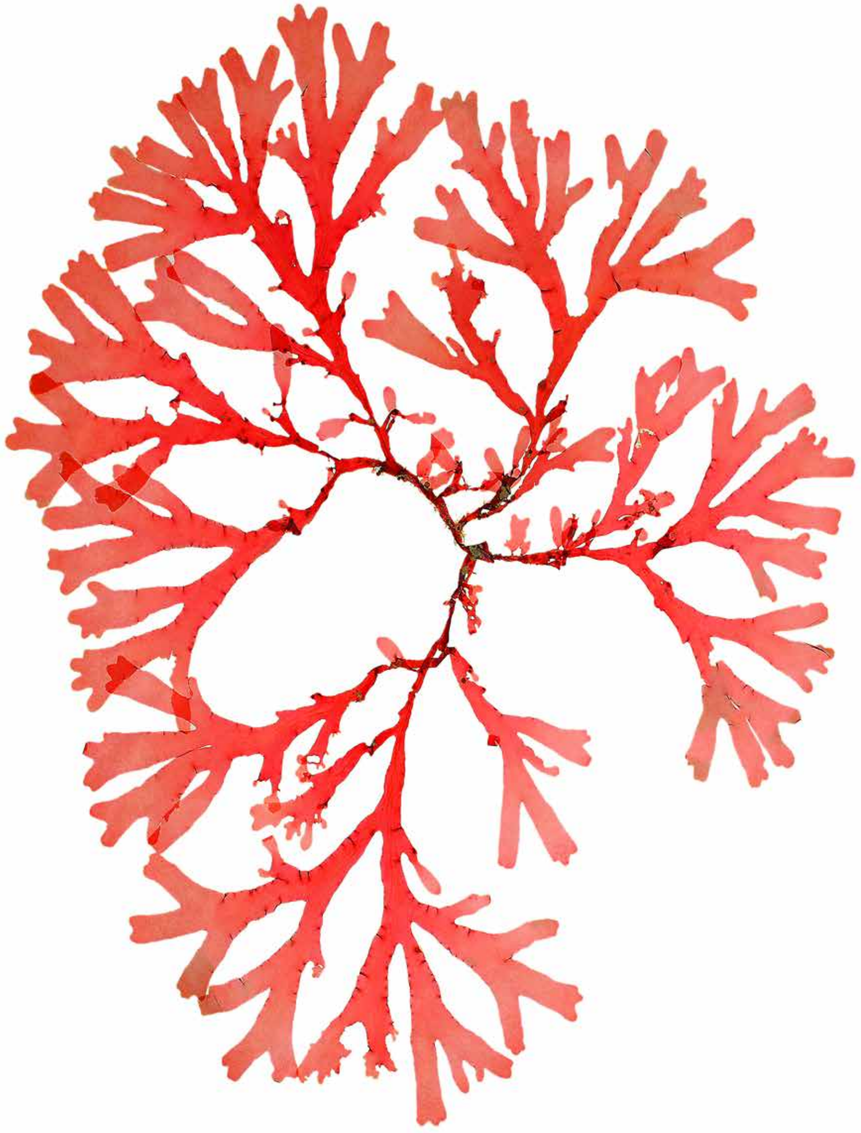
(Hudson) Stackhouse

Red algae (Rhodophyta)

The three groups of macroalgae are the red algae, the green algae and the brown algae. *Osmundea pinnatifida* is a typical member of the red algae – Rhodophyta. This group contains 7145 species according to Algaebase. Most red algae are found in marine habitats in coastal seawater. There are only a few genera living in freshwater or in terrestrial habitats. Some extremophilic species like *Galdieria* and *Cyanidioschyzon* are adapted to hot and acidic fonts. Most red algae are multicellular, but especially the terrestrial and the extremophilic species are unicellular. There is a high diversity in the red algae which is reflected by the division into 8 classes: Bangiophyceae, Compsogonophyceae, Cyanidiophyceae, Florideophyceae, Porphyridiophyceae, Rhodellophyceae, Stylonematophyceae and a group named "Rhodophyta incertae sedis". The class Florideophyceae is by far the largest group of the red algae containing more than 6794 species (95%). That's why most of the red algae shown in this book belong to the Florideophyceae.

Osmundea pinnatifida is found at the low tide level on rocks and normally doesn't exceed a size of 10 cm. The traditional phycologists – people that are familiar with algae taxa– perhaps know this alga better under its former name "*Laurencia pinnatifida*". The genus *Osmundea* consists of 22 accepted species.





Cryptopleura ramosa

(Hudson) L. Newton

Red algae (Rhodophyta)

Modern taxonomists try to group the organisms according to their phylogenetic relationships. The lowest taxonomic level is the species. Closely related species are united into a genus; related genera are pooled in a family; families are united to an order; related orders can be combined to classes and classes to a phylum. Since Carl von Linné the rule of binominal nomenclature prescribes that the scientific name of every species has to be a combination of a genus name and a so called epitheton. In our case the species name is *Cryptopleura ramosa*. "*Cryptopleura*" is the name of the genus, "*ramosa*" is the "epitheton":

- 20 different species belong to the genus *Cryptopleura*.
- 140 genera (452 species) are united to the family Delesseri**aceae**.
- 10 families (3640 species) constitute the order Cerami**ales**.
- The class Florideo**phyceae** comprises 33 orders (6790 species).
- And the phylum Rhodopyta contains 8 classes (7145 species)

Apart from the binominal species name there are special endings for

- families: "-**aceae**"
- orders: "-**ales**"
- classes: "-**phyceae**"
- and phyla: "-**phyta**"

Chaetomorpha aerea

(Dillwyn) Kützing

Green algae (Chlorophyta, Ulvophyceae)

Green plants – Viridiplantae – can be divided in two lineages: The Chlorophyta (6429 species) and the Streptophyta (4939 algal species). The streptophytic algae and the land plants are sister groups regarded from the phylogenetic point of view and are almost completely restricted to freshwater and terrestrial habitats. In contrast, the Chlorophyta contain freshwater- and marine species. So the green algae shown in this book are exclusively members of the Chlorophyta.

In recent systematics the Chlorophyta comprise numerous classes of complex phylogenetic relationship. Only a few are mentioned here: Prasinophyceae, Pyramimonadophyceae, Chlorodendrophyceae, Tebouxiophyceae, Chlorophyceae and Ulvophyceae. The first classes contain only forms of microscopical size, while in the latter two classes there are species that can be seen with the naked eye. They belong to different orders of Chlorophyceae that contain species with multicellular filaments but hardly suitable for a herbarium,, and the class Ulvophyceae containing a lot of macroalgal genera like *Ulva*, *Acetabularia*, *Halimeda*, *Caulerpa* and others.

Chaetomorpha aerea is an example for a large celled, unbranched filamentous marine green alga which is distributed worlwide. The genus *Chaetomorpha* consists of 67 accepted species. The filaments of this species can reach a length of 20 cm and a diameter of 0.5 mm.

Ulva flexuosa

Wulfen

Green algae (Chlorophyta, Ulvophyceae)

The genus *Ulva* is the origin of the names for the class "Ulvophyceae" , the order "Ulvales" and the family "Ulvaceae". Note the appropriate endings for the different taxonomic groups. According to the rules of nomenclature the higher taxonomic levels have to be based on a genus to which endings must be attached. Looking on the herbarium sheet you find the species name "*Enteromorpha lingulata*". This name is not at all similar to the name "*Ulva flexuosa*" given above. But this name is not due to a misidentification. It rather reflects the progress in taxonomy and scientific knowledge. In former times only two genera were strictly separated. Species with tubular thallus had to be assigned to the genus *Enteromorpha* whereas species with a flat two-layered thallus were identified as the genus *Ulva*. Checking the molecular phylogeny of this group where the relationships of different taxa are shown as a tree or "dendrogram", it could be shown that *Enteromorpha*- and *Ulva*-species are completely mixed up in the resulting trees: The identification of two genera on the basis of tubular or flat thalli is obsolete and the two genera have to be united. The rules of nomenclature say that in such a case the older genus name must be chosen. Currently the genus *Ulva* consists of 129 species. *Ulva flexuosa* is distributed worldwide. 10 forms and varieties are accepted.

The specimen shown has a length of ca. 25 cm.

Ulva linza

Linnaeus

Green algae (Chlorophyta, Ulvophyceae)

Ulva linza is a species that is also known under its old name "*Enteromorpha linza*". *Enteromorpha* was the former name of *Ulva* plants with a tubular thallus. *Ulva linza* has thalli that are up to 30 cm long and ca. 5 cm broad, tapering gradually towards the basis, attached to the ground by rhizoids. Very characteristic is the frilled margin of the plant. The thallus is tubular, but this is only visibleat the margins. In the middle of the flat leaflike thallus, the cells of the outer layers are pressed together resembling a tissue. Thalli are frequently in patches of more than 20 individuals on mussels and stones at the upper to lower eulitoral level, but also in rock pools. The life cycle probably is like that in *Ulva lactuca*, where sporophytes release haploid quadriflagellate zoospores. From these arise the gametophytes that release biflagellate gametes identical in size. After fusion of the isogametes a diploid sporophyte is built again. This isomorphic and isogamous life cycle was reported from North America and Japan. But from different parts of the world also populations are reported where only asexual reproduction occurs without meiosis. This can involve biflagellate as well as quadriflagellate zoospores. The sporophytes can be haploid or diploid. So the reproduction biology of *Ulva linza* needs further investigation.

chapter 2
Red, brown and green – three classes of macroalgae

Ulva linza

Linnaeus

Green algae (Chlorophyta, Ulvophyceae)

The genus *Ulva* is used in science for the research of morphogenesis. It was assumed in earlier times that interaction with bacteria could be a factor responsible for morphogenesis in the genus *Ulva*. For examinations of the interrelationship with other organisms, axenic cultures are needed. This can be achieved by the isolation of zoospores or zygotes and cultivation in sterile culture media. In experiments with axenic zoospores of *Ulva* it could be shown that no coordinated growth of *Ulva* thalli was possible in the absence of bacteria. They only perform some uncontrolled division and the cell aggregate doesn t look like *Ulva*. Isolation of different bacteria strains from the habitat of *Ulva* and cultivation of young *Ulva* in presence of the isolated bacteria showed that only a combination of *Ulva* with two strains of bacteria allowed the alga to perform a normal growth. They were the Bacteria *Roseobacter* and *Cytophaga*. The *Roseobacter* bacterium is responsible for the growth of the algal cells in one plane. *Cytophaga* is responsible for the formation of rhizoids that are responsible for the attachment of the *Ulva* plant to the substrate. Only the combination of these two bacteria allows the formation of the *Ulva*-thallus. The experiments were performed with *Ulva mutabilis*. But similar effects may be expected in other *Ulva* species like *Ulva linza*. And surely also in other Algae groups the examination of the interrelationships between different groups of organisms promise new results.

Ulva prolifera

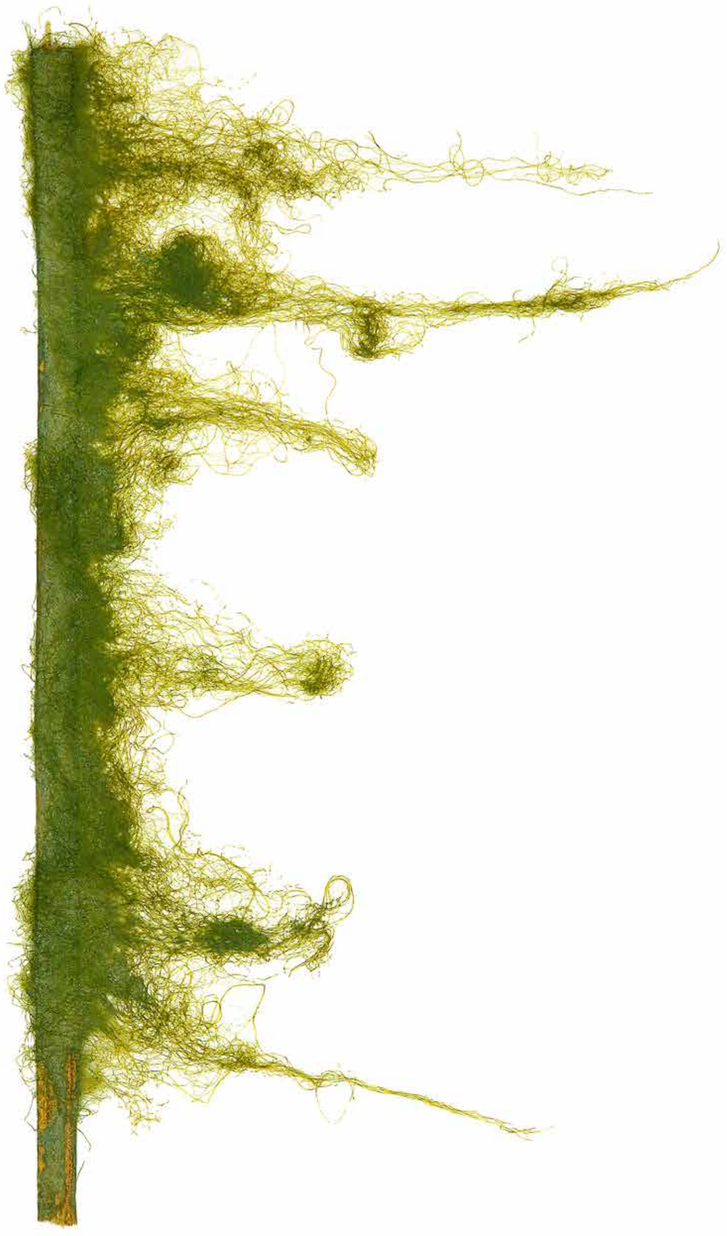
O. F. Müller

Green algae (Chlorophyta, Ulvophyceae)

Unlike *Ulva linza* *Ulva prolifera* is a species with a throughout tubular thallus. The central cavity measures only 12-15 µm. The thallus is branched which is also a difference to *Ulva linza*. When found in nature, the tubular thalli often form an interwoven network. A high variability in morphology is described. In which way the different morphotypes can be assigned to one or more species must be left for future examinations. *Ulva prolifera* has an isomorphic life cycle with a sporophyte producing quadriflagellate zoospores and a gametophyte producing biflagellate gametes.

The plant is found in different habitats like stones and mussels in eulittoral, epiphytic on other algae but also on the mud of estuaries. Some species like *Enteromorpha ahneriana* and *Enteromorpha torta* have been included in recent times. This is perhaps the reason for the high morphological plasticity of *Ulva prolifera*.

A lot of other Ulva species that were formerly assigned to the genus *Enteromorpha*, are described. They are all not easily to be recognized by their morphology. Maybe that in the *Enteromorpha*-like species of Ulva the molecular assay is the more effective way to identify species. But also the morphological plasticity of the *Enteromorpha*-like members of the genus *Ulva* has to be taken in account. The specimen shown is a fragment of seagrass of about 10 cm length.



Ulva sp.

Green algae (Chlorophyta, Ulvophyceae)

Ulva sp. shown left is a specimen of the old genus *Enteromorpha* which could not be assigned to a certain species. This is possibly a problem within all species of *Ulva* and the old genus *Enteromorpha*: The assignment to the *Ulva/Enteromorpha* complex is very clear, but the differentiation on the species level is difficult. In the class Ulvophyceae there are some orders in which the identification of species is equally problematic as in *Ulva*: In the order Ulotrichales containing the filamentous genera *Ulothrix*, *Acrosiphonia*, *Spongomorpha* etc. it is especially difficult to distinguish species within the genus *Ulothrix*. Also in the order Cladophorales, containing the genera *Cladophora*, *Anadyomene*, *Pithophora* etc., the differences between the species are almost undistinguishable. This is a problem especially in the freshwater species of the genus *Cladophora*.

And also in the order Bryopsidales, containing the siphonous genera *Caulerpa*, *Codium*, *Bryopsis*, *Derbesia*, *Halimeda* and *Udotea* the species delineation is sometimes difficult. Some authors don't accept the differentiation between *Bryopsis hypnoides*, *Bryopsis plumosa* and *Bryopsis lyngbyei*. Some species of the Byopsidales have a strongly heteromorphic life cycle (*Derbesia*) or their life cycle is diplontic (*Codium*). The specimen of *Ulva sp.* shown here has a length of about 10 cm.

Fucus vesiculosus

Linnaeus

Brown algae (Phaeophyceae)

Fucus is one of the most abundant members of the brown algae (Phaeophyceae) in Europe. Although there are a lot of classes with plastids that arose by secondary endocytobiosis, only the brown algae have macroscopic representatives. All the other classes – Chrysophyceae, Cryptophyceae, Dinophyceae, Haptophyceae and the large group of diatoms (Bacillariophyceae) – are microscopic algae occurring in the marine and freshwater phytoplankton. In contrast to this the brown algae exclusively contain multicellular representatives, one being the largest algae that exist. *Macrocystis*, a macroalga occurring in the Pacific Ocean, reaches a length of 45 m. Compared to *Macrocystis*, *Fucus vesiculosus* is rather small with its length of approximately 30 cm. The typical habitat of brown algae is the upper tidal zone in coastal regions all over the world. The distribution of *Fucus vesiculosus* is restricted to the northern half of the Atlantic; it is missing in the southern hemisphere and in the Pacific Ocean. As all seaweeds in the upper tidal zone, *Fucus* is resistant against wave action and also against drought. The thalli must survive more than 8 hours during low tide. During high tide they can stand upright in the water due to the series of gas bladders left and right of the central strand of the thallus. *Fucus vesiculosus* is the type species of the genus; this means that *F. vesiculosus* is the first Fucus species ever described.

Dictyopteris polypodioides

(A.P. De candolle) J.V. Lamouroux

Brown algae (Phaeophyceae)

Another brown algal species, more distributed in the Mediterranean region, is *Dictyopteris polypodioides*. It can't be confused with *Fucus vesiculosus*, as the typical gas bladders are missing and the thallus is only a little bit larger than 10 cm. In spite of the similarity to *Fucus* it is more related to *Dictyota* and is thus classified to the order of "Dictyotales". Fucus is naming its own order "Fucales". There are a lot of additional orders in the brown algae e.g. Laminariales and Desmarestiales that are named after genera and species represented in this book. For the classification of genera into the different orders the following characters are evaluated:

- Morphology of the thallus
- Reproductive structures
- Mode of growth
- Life cycles

So for the Fucales diplontic life cycles and "receptacles" are characteristic, whereas for the Dictyotales isomorphic life cycles and reproductive structures that are not arranged in receptacles are characteristic.

The genus *Dictyopteris* consists of 35 species. On the labels of the herbarium sheets the algae are named "*Dictyopteris membranacea*". According to the rule of priority, the species name is now *Dictyopteris polypodioides*.

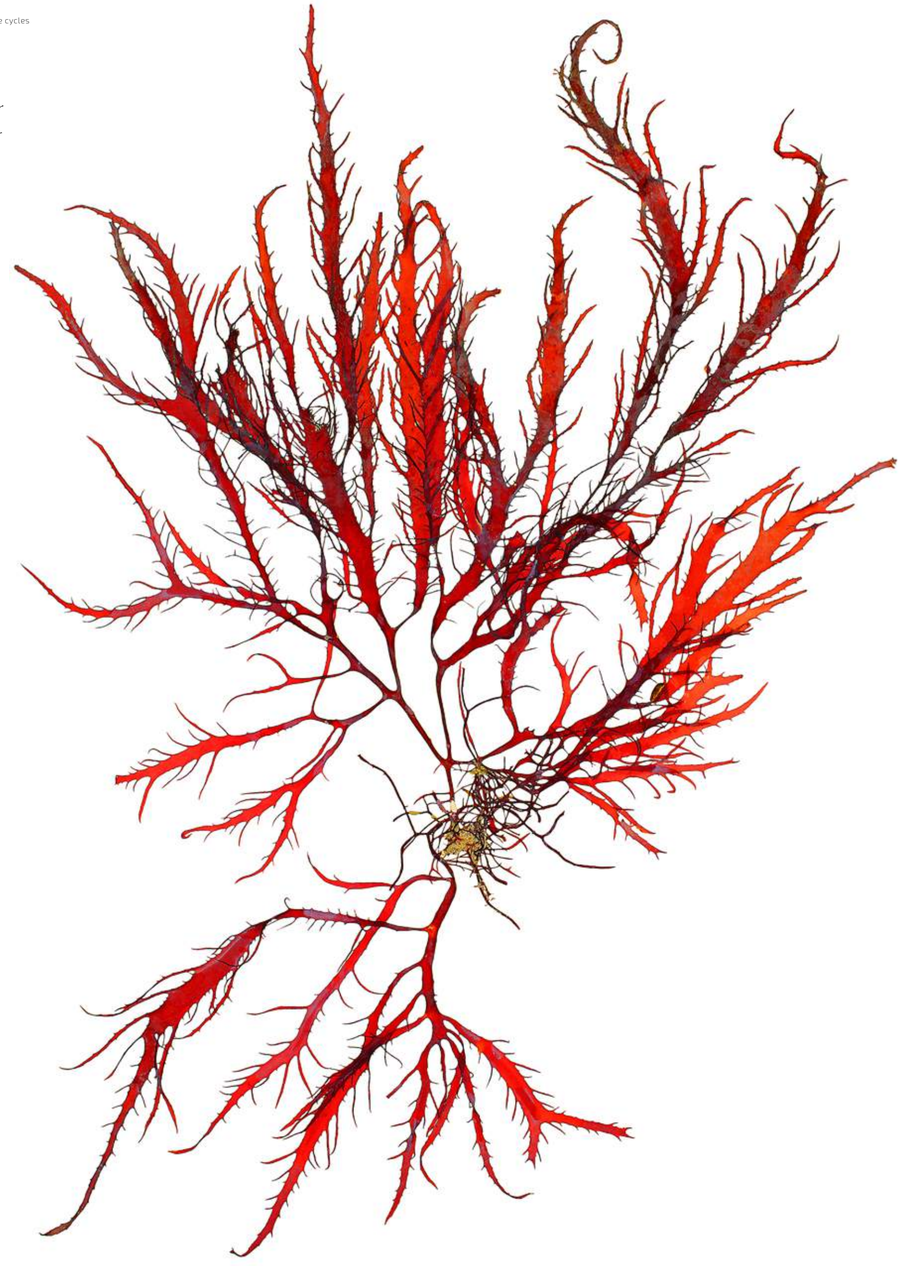
Calliblepharis jubata

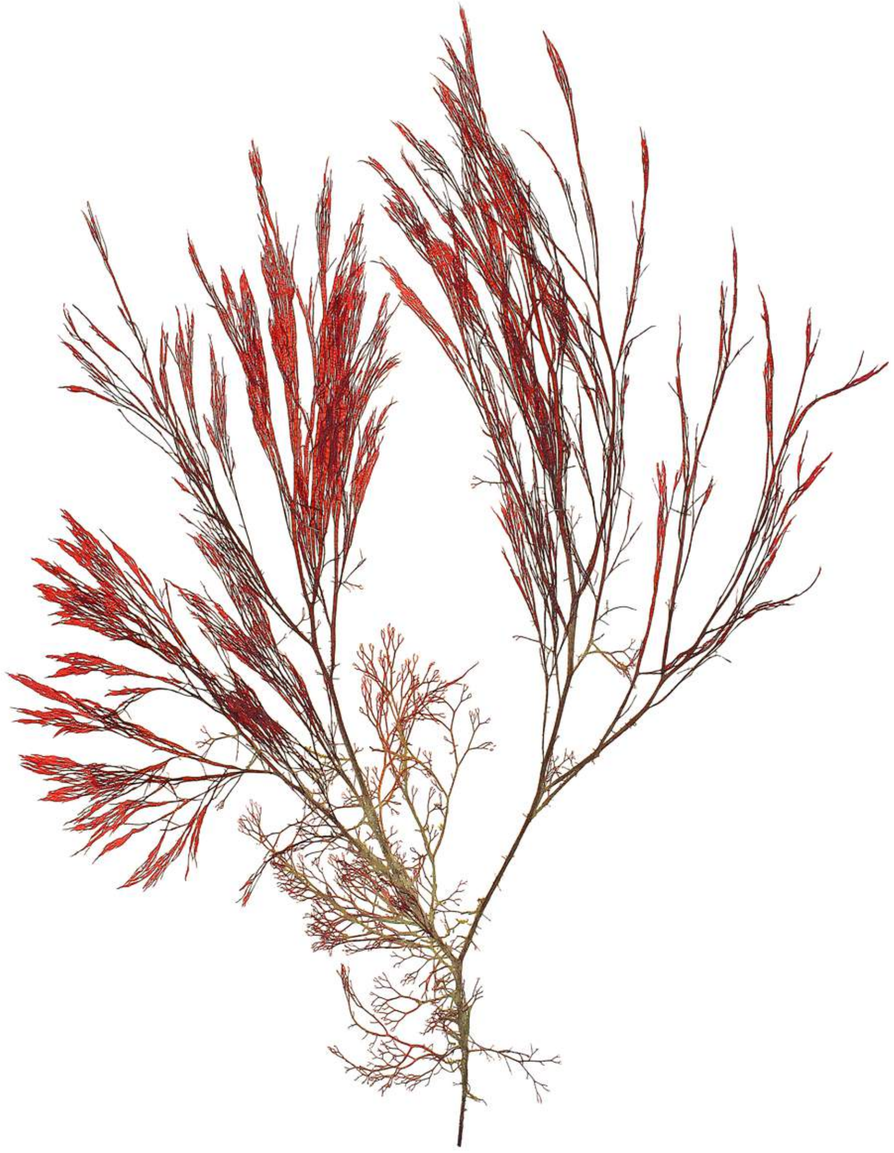
(Goodenough & Woodward) Kützing

Red algae (Florideophyceae)

Calliblepharis is a representative of the red algae. The scientific name of this class as well as the trivial name corresponds to the most evident character of the class: its red colour. Additional to chlorophyll a there are red and blue accessory pigments:phycoerythrin, phycocyanin and allophycocyanin. They mask the green colour of the chlorophyll. In the red algae the red pigment phycoerythrin is often dominant, possibly as an adaptation to their occurrence in deeper water where the light composition is shifted to the blue light. Furthermore the red algae never have flagellated cells in their life cycles. In most other algal groups at least during reproduction flagellated cells are present. Red algae have a unique life cycle in which additionally to the gametophyte and the sporophyte a new type of generation is developed: the carposporophyte. Details to these complex life cycles of red algae are mentioned later in this book. It must be stated that due to pigment composition not all red algae are red. The amount of phycoerythrin which is sensible to sunlight can be low in species that occur in sunny locations. The colour of the thallus then is more brownish or olive green.

Calliblepharis is a marine algal genus currently comprising nine species. The thalli of Calliblepharis jubata can reach a size of 25 cm.





Polysiphonia elongata

(Hudson) Sprengel

Red algae (Florideophyceae)

Microscopy of the thallus of the red algae has revealed that there is no real tissue known in the leaves and stems of higher plants. In contrast there is a network of interwoven filaments – a so called pseudoparenchyma – similar to that known infungi. Two completely different architectures have been found:

1. The **multiaxial** type consists of a lot of filaments running parallel and branching near to the surface of the thallus.

2. In the **uniaxial** type a central filament is building a main axis and lateral subordinate branches surround the central filament or build up a leaf-like pseudoparenchyma. An example for the multiaxial type is *Calliblepharis* (see left page) whereas *Polysiphonia elongata* belongs to the uniaxial type. Here the thallus is thread-like and shows a central filament which is surrounded by four and more pericentral cells. The distribution of *Polysiphonia elongata* is worldwide in coastal water. The threads can reach a length of 30 cm. With 991 species the genus *Polysiphonia* is one of the largest genera in red algae. Characters for the differentiation of the species are:

- Diameter of the thallus.
- Length of the thallus.
- Number of the pericentral cells.
- Additional cortication of the thallus.

Students learn the complex life cycle of red algae by *Polysiphonia*. The specimen shown has a length of ca. 20 cm.

Calliblepharis ciliata

(Hudson) Kützing

Red algae (Florideophyceae)

In contrast to *Calliblepharis jubata*, *Calliblepharis ciliata* has a broader thallus (7 cm). The length of the thallus can reach 30 cm. The proliferations at the margin and on the surface of the thallus normally reach a length of ca. 0.5 cm. The thallus is fixed on the substrate with long branched rhizoids. At the top of the thallus the lobes can be branched dichotomously. The structure of the thallus is uniaxial, visible only at the top of the thallus. In cross-sections no central filament can be recognized. The flat thallus feels somewhat cartilaginous. The gametophytes are dioecious; gametophytes and tetrasporophytes are isomorphic. In male plants the spermatangia are in larger groups (sori) on the surface of the Thallus. In female plants the carpogonia and later on the carposporophytes are found near to or in the proliferations at the margin of the blade. On tetrasporophytes also the tetrasporangia are in sori on the surface or at the margin of the thallus. In the tetrasporangia the spores are arranged in rows of four. The plants are variable in size and shape. They are annual, occurring attached on rocks and epiphytic on other algae during the summer. In late autumn to spring they are detached and swim in the drift.

Calliblepharis ciliata is a plant mainly of the sublittoral and is distributed in the North- and South Atlantic. Detached specimens are found also in the eulittoral. The specimen shown has a diameter of about 20 cm.

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Lifestyle – the major groups of algae are characterized by their life cycles

Calliblepharis ciliata

(Hudson) Kützing

Red algae (Florideophyceae)

Calliblepharis ciliata is a member of the order Gigartinales. This order, containing 906 species, is characterized by mostly erect pseudoparenchymatous thalli: in rare cases the thalli can be crustose. The carpogonium arises from an apical cell and the carposporophyte is starting with the development when after fertilization the zygote nucleus is transferred to an "auxiliary cell", which is normally an undifferentiated cell of the carpogonial branch. Interestingly, in some genera not only one carpospores, but four spores (carpotetrasores) are released from the carposporangium. Gametophytes in this order can be isomorphic to the tetrasporophytes or strongly hetermorphic. The delineation from the closely related order "Cryptonemiales" is sometimes difficult. Here are some families, whose genera are mentioned in this book:

- Polyideaceae: *Polyides rotundus*
- Fucellariaceae: *Furcellaria lumbricalis*
- Phyllophoraceae: *Phyllophora sicula*, *Calliblepharis ciliata*, *Calliblepharis jubata*
- Plocamiaceae: *Plocamium cartilagineum*
- Gigartinaceae: *Chondracanthus teedei*, *Chondrus crispus*

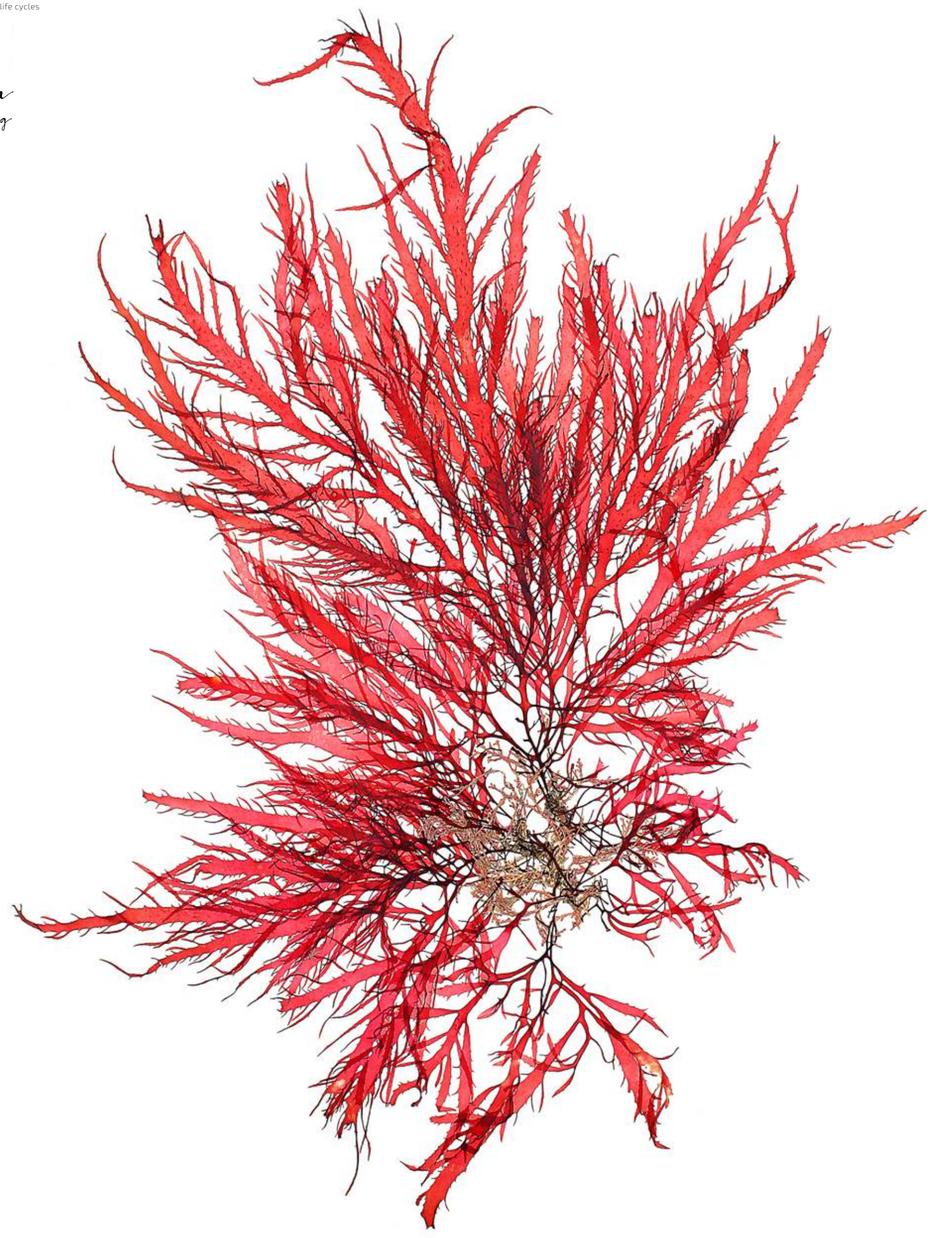
In this order species with uniaxial as well as multiaxial thalli occur.

Calliblepharis jubata

(Goodenough & Woodward) Kützing

Red algae (Florideophyceae)

Calliblepharis jubata is a red alga with a flat pinnate thallus. Surveying alcohol preserved material in the microscope reveals that the cytoplasm is fixed to every cross wall where descendent cells are connected. This is the case because in the Florideophyceae every cross wall is closed by a "pit connection" and the plasma membrane is going through this pit. Here the plasma membrane is adhering to the common cross wall. On the ultrastructural level it can be seen that the cell division is incomplete and an open whole between the cells is closed by a proteinaceous plug. In reality this pit is not a pit and the connection is not a connection. So in the microscopical picture it is easy to see which cells are derived from one another. These "connections" are the primary pit connections. In many Florideophyceae there are also secondary pit connections. In *Polysiphonia* for example the pericentral cells are connected to one another in longitudinal direction. Such secondary pit connections can occur in all Florideophyceae. In the microscope secondary pit connections cannot be distinguished from the primary ones. Also in *Calliblepharis* where the thallus structure is uniaxial there are many secondary pit connections between the central axis and the basal cells of the lateral branches. Due to the lot of secondary pit connections it is often impossible to identify the central filament of *Calliblepharis* in microscopical sections. The specimen shown has a length of about 15 cm.



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Lifestyle – the major groups of algae are characterized by their life cycles

Calliblepharis jubata

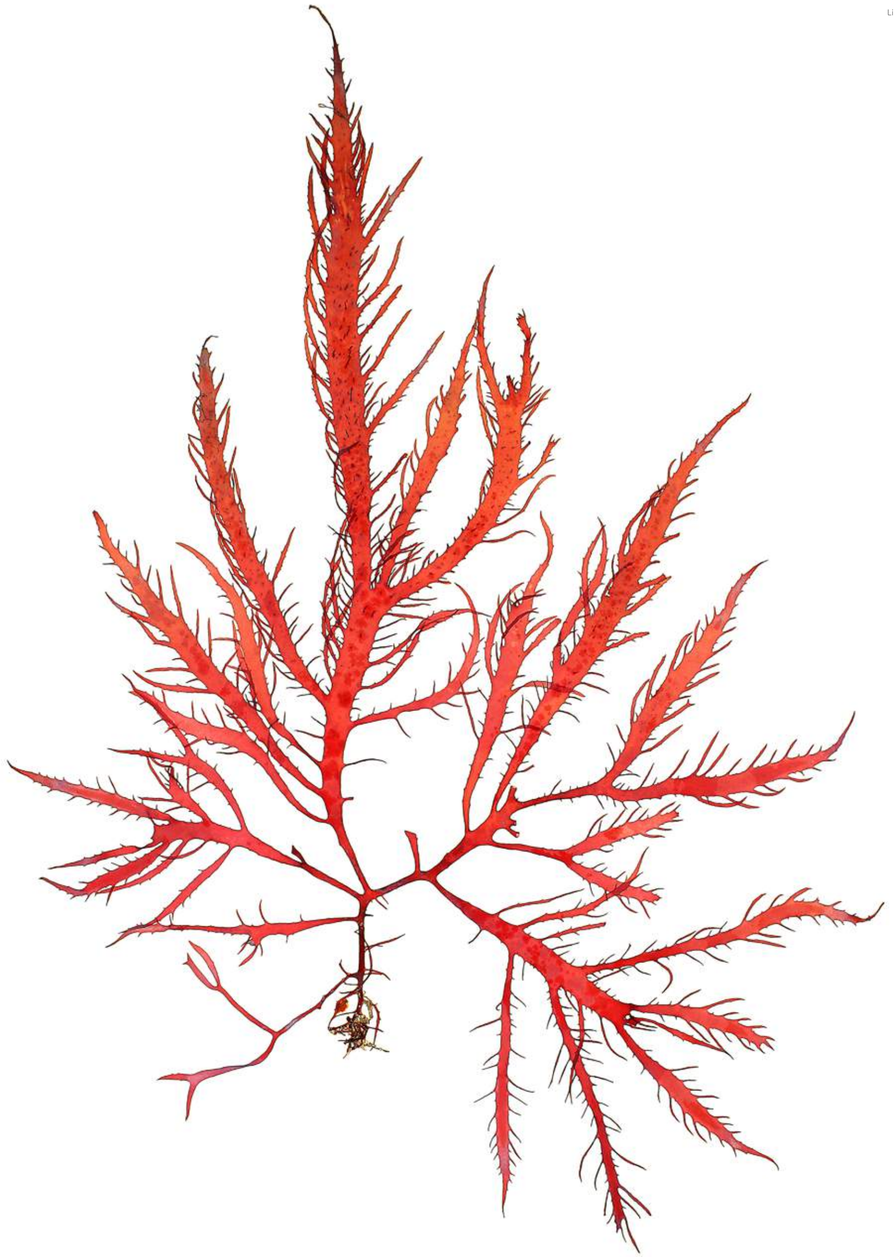
(Goodenough & Woodward) Kützing

Red algae (Florideophyceae)

Calliblepharis jubata is a red alga with a flat pinnate thallus. In the microscope red algae show starch grains that are not included in the rhodoplasts, the so called "floridean starch". This is thought to be the long term storage of energy in the red algae. Analysis of the products of photosynthesis in red algae shows that the primary product is floridoside (O-α-D-galactopyranosyl-(1,2)-glycerol). This substance is increasing in amount with the salinity of the surrounding medium and it can be concluded that it is responsible for the osmoregulation of the red algae. Looking for the reserve polysaccharides in algae it can be said that only in the green algae and the higher plants reserve polysaccharides are produced inside of the chloroplast (plastidial starch). In all the other groups of algae the polysaccharides are deposited outside of the plastids. The most important:

- Red algae: Extraplastidial floridean starch
- Euglenophyceae: Extraplastidial paramylon
- Brown algae and diatoms: Extraplastidial chrysolaminaran in vaculoles
- Dinophyceae: Extraplastidial starch.

The specimen shown has a length of about 10 cm.



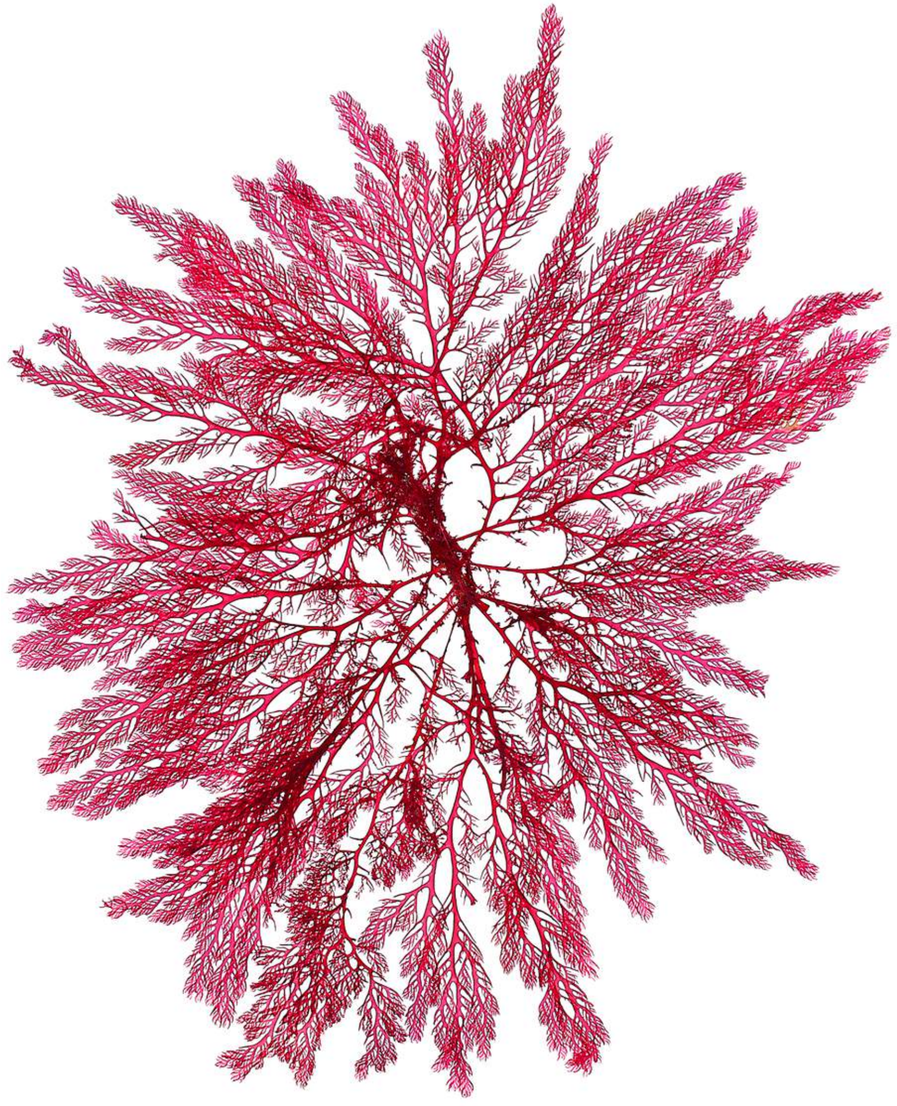
Plocamium cartilagineum

(Linnaeus) P. S. Dixon

Red algae (Florideophyceae)

Plocamium cartilagineum is an alga of the class Florideophyceae, the red algae. The red colour of most members of this class is resulting from the additional red pigment phycoerythrin. This is a protein associated with phycoerythrobilin which is strictly spoken the component giving the red colour to the protein. There are other pigments of the same chemical class: Phycocyanin and allophycocyanin that are blue in colour. Also in these cases the component giving the colour to the protein is phycocyanobilin. These pigments are called "phycobilins". Phycoerythrin, phycocyanin and allophycocyanin are arranged in superstructures which are called "phycobilisomes". The centre of this phycobilisome consists of three allophycocyanin - units from which 6 rays of phycoerythrin and phycocyanin are radiating. The relative amounts of phycoerythrin and phycocyanin are of great influence on the colour of the alga. So in *Plocamium cartilagineum* and many of the marine red algae phycoerythrin is the dominant component. The freshwater red algae *Lemanea* and *Batrachospermum* are more olive in colour because phycocyanin is predominant.

Phycobilisomes are not only present in red algae but also in Glaucophyta and the cyanobacteria, a strong evidence that the plastids of Glaucophyta and Rhodophyta are derived from endosymbiotic Cyanobacteria. The specimen shown has a length of about 10 cm.



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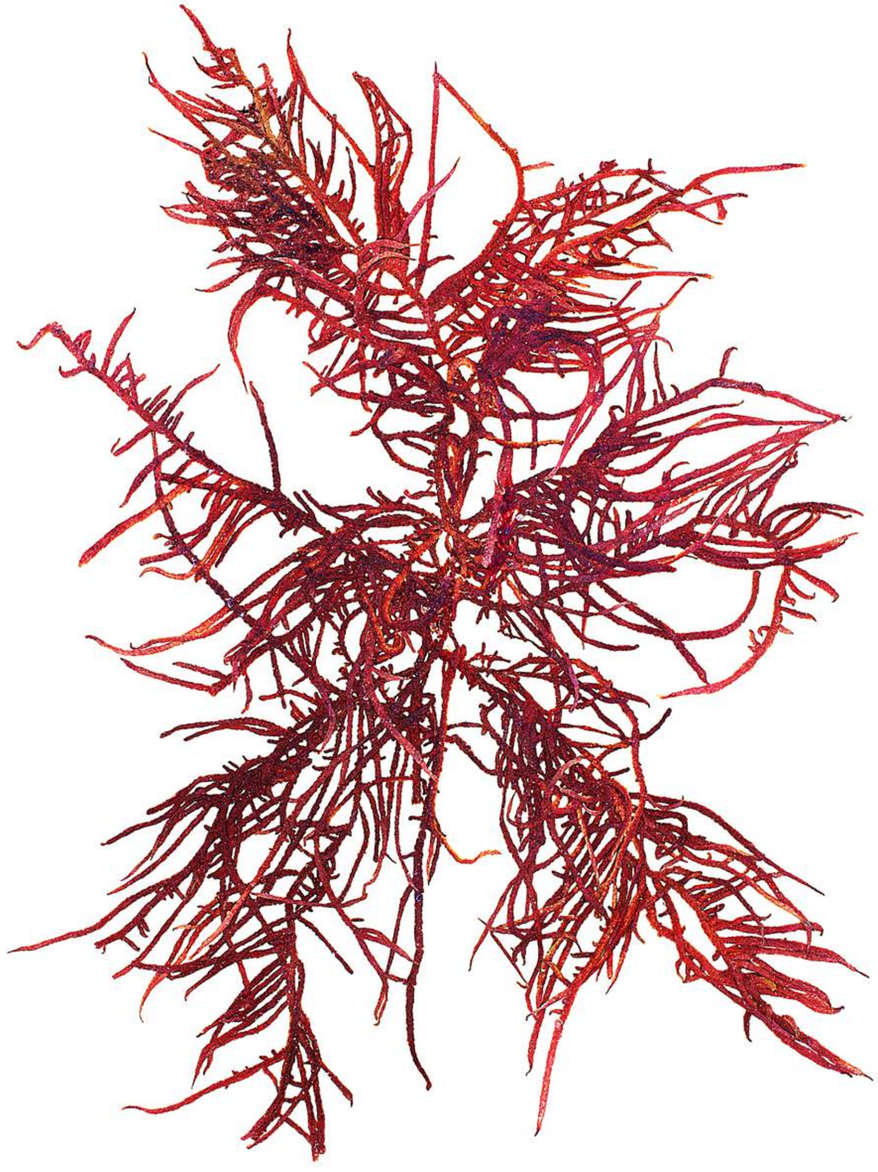
Lifestyle – the major groups of algae are characterized by their life cycles



Halurus equisetifolius

(Lightfoot) Kützing

Red algae (Florideophyceae)

Halurus equisetifolius is a red alga which is easy recognized by its thallus bearing verticillate branches. The thallus is attached to the substrate by an up to 1 cm broad disc. From this disc afew main axes are arising that normally are branched again. The diameter of the axis including the whorls of lateral branches is 2-3 mm. These lateral branches are again branched.

The main axis of this uniaxial thallus consists of large cells that are covered by rhizoidal cells later on. The plant has a dark red colour. The gametophytes are dioecious. Spermatangia are arranged in heads and are located at the basis of the whorl branches. Carpogonia are at the end of whorl branches. Tetrasporangia also at the end of whorl branch in an adaxial arrangement. Tetrasporophyte and gametophytes are isomorphic.

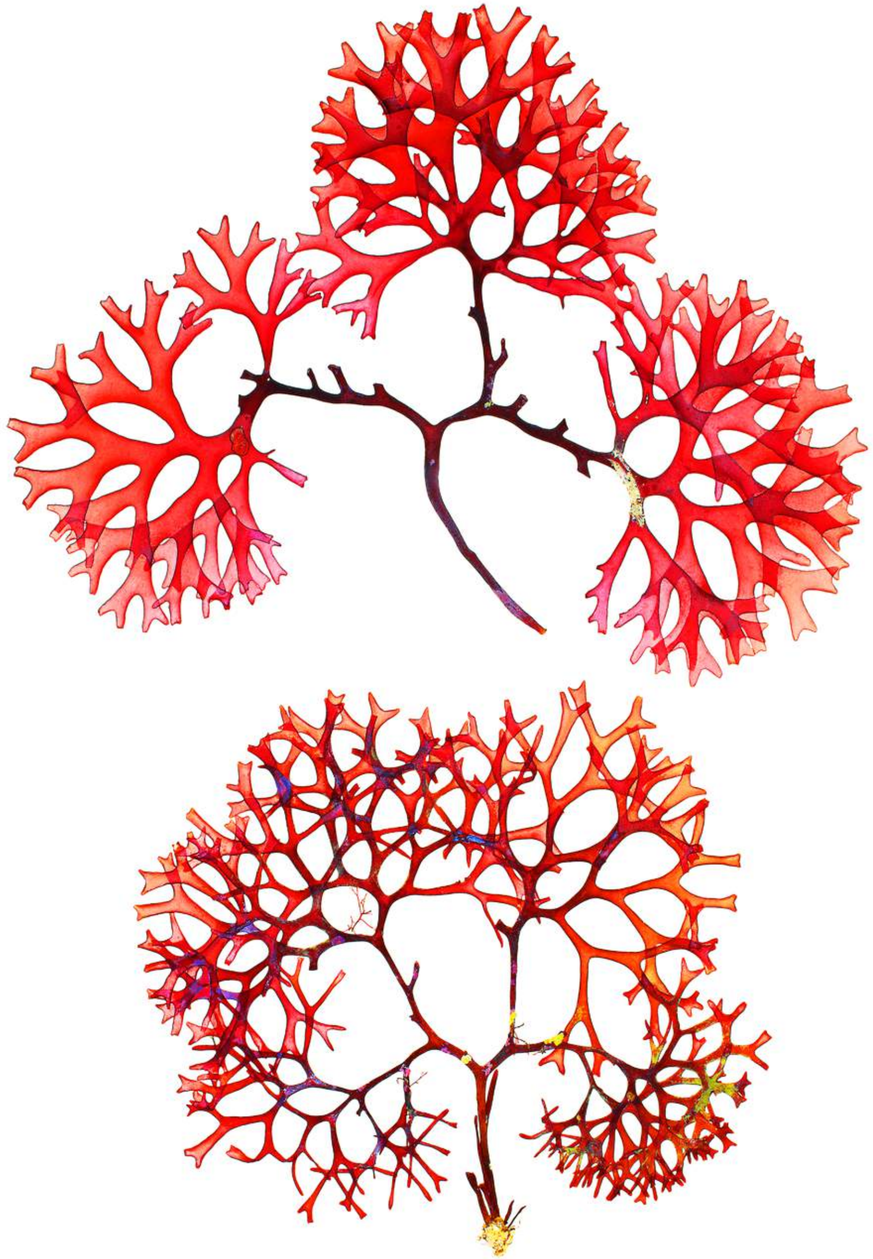
Halurus equisetifolius is a typical representative of the sublittoral and can be best found in the kelp forest down to a depth of 15m. Its distribution is worldwide in the mediterranean and moderate climate. The genus belongs to the family of Ceramiaceae and the order of Ceramiales. The second European member of the genus is *Halurus flosculosus* which can t be confused with Halurus equisetifolius: They miss the whorls of subordinate branches. The specimen shown has a length of about 15 cm.

Phyllophora sicula

(Kützing) Guiry & L.M. Irvine

Red algae (Florideophyceae)

Phyllophora sicula is a red alga in the order Gigartinales building its own family Phyllophoraceae. It has a richly sympodially branched thallus and the branching is in one plane. The thallus is compressed. The thallus structure is multiaxial; the medullar cells are large with a thick wall and colourless whereas the cortical cells are small and red in colour. The thallus is attached to the ground by a small disc and a short stalk. This is a typical case where the original identification was wrong: The name on the herbarium sheet was *Phyllophora epiphylla* but this plant is according to Algaebase synonymous to *Phycodrys rubens* (see there). This specimen is definitely not *Phycodrys*. According to Dixon and Irvine (1977) the species must be *Phyllophora sicula*. The collector in the 1970ties used the old identification key of Lily Newton and in this book *Phyllophora epiphylla* is the appropriate name. This is a species where gametophytes are unknown. Thus the specimen on our sheet must be a tetrasporophyte. May be this species is also one of those where the gametophyte has a different morphology. The species is distributed in the Western Atlantic and the Mediterranean Sea. It is attached to rocks of the lower eulittoral and the sublittoral. The specimens shown have a length of about 8 cm.



Chondrus crispus

Stackhouse

Red algae (Florideophyceae)

Chondrus crispus is a red alga in the order Gigartinales and in the family Gigartinaceae. It has a richly sympodially branched thallus and the branching is in one plane. The thallus is compressed. The thallus structure is multiaxial; the medullar cells are large with a thick wall and colourless, whereas the cortical cells are small and red in colour. The thallus is growing by the activity of apical uninucleate cells; the older cells can get multinucleate, which means that there are a lot of nuclei in one cell. Multinucleate cells are not rare in the red algae. So the genus *Callithamnion* can be differentiated from the genus *Aglaothamnion* by its multinucleate cells. Another way to enhance the DNA content of larger cells is polyploidy: Not the number of nuclei but the number of chromosomes in the nucleus is enhanced. In the red algae many possibilities are realized:

In *Acrochaetium* the apical cell and all the other cells are uninucleate and non-polyploid.

In *Chondrus* and many other red algae the apical cell is uninucleate, but the subapical cells are getting multinucleate.

In *Antithamnion* the subapical cells are getting polyploid.

In *Bornetia* the apical and the subapical cells are multinucleate.

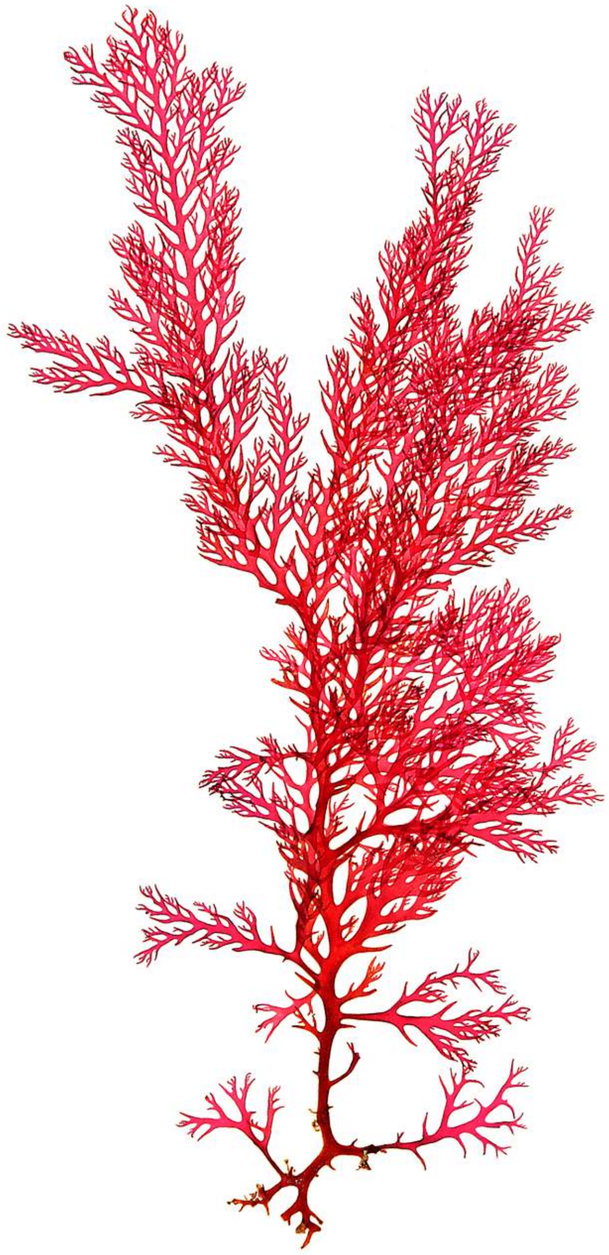
And in *Polysiphonia* and *Bostrychia* the apical cell is polyploid, whereas the subapical cells reduce their nuclear chromosome numbers. In contrast these cells get multinucleate. The specimen shown has a length of about 12 cm.

Plocamium cartilagineum
(Linnaeus) P.S.Dixon

Red algae (Florideophyceae)

Plocamium cartilagineum is a red alga in the order Gigartinales and builds its own family Plocamiaceae. It has a richly sympodially branched thallus and the branching is in one plane. The thallus is compressed. The final ramuli are incurved, unilaterally branched and the branchlets are all directed to the top of the filaments. The general structure of the thallus is uniaxial well visible at the top of the filaments. In cross sections of older parts only a differentiation into large central mostly colourless cells and a cortex of small red peripheral cells can be seen. The thallus is normally attached to solid substrate by a small disc and has a length of 15 cm. It is also found on the stipes of *Laminaria* in upper sublittoral. *Plocamium cartilagineum* was found in a depth of at least 30 m. It feels cartilaginous as suggested by the scientific species name.

Gametophytes are dioecious and isomorphic. Tetrasporophytes and gametophytes are isomorphic. Spermatangia, which release nonflagellated spermatia, are found on the surface of the terminal branches of the male plants. Carposporangia or carposporophytes are found also on branchlets of last order. The cystocarps surrounding the carposporophytes are globose and don't have a pore. The plants are perennial, but frequently detached and then found in the drift for a longer time. The specimen shown has a length of about 5 cm.



chapter 3
Lifestyle – the major groups of algae are characterized by their life cycles

Plocamium cartilagineum
(Linnaeus) P.S.Dixon

Red algae (Florideophyceae)

According to Algabase the distribution of *Plocamium cartilagineum* is worldwide.

A lot of variabilities were described in *Plocamium cartilagineum*, resulting in the description of new species. Sequence data revealed that some of the European species described in recent times are in fact only variants of *Plocamium cartilagineum*, whereas specimens from the Pacific region and Australasia united under the name "*Plocamium cartilagineum*" are in fact new undescribed species.

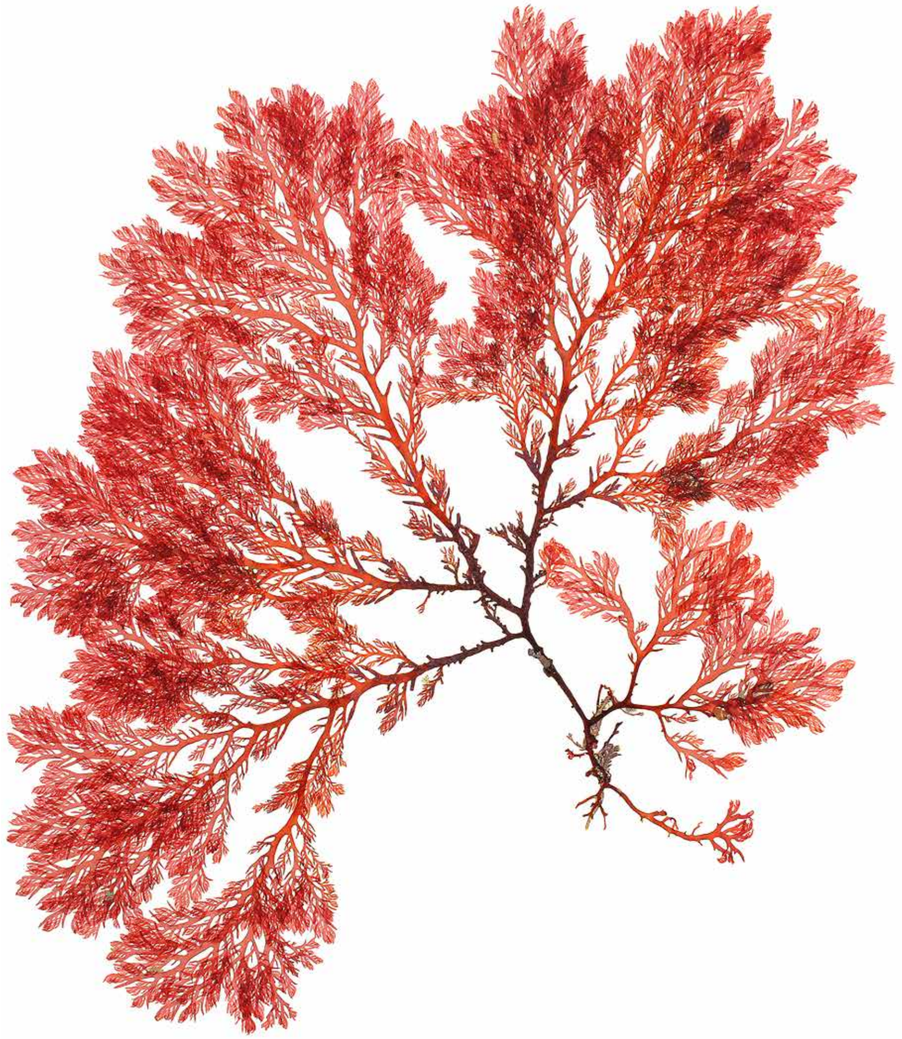
There is one close related species in the European flora, with which *Plocamium cartilagineum* can possibly be confused. This is *Sphaerococcus coronopifolius*. It also has a flattened thallus, is branched in one plane, feels cartilaginous and is with a length of 15 cm of the same size as *Plocamium cartilagineum*. In contrast to this species the cystocarps are stalked and the branching of the terminal ramuli is not unilateral. As *Plocamium*, also *Sphaerococcus coronopifolius* belongs to the order Gigartinales but to an own family Sphaerococcaceae. Both species have the same type of distribution and are occurring fixed on solid materials and *Laminaria* stipes. The specimen shown has a length of about 15 cm.

Plocamium cartilagineum

(Linnaeus) P.S.Dixon

Red algae (Florideophyceae)

Plocamium cartilagineum is a red alga in the order of Gigartinales and is building its own family Plocamiaceae. If looking in different textbooks or databases, the allocations of the genus or family are divergent. In modern systematics more and more molecular data are used to evaluate the taxonomic positions of species. In a fast evolving group like the red algae the resolution is low using genes commonly used for molecular systematics. Sequences from the rubisco genes and from ribosomal RNAs are the preferred markers applied in plants. In red algae up to 14 different genes were analysed in parallel to enhance resolution. So it could be confirmed the Florideophyceae build up monophyletic group. The order Gigartinales, the group in which Plocamium is included, appears to be the group which has most recently evolved. The class of Bangiophyceae containing the genera Porphyra, Pyropia and Bangia is an own monophyletic group and is the sister group to the Florideophyceae. And there are additional monophyletic groups at the basis of the red algae that are not near correlated to the Florideophyceae: The Rhodellophyceae (unicellular), the Compsopogonophyceae (smaller macroalgae) and the Porphyridiophyceae (unicellular). Most basal in the system are the Cyanidiophyceae, interestingly an extremophilic group living in hot and strongly acidic springs. . The specimen shown has a length of ca. 15 cm.



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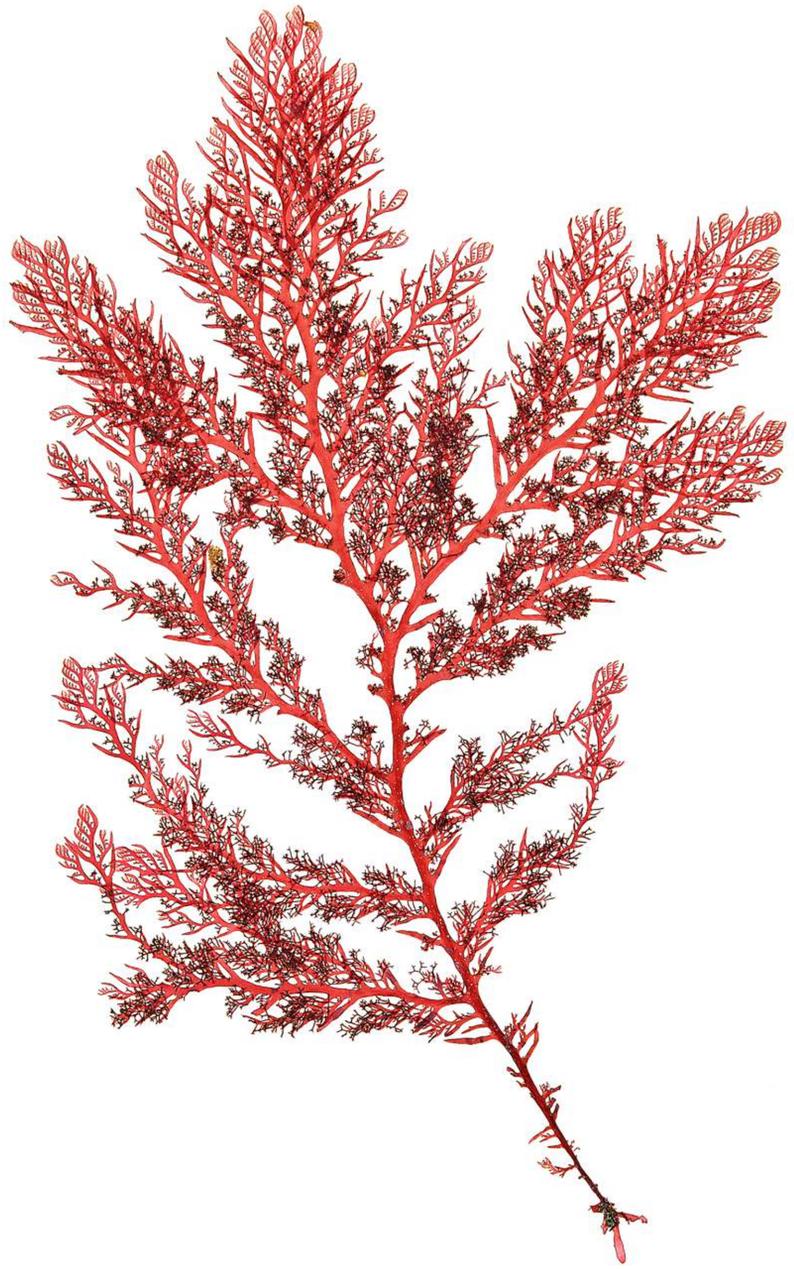


Plocamium cartilagineum

(Linnaeus) P.S.Dixon

Red algae (Florideophyceae)

Plocamium cartilagineum was taken in the last years for molecular sequencing. So ribosomal sequences are known, rubisco-genes have been sequenced and the complete plastid genome is known for Plocamium cartilagineum. Comparisons of DNA-sequences and molecular analyses have elucidated the general evolution of eucaryotic organisms. So it could be shown that the plastids of the algal groups with primary endocytobiosis (green algae, red algae and glaucophytes) come most probably from a single uptake or a cyanobacterium. It also could be shown that in the process of secondary endocytobiosis the ancestors of the todays Heterokontophyta (brown algae, diatoms, gold algae) took up a red alga. The phycobilisomes characteristic for red algae were lost in all classes of the Heterokontophyta during evolution. Also this uptake was most probably a single event. And the Euglenophyta and the Chlorarachniophyta took up green algae in two different events. And in the case of the dinoflagellates even a tertiary endocytobiosis has taken place, where for example a cryptophyte alga was taken up. All this knowledge is the result of comparative DNA-sequencing. The specimen shown has a length of about 15 cm.

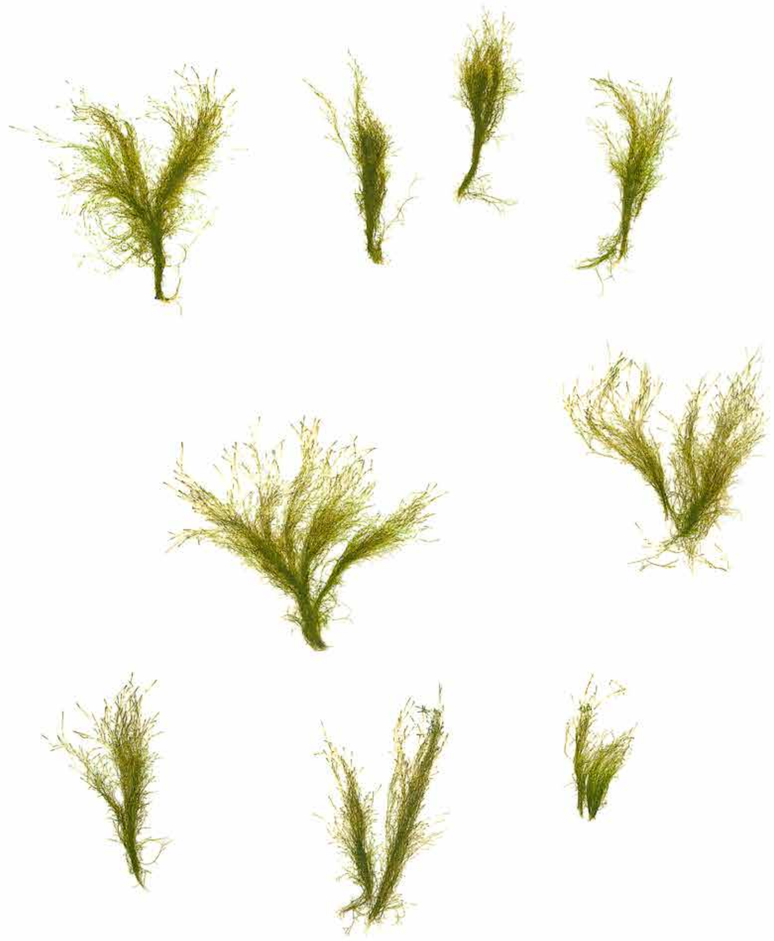
Acrosiphonia spinescens

(Kützing) Kjellman

Green algae (Chlorophyta, Ulvophyceae)

Acrosiphonia spinescens is a green alga. It is a uniseriate alga composed of branched filaments growing mostly attached on rocks and epiphytic on other algae.

The green algae are the group most related to the streptophytes and the land plants. So they share a lot of characters. There is the cell wall which consists of cellulose in most cases. The chloroplasts are surrounded by an envelope of two membranes, an indication for their origin by a primary endocytobiosis effect. They have a characteristic combination of pigments. There is a specific set of carotenoids and especially the combination of chlorophyll a and b is a strong indication for a green alga. Only two other classes with this pigment combination excist, the Euglenophyceae and the Chlorarachniophyceae. Of both classes it is known that an ancestor of them took up a green alga in early times of evolution. *Acrosiphonia* builds thalli of up to 10 cm attached to rocks or other algae. The branching is unilateral; the tips of the filaments normally are incurved like a hook. Similar to genus *Cladophora* they have multinucleate cells. This is in contrast to the similar Genus *Spongomorpha*. The genus *Acrosiphonia* contains 13 accepted species according to Algaebase. The specimens shown have a length of about 5 cm.



Halimeda tuna

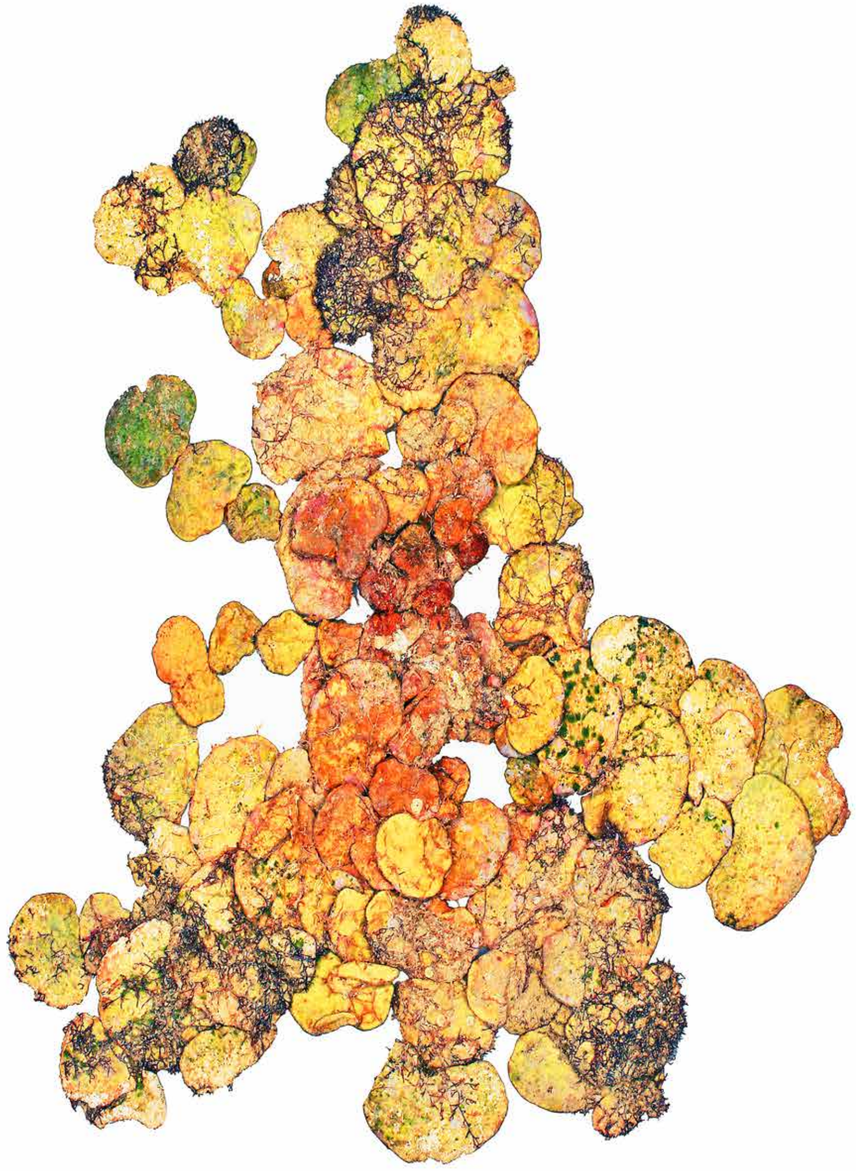
(J. Ellis & Solander)

Green algae (Chlorophyta, Ulvophyceae)

Our second example of a green alga is *Halimeda tuna*, a macroscopic alga with an articulate thallus. The alga really looks like a tuna (cactus of the genus *Opuntia*), having flattened calcified clades sitting on one another joined by soft tissue. It can be found on rocks in coastal regions with a Mediterranean climate. On the microscopic level it consists of interwoven siphonous filaments. This means that there are no crosswalls separating one cell from the other so that the filaments are multinucleate.

The reserve carbon hydrate of the green algae and the higher plants is starch which is deposited inside of the chloroplasts. This is in contrast to all other algal groups where the storage of carbon hydrates is outside of the plastids. In the other groups the storage products are mostly different from starch: Chrysolaminaran in the brown algae and diatoms, paramylon in the Euglenophyceae.

There are 44 species of the genus *Halimeda* worldwide the most of which are adapted to warm climate. *Halimeda tuna* has a worldwide distribution in regions with Mediterranean climate. Friends of seawater-aquaria can obtain cultures of *Halimeda sp.* in special stores. The specimen shown has a length of about 15 cm.



Acrochaetium secundatum

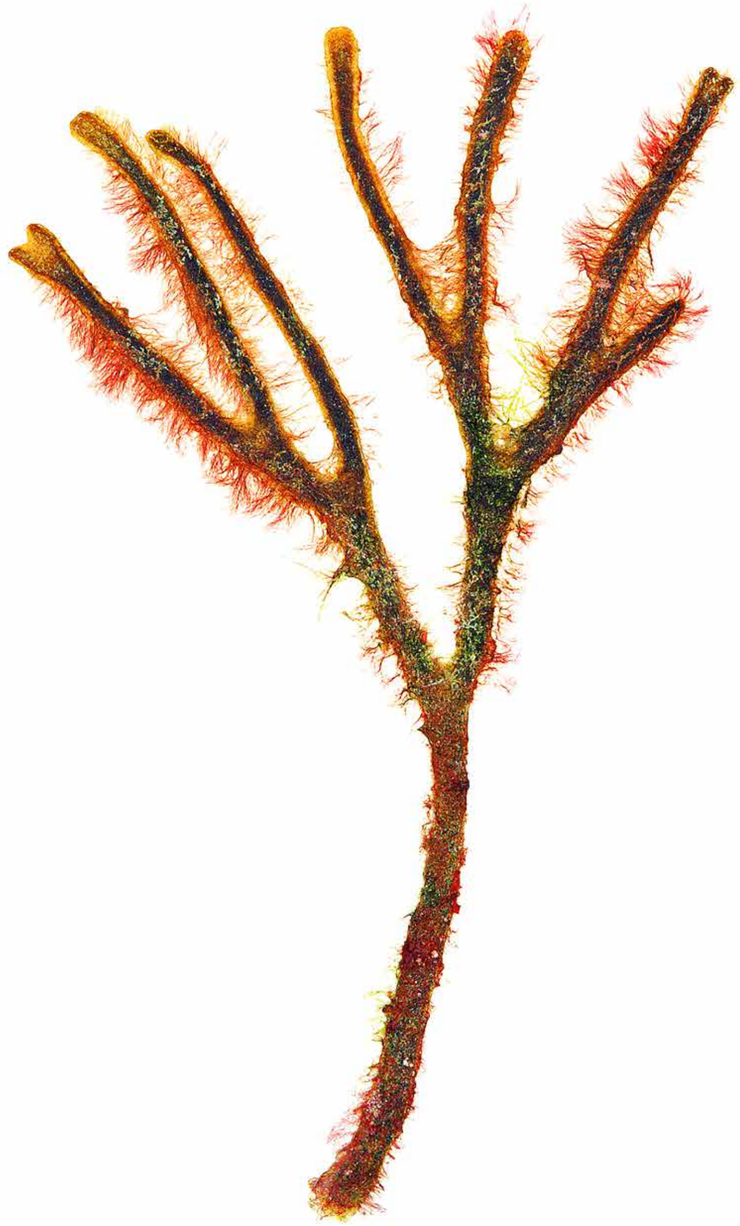
(Lyngbye) Nägeli in Nägeli & Cramer

Red algae (Florideophyceae)

Acrochaetium secundatum is an epiphytic red alga found frequently on macroalgae. In our case the red alga is growing on the green alga Codium sp. (see above). The thallus consists of uniseriate branched filaments, some of which are prostrate creeping, building a disc. From this disc some filaments emerge. They reach a length of ca. 2 mm. The filaments are branching in a variable manner but often the branchlets are unilateral. End cells of these branches often release monospores. These are asexual spores which grow out to descendants that are genetically identical to the mother-plant. Vegetative cells contain one plastid (rhodoplast) which is star-shaped and has a single pyrenoid.

From *Acrochaetium secundatum* no gametophytes are known. Only plants bearing tetrasporangia and monosporangia can be found and the two sporangial types occur mixed on one and the same plant. Thus sexual reproduction appears not to occur in this species.

The next related species is *Acrochaetium virgatulum*. This species differs from *Acrochaetium secundatum* only by branching pattern and size. The characters of both species are overlapping. The species has a worldwide distribution. It is the type species of the genus. The genus *Acrochaetium* builds its own family Acrochaetiaceae and an own order Acrochaetiales. The specimen shown, the branch of *Codium* with epiphytic *Acrochaetium*, has a length of about 12 cm.



Halimeda tuna

(J. Ellis & Solander)

Green algae (Chlorophyta, Ulvophyceae)

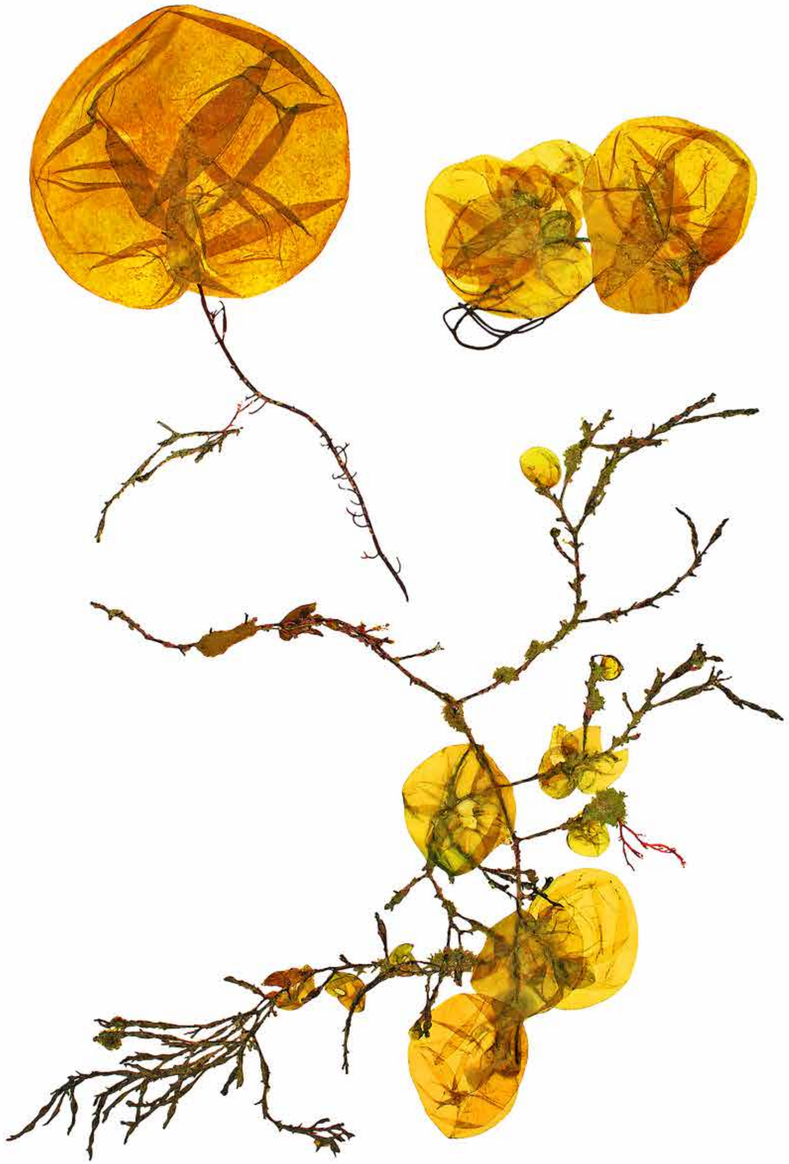
Halimeda is one of the most important algae in subtropical and tropical reefs. The segmented thallus is constructed of siphonous filaments that are interwoven and building calcified disc-like segments that are alternating with the non-calcified hinges. The plants are anchored in the substrate by rhizoids or with a bulb. Examining the reproduction of *Halimeda*, it could be shown the life cycle is diplontic. The gamete producing plants are diploid and dioecious. For the production of gametes filaments are growing out of the last segments of the thallus which produce gametangia. In these gametangia meiosis is taking place. The gametes are biflagellate and their size is somewhat different. The plant with the larger gametes is defined as female, that with the smaller ones as male. The gametes fuse to a zygote that germinates forming firstly a basal rhizoid with which it is anchored in the substrate. The other end of the zygote grows out to a branched filamentous system that doesn't look like *Halimeda*. Here photosynthesis is taking place producing material for the establishment of a rhizoidal system. These rhizoids are growing in the substrate and are later on at certain points growing as an interwoven ball which is the starting point of a *Halimeda* thallus. Such a system of upright filaments before the initiation of the genuine thallus is a unique feature of the genus *Halimeda*. This life cycle was revealed from our Mediterranean *Halimeda tuna*. The specimen shown has a length of about 5 cm.

Colpomenia peregrina

Sauvageau

Brown algae (Phaeophyceae)

Colpomenia peregrina, a brownish ball-like alga of up to 9 cm diameter, is growing on rocks and sometimes epiphytic in the tidal and in the subtidal zone. It is an introduced brown alga and is found in Europe and the northern Atlantic since the beginning of 20th century. Its habit is, compared to the native European brown algae, somewhat strange as most of them have leaf-like or cylindric thalli. But it has all essential characters of brown algae: The plastids are surrounded by four membranes, a strong indication for their origin by secondary endocytobiosis. This and the mastigonemata – small hair-like structures on one of the two flagella – are properties that can only be seen in the electron microscope. But the brownish colour is rather obvious and is a distinctive feature of the brown algae. There are more algae with brown colour – e.g. the diatoms (Bacillariophyceae) and the gold algae (Chrysophyceae), but they are almost all microalgae. All brown algae are macroalgae, visible with the naked eye, and the largest algae worldwide are among them. The brown algae have a special pigment composition: They contain chlorophyll a and c and in addition fucoxanthin, which is responsible for the brown colour. This pigment composition as well as the four plastid membranes and the mastigonemes are common features of brown algae, diatoms and gold algae. They all belong to the phylum Heterokontophyta. The specimen shown has a length of about 7 cm.



Saccharina latissima

(Linnaeus) C. E. Lane, C. Mayes, Druehl & G. W. Saunders

Brown algae (Phaeophyceae)

Saccharina latissima is one of the largest brown algae in Europe. It can reach a length of 7 m and grows on rocks at the subtidal level. The organisation of the thallus is like that of higher plants: A strong holdfast resembles the root of the higher plant and is needed for the attachment to the substrate even in strong wave action. A kind of stem, the cauloid, is needed for the flow of photosynthesis products, and a phylloid, a leaf-like structure, is responsible for photosynthesis. Variations of this architecture can be seen in different genera and species of the order Laminariales, e.g. *Alaria esculenta* and the species of the genus *Laminaria*. When the algae were collected in the 70ies of the last century, they were labelled as "*Laminaria saccharina*". This species and some other were transferred in an own genus *Saccharina*. *Laminaria*- and *Saccharina*-species are harvested in large scale in the coastal regions of the Atlantic to extract the carbon hydrates of their cell walls. These so called "alginates" are specific components of the brown algal cell wall. Large amounts of alginates are processed in food industry.

Saccharina latissima has a worldwide distribution.

The genus *Saccharina* consists of 22 different species according to Algaebase. The specimen shown has a length of about 35 cm.

asparagopsis armata

Harvey 1855

Red algae (Florideophyceae)

Asparagopsis armata is a red alga that was introduced into the Mediterranean algal flora, first found near Elba in 1880. It has now spread over the Mediterranean and the north-eastern Atlantic. It is native to the southern hemisphere being described first in Australia. *Asparagopsis* is interesting because its life cycle shows a drastical difference between two generations: The gametophyte, having only one set of chromosomes (haploid) and the sporophyte, having two sets of chromosomes (diploid). They are so different in shape that they had been described as different genera by former taxonomists. The haploid gametophytic generation is a plant type where sexually determined cells – the gametes – are formed: in red algae the female cells – the carpogonia – are strongly different from male cells – the non-motile spermatia. The carpogonia are fusing with the spermatia and build a diploid zygote. This gametophytic generation is named *Asparagopsis armata*. The diploid sporophyte generation which is producing haploid spores after meiosis is so different in morphology that it was described as a different genus "*Falkenbergia rufolanosa*" (see next page). That these two genera are manifestations of one and the same organism could only be proven by culture experiments. The meiotic spores – in meiosis always four spores are produced – are called "tetraspores". If these *Falkenbergia*-spores are isolated and cultivated separately, an *Asparagopsis* thallus is growing. The specimen shown has a length of ca. 15 cm.

asparagopsis armata

Harvey 1855

Red algae (Florideophyceae)

On *Falkenbergia rufolanosa* sporangia with four spores are found, the tetrasporangia. This is the location where meiosis is taking place. The four meiotic spores that are built in meiosis are called "tetraspores". If these *Falkenbergia*-spores are isolated and cultivated separately, *Asparagopsis* plants are growing out. So we could see on the left page that there are two different generations, the gametophyte "*Asparagopsis armata*" and the carposporophyte which forms diploid spores. And we see that "*Falkenbergia rufolanosa*" is another, third diploid generation in which meiospores, the so called tetraspores are formed. Thus *Falkenbergia rufolanosa* is only a generation in the life cycle of *Asparagopsis armata*. This generation is called "tetrasporophyte". Most of the red algae have this type of "triphasic" life cycle: The haploid gametophyte, the diploid carposporophyte which is growing on the gametophyte and the diploid tetrasporophyte where meiosis is taking place. In contrast to *Asparagopsis* in most other red algae gametophyte and tetrasporophyte are identical in morphology; they are "isomorphic". In *Asparagopsis* they are strongly "heteromorphic".

Only three species worldwide are included in the genus *Asparagopsis*. *Asparagopsis armata* can be easily distinguished from other red algae when the harpoon-like portion of the gametophyte is developed. With their hooks it is often attached to other algae, especially to the thalli of *Ulva*.

asparagopsis armata

Harvey 1855

Red algae (Florideophyceae)

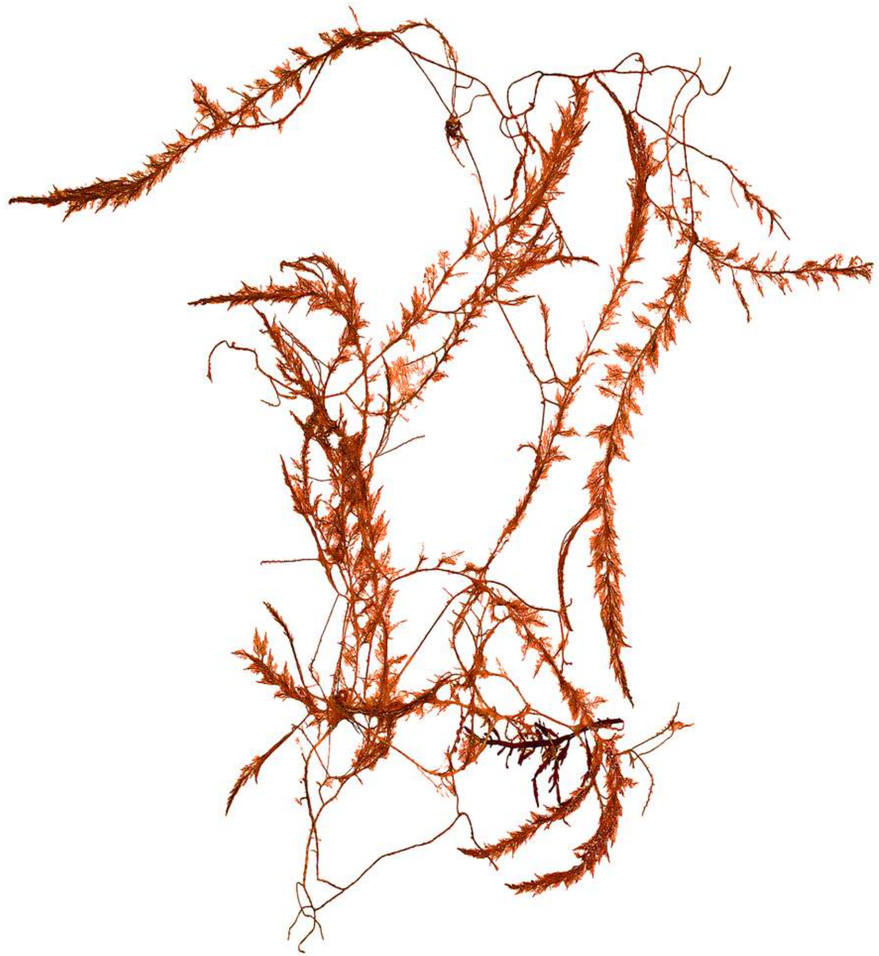
Asparagopsis armata is a red alga with a strong heteromorphic life cycle. It belongs to the order Bonnemaisoniales and the family Bonnemaisoniaceae. One species, *Bonnemaisonia hamifera*, is frequently found in Brittany and British Isles. The dark red gametophyte grows opposite short branches of different length. The longer branch is sterile, the shorter one can develop to reproductive structures. In male plants it develops to spermatangial cones, in female plants to carpogonia and later carposporophytes that are surrounded by a pericarp that is open by an ostiolum. Both sexual reproduction structures sit on a short stalk. The species is dioecious. The carpospores grow out to a tetrasporophyte that is so different from the gametophytes, that it was described before as an own species "*Trailliella intricata*" This is a plant with dark red uniseriate and branched filaments. At the borders between two large cells small cells with a high refractive appearance are found. And when we see the cruciate tetrasporangia we can be sure the we see the tetrasporophyte. Culture experiments are needed to see that *Trailiella intricata* is the tetrasporangial phase in the life cycle of *Bonnemaisonia hamifera*. So we have very similar heteromorphic life cycles in Asparagopsis and Bonnemaisonia. Some authors argue that the two genera should be united to one genus. The specimen of *Asparagopsis* shown has a length of about 15 cm.

chapter 4
Diversity – variations in the life cycles of algae

asparagopsis armata

Harvey 1855

Red algae (Florideophyceae)



Asparagopsis armata is a red alga with a strong heteromorphic life cycle. Strongly heteromorphic life cycles occur in different algal classes. So in red algae the *Bonnemaisonia* example is known (see left page), in brown algae all members of the order Laminariales have heteromorphic life cycles and in green algae the pair of *Derbesia* (sporophyte) and *Halicystis* (gametophyte) is known. A lot of more examples can be found in different algal classes can be found. And when we have a look to the evolution of the higher plants, heteromorphic life cycles are the standard: In mosses the gametophytic phase is the dominant green plantlet and the sporophytic phase is the brownish capsule growing at the top of the green gametophyte. And in ferns the gametophytic phase is a small plantlet of a few mm bearing male and female gametangia and the sporophyte is the very dominant phase. And also in the flowering plants there is a regular change between sporophytes, the very dominant phase, and gametophytes, hidden in the flowers. So the embryo sac which is later on developing to the seed was homologized with the female gametophyte and the pollen grain with the male gametophyte. Thus heteromorphic life cycles as found in Asparagopsis have evolved separately in very different systematic groups. The specimen shown has a length of about 15 cm.

Polysiphonia stricta

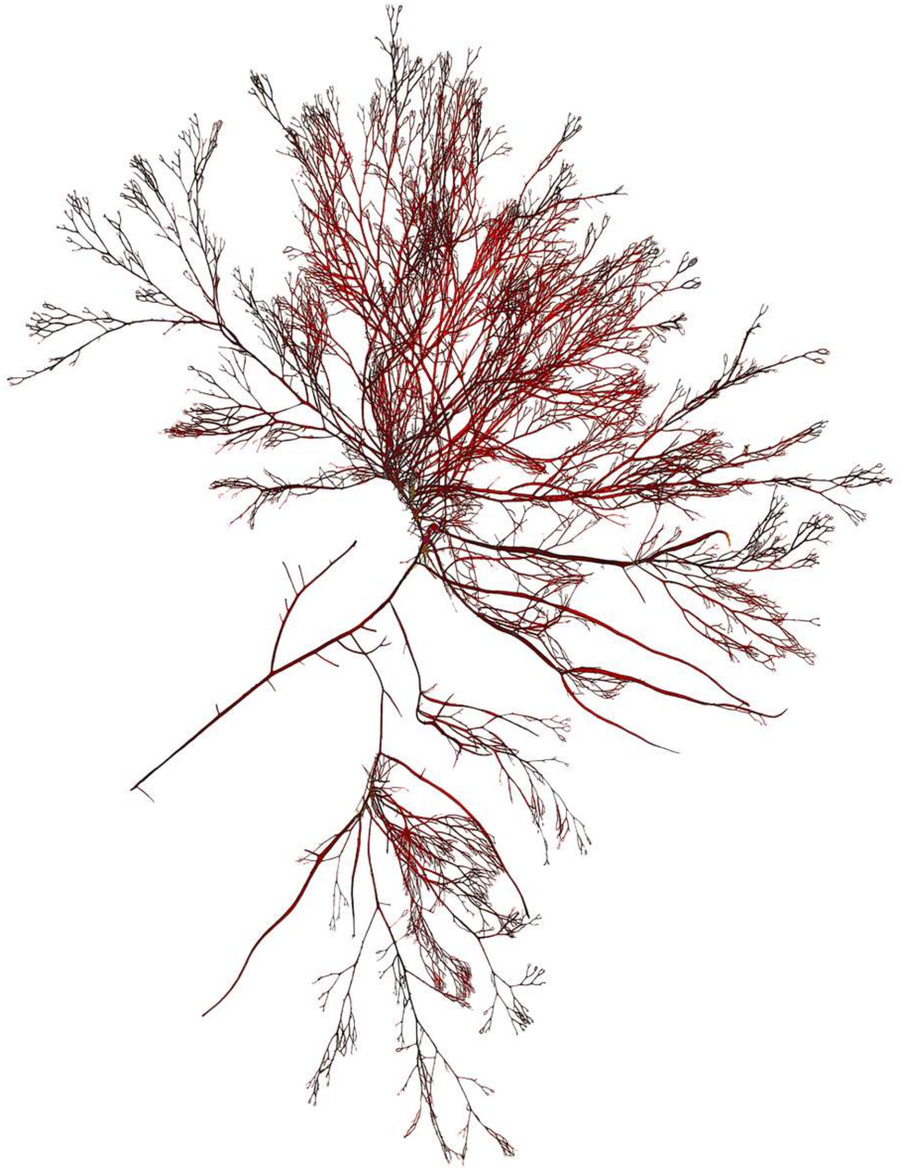
(Dillwyn) Greville

Red algae (Florideophyceae)

Polysiphonia stricta, among phycologists better known as *Polysiphonia urceolata*, has the "typical" life cycle of red algae. In contrast to *Asparagopsis armata* tetrasporophyte and gametophyte are usually identical. The general structure is as described for *Polysiphonia elongata*: A central filament is surrounded by four pericentral cells. The tetrasporangium – this is the cell in which meiosis is taking place – is located between the central filament and the pericentral cells. On the gametophyte the female cells, the carpogonia, are located on side branches. In order to enhance the probability of fertilisation, a long filamentous "trichogyne" is growing out of the carpogonium. The carpogonium and the carposporophyte, which is growing when fertilisation was successful, are protected by a sheath of gametophytic cells. This structure with gametophytic mantle is called "cystocarp" and is visible with the naked eye. Like the oogonia, also the male gametangia are located at the end of side branches. They are arranged in a strobilus-like structure.

Polysiphonia stricta can be distinguished from *P. elongata* by the missing cortex. The cortex is an additional parenchyma-like layer outside of the pericentral filaments.

The filaments are 15 to over 20 cm long, growing on rocks, epiphytic on large algae and on shells of limpets. The specimen shown has a length of ca. 15 cm.



Ceramium virgatum

Roth

Red algae (Florideophyceae)

Among phycologists *Ceramium virgatum* is better known as *Ceramium rubrum*. Members of the genus *Ceramium* are easy to identify by their dichotomous branching and the ends of the branches incurving inwards sometimes resembling hearts. A central filament of large colourless cells is surrounded by cells of irregular order that look like a parenchyma. This cortex cells are rich in rhodoplasts and so responsible for the red colour of the filaments. In truth this mantle is built by side-branches that are creeping over the surface of the large central cells. In some cases this mantle is incomplete and a part of the colourless central cells is not coated. This results in a sort of banding like a barcode: red-white-red-white and so on. This habit is unique in the red algae and only occurs in the genus *Ceramium*. In *Ceramium virgatum* the central filament is completely covered by cortex cells. Nevertheless transverse stripes are visible.

Ceramium virgatum is one of the most abundant species of the genus *Ceramium* in the North Atlantic region. It is growing to a length up to 30 cm on rocks as well as epiphytic on larger algae. The species of the genus *Ceramium* can be differentiated by size, grade of banding, incurvation of the ends of filament and the presence/absence of spines on the surface. The specimen shown above was labelled with the former name "*Ceramium rubrum*". The specimen shown has a length of ca. 10 cm.

Polysiphonia fucoides

(Hudson) Greville

Red algae (Florideophyceae)

Polysiphonia fucoides is a red alga with the typical *Polysiphonia* habit. It has a central filament with pericentrals. The thallus therefore looks segmented. The branching pattern is variable. Characteristic are the prostrate filaments that form rhizoids and are attached to the substrate. Additional cortication is missing. The gametophytes are dioecious and the tetrasporophyte is isomorphic in regard to the gametophytes. Spermatangia are found in cone-like arrangements at the end of lateral branches, one cone per segment. Carpogonia and carposporophytes are on stalks, surrounded by a pericarp and with an ostiolum. Tetrasporangia are formed at the end of terminal branches, between central filament and the pericentral cells. The plant reaches a length of ca. 20 cm. But due the prostrate creeping branches the whole plant can be larger. The old name of the plant was *Polysiphonia nigrescens*. This was also the name on the herbarium sheet.

The species has a more or less worldwide distribution with emphasis to the Atlantic and Mediterranean. It is a plant of the upper sublittoral and the lower eulittoral. It is also frequently found in low tidal rock pools.

Vertebrata lanosa

(Linnaeus) T.A.Christensen

Red algae (Florideophyceae)

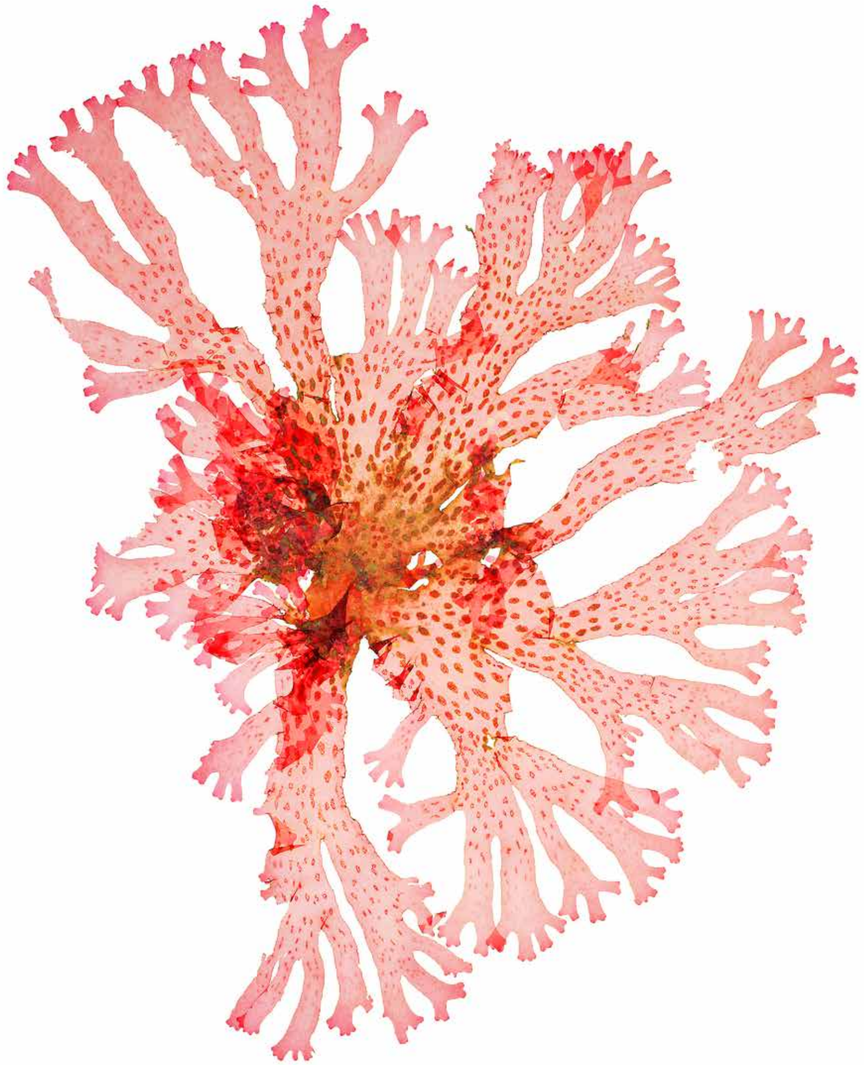
Vertebrata lanosa is a red alga easily to be identified because it is nearly exclusively found on the thalli of the brown alga *Ascophyllum nodosum*. On the herbarium sheet it is noted as *Polysiphonia nodosa* and it is discussed which of both names is appropriate. In Algaebase we find "currently recognized as a distinct genus" although even here the assignation to *Polysiphonia* is discussed. The thallus is fixed by rhizoids penetrating the tissue of *Ascophyllum*. The colour is dark brownish red to nearly black. The plant grows scrubby and is building secondary branches growing over the host. The thallus structure is uniaxial and at the tip there is a large apical cell. The deriving cells of the central filament are soon surrounded by 12-24 pericentral cells, so that the complete thallus looks segmented. The gametophytes are dioecious. Spermatangia are growing at the tips of filaments in cone-like structures. Carposporophytes surrounded by sterile gametophytic pericarp and so forming a large ovoid cystocarp. Tetrasporophytes are isomorphic in regard to the gametophytes. Carpospores as well as tetraspores are germinating preferentially on *Ascophyllum*. *Vertebrata lanosa* is found rarely on other members of Fucaceae, for example on Fucus species when their thalli are wounded. The plant is found in the Northern Atlantic. The specimen shown has a length of about 10 cm.

Nitophyllum punctatum

(Stackhouse) Greville

Red algae (Florideophyceae)

Nitophyllum punctatum is a red alga with a blade like thallus that is very diverse in habit: It can be a dichotomously branched ribbon or a fan shaped blade where dichotomous branching is not easy to see. And all intermediates between these morphologies are possible. The thalli can reach a length up to 50 cm. They are attached to the substratum by a small disc which is proliferating and can give rise to new thalli. Also the thallus can form secondary holdfasts when getting contact with the substrate. Starting with an apical cell, the thallus later on is growing with a meristematic margin. In the marginal the lamina is an unicellular layer, getting later more than one cell thick. The gametophytes are dioecious and are isomorphic to the tetrasporophyte. When fertile, the reproductive structures are scattered evenly over the whole thallus with the exception of the most basal parts. This might have led to the Epitheton "punctatum". The spermatangia and also the tetrasporangia are arranged in sori so that they are visible as scattered Points on the thallus as well as the large cystocarps. 33 species belong to the genus Nitophyllum. Nitophyllum punctatum is the type species of the genus. The species is mostly confined to the Atlantic region. The leafy red algae are a difficult morphological group. The genus can be confused with *Drachiella*, *Haraldiophyllum*, *Rhodophyllis* and more genera. The specimen shown has a length of about 15 cm.



Gracilariopsis longissima

(S. G. Gmelin) M. Steentoft, L. M. Irvine & W. F. Farnham

Red algae (Florideophyceae)

Gracilariopsis longissima is a red alga which is normally brownish to olive green, never being really red. Phycoerythrin is part of the pigment composition but it is present in low concentrations. The thallus is cylindrical and string-like. In cross section there is no visible central filament; the cells are large and isodiametric. The outer cells are smaller and contain rhodoplasts. The thallus is branched and reaches a length of up to 60 cm. There are male and female plants. Thus the plant is dioecious. The old name of the species was *Gracilaria verrucosa* which means that the plant is warty. But this is only the case in female plants, where the carposporophytes are within the warts. Male plants are bearing spermatangia which release spermatia, male gametes that are not flagellated. In red algae there never are flagellated cells. In the case of *Gracilariopsis* groups of spermatangia are formed in pits. Structures for the formation of spermatia are different in the diverse groups. They can be formed in sori in the family of Delesseriaceae or in cone-like structures in *Polysiphonia*. Through the loss of flagella the male gametes cannot swim actively to the female cells and a gamete attraction by pheromones as found in the brown algae is impossible. The chance for a successful fertilization is decreased. The mass of the spermatia produced and the increase of the surface for fertilization by a filamentous trichogyne enhances the chance a little bit. The specimen shown has a length of about 15 cm.

Gracilariopsis longissima

(S. G. Gmelin) M. Steentoft, L. M. Irvine & W. F. Farnham

Red algae (Florideophyceae)

The female plant of *Gracilariopsis longissima* is forming the "warts". Surveying cuts through these warts in the microscope, reveals the carposporophyte. But before these warts are built fertilization must have taken place. During the time of fertilization the female gamete of *Gracilariopsis* is hidden under the surface of the female thallus. Only a filamentous outgrowth reaches the surface, the "trichogyne". To this sticky filament the spermatium binds and the male nucleus is transferred to the female nucleus. The two nuclei fuse to a diploid zygote nucleus. Then a process follows where the zygote cell fuses with neighboured cells and these cells build a diploid plantlet which is dependent on the female "mother"-plant. This is a small branched globose generation, in which at the end of the branches sporangia are formed. This generation is called "carposporophyte". The spores which are released by the carposporangia are called "carpospores". They are genetically identical to the zygote. Thus from one fertilization hundreds of identical new plants arise. So the disadvantage of the missing flagella is retrieved by this clonal multiplication of the zygote. Some authors characterize the life style of the carposporophyte as "parasitic". But this is not the case because this is only a reproductive stage in the life cycle of the red algae. The diploid carpospores then grow out to a plant which is also diploid and is isomorphic to the gametophytes: the tetrasporphyte.

Gracilariopsis longissima

(S. G. Gmelin) M. Steentoft, L. M. Irvine & W. F. Farnham

Red algae (Florideophyceae)

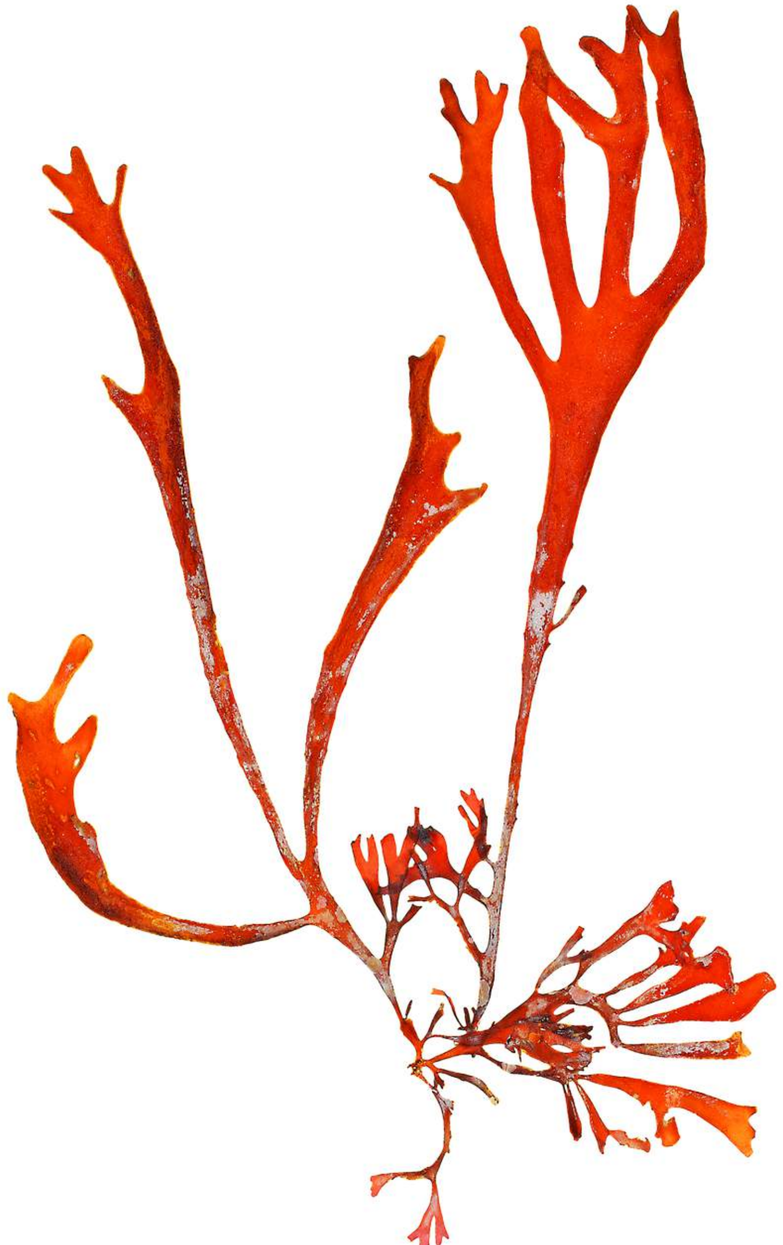
As all red algae also the plastids of *Gracilariopsis longissima* contain the pigments phycocyanin and phycoerythrin. It is broadly accepted that cyanobacteria are the precursors of all plastids. In the case of red algae the similarity of the rhodoplasts with unicellular blue green algae can be easil shown: The phycobilins, phycoerythrin and phycocyanin are arranged in phycobilisomes which are completely identical in structure. They are bound to photosynthetic lamellae that are singular and not stacked as it is the case in other classes. These lamellae are running parallel to each another in both groups. And a rest of the cyanobacterial genome which comprises 3.5 billion base pairs in free living cyanobacteria is in fact present in plastids, not only in rhodoplasts but also in all algal classes including the higher plants. But this "plastid genome" is strongly reduced and is similar in size in nearly all taxonomic groups: The size is about 150000 base pairs (5% of the original cyanobacterial genome). Sequence comparisons have shown that an endosymbiotic process has occurred most probably only once in evolution. In the last years a second endocytobiosis could be demonstrated: The amoeba *Paulinella chromatophora* contains two blue green inclusions that are former bluegreen algae. This must be a younger endocytobiosis process, because here the genome is only reduced to one billion base pairs, so only 2/3 of the original cyanobacterial genome was lost. The specimen of *Gracilariopsis* shown has a length of about 15 cm.

Gracilariopsis longissima

(S. G. Gmelin) M. Steentoft, L. M. Irvine & W. F. Farnham

Red algae (Florideophyceae)

As in *Gracilariopsis longissima* the most tetrasporophytes are identical in morphology to the gametophytes. But in some cases, for example in *Asparagopsis armata* the tetrasporophyte is so different from the gametophytes that it was described as a separate genus "*Falkenbergia rufolanosa*". The function of the tetrasporophyte in the life cycle is to perform meiosis. This is done in special sporangia, the so called "tetrasporangia". They are called so because in meiosis always four products are formed. And these four (Greek: tetra) spores are united in this sporangium. The tetrasporangia are embedded in the surface of the Tetrasporophyte. In the keys for the identification of species often the exact arrangement of the spores in the Tetrasporangium is asked. This order can be cruciate, when the four spores are in one plane and the gaps between then are like a cross. Or they are in the form of a tetrahedron. And the third option is that they are in on series and then called "zonate". The tetrasporangium in *Gracilariopsis longissima* is of the cruciate type. If one would isolate the four spores from one tetrasporangium and cultivate each spore separately two male and two female thalli would arise. This description of tetrasporophytes is true for most members of Florideophyceae. In the Bangiophyceae also a sporophyte exists. But here the spores released are diploid and meiosis takes place during germination of the spores. The specimen shown has a length of about 20 cm.



Gracilaria foliifera

(Forsskål) Børgesen

Red algae (Florideophyceae)

Gracilaria foliifera is a red alga with a flat ribbon-like thallus that is irregularly subdichotomously branched. The thallus is thick and cartilaginous. The colour can be from dull purple to brownish. It has a length up to 25 cm and is attached to the substrate with a small disk-like holdfast. The stipe is compressed. The gametophytes are dioecious. The spermatangia are in pits that are scattered over the thallus. This is also the case with the carpogonia and the cystocarps that are protruding as warts from the surface and resembling so the female gametophyte of *Mastocarpus stellatus*. The cystocarps have a distinct pore (ostiolum). The tetrasporophyte is isomorphic to the gametophytes. Microscopical cross sections reveal a central part of large storage cells and a peripheral layer of red assimilatory cells containing rhodoplasts.

The plant is found in the eulittoral and in the sublittoral up to a depth of 15 m. The species has a worldwide distribution. The closely related *Gracilariopsis verrucosa* was formerly a member of the genus *Gracilaria*. Both species are collected for the preparation of agar. *Gracilaria* is the name giving genus for the family Gracilariaceae and the order Gracilariales. The specimen shown has a length of about 15 cm.

Lemanea fluviatilis

(Linnaeus) C. Agardh

Red algae (Florideophyceae)

Lemanea fluviatilis is one of the few red algae occurring in freshwater habitats. It is a red alga of the uniaxial type. Whorls of lateral branches grow in a way that they build up a hollow thallus. In the inner of this hollow cylinder spermatangia and carpogonia are differentiated. So we know that this is the gametophytic phase. And from the fertilized carpogonia carposporophytes, visible as dark dots, are developed. Compared to the life cycle of *Polysiphonia* where a gametophytic phase, the carposporophyte and the tetrasporophyte can be distinguished, the latter phase is missing. The fate of the carpospores could not be examined until culture experiments were done. In culture they grew out as a plants which formerly had been described as an own genus *Chantransia*. From this *Chantransia* a new *Lemanea* gametophyte is growing out. Meiosis is taking place in vegetative cells so that from the diploid *Chantransia* – phase a haploid *Lemanea* gametophyte can grow. So tetrasporangia as found in most red algae are missing in the life cycle of *Lemanea*. And *Chantransia* is only a phase in the life cycle of *Lemanea*.

Lemanea species don't really look like red algae because most of them are greenish to olive in colour. Their typical habitats are waterfalls and rapids in streams. There are 17 accepted species of *Lemanea* worldwide according to Algaebase. The specimen shown has a length of about 10 cm.

Batrachospermum gelatinosum

(Linnaeus) De Candolle

Red algae (Florideophyceae)

Batrachospermum is like *Lemanea* one of the few red algae occurring in freshwater habitats. On a central filament there are growing whorls of lateral tufts so that the thallus looks macroscopically like the filamentous spawn of a toad. In the microscope we can see spermatangia and carpogonia so that we know that this is the gametophytic phase in the life cycle of this red alga. After fertilization the carposporophytes can be seen with the naked eye as dark dots. And, as in *Lemanea*, the diploid carpospores are germinating to a *Chantransia* stage in which meiosis occurs in vegetative cells regenerating the *Batrachospermum* gametophyte. So in spite of their drastic morphological difference the common life cycle reveals that these two genera are close related. As in *Lemanea* also in *Batrachospermum* the thalli are rarely red but more greenish to olive. Nevertheless the red pigment phycoerythrin which is characteristic for red algae is present in the plastids in low concentrations. Most *Batrachospermum* species are occurring in cool waters near to the fonts of streamlets and are indicative for clean water. The genus includes 97 accepted species. *Batrachospermum gelatinosum* is one of the most frequent species although all in all *Batrachospermum* species are rarely found. Some phycologists rather know *Batrachospermum gelatinosum* under its old name *Batrachospermum moniliforme*. The specimens shown have a length of about 5 cm.

Ulva lacuta

Linnaeus

Green algae (Chlorophyta, Ulvophyceae)

Ulva lactuca is one of the most common seaweeds in the coastal waters of Europe. Therefore it is one of the few species having a common name: Sea lettuce. It is in fact used by the friends of seafood as a component of their meals. *Ulva lactuca* is an example of an isomorphic life cycle: Gametophyte and sporophyte cannot be distinguished. Often *Ulva*-thalli are found with a white margin. In this whitish zone cells have released flagellated cells. In natural habitat or in experimental assays the flagellated cells can be examined in the microscope. If they bear four flagella they are zoospores that have undergone meiosis prior to their release. The plant, from which they have arisen, was a sporophyte. The zoospores settle on the ground and grow out to a gametophyte. If the flagellated cells bear only two flagella, they are gametes and with some luck the fusion of gametes can be seen in the microscope. This type of fertilisation is called isogamous fertilisation, because the gametes are of the same size. The resulting zygote grows to a sporophyte.

Ulva lactuca has a worldwide distribution in coastal waters. The genus, including the old genus "*Enteromorpha*", contains as much as 129 species according to Algaebase. Thalli can reach a size up to 50 cm. In cross sections the thallus is two cell-layers thick.

Ulva sp.

Linnaeus

Green algae (Chlorophyta, Ulvophyceae)

The *Ulva sp.* specimen shown above is labelled as "*Enteromorpha sp.*" on the herbarium sheet. Examination of *Enteromorpha* species has revealed that their life cycles are completely identical to that of *Ulva lactuca*: Gametophyte and sporophyte are identical in morphology, zoospores have four flagella, gametes two, the fertilisation is by isogamy. Also this facts strengthen the joining of the two genera into the one genus *Ulva* as stated in (2-2). If one tries to identify the algae after collection, more than one literature must be used. With older literature the result of determination for the shown alga perhaps would be "*Enteromorpha intestinalis*". Searching for this name in Algaebase (www.algaebase.org/) one finds the name: "*Enteromorpha intestinalis* (Linnaeus) Nees"; some lines later under „status of the name", one can learn that this name is actually regarded as a synonym of the name *Ulva intestinalis* Linnaeus. From these lines one can reconstruct the history of naming: Carl von Linné described this species as *Ulva intestinalis*; later Nees transferred the tubular species into an own genus "*Enteromorpha*" and again later due to new results of research the former name *Ulva intestinalis* was reactivated.

The genus *Ulva* currently contains 129 species. All species are distributed in marine environments. Only *Ulva intestinalis* can also be found in freshwater habitats. A length of more than 1m was reported. The specimen shown has a length of about 15 cm.

Cladophora rupestris

(Linnaeus) Kutzing

Green algae (Chlorophyta, Ulvophyceae)

Cladophora rupestris is a uniseriate branched filamentous alga growing on rocks in the tidal zone. Normally the branching is lateral, in a few cases it can be nearly dichotomous. The cells are large, up to 200 µm, multinucleate, having a net-like peripheral chloroplast or numerous small chloroplasts. The filaments usually grow by the division of the apical cell of the filament. The reproduction is similar to that in *Ulva*: Terminal cells of the filaments of the diploid sporophyte release zoospores with four flagella formed after meiosis. They settle and grow up to a haploid gametophyte which releases biflagellated cells. These fuse to build a zygote. After settlement and germination again a sporophyte is formed. *Cladophora* is a genus with species in freshwater and in marine habitats. Only in the marine species this type of life cycle could be found. Although there were more than thousand species described, 217 are currently accepted. The species *Cladophora* appear to be adapted to nutrient-rich condition, at least in freshwater habitats. Most species are growing attached to rocks. One exception is *Cladophora aegagropila* that is growing as a ball of interwoven filaments.

The genus *Cladophora* consists of 196 species occurring in freshwater- as well as in marine environments. The specimen shown has a length of about 10 cm.

Cladophora flexuosa

(O. F. Muller) Kutzing

Green algae (Chlorophyta, Ulvophyceae)

Compared to *Cladophora rupestris* on the left page which is dark green in colour and has straight main axes and side branches, *Cladophora flexuosa* is light green and the side branches are flexuous throughout the thallus.

The general life cycle described on the left page has many variations. Two-flagellated cells can serve as zoospores. Also akinetes are known from *Cladophora*. Also a haplontic life cycle is described, where the zygotes germinate under meiosis and four quadriflagellate haploid zoospores are released. Also a diplontic life cycle is known in *Cladophora glomerata* ,where quadriflagellate zoospores arise without meiosis; in contrast, the two-flagellated gametes are built during meiosis; the resulting zygote grows into a diploid filament.

Cladophora species can be distinguished from one another by size, colour, diameter of the cells, mode of branching, and form of the filaments and cells.

The genus *Cladophora* consists of 196 species occurring in freshwater- as well as in marine environments. The specimens shown have a length of about 10-15 cm.

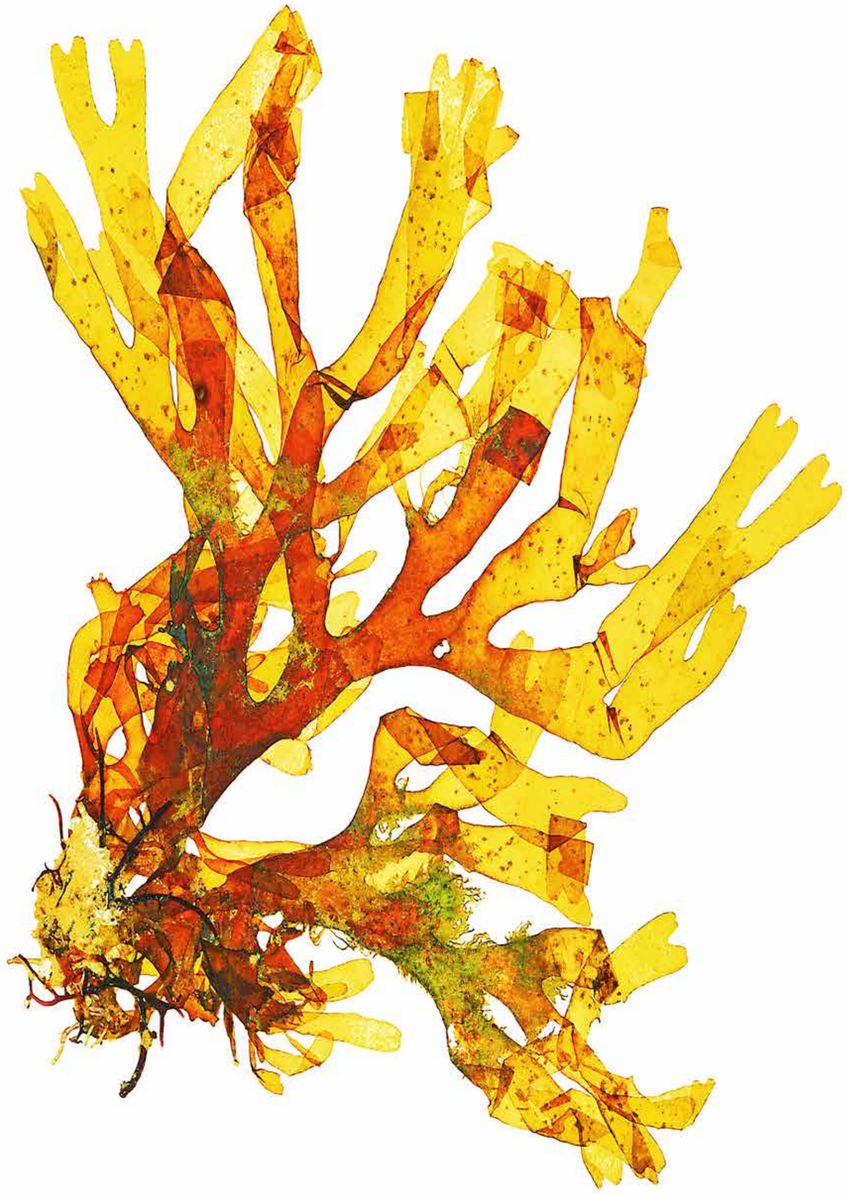
Dictyota dichotoma

(Hudson) J. V. Lamouroux

Brown algae (Phaeophyceae)

In brown algae different types of life cycles are known: The isomorphic, the heteromorphic and the diplontic life cycle. *Dictyota dichotoma* is an example for the isomorphic life cycle. Gametophyte and sporophyte cannot be distinguished when reproductive structures are missing. When they are present, on the sporophyte sporangia can be found in which meiosis happens. The four cells resulting from this meiosis are arranged in the sporangium as a tetraeder. After their release these haploid spores germinate and grow to gametophytes.

Gametophytes bear either oogonia on female plants or antheridia on male plants, i.e. the gametophytes are dioecious. The oogonia contain egg cells, large non-flagellated cells, rich in nutrients. The male plants develop antheridia, which release many biflagellated cells. These are called spermatotzoids finding their fertilization partner with the help of pheromones that are excreted by the egg cell. After fertilization the diploid zygote develops into the sporophyte. The specimen shown has a length of about 5 cm.



chapter 4
Diversity – variations in the life cycles of algae

Dictyota dichotoma

(Hudson) J. V. Lamouroux

Brown algae (Phaeophyceae)

Dictyota is the genus responsible for the name of the order Dictyotales and of the family name Dictyotaceae. The Dictyotaceae are the only family of the Dictyotales and contain 279 species. Different genera of the Dictyotaceae are handled in this book:

The most species-rich genus is *Dictyota* (91 species) represented here by the species *Dictyota dichotoma*.

The second species-rich genus is *Padina* with 52 species represented here by the species *Padina pavonica*.

Dictyopteris is the third species-rich genus with 35 species represented here by *Dictyopteris membranacea*.

The next species-rich genera, not represented in this book, are *Lobophora* (25 species), *Spatoglossum* (20 species) and *Zonaria* (14 species).

Taonia (6 species) is represented here by *Taonia atomaria*.

Most of the species in this family form thalli that are dichotomously or subdichotomously branched. Typical for this family is the isomorphous life cycle with mostly dioecious gametophytes, the male producing spermatozoids and the female producing eggs. The sporophytes release four unflagellated spores in one sporangium built during meiotic division.

Taonia atomaria

(Woodward) J. Agardh

Brown algae (Phaeophyceae)

Taonia atomaria is a brown alga which is rarely found and resembles *Dictyota* belonging also into the order Dictyotales.

The flat thallus reaches a length of 20 cm (maximal 30 cm) and is dichotomously branched. At the basis the thallus is terete soon changing into flat ribbon like bands of ca. 1 cm width. The width is not as regular as in *Dictyota* and the branches are often attenuated towards the basis. Compared to *Dictyota* the ends of the thalli are not rounded but rather irregular. And in contrast to *Dictyota* the thallus in not homogenous in colour but characterized by darker concentric stripes wandering across the thallus bands. This pattern is visible from both faces of the thallus. In the microscope hairs and reproduction stages can be seen in these zones. A midrib as seen in *Dictyopteris* is missing.

It is a species of the sublittoral, reaching a depth of 10 m. The species occurs in the Northeast- Atlantic region in Britain, Brittany, the Atlantic coast in France and Portugal to Mauretania and in the Mediterranean region. *Taonia atomaria* is the type species of the genus. The genus *Taonia* consists of 6 species according to Algaebase. As a member of the order Dictyotales, *Taonia atomaria* has an isomorphic life cycle. This means that gametophytes and sporophytes cannot be distinguished with the naked eye. In the microscope gametophytes can be recognized by their oogonia or antheridia. As in *Dictyota* the oogonia and the antheridia are arranged sori.

chapter 4
Diversity – variations in the life cycles of algae

Taonia atomaria

(Woodward) J. Agardh

Brown algae (Phaeophyceae)

In the oogonia eggs are formed; in the antheridia spermatozoids are released. These spermatozoids bear the typical heterokont flagella with mastigonemes characteristic for all brown algae. After fertilization the zygote grows to a diploid sporophyte which is identical to the gametophyte. Here meiosis takes place in special sporangia that are called "tetrasporangia" in analogy to those of the red algae. As in the red algae the four spores are unflagellated. When released they develop new gametophytes.

Alaria esculenta

(Linnaeus) Greville

Brown algae (Phaeophyceae)

Alaria esculenta belongs to the order Laminariales known for their extremely heteromorphic life cycles. What we see on the herbarium sheest on the left as well as on the right page are sporophytes. The gametophyte is of microscopic size and never seen on a herbarium sheet. In contrast to other European Laminariales, *Alaria* has developed specialized wings for spore production at the basis of the leaf-like phylloid. These wings can be seen as an isolated structure on the left page. Here meiosis takes place and zoospores – flagellated unicells – are released and swim away to build the gametophytic generation. The gametophytes were first recognized, when zoospores were fished with a pipette and were allowed to grow up in a petri-dish. At the tips of the few-celled filaments eggs are set free, on other filaments spermatozoids: The gametophyte is dioecious. As possibly in all brown algae, the egg produces a specific pheromone to attract spermatozoids and after fertilization the zygote immediately grows out as a new sporophyte. *Alaria esculenta* can be easily recognized by its distinctive bright yellow midrib and, if present, by the wing-like outgrowths of sporogenic tissue. The specimen shown has a length of about 25 cm.

Alaria esculenta

(Linnaeus) Greville

Brown algae (Phaeophyceae)

Alaria esculenta is growing attached to exposed rocks with heavy wave breaking near to the low-water-line. Its thallus can reach a length of more than 2, 5 m.

The distribution is circumboreal (North Atlantic, North Pacific) as most of the other species of this genus. There are 15 species accepted currently of which *Alaria esculenta* is the only European species. There is a decline of the population of *Alaria esculenta* in Europe, possibly due to the warming in last decades. The epitheton "*esculenta*" means that the plant is edible. At natural locations the species can form abounding populations. There is only one species in Europe, an introduced species from East Asia, *Undaria pinnatifida* that has also a midrib and wing like sporogenic outgrowths. It cannot be confused with *Alaria esculenta* as it is much broader, shorter than *Alaria*, the margin is pinnate (feather-like) and the midrib is not light yellow. *Undaria* is also an edible plant and this is the reason why it was introduced. In East-Asia *Undaria pinnatifida* is cultivated as a delicacy under the name "Wakame". In the last century it was cultivated first in Brittany and from there it is expanding as an invasive species. The specimen shown has a length of about 35 cm.

Halidrys siliquosa

(Linnaeus) Lyngbye

Brown algae (Phaeophyceae)

Halidrys siliquosa is aseaweed that is not found very frequently because it is growing at the subtide level. It is washed up after stormy weather to the coast. It grows attached to rocks and can reach a length of over 2.5 m. At the tips of branches there are silique-like structures which are filled with gas. These "pneumatocysts" – occurring also in other genera of the order "Fucales" – help the thalli to grow upright in the water. Additionally to these floating bodies there are thallus lobes similar to the "siliques" called "receptacles". In microscopical cross-sections these receptacles show pear-shaped invaginations. These "conceptacles" bear oogonia and/or antheridia. In the oogonia meiosis takes place and eggs are developed and set free. In the antheridia spermatozoids are formed also after meiosis. They are released in small vesicles that later disintegrate. A spermatozoid fuses with an egg and the resulting diploid zygote germinates without a longer retarding period. The resulting plant is also diploid. A life cycle, in which all parts are diploid and only the gametes are haploid due to meiosis, is called "diplontic. An organism with diplontic life cycle is a "diplont". Among the numerous orders of brown algae the Fucales are the only one with a diplontic life cycle. Important genera like *Fucus* and *Ascophyllum* are members of the order Fucales. The fragment shown has a length of about 8 cm.

Ascophyllum nodosum

(Linnaeus) Le Jolis

Brown algae (Phaeophyceae)

In contrast to *Halidrys siliquosa* another member of the Fucales, *Ascophyllum nodosum*, is growing on rocks near to the upper tide level. Similar to *Halidrys*, there are gas bladders: thick ovoid bubbles in the middle of the thallus. As in all members of the order Fucales *Ascophyllum* has a diplontic life cycle. Gametangia are located in conceptacles that are found in a specialized thallus portion, the receptacle. *Ascophyllum* is dioecious, so male and female thalli exist. The receptacles of the male plants are orange in colour. Those of the females are green to olive. In the oogonia 4 eggs are produced. In the genus *Fucus* there are eight eggs. As an inhabitant of the upper tide level *Ascophyllum* must be resistant to wave action as well as to drought. It has to survive 10 and more hours of dry condition on summer-days.

Ascophyllum nodosum is monotypic; this means that it is the only species of the genus. It occurs only in the Northern Atlantic on rocky shores. The thallus of *Ascophyllum nodosum* is frequently found with a hemiparasitic red alga *Vertebrata lanosa*. This alga is closely related to *Polysiphonia*; on the herbarium sheets the specimens are labelled as "*Polysiphonia lanosa*". The specimen shown has a length of about 10 cm.

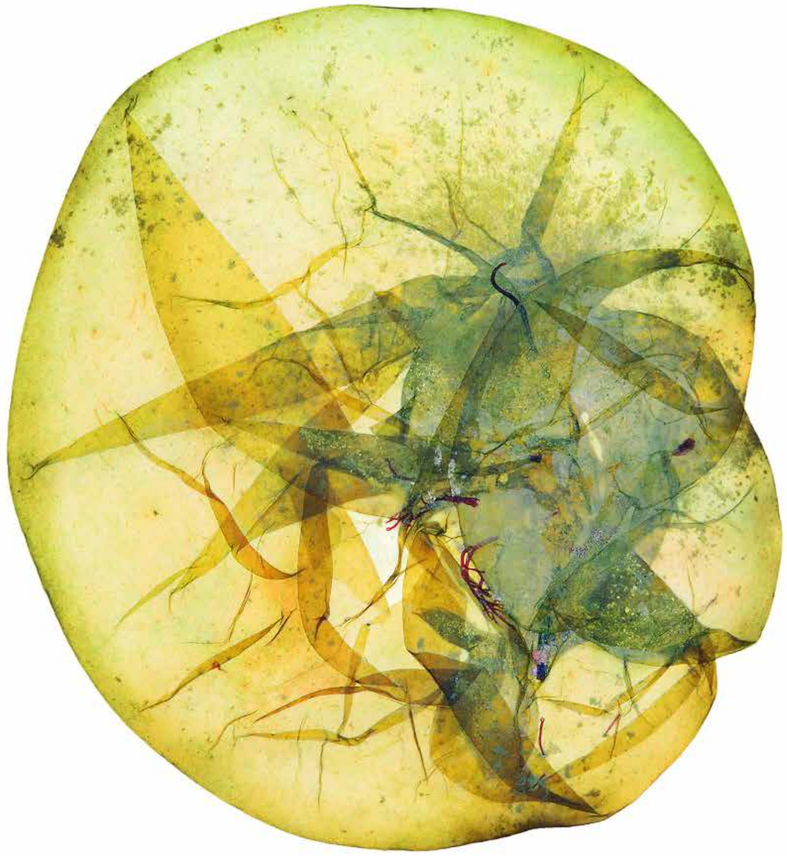
Colpomenia peregrina

sauvageau

Brown algae (Phaeophyceae)

Colpomenia peregrina is a brown alga which differs from most other brown algae by its bladder like form. The bladders are hollow, are surrounded by a thin yellowish to olive brown layer of few cells and have a diameter of up to 9-10 cm. Younger bladders are mostly globose, the older and larger ones mostly deformed. They normally grow on rocks or frequently epiphytic on other marine macroalgae. *Colpomenia peregrina* can only be confused with *Colpomenia sinuosa* which forms larger thalli and has a surrounding layer which is thicker (more than 5 cells thick). The second species with which it can be confused is *Leathesia difformis*, a species with a stable cartilaginous outer layer and a brain like winded surface.

The species are found in the low eulittoral, in the sublittoral and also in rock pools that retain the seawater during the period of low tide. Both *Colpomenia* species are known to be introduced from the Pacific region. *Colpomenia sinuosa* is known in the European flora since middle of the 19th century. *Colpomenia peregrina* is present in our flora since the beginning of the 20th century. Especially *Colpomenia peregrina* has properties of an invasive species by displacing native algae. The specimen shown has a length of about 6 cm.



Scytosiphon lomentaria

(Lyngbye) Link

Brown algae (Phaeophyceae)

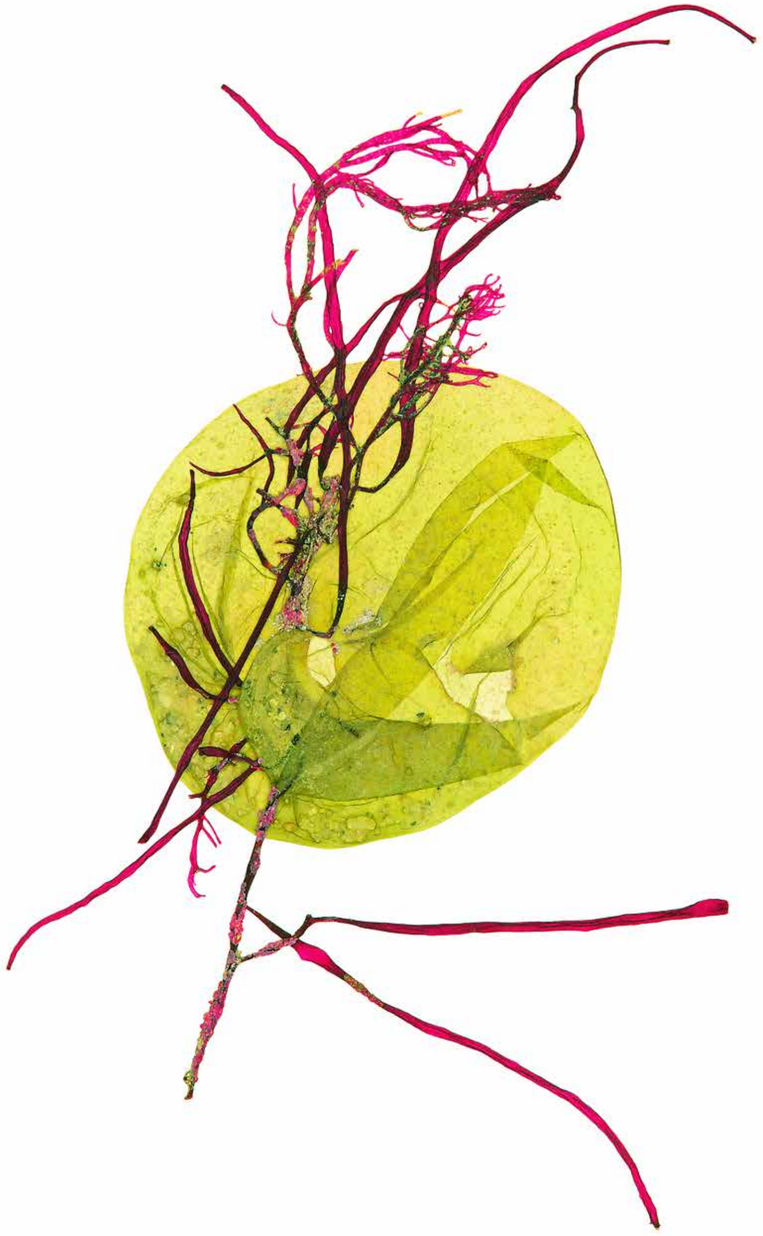
Scytosiphon lomentaria is a brown algal species which is characterized by a brown tubular thallus of 5 mm diameter and a length of ca 30 cm. In rare cases a length of 90 cm and a diameter of 1 cm can be found. Regularly small portions of the thallus are flattened so that the long unbranched thallus is interrupted into some chambers. The tubular thalli are tapering to the basis and the end of the tube. Usually more than one of these erect thalli are arising from a common basis which is a round disc of ca. 1 cm diameter. This species normally cannot be confused with other species. The species *Scytosiphon lomentaria* occurs at the lower level of eulittoral and in the upper sublittoral. It is also often found in rock pools that are filled with water during the low tide. The species is distributed worldwide in cold and moderate marine habitats. The genus *Scytosiphon* contains 7 accepted species according to Algaebase. It forms an own family Scytosiphonaceae and is classified into the order Ectocarpales. Also the genus *Colpomenia* (left side) with its invasive species *Colpomenia peregrina* belongs to this family. The specimen shown has a length of about 15 cm.

Colpomenia peregrina

sauvageau

Brown algae (Phaeophyceae)

Colpomenia peregrina has a complex heteromorphic life cycle. The bladders are the gametophytes. They are heterothallic and therefore male and female gametophytes exist. Under certain conditions plurilocular gametangia are formed and anisogametes are released. The resulting zygotes germinate as small filamentous diploid sporophytes. At terminal branches unilocular sporangia appear in which meiosis occurs. The meiospores grow out either to male or to female gametophytes which are bladder-like. So far this is a normal heteromorphic and heterophasic life cycle. But parallel to this mode of reproduction also other behaviour of the spores and gametes was detected: Anisogametes that came not up to fusion can grow out to sporophytes that look like those which grew out of the zygotes. But in contrast to the zygote-born sporophytes the gamete-born sporophytes are haploid. Also these sporophytes build plurilocular sporangia containing mitospores and regenerating the corresponding gametophyte. And last but not least on the gametophytes the flagellated cells that normally should be gametes and fuse to a zygote can also function as spores that directly generate new gametophytes. Since the detection of this opportunistic behaviour of the flagellated stages in brown algae a lot of such complicated life cycles were detected. The specimen shown has a length of about 5 cm.



Scytosiphon lomentaria

(Lyngbye) Link

Brown algae (Phaeophyceae)

For the species *Scytosiphon lomentaria* sexual reproduction is not described. But in the last years a monophasic developmental cycle between *Scytosiphon lomentaria* and a phase which was described as a different species *Microspongium gelatinosum* was detected. On the surface of the *Scytosiphon lomentaria* thallus plurilocular sporangia are formed. These are sporangia composed of many cells from which only one flagellated spore is released. Isolating these spores and cultivating them separately reveals that microthalli develop from these spores creeping over a substrate. This is the former species *Microspongium gelatinosum*. On this microthallus another type of sporangium, the so called "unilocular" sporangium, develops. This is a sporangium not separated in different chambers as the plurilocular sporangia. And this sporangium is releasing many flagellated spores. These, when germinating, build up a new thallus of the *Scytosiphon lomentaria* type. As on both thalli only spores are produced and never gametes were seen, we can call this cycle a homophasic heteromorphic cycle. Homophasic means that no change in chromosome number occurs (no meiosis). Heteromorphic means that two generations occur that look quite different. The normal condition in life cycles is a heterophasic change between gametophyte and sporophyte. The specimen shown has a length of about 15 cm.

Pelvetia canaliculata

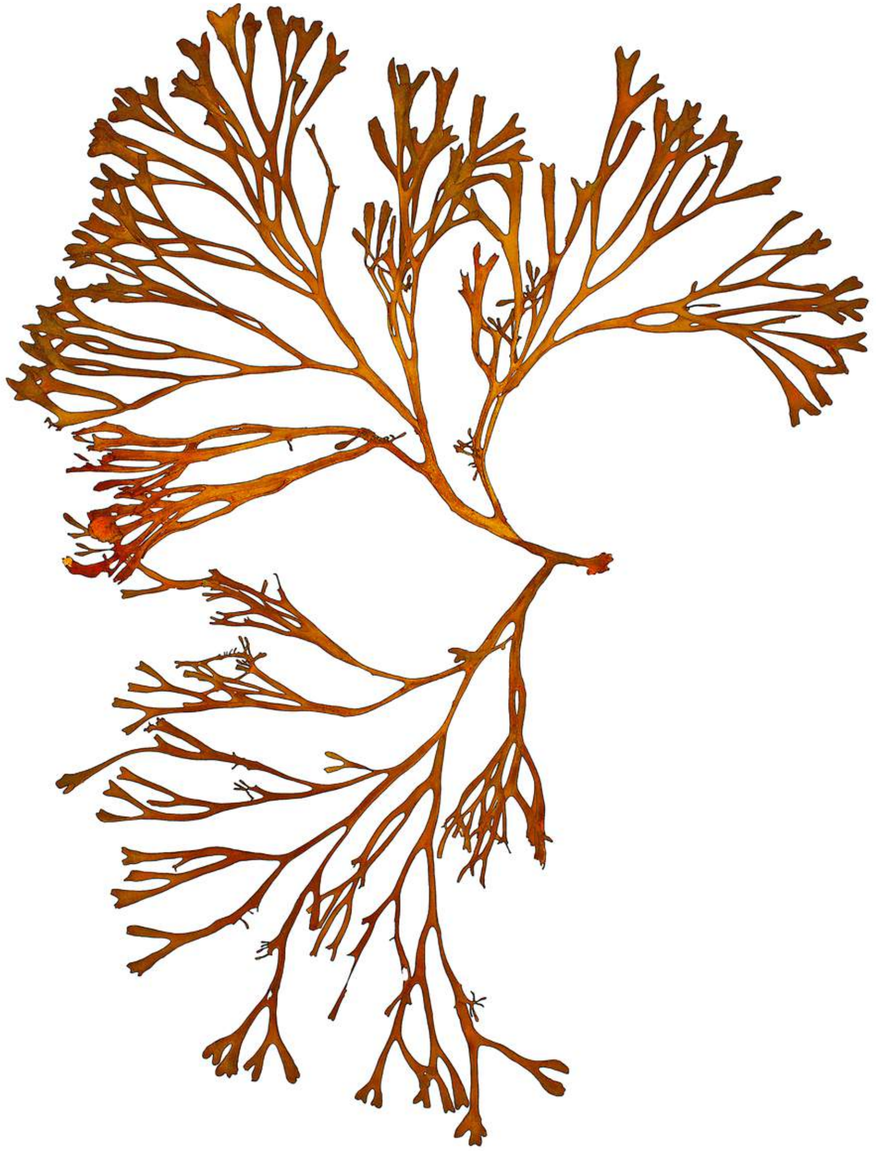
(Linnaeus) Decaisne & Thuret

Brown algae (Phaeophyceae)

The different macroalgal species occurring in the small coastal seam are adapted to very different ecological conditions. So the brown algal species *Pelvetia canaliculata* is found only on rocks at the most upper level of sea- water and rarely occurs in areas where it would be covered by water for longer times. Ecologists named this level the "supralittoral". In contrast the so called "eulittoral" is falling regularly dry and is regularly flooded, the area between high-tide line and low-tide-line. The eulittoral is particularly species-rich because the diversity of ecological conditions is very high. Here a lot of species occur that are more specialized to the upper, the mid- and the lower eulittoral. Especially here brown algae of the order Fucales are predominant. The area permanently covered with water is called "sublittoral". Here large species of brown algae, especially those of the order Laminariales, are dominating the vegetation, the "kelp-forest". Here also a large number of red algae which are sensible to wilting and adapted to weak-light-conditions have their principal dispersion area. Due to their special pigment composition, the red algae are getting more abundant with increasing depth and decreasing light intensity.

As an indicative species of the supralittoral *Pelvetia canaliculata* is the most draught resistant member of the order Fucales. The specimen shown has a length of ca. 5 cm.

chapter 5
Each alga has its place – about the vertical zonation of algae



Pelvetia canaliculata

(Linnaeus) Decaisne & Thuret

Brown algae (Phaeophyceae)

Pelvetia canaliculata is a member of the order Fucales. The epitheton "*canaliculata*" is referring to the channel-like habit of the thallus. The receptacles are yellowish lobes of the thalli, on which the openings of the conceptacles can be seen. In the conceptacles oogonia and antheridia are visible, so the species is monoecious. In contrast to the genus *Fucus*, where the oogonia release eight eggs, in *Pelvetia* only two eggs are developed. *Pelvetia* is one of the most draught resistant species among the Fucales. And, corresponding to this fact it also has to resist high UV-radiation. For successful reproduction the species has to synchronize the release of eggs and spermatozoids. In the order Fucales this synchronization is directly coupled to the moon phases. Zygotes very fast and firmly attach to the surrounding substrate. So the plants ensure that new thalli develop in an appropriate environment.

The thallus regularly is infected by the fungus *Mycophycias* (*Mycosphaerella*) *ascophylli*. This infection takes place early after germination of the zygote. It was shown that growth of the thallus is faster in symbiosis with *Mycophycias* and that the thallus is more draught resistant. The genus *Pelvetia* consists of only one species and is therefore called a "monotypic" genus. The specimen shown has a length of about 15 cm.

Fucus spiralis

Linnaeus

Brown algae (Phaeophyceae)

Fucus spiralis is growing a little bit below the "*Pelvetia* belt" and also fixed to solid substrate. This species is characteristic for the upper eulittoral and is recognized by its thick inflated terminal receptacles. In microscopic cross-sections oogonia as well as antheridia can be found. So *Fucus spiralis* is a monoecious species. This is in contrast to *F. vesiculosus* and *F. serratus* that are dioecious. Perhaps monoecy is advantageous for those species that are covered with water only for a short time. Thus the probability of successful fertilization is significantly enhanced. Compared to the most common *Fucus vesiculosus*, gas vesicles (pneumatocysts) are missing in *F. spiralis*. Zygotes are sticking fast and firm on the substrate in order to occupy their appropriate habitat. To teach students the life circle of Fucales , *F. spiralis* is a favourite object, because the male and the female reproduction cells (in antheridia and in oogonia) can be seen in the microscope.

In the beginning of modern systematics, Carl von Linné described nearly all marine macroalgae as "*Fucus*" thereby mixing so different groups as red algae and brown algae. With increasing knowledge red algae and brown algae were assigned to different classes and numerous new genera of brown algae were defined. Today the genus *Fucus* contains 67 accepted species. *F. spiralis* is found in North-America and Europe. The specimen shown has a length of ca. 20 cm.

Ascophyllum nodosum

(Linnaeus) Le Jolis

Brown algae (Phaeophyceae)

Similar to *Fucus spiralis*, *Ascophyllum nodosum* form large populations in the upper eulittoral on the coastal rocks. This species, characterized by the large pneumatocysts in the middle of the ribbon-like thalli, is dioecious. Male plants can be distinguished from females by the orange colour of the long stalked receptacles. The eulittoral is dominated by members of the order Fucales, for example *Pelvetia*, *Ascophyllum* and diverse *Fucus*-species. The success of members of the Fucales in the eulittoral may be due to the diplontic life cycle. Among algae there often is a regular change between sporophyte and gametophyte. This is the case in all other orders of brown algae but Fucales, because perhaps both generations would have to adapt to the temporary dry condition. So these other brown algal orders prefer habitats of the lower eulittoral and the sublittoral. *Ascophyllum* and most of the other genera of Fucales are growing in dense populations and at low-tide-conditions only the outermost parts of the vegetation are exposed to draught and irradiation. So less than 20 % of the thalli is stressed by these factors. As described for Pelvetia, also the thallus of *Ascophyllum* is regularlyinfected by the fungus *Mycophycias* (*Mycosphaerella*) *ascophylli* resulting in a better growth and resistance against drought stress. Similar to *Pelvetia*, *Ascophyllum* is a monotypic species. Its distribution is the coastal rocks of North America and Europe, in the south reaching Brazil and Portugal.

Fucus vesiculosus

Linnaeus

Brown algae (Phaeophyceae)

The distribution of the algal species characteristic for the different zones of the eulittoral is not strict. *Fucus spiralis* can be found intermixed with *Ascophyllum nodosum* as well as with the two following species, *Fucus vesiculosus* and *Fucus serratus*. These two species are normally found somewhat below *Ascophyllum nodosum*. *Fucus vesiculosus* cannot be confused with *A. nodosum* due to the fact that there is a midrib in the ribbon-like thallus and the globose pneumatocysts are smaller than those of *Ascophyllum*; they are arranged in regular distances on the left and right of the midrib. Like *A. nodosum* and the later shown *F. serratus* the species is dioecious. The receptacles are less swollen compared with *F. spiralis*. When ready for fertilization, male receptacles differ from the females by the orange colour of the apertures. Receptacles mature in a lunar-periodic manner every two weeks. Receptacles are restricted mostly to the winter term; more rarely they are found in summer. *Fucus vesiculosus* was the first *Fucus* species described by Carl von Linné and is therefore the type species of the genus. In "Algaebase" there are 1079 species but only 63 are accepted as real taxa today. This is due to the fact that in former times of systematics nearly all marine macroalgae were subsumed to the genus *Fucus*. *F. vesiculosus* is a species of the North Atlantic occurring in North America and Europe. Normal thalli have a size of 50 cm; maximal length: 90 cm. The specimen shown has a length of about 15 cm.

Fucus serratus

Linnaeus

Brown algae (Phaeophyceae)

Fucus serratus is normally found somewhat below *Fucus vesiculosus*, but both are also frequently found in mixed populations. *Fucus serratus* cannot be confused with other species due to its serrate margin of the thallus. It can also be recognized by its flat receptacles, the margins of which are serrate as the vegetative thallus. The species is dioecious and male receptacles can be recognized by the orange colour of the pores where the spermatozoids are released. The spermatozoids and the egg-cells are not set free directly from the gametangia, but via small vesicles that later disintegrate to release the gametes.

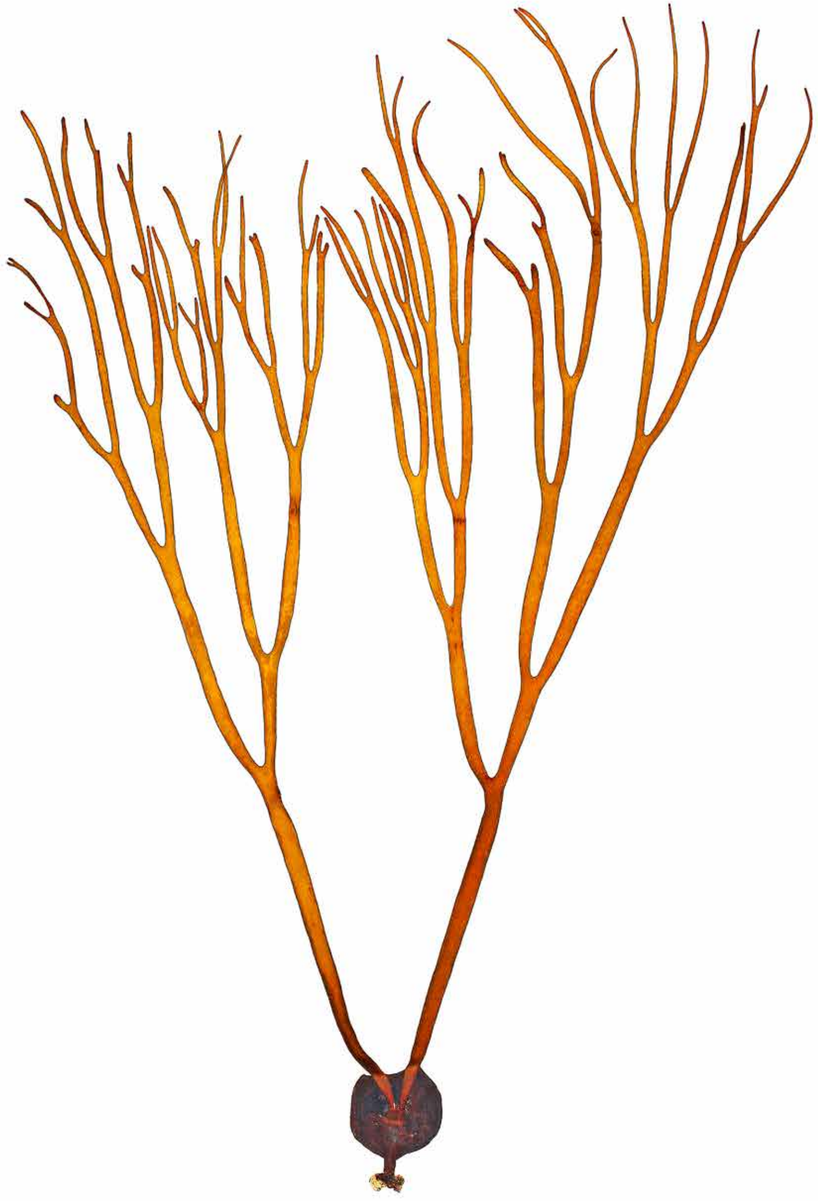
As described for *F. vesiculosus*, receptacles mature in a lunar-periodic manner and are restricted mostly to the winter term. In summertime new receptacle areas develop at the ends of young thallus lobes. The old ones degenerate. As receptacles develop from the dichotomous vegetative thallus, in *F. serratus* they can also be dichotomous. *F. serratus* is a species of the North Atlantic occurring in North America and Europe. Normal thalli are 60 cm long; maximal length: 180 cm. The specimen shown has a length of about 20 cm.

Himanthalia elongata

(Linnaeus) S.F. Gray

Brown algae (Phaeophyceae)

Himanthalia elongata is a species of the order Fucales which is not very similar to the genera *Fucus*, *Pelvetia* and *Ascophyllum*. The thallus is starting after zygote germination with small green spinning tops of 2-5 cm diameter, often 5-20 of them in a group. In the centre of each of these tops two sprouts, flat and ribbon-like, are starting with growth, branching dichotomously and reaching finally a length of 5 m and more. On the complete surface of older ribbons dark points are visible, that turn out to be conceptacles when cross-sections are examined in the microscope. They are containing either oogonia or antheridia. The plant is dioecious. So the complete ribbon-like thallus is composed of two gigantic receptacles. In *Fucus* and *Ascophyllum* the receptacles are confined to small lobes at the ends of vegetative thalli. In *Himanthalia* the vegetative thallus is the small green spinning top of 2-5 cm diameter. In contrast to *Fucus*, where eight eggs are released from one oogonium, there is only one egg in the oogonium of *Himanthalia*. In Brittany the young thalli are harvested and served as "Haricots" or "Spaghetti de la mer".



chapter 5
Each alga has its place – about the vertical zonation of algae

Himanthalia elongata

(Linnaeus) S.F. Gray

Brown algae (Phaeophyceae)

Himanthalia elongata grows mostly in the lower eulittoral and the upper sublittoral, so that thalli are rarely and only shortly exposed to the dry air. Together with *Saccharina latissima* and the species of the genus *Laminaria Himanthalia* constitutes the "kelp forest". Thalli of the macrophytic brown algae are frequently colonized by filamentous brown algae of the order "Ectocarpales". Some of these "epiphytes" are species- or genus-specific, i.e. *Elachista fucicola* is a specific inhabitant of the genus *Fucus*. Other epiphytes like *Pylaiella littoralis* are less specific, growing mostly on *Fucus serratus*, but also on other *Fucus*-species, on sea-grasses and epilithic. Beside from less specific epiphytes (*Pylaiella*, *Ectocarpus*) *Himanthalia elongata* harbours two very specific species that are only found on the receptacles of this species: *Elachista scutulata* and *Herponema velutinum*. *Elachista scutulata* infects conceptacles and then builds colonies on the thallus of appr. 2 cm length, the filaments growing out up to 1 cm. *Herponema* grows more inside of the *Himanthalia* thallus and only short brownish filaments are visible in the infected area. *Himanthalia*, which is harmed at least by the shading of the own thallus tries to get rid of the epiphyte by shedding the own cell wall.

The genus *Himanthalia* comprises only two species. *H. elongata* is a European species with an extraterritorial occurrence in Ghana. The specimen shown has a length of about 25 cm.

Saccharina latissima

(Linnaeus) C.E. Lane, C. Mayes, Druehl & G.W. Saunders

Brown algae (Phaeophyceae)

Saccharina latissima, a member of the order Laminariales, grows thalli of more than 5 m length, fixed with a strong holdfast to the substrate. A relatively short flexible stalk, the cauloid, bears the long narrow leaf like phylloid. The inner third of the phylloid is curly and bears dark brown sporangia sori in winter. Thusthe macrophytic plant is the sporophyte generation in the life cycle of *Saccharina latissima*. Transferring a part of the sporangia sori in culture medium or sea water, the slipping and further development of zoospores can be seen. They germinate to tiny filaments of around 1mm. These branched filaments develop gametangia at their tips, from which eggs are set free (female filaments) or spermatozoids (male filaments). The tiny filaments are therefore the gametophytic generation of this alga. And this generation is heterothallic because male and female filaments exist. After the fertilization the zygote grows to a new sporophyte. This strongly heteromorphic life cycle is typical for all members of the order Laminariales (*Alaria*, *Laminaria*, *Saccorhiza*, *Saccharina*, *Undaria*). *Saccharina latissima* is worldwide distributed and is the only European species. It is the type species of the genus. The species is found in the sublittoral and the low eulittoral. The genus *Saccharina* contains 20 species worldwide. The specimen shown has a length of about 25 cm.

Laminaria hyperborea

(Gunnerus) Foslie

Brown algae (Phaeophyceae)

Laminaria hyperborea, a member of the order Laminariales, grows thalli of more than 2 m length, fixed with a strong holdfast to the substrate. A long stable and upright stalk, the cauloid, with a diameter of up to 5 cm, carries a broad digitate phylloid. The species can be distinguished from *Laminaria digitata* occurring in the same locations in the upper sublittoral by the much stronger cauloid, the general size and the connecting region between cauloid and phylloid. This is cuneate in the case of *Laminaria digitata* and broad shouldered in *Laminaria hyperborea*.

According to the description of *Saccharina latissima* the sporangia are developed on the phylloids in winter (November to April) and tiny filaments form the gametophyte. As in all Laminariales the life cycle is strong heteromorphic. In late winter the connecting region begins to build a new phylloid and the old one is torn off during spring storms. In the strong stalks of *Laminaria* transport elements were found which resemble the sieve elements of higher plants and which are responsible for the transport of assimilates in the cauloid. These elements are called “trumpet hyphae” because of their characteristic form. The genus *Laminaria* comprises 29 species. *Laminaria hyperborea* is a European species. *Laminaria* species are the main components of the so called algal forest in the sublittoral. The crowns of the *Laminaria* plants can be seen only in the times of extremely low tides. The specimen shown has a length of about 25 cm.

Phycodrys rubens

(Linnaeus) Batters

Red algae (Florideophyceae)

Phycodrys rubens is one of the red algae the thallus of which mostly resembles branches and leafs of higher plants. The "leafs" have the habit of oak leafs in form and also in venation. The typical habitat is the sublittoral and it is growing frequently on the stalks of the large *Laminaria* species. The red algae are known to occur in deeper water thus having a pigment composition different from green algae and diatoms. The absorption spectrums of chlorophyll a and b exhibit a so called green gap, with wave lengths between 500 and 620 nm that are not absorbed by green algae and diatoms. So this light reaches deeper regions and red algae with their phycoerythrin can use this light for photosynthesis. Also the absorption spectrum of water allows that blue light penetrates deeper water levels and can be absorbed by red algae. Phycoerythrin and phycocyanin are also present in the classes Cryptophyceae and Cyanophyceae so that also species of these classes can use the light in deeper water. In the case of red algae this is most evident because they are macroalgae.

Phycodrys rubens is distributed in the northern hemisphere. 25 Species of *Phycodrys* are accepted worldwide. It belongs to the species-rich family of Delesseriaceae, the members of which predominantly develop leafy thalli. The specimen shown has a length of about 20 cm.

Plumaria plumosa

(Hudson) Kuntze

Red algae (Florideophyceae)

Plumaria plumosa is a small dark red alga of ca. 10 cm length. Its ramuli are in one plane and the branching is multiple. The basal branches have a cortex around the central filament; the terminal ends are ecorticate. According to the construction of the thallus they belong to the uniaxial type. The branching in the basal parts is alternate, whereas the terminal branches are opposite, the outermost larger than the inner ones. The plants are attached to solid substrate or to other algae with a disc.

Plumaria plumosa is an alga of the lower eulittoral and the sublittoral. With its dark red colour it is well adapted to deep water conditions. When reproducing, on the gametophyte the gametangia, the carposporophyte and in the tetrasporophyte the tetrasporangia are on the outermost cells at the top of the thallus. Gametophyte and tetrasporophyte are isomorphic.

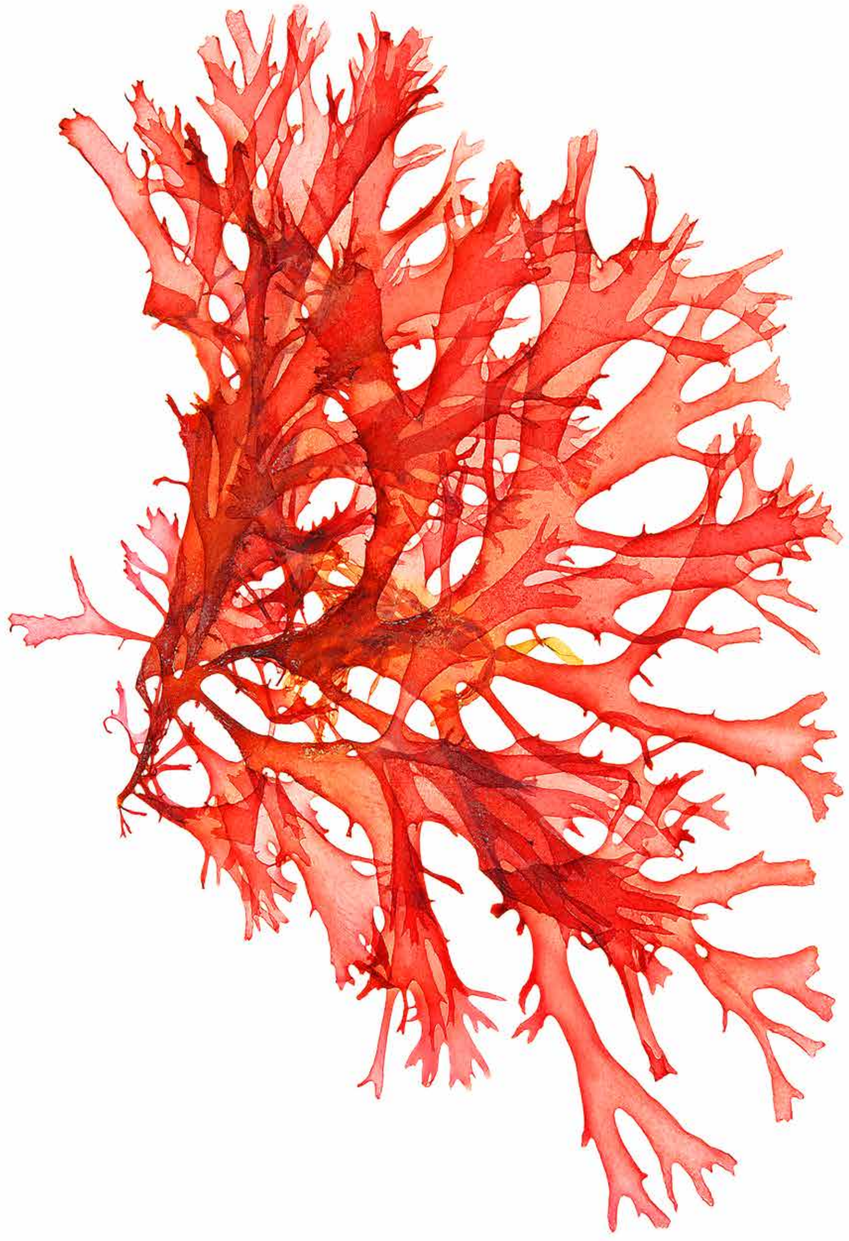
The genus *Plumaria* is monotypic; this means that *Plumaria plumosa* is the only species of this genus. The next relative is the genus *Ptilota*, with which *Plumaria* can be confused macroscopically. But in the microscope it can be easily distinguished by its mode of branching. Both genera belong to the large family of Ceramiaceae. The specimen shown has a length of about 10 cm.

Apoglossum ruscifolium

(Turner) J. Agardh

Red algae (Florideophyceae)

Apoglossum ruscifolium is a species of the family Delesseriaceae. Members of this family frequently have thalli with phylloids that look like leafs on higher plants: Median and lateral veins are visible and also the outline of the "leafs" resembles those of higher plants. In *Apoglossum ruscifolium* the median is easily visible whereas the lateral veins are only distinguishable in the microscope. The general structure is of course of the uniaxial type. Typical for *Apoglossum* is the branching of the thallus: Branches arise from the midrib so that the younger phylloids are sitting on the older ones. In the microscope a very regular pattern of central filament and lateral descendants is seen. The leaf-like thallus is in principal a central filament where the lateral branches are touching one another in one plane. Gametophytes are dioecious. In male plants the spermatangia are arranged in sori near to the midrib. In female plants the carpogonia and later on the carposporophytes are next to the midrib. They are surrounded by a layer of sterile cells forming a cystocarp. Carpospores are released from the cystocarp by a pore. *Apoglossum ruscifolium* is a plant of the sublittoral occurring on stipes of *Laminaria* but also below the kelp forest in depths to 20 m. It also can be found in rock pool in the intertidal region. It is a plant of the Western and Eastern Atlantic. 7 species are included in the genus *Apoglossum*. The specimen shown has a length of about 10 cm.



Palmaria palmata

(Linnaeus) F. Weber & D. Mohr var. sarniensis

Red algae (Florideophyceae)

Palmaria palmata is a frequent species on Northeast Atlantic seashores. The tough plants can reach a length of more than half a meter, the normal length is 30 cm. The flat thalli are divided dichotomously or hand-formed and are attached to the substrate with a short stalk and a disc. The plant occurs in the lower eulittoral and sublittoral attached to rocks and epiphytic on larger algae. Plants are collected in Brittany as seafood under the name "Dulse".

The large isomorphic thalli are either tetrasporophytes or male gametophytes. The female gametophytes were unknown for a long time; they are reduced to a small disc-like thallus bearing carpogonia but no carposporophytes. The fertilized carpogonia directly develop to tetrasporophytes.

Palmaria is a genus containing 11 species worldwide. The genus' name was taken to create the family (Palmariaceae) and an order (Palmariales). There is one variety *Palmaria palmata* var. sarniensis shown on the left. This variety is restricted in its distribution to Brittany and the channel going up to Ireland in the north. According to Algaebase it is not anymore an variety despite its clearly different morphology. The distribution of *Palmaria palmata* is worldwide. On the herbarium sheet the alga is named under its former name *Rhodymenia palmata*. The specimen shown has a length of about 15 cm.

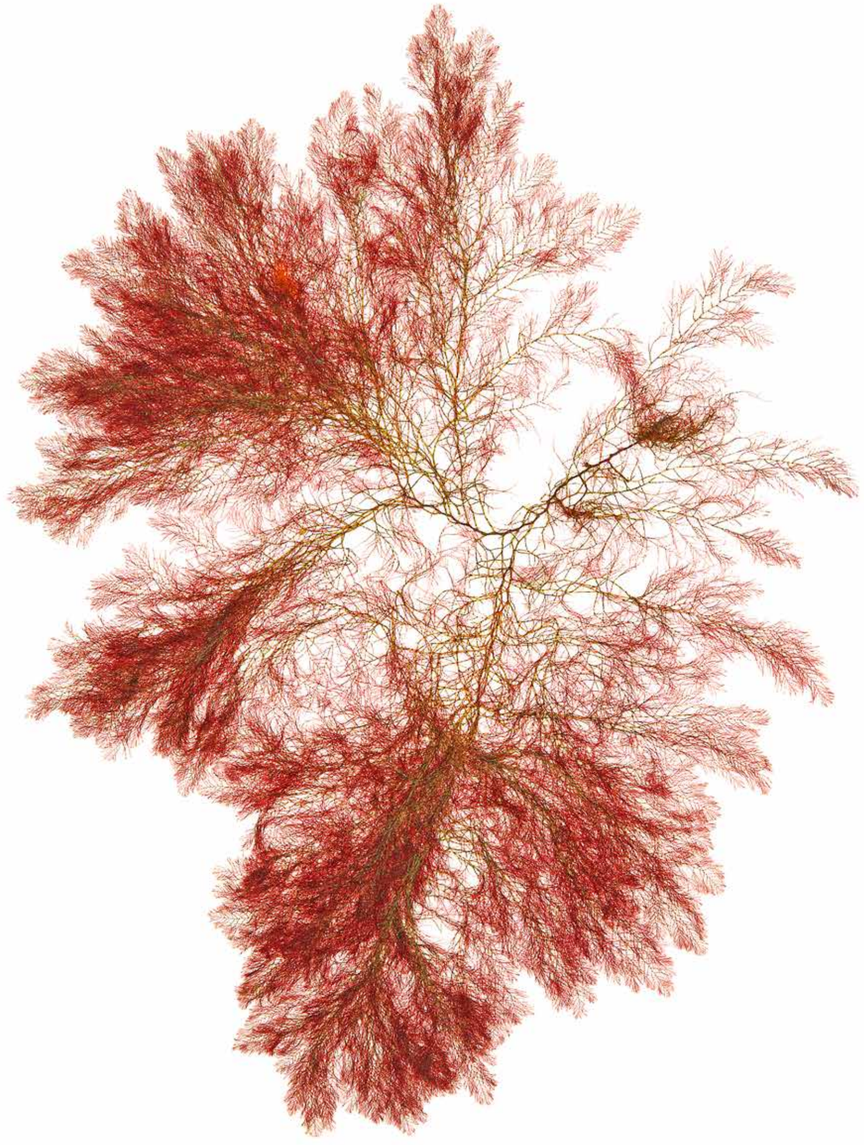
Callithamnion sp.

Lyngbye

Red algae (Florideophyceae)

The genus *Callithamnion* is not easily recognized. It grows up to 10 cm. The filaments are uniseriate, sometimes surrounded by rhizoids. Branching is irregular and the branchlets arise from every cell of the main axis. In contrast to similar genera the cells are multinucleate. Carposporophyte, spermatangia and tetrasporangia are located on special branches near to the tips of the thalli. Life cycles appear to be isomorphic. Species delineation is according to Algaebase difficult. Maybe that also the delineation of genera of similar habit is insufficient. According to Algaebase there are 90 species of *Callithamnion* of which 15 occur in Europe. The genus is distributed worldwide.

Confusion is possible with the very similar genus *Aglaothamnion*. The genus is a member of the family Ceramiaceae and the large order Ceramiales. Most *Callithamnion* species grow on rocks or are epiphytic on other algae. The specimen shown has a length of about 10 cm.



Callithamnion sp.

Lyngbye

Red algae (Florideophyceae)

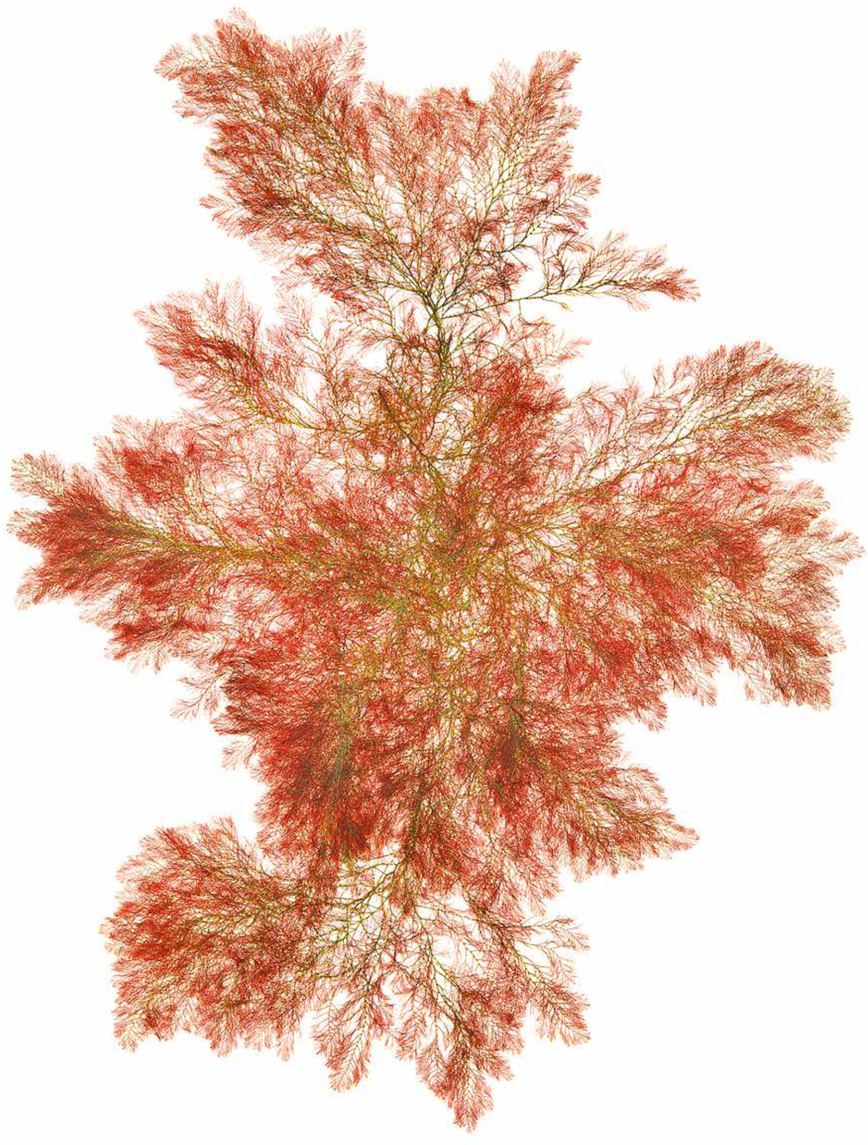
There are a lot of genera that can be confused with *Callithamnion*:

Aglaothamnion resembles strongly the genus *Callithamnion*. The cells of *Aglaothamnion* are uninucleate in contrast to the multinucleate cells of *Callithamnion*. As the number of nuclei is not easy to be count, the differentiation of both taxa is not easy. Also the arrangement of the carpogonia and carposporophytes is different in both genera. The genus *Aglaothamnion* comprises 34 species according to Algaebase. *Aglaothamnion fucellariae* is the type species of the genus.

Antithamnion has opposite or cruciate branches in contrast to *Aglaothamnion* and *Callithamnion*. 42 species are accepted currently in Algaebase. Also *Antithamnionella* must be taken in account comprising 26 species worldwide.

Rhodochorton has a divergent life cycle in which tetrasporophytes (or tetrasporangia) directly arise from fertilized carpogonia. Free carpospores don't exist. Ten species are currently present in the genus *Rhodochorton*.

Acrochaetium is easily distinguished from *Callithamnion* because of its small size (less than 3 cm). The life cycle of *Acrochaetium* is heteromorphic. 184 species are included in the genus. The specimen shown has a length of about 10 cm.

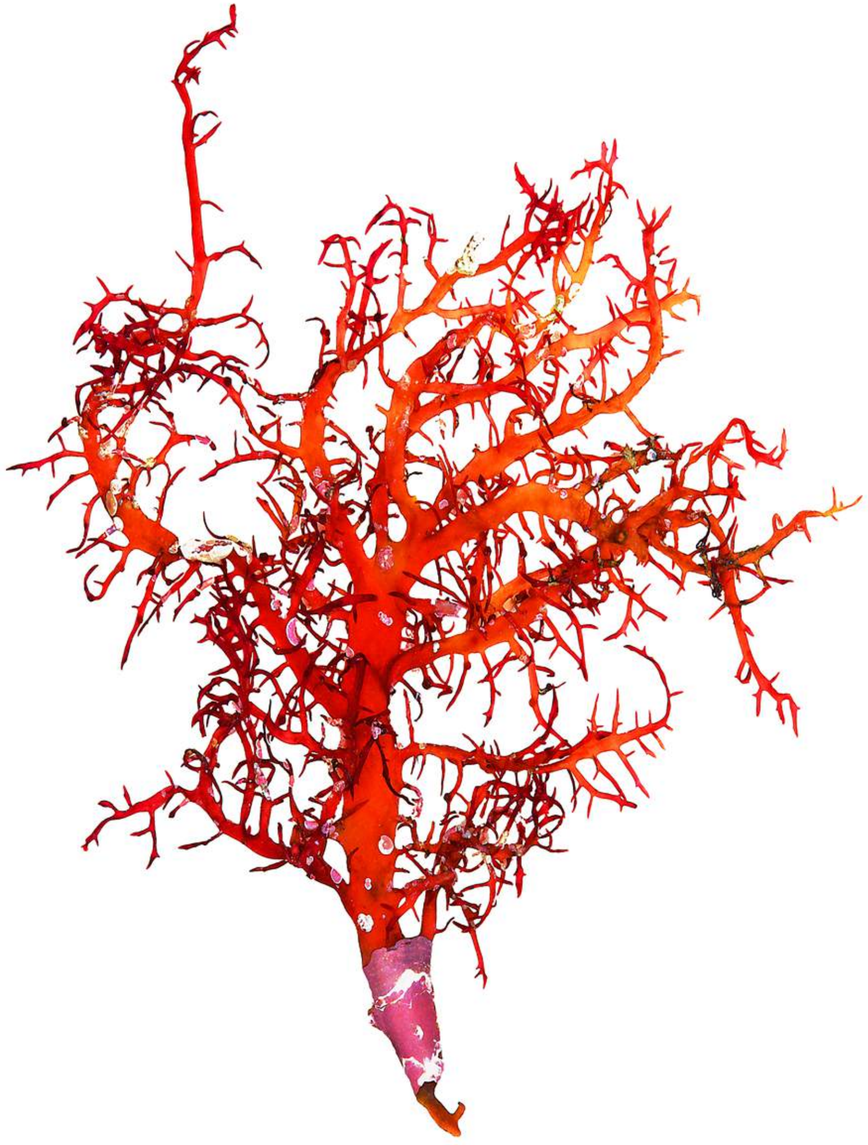


Chondracanthus teedei

(Mertens ex Roth) Kutzing

Red algae (Florideophyceae)

Chondracanthus teedei, better known as "*Gigartina teedei*" to most phycologists, is a red alga of worldwide distribution. The thallus has a multiaxial structure with large filamentous cells in the centre surrounded by radially arranged cells getting gradually smaller towards the surface. The outermost cells are photosynthetic with rhodoplasts. The thallus is flat in cross-section, up to 30 cm in length and feathery branched. The gametophytes are described to be dioecious or monoecious in the genus *Chondracanthus*, but in literature it is stated that the male gametophyte is unknown. When spermatangia are formed in other species of *Chondracanthus*, they are in superficial sori. May be that the male gametophyte is of different morphology. The carpogonia and later the cystocarps are at the end of younger branches and reach a diameter of about 1 mm. The tetrasporophyte is isomorphic to the female gametophyte. Tetrasporangia are arranged in sori that are located at the end of younger branches. Interestingly also in *Chondracanthus acicularis* the male gametophyte is unknown. The species has a more or less worldwide distribution. This is a species found on rocks in the upper sublittoral. The specimen shown has a length of about 15 cm.



Chondracanthus teedei

(Mertens ex Roth) Kutzing

Red algae (Florideophyceae)

Chondracanthus teedei, also known as "*Gigartina teedei*", is one of the red algae collected for agar production. It is fixed with a small disc to stones. Branching of 2nd to 4th order can occur. All ends of branchlets are acute. The uppermost branches are round in cross-section, the basal ones mostly flat. Branching takes place in one plane. The thallus is cartilaginous and members of the genus are frequently collected for agar production. Tetrasporophyte and female gametophyte are isomorphous.

The family Gigartinaceae comprises 151 species in 10 genera. Three of the genera are relevant for the European flora:

- The genus *Chondracanthus* with 21 species
- The genus *Gigartina* with 41 species
- The genus *Chondrus* with 19 species

The order Gigartinales with its 905 species is the second largest order within the red algae. All the three genera mentioned above contain species that are collected for agar production. In the herbarium sheets *Chondracanthus teedei* is mentioned as"*Gigartina teedei*". The specimen shown has a length of about 15 cm.

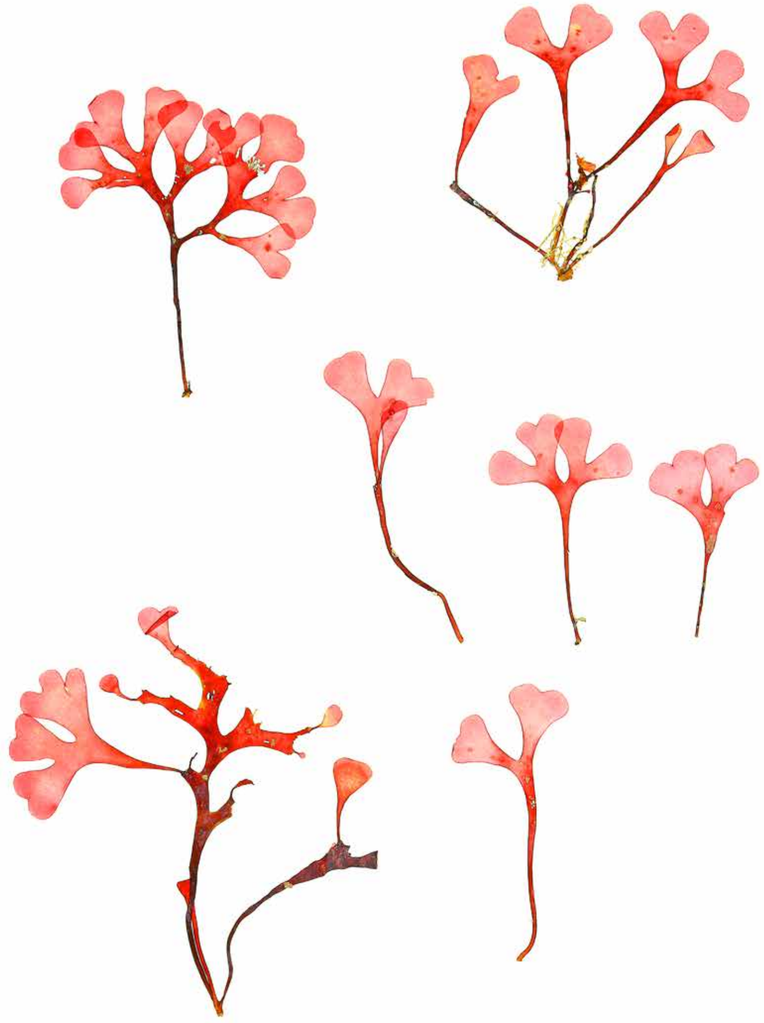
Palmaria palmata

(Linnaeus) F. Weber & D. Mohr

Red algae (Florideophyceae)

Palmaria palmata is one of the red algae that have a multiaxial construction of the thallus. This means that in microscopical cross-sections or longitudinal section a lot of filaments are arranged in parallel order. This is in contrast to the uniaxial thalli found in *Polysiphonia* and *Delesseria* where the central axis is easy to identify. Normally the thalli of multiaxial organization are thick and the central filaments which don't contain coloured plastids are curved outwards. Only the outer parts of the filaments contain coloured rhodoplasts. The consistency of the thallus resembles a real tissue, but as thalli are in principle filamentous, these plants are called "pseudoparenchymatic". There are numerous genera which have thalli with multiaxial structure. Often the space between the filaments is filled with the carbon hydrates of human interest and the plants are collected for agar production. *Chondrus crispus*, *Gracilaria verrucosa*, *Mastocarpus stellatus* and *Furcellaria fastigiata* are the major species for agar production. *Palmaria palmata* is also collected but in this case it is for human nutrition. It is one of the most frequent algae in Brittany and Ireland used as seafood.

Other species mentioned in this book are of the multiaxial type: *Dumontia contorta*, *Lomentaria articulata*, *Lomentaria clavellosa*, *Chylocladia verticillata* and a lot of more species. The specimen shown has a length of about 15 cm.



Phyllophora sicula

(Kutzing) Guiry & L.M. Irvine

Red algae (Florideophyceae)

Phyllophora sicula is a member of the order Gigartinales and in this order forms an own family, the Phyllophoraceae. According to Algaebase the genus *Phyllophora* comprises 12 species. The thalli are flat, sitting on long stalks and are dichotomously branched. They reach a length of 15 cm. With their rounded lobes they somewhat resemble *Palmaria palmata*. But this species is larger and the thallus is much thicker. They occur in the sublittoral to a depth of 15 m. Typical habitats are rocks and the stipes of *Laminaria* in the upper sublittoral. The species occurs in the Mediterranean and in the North Atlantic. Members of the genus are collected as a source of agar and carrageenan. The genus contains 12 accepted species according to Algaebase. It belongs to the family Phyllophoraceae and to the order Gigartinales. The family Phyllophoraceae contains 131 species distributed in different genera. Irrespective of *Phyllophora*, the most important genera of this family are: *Ahnfeltiopsis* (29 species), *Gymnogangrus* (29 species) and *Mastocarpus* (15 species). *Mastocarpus stellatus* is a species which is mentioned in this book. The Gigartinales is one of the larger orders (905 species) in the red algae. On the herbarium sheet the specimen was named *Phyllophora membranifolia*. But according to modern literature it must be called *Phyllophora sicula*. The specimens shown have a length of about 8 cm.

Phyllophora sicula

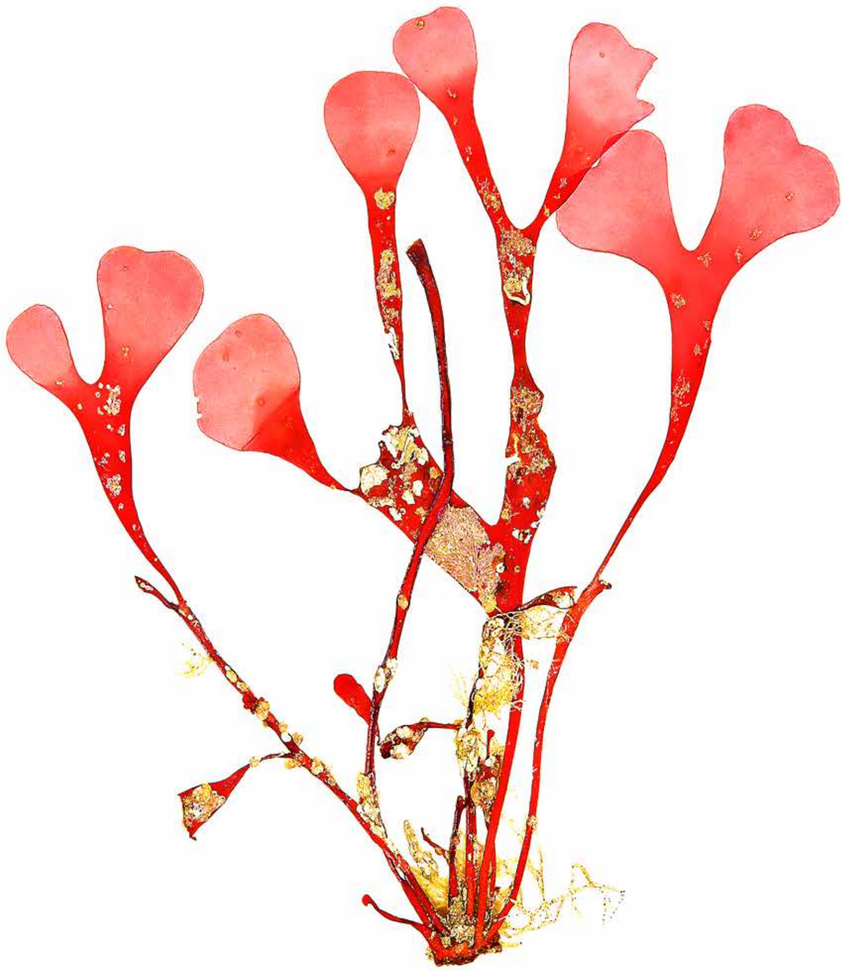
(Kützing) Guiry & L.M. Irvine

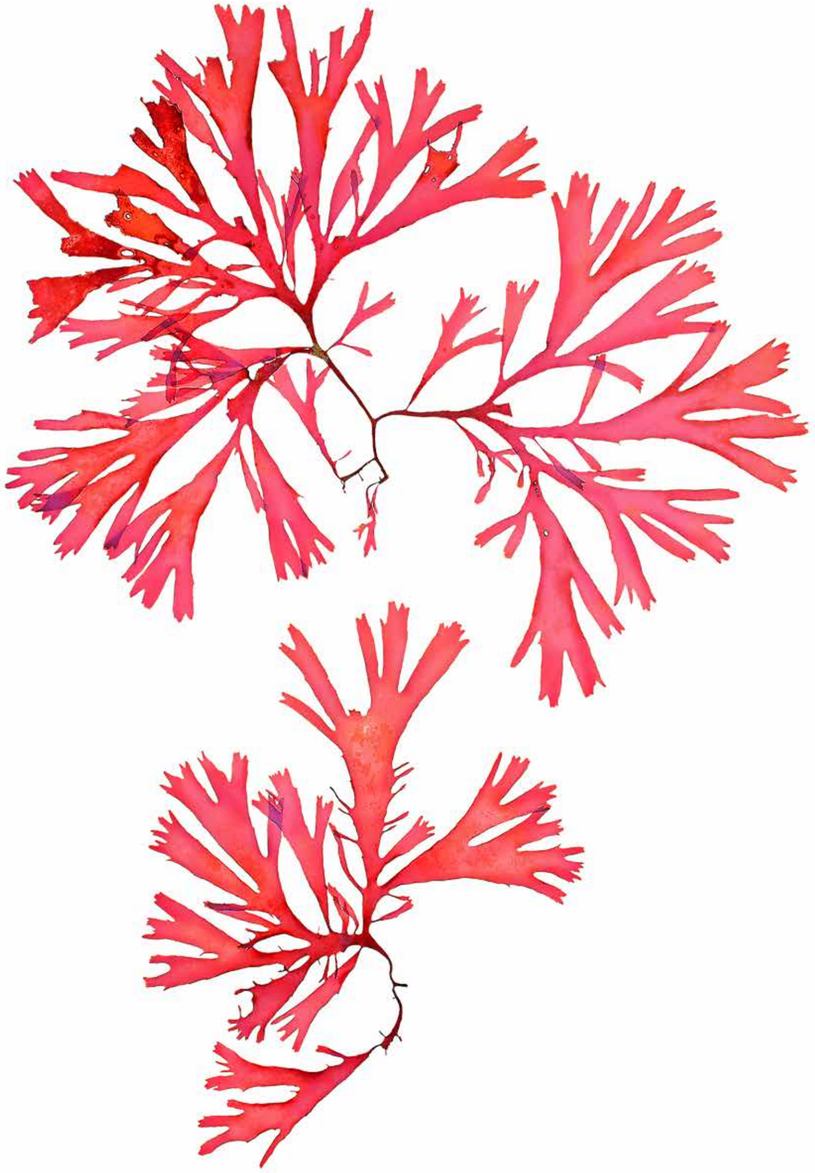
Red algae (Florideophyceae)

Phyllophora sicula is a red alga in the order Gigartinales building its own family Phyllophoraceae. The name on the herbarium sheet was *Phyllophora epiphylla*, but this plant is, according to Algaebase, synonymous to *Phycodrys rubens* (see there and also 3-5). Pyllophora is a plant of the upper sublittoral found on rocks up to 15 m depth. Rarely the plant grows on stipes of *Laminaria hyperborea*. In the upper sublittoral the predominating vegetation is the "kelp forest". This is the most species-rich seam in the coastal seashore and the location of highest productivity. Here the largest species are found especially giving an ecological niche to the numerous epiphytic red algae that are growing for example on *Laminaria* stipes. The life conditions in the upper sublittoral are:

- Covered by water all over the year.
- No drought stress.
- No frost in winter.
- No UV stress.
- Good supply of fresh water and nutrients.
- Enough light to grow even under high-tide-conditions.
- Wave action less intense than in eulittoral.

The dominating planst in sublittoral are: *Laminaria*, *Saccharina*, *Saccorhiza*, *Himanthalia* and the bulk of leafy red algae of the upper sublittoral. The specimen shown has a length of about 12 cm.





Palmaria palmata

(Linnaeus) F. Weber & D. Mohr

Red algae (Florideophyceae)

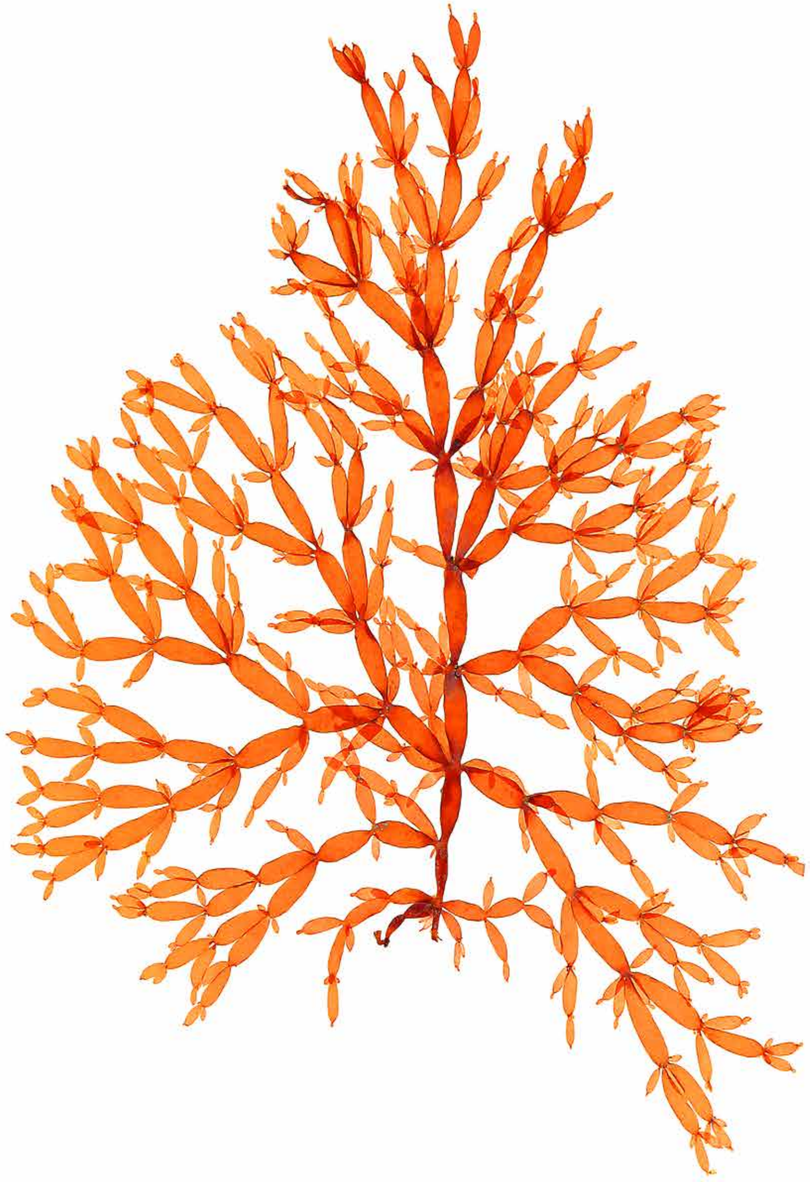
Palmaria palmata is one of the red algae that are most frequently found at the seashore of Brittany. The deep red colour derives from the water soluble pigments phycoerythrin and phycocyanin that are relics of the pigmentation of the blue-green alga taken up in early evolution. The names of these pigment are derived from the Greek, where "phycos" is the word for a kelp, "erythro-" is the word for the red colour and "cyano-"is the word for blue colour. There are two additional classes of algae where these pigments occur: The Glaucocystophyceae and the Cryptophyceae. The pigmentation of the algae is a prominent character for the allocation of the algae to their classes. Especially some carotenoids are classical characters for certain algal classes: So "fucoxanthin" is indicative for most of the classes of Heterokontophyta, for example brown algae, diatoms and gold algae. The name is derived from the genus *Fucus*, out of which this pigment was first isolated. And "xantho-" is the Greek term for yellow, although this pigment is more brownish. But most pigments of this class of molecules, the xanthophylls, are yellow. One class of the Heterokontophyta is not brown but green, because fucoxanthin is missing in the plastids. This is the class "Xanthophyceae", where fucoxanthin is replaced by "vaucheriaxanthin", a pigment which was first isolated from *Vaucheria*. And another xanthophyll characteristic for phototrophic dinoflagellates, "peridinin", was isolated from the dinophycean alga *Peridinium*. The specimen shown has a length of about 15 cm.

Lomentaria articulata

(Hudson) Lyngbye

Red algae (Florideophyceae)

Lomentaria articulata is a red alga which is characterized by the segmented "articulate" thallus. The thallus is completely hollow in the centre and the general structure is multiaxial. There are no cellular septa at the constrictions. At the constrictions two or more subordinate branches are standing in a whorl. Branching of second order can occur. The gametophytes are dioecious. Spermatangia are arranged in sori on the surface of the male gametophyte. The carpogonia are scattered over the thallus. Most cells of the carposporophyte are developing to carposporangia. Carposporophytes are protected by a gametophytic pericarp building large cystocarps with a distinct pore. Tetrasporophyte and gametophytes are isomorphic. The tetrasporangia are formed in sori on the surface. They are located in pits. The four spores are arranged as a tetrahedron in the tetrasporangium. The plants are found in rock pools in lower eulittoral and in the sublittoral. They are growing epiphytic or epilithic. There are 40 accepted species of *Lomentaria* worldwide. *Lomentaria articulata* is the type species of the genus. It is a species of worldwide distribution. *Lomentaria* builds its own family "Lomentariaceae" in the order Rhodymeniales. The plant can reach a length of 10 cm.



Callophyllis laciniata

(Hudson) Kutzing 1843

Red algae (Florideophyceae)

Callophyllis laciniata (Gigartinales, Kallymeniaceae) is a red alga with a flat ribbon-like thallus that is branched strictly or irregularly dichotomous. It belongs to a genus containing 61 species worldwide. Even phycologists with great experience have their problems identifying the flat dichotomous or subdichotomous species of red algae. For identification additional characters like the arrangement and design of reproductive organs are needed. Looking through this book some species occur that can be confused with *Callophyllis laciniata*:

- *Cryptopleura ramosa* (Ceramiales, Delesseriaceae)
- *Chondrus crispus* (Gigartinales, Gigartinaceae)
- *Nitophyllum punctatum* (Ceramiales, Delesseriaceae)
- *Palmaria palmata* var. *sarniensis* (Palmariales, Palmariaceae)
- *Membranoptera alata* (Ceramiales, Delesseriaceae)
- *Palmaria palmata* (Palmariales, Palmariaceae)
- *Polyneura bonnemaisonii* (Ceramiales, Delesseriaceae)

And there are a lot of other species that can be confused with *Callophyllis*. Some of them can be identified by vegetative characters (veination, general size, consistency). The specimen shown has a length of about 15 cm.

Lomentaria articulata

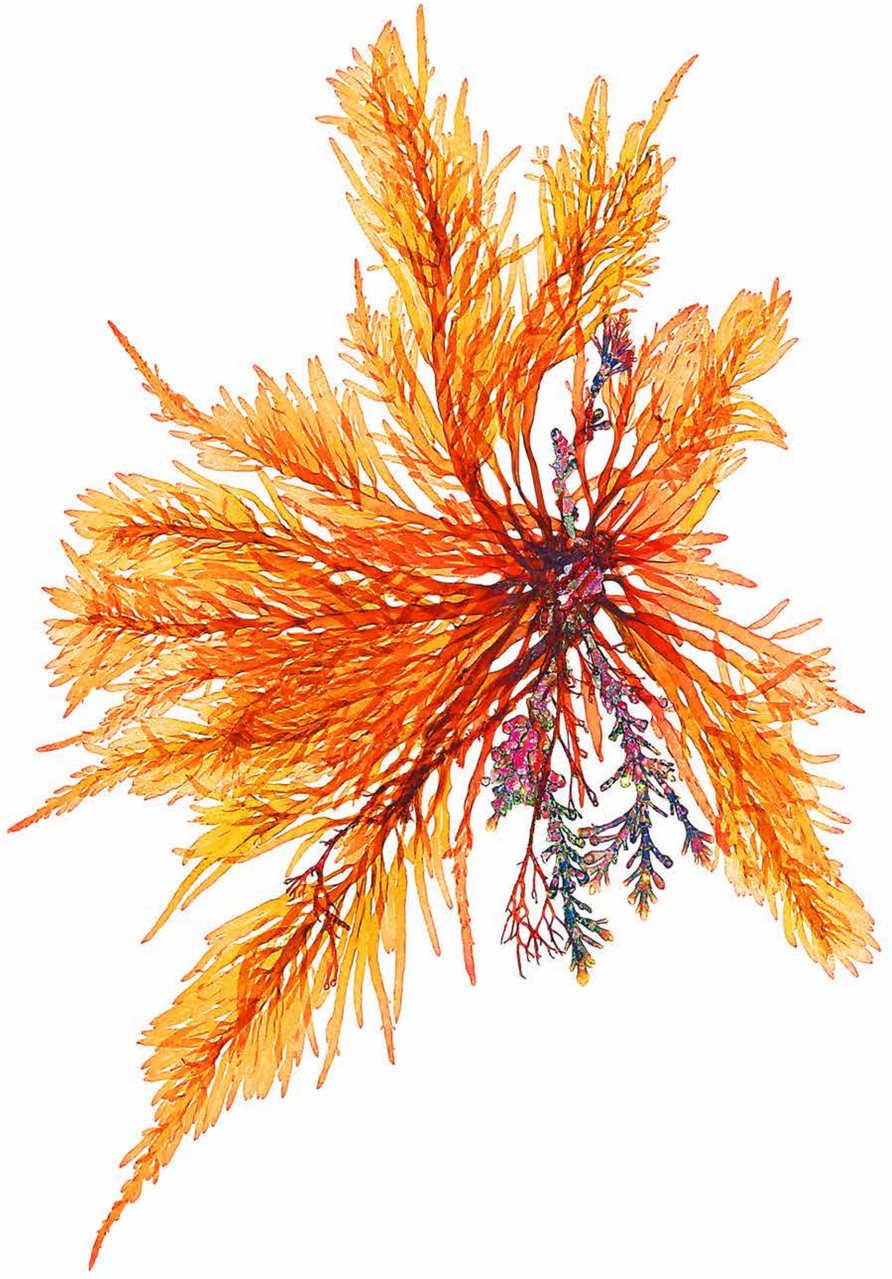
(Hudson) Lyngbye

Red algae (Florideophyceae)

Lomentaria articulata is a red alga which is characterized by the segmented "articulate" thallus. This species and the next species *Lomentaria clavellosa* are frequently confused with other species. So *Lomentaria articulata* can be confused with *Chylocladia verticillata*. In *Chylocladia* the segments are more barrel-like. The pericarps are not opened by an ostiolum. And the spermatangia are not hidden in a pit. It was proposed by some authors to make two separate genera: Species with constrictions would remain in the genus Lomentaria, because the type species is *Lomentaria articulata*, the species with constrictions.

Species without these constrictions would change into a new genus "*Chondrothamnion*", a name which was used by the phycologist Kuetzing a long time ago.

There are some other species which can be confused with species of the genus *Lomentaria*: So the stiff forms from exposed locations can be confused with *Gelidium sp*. Also a confusion with *Gloiosiphonia* is possible, when the plant is not fertile. But in this genus the cystocarps are in the inner side of the thallus. Finally, confusion with the genus *Dasya* and with other species of *Lomentaria*, for example *Lomentaria orcadensis* is possible. The specimen shown has a length of about 15 cm.



Lomentaria clavellosa

(Lightfoot ex Turner) Gaillon

Red algae (Florideophyceae)

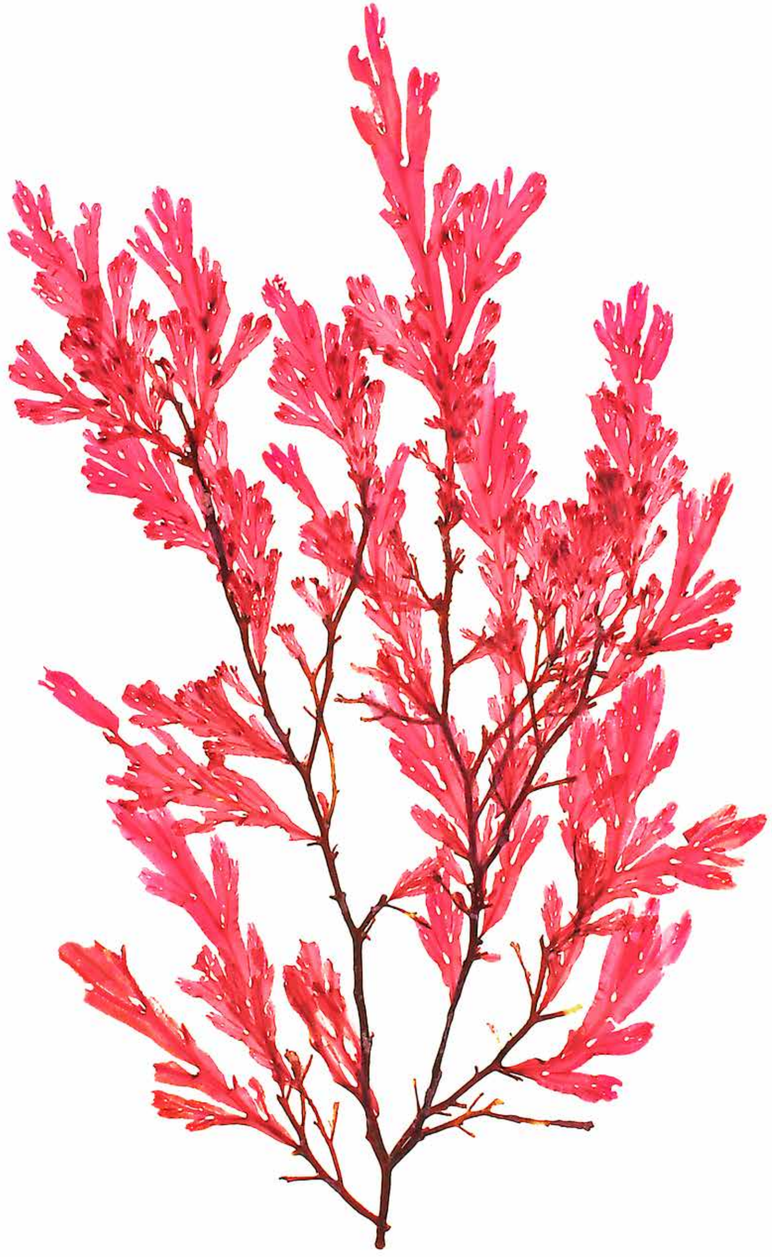
Lomentaria clavellosa is a red alga which is, in contrast to *Lomentaria articulata*, not segmented. The thallus is completely hollow in the centre and the general structure is multiaxial. The plant can reach a length of 40 cm and is much larger than *Lomentaria articulata*. There is a dominant main axis. The branching can be multidirectionally but also plants are found with distichous branching in one plane. The gametophytes are dioecious. Spermatangia are arranged in sori on the surface of the male gametophyte. The carpogonia and the carposporophyte are surrounded by a thick pericarp which is open with a visible pore. The carposporangia are large. Tetrasporophyte and gametophytes are isomorphic. The tetrasporangia are formed in sori on the surface near the tips of branches. They are located in pits. The four spores are arranged as a tetrahedron in the tetrasporangium. The plants are found epiphytic or epilithic in rock pools in lower eulittoral and in the sublittoral. There is some variability in the habit of the plants. Cross-section can be terete or flattened. Often the distichous are those that are flattened. And it was described that the consistency can be variable dependent on the exposition of the plants: Plants exposed to wave action feel stiff whereas plants of sheltered locations are soft in texture. *Lomentaria clavellosa* is an Atlantic species. The specimen shown has a length of about 20 cm.

Membranoptera alata

(Hudson) Stackhouse

Red algae (Florideophyceae)

Membranoptera alata is a red alga of the family Delesseriaceae. Large plants reach a length of 20 cm, normal plants are about 10 cm. They are fixed to the substrate with a disc-like holdfast, from which diverse erect thalli arise. The thalli are leaf-like with a conspicuous midrib and a width of about 2 mm. Lateral veins can only be seen in the microscope. Thalli are regularly branched subdichotomously in one plane so that the plants can form dense tufts. New branches also can arise from the midribs. The thallus structure is of the uniaxial type and grows with an apical cell. The blades consist of one cell layer in the lamina and are thicker in the region of the midrib. The plants are dioecious. Spermatangia are formed in sori near the apex. Carpogonia and carposporophytes are enclosed in subglobose pericarps with an ostiolum. Tetrasporophytes are isomorphic to the gametophytes; tetrasporangia are built in the region of the midrib. The species is found in rock pools in the lower eulittoral and in the sublittoral on stipes of *Laminaria*. *Membranoptera alata* can be confused with smaller specimens of *Apoglossum ruscifolium*. There are 11 species of *Membranoptera* worldwide. *Membranoptera alata* is the type species of the genus. The species is restricted to the North Atlantic. The specimen shown has a length of about 15 cm.

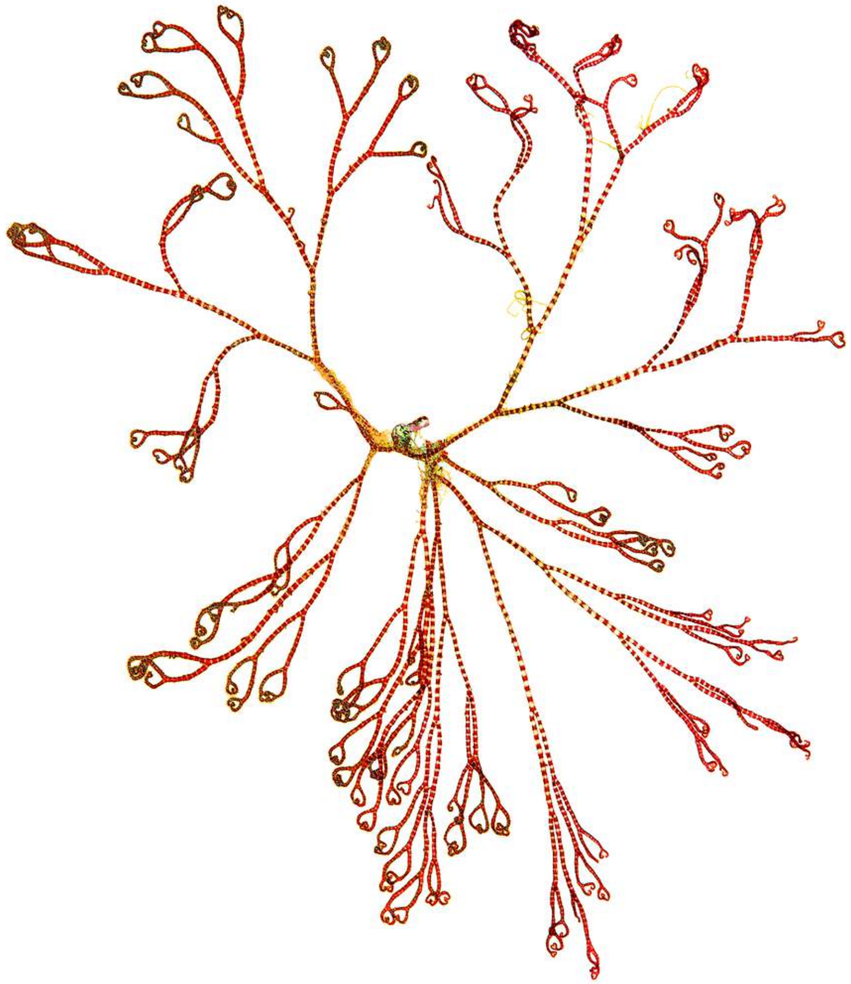


Ceramium ciliatum

(J.Ellis) Ducluzeau

Red algae (Florideophyceae)

Ceramium ciliatum is a small species of this genus with a length of about 8 cm (max. 15 cm). It is creeping over substrate with erect branches that are pseudodichotomously branched. This means that a side branch is becoming so dominant that it is equivalent to the main filament. The most obvious character of this species is the strong horizontal red stripes. These stripes are branches which cover the large cells of the central filament. They form a cortex upwards and downwards. This doesn t cover the complete central cells. As the central cell is poor of plastids whereas the cortex cells are red due to rhodoplasts, the thallus seems striped. Very characteristic for the genus *Ceramium* is the fact that the very last branches are incurved inwards and are so building the form of a heart. Especially in younger plants there is a whorl of "spines" at every segment of the filamentous thallus. The gametophytes are dioecious in this plant and the tetrasporophyte is isomorphic to the gametophytes. The carposporophyte is only surrounded by a whorl of filaments and not by a right pericarp. This is a species of the subtide level also occurring in lower intertidal rock pools. With 212 species *Ceramium* is a large genus. The family Ceramiaceae contains 759 species and the order Ceramiales is the most species- rich order of red algae (2642 species). The species seems to be restricted to the Atlantic region. The specimen shown has a length of about 15 cm.

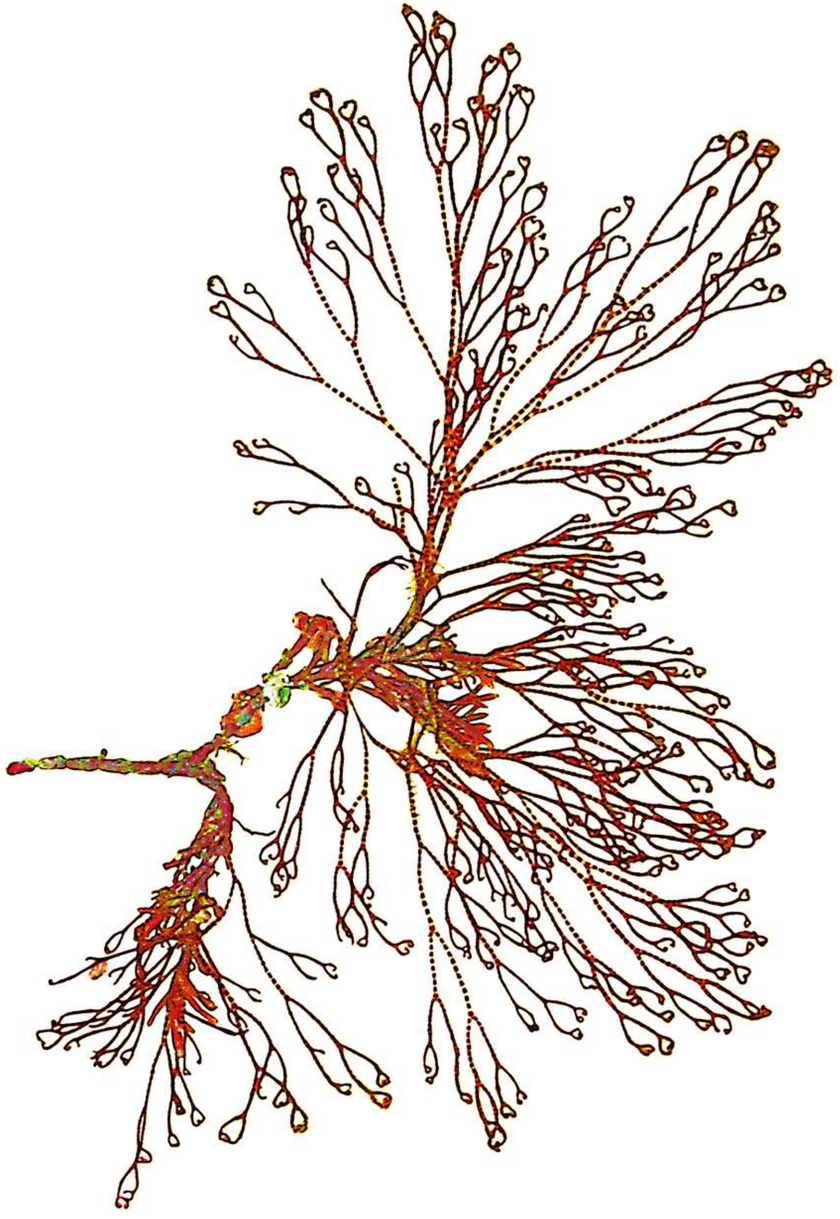


Ceramium ciliatum

(J.Ellis) Ducluzeau

Red algae (Florideophyceae)

Ceramium ciliatum is a filamentous alga. In order to describe algae they are classified into different morphotypes. We differentiate them into unicellular and multicellular algae. The unicellular algae can be motile by flagella (*Euglena*); then they are "monadoid". If they don't have flagella and are surrounded by a cell wall (*Chlorella*) they are called "coccoid". In some groups algae exist without cell walls which are motile like an amoeba (*Chlorarachnion*); this form of organization is called "rhizopodial". Among the multicellular algae there are also monadoid (*Volvox*) and coccoid forms (*Scenedesmus*). All these forms are microscopic and therefore not found in classical herbaria. When cells don't separate after division and the plane of cell division is ever the same, "unbranched filaments" are formed (*Chaetomorpha*). And if a change in the direction of cell division occurs, "branched filaments" will arise (*Cladophora*, *Ceramium*). In some cases (*Ceramium*, *Chara*) filaments are functionally and morphologically differentiated. These forms are called "heterotrichous". Forms without cross walls and many nuclei are called "siphonous" (*Vaucheria*, *Codium*); in the latter the filaments are interwoven, building a tissue-like thallus which is called "plectenchymatic". Many red algae, which are in principal branched filaments, are arranged in a tissue-like thallus where the filaments are even connected by secondary pits (*Delesseria*). True three dimensional tissues are realized in the orders Fucales and Laminariales.



Ceramium sp.

Red algae (Florideophyceae)

Ceramium is a filamentous red alga. It is easy to see that this is an alga of the uniaxial type. At least in the species that are only partially corticated the central cells are directly visible in the microscope. Also *Polysiphonia* has a thallus of the uniaxial type. There is also a central filament which is surrounded by four or sometimes more pericentral filaments so that the complete thallus appears segmented. And in some species of *Polysiphonia* or *Ceramium* an additional irregular cortex is formed at older parts of the thallus. In the gametophytes of the freshwater alga *Batrachospermum* the central filament can be easily seen. At the nodes whorls of photosynthetic filaments are formed; in older parts of the alga the central filament is surrounded by rhizoid-like outgrowths. Also in the freshwater *Lemanea* occurs, in which the central filament is not so easily seen. Here longitudinal sections help to find the central filament and it is obvious that like in *Batrachospermum* the thallus is segmented. Secondarily a mantle of pseudoparenchyma surrounds the central filament like a tube. In the Delesseriaceae the central filament is sometimes visible with the naked eye as a midrib. In order to give stability to the thalli in *Delesseria* and *Polysiphonia* cells are secondarily interconnected by secondary pits. This is probably also the case in most of the other genera of red algae. The specimen shown has a length of about 8 cm.

Saccharina latissima

(Linnaeus) C. E. Lane, C. Mayes, Druehl & G. W. Saunders

Brown algae (Phaeophyceae)

Looking on the thallus of *Saccharina latissima*, the analogy with the structure of a higher plant is evident. There is a root-like structure, the rhizoid or "holdfast". Holdfast is indeed the better term because its only function is to keep the plant attached to the ground. And it has to withstand the raging watercurrents in autumn and spring. This is in contrast to the higher plants where the roots take up water and minerals from the soil. The uptake of minerals into marine algae is performed by the complete surface of the alga. The cauloid, corresponding to the stem of higher plants, has similar functions: The transport of assimilates and the carrier of the phylloid. The cauloid in *Saccharina latissima* is very solid but also flexible because it has to bear the currents from all directions. And it has a high tensile strength because of the strong mechanical forces acting on the phylloid. The phylloid is corresponding to the leaf of higher plants and its primary function is photosynthesis as in the leaf. Also the phylloid must be resistant to the strong mechanical forces of water movements. A special feature of *Saccharina latissima* is the wavy surface in the centre of the "leaf" and its undulated margin. A special function of the phylloids of the sporophytes of Laminariales is the development of sporangia. Here the spores arise by meiosis and germinate as small gametophytes.

The small specimen shown has a length of ca. 40 cm. Thalli can reach a length of more than 5 m.

Laminaria digitata

(Hudson) J. V. Lamouroux

Brown algae (Phaeophyceae)

In principle *Laminaria digitata* has the same thallus structure as *Saccharina latissima*: A strong holdfast, a longer but also flexible cauloid and a leathery phylloid. In contrast to *Saccharina latissima*, where the phylloid is long and lanceolate, in *Laminaria digitata* the phylloid is broad and split in a digitate manner. This is similar also in the other *Laminaria* species, *L. hyperborea* and *L. ochroleuca*. In the species of the genus *Saccharina* the undivided lanceolate phylloid is a common feature.

In most higher plants the foliage is falling during autumn. Also in the Laminariales phylloids are removed in winter: The old "leafs" transfer their nutrients to the stalk where then a new phylloid is built. In the initial stages this new "leaf" is undivided and the old one is hanging at the end of the new one. Later, during storms in spring, the old phylloids are torn off and the new phylloid gets divided in a digitate way in the case of *Laminaria digitata*. Most species of the order Laminariales have a thallus structure as in *Laminaria digitata* and *Saccharina latissima*. In *Laminaria ochroleuca* and *Laminaria hyperborea* the cauloids are much stronger than in *Laminaria digitata*. In *Undaria pinnatifida* and *Alaria esculenta* spores are produced at special lobes. And in *Saccorhiza polyschides* the rhizoid is inflated and the cauloid is ribbon-like. The specimen shown has a length of about 30 cm.

Fucus serratus

Linnaeus

Brown algae (Phaeophyceae)

In most brown algal orders with the exception of Laminariales the clear division of the thallus in rhizoid, cauloid and phylloid is missing. In *Fucus serratus* and in other species of *Fucus* the rhizoid is replaced by a small but strong disc. The cauloid is replaced by a short stalk and the rest of the thallus is a flat dichotomously branched ribbon-like thallus. So photosynthesis is performed by the whole thallus. The disc-like holdfast and the thallus must withstand the same mechanical forces as the large thalli of Laminaria. In *Fucus serratus* the margins of the thallus are incised in a serrate way (name!). That's why the species is easy to identify. The thallus reaches a length of 80 cm. Reproduction in *Fucus* is performed in terminal parts in which conceptacles with oogonia and antheridia are embedded. These parts are called "receptacles". Compared to the other larger *Fucus* species where the receptacles are inflated, in *Fucus serratus* they are flat like the rest of the thallus. Most *Fucus* species, like *Fucus serratus*, are dioecious which means that there are female, egg-producing plants and male plants producing spermatozoids. Only in the monoecious species *Fucus spiralis* antheridia and oogonia are in one and the same conceptacle. At least eight *Fucus* species are found at European coasts. Some of them are specialized on special habitats like salt marshes and estuaries. The specimen shown has a length of ca. 30 cm.

Padina pavonica

(Linnaeus) Thivy in W. R. Taylor

Brown algae (Phaeophyceae)

Padina pavonica is a brown alga of the order Dictyotales. The thallus is leaf-like growing attached to stones with a small disk and a stalk. Starting from the disc-like attachment point a flat stalk is broadening continuously so that the outline of the thallus is fan-shaped. The "fan" can be divided into some lobes. The thallus reaches a length of ca. 13 cm. Very characteristic is the zonation of the thallus which is achieved by the concentric arrangement of hair rows. Sporophyte and gametophyte are of identical morphology (isomorphic). On the sporophyte sporangia are standing in large groups (sori). During meiosis four spores are produced that are not flagellated; in analogy to the red algae where also four spores without flagella are in one sporangium this container is called tetrasporangium by some authors. Antheridia and oogonia are arranged in concentric linear sori. *Padina* is a genus of predominantly tropical to subtropical distribution. *Padina pavonica* is a Mediterranean species which is common in the North Sea, Brittany (bay of Brest) and the Atlantic south of England. But it is also distributed all over the world in regions with subtropical climate. The genus contains 52 species worldwide according to Algaebase.

Pelvetia canaliculata

(Linnaeus) Decaisne & Thuret

Brown algae (Phaeophyceae)

Pelvetia canaliculata is known as one of the uppermost algae occurring in the algal zonation. Whereas the algae of the low tide condition profit from leaf-like thalli, because thus they can collect more sunlight energy, the sun-exposed *Pelvetia* has to avoid sun stress. So *Pelvetia canaliculata* has a split thallus which is more resistant against wave action. The alga is named in English "channelled wrack". The channel-like structure of the thallus is giving certain stability so that, after high tide, the lobes are not sticking together. The channels also retain the seawater longer so that the process of drying after high tide is slowed down. The retaining of water during low-tide-conditions is also the function of the mucus of the brown algae in the upper eulittoral. On the other hand *Pelvetia* is known as a plant that needs the regular drying out for survival. So *Pelvetia* cannot survive when it is covered by water more than 6 hours during one tide period. This could easily be shown by transplantation experiments. When the plant is fertile, the channelled branches end with receptacles. These receptacles are ochre in colour and the ostioli of the conceptacles can easily be seen. In most cases the receptacles are branched. The plant is monoecious and antheridia and oogonia are found in one conceptacle. *Pelvetia canaliculata* is monotypic and the species is restricted to the North Atlantic. The specimen shown has a length of about 15 cm.

Cystoseira sp.

Brown algae (Phaeophyceae)

Cystoseira sp. is a genus in the order Fucales and the class Phaeophyceae. One level of taxonomy higher we are in the phylum "Heterokontophyta" which is characterized by mastigonemes on one of the heterokont flagella. The photoauto-trophic members of this phylum have plastids that are surrounded by four membranes. This unique combination of features is shared by 15 different classes. Besides of the Phaeophyceae the only class containing macroscopic species, there are some important classes:

The diatoms are coccoid algae of the freshwater and the sea they are most important in ecology as one of the main oxygen producers worldwide. The colour of most species is brownish.

The gold algae are more or less restricted to freshwater habitats. They especially can form blooms in spring and become more rare in summer. This class contains unicellular monadoid species or species forming flagellated colonies. The colour is like the name of the class: gold-brown.

Another class, the Xanthophyceae, is closely related to the brown algae although not at all similar to any member of this class. All members of this class are bright green and some can be flagellated, coccoid, rhizopodial, unbranched filaments and branched siphonous filaments. The specimen shown has a length of about 20 cm.

Pyropia leucosticta

(Thuret) Neefus & J.Brodie in Sutherland et al.

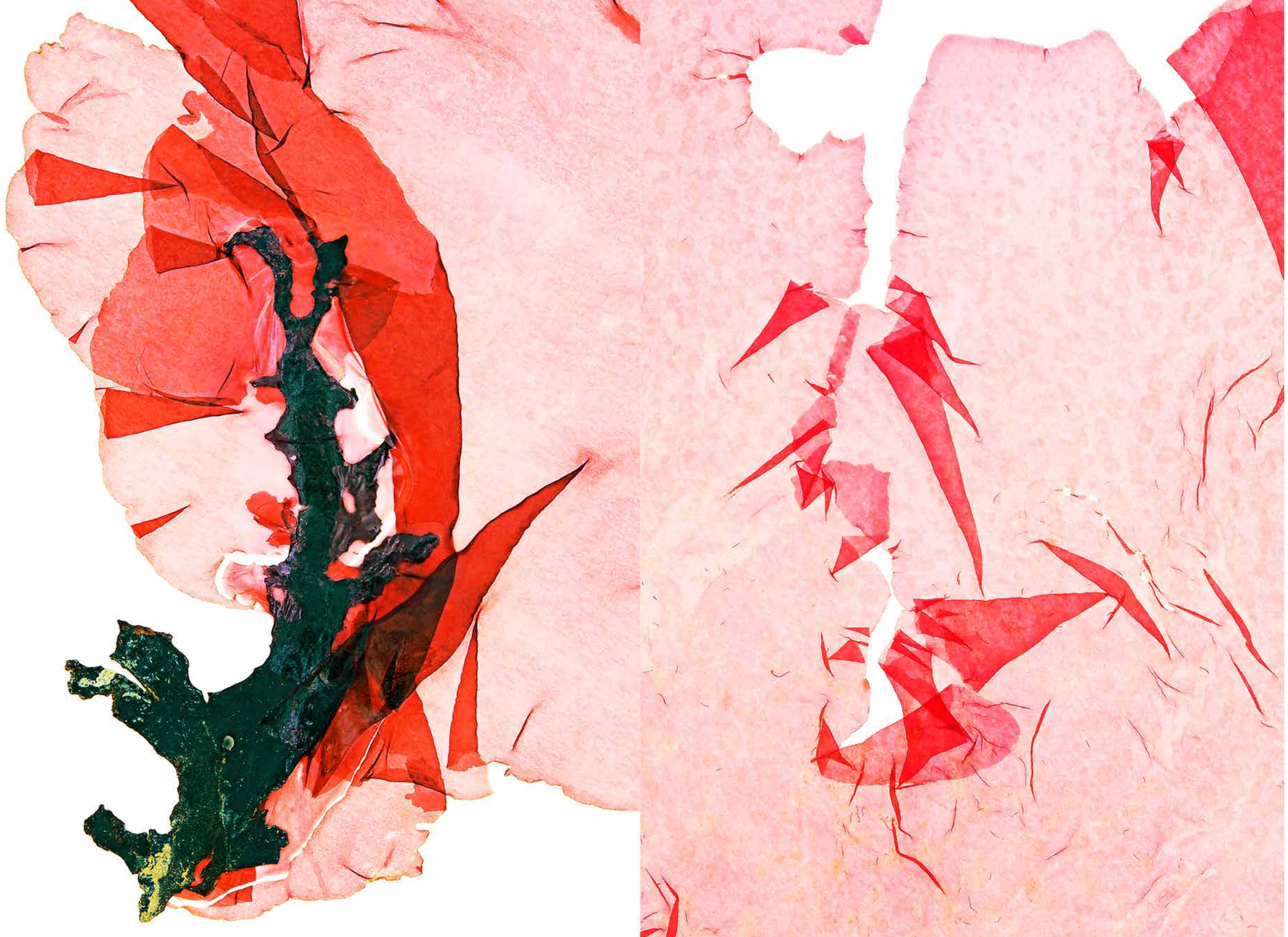
Red algae (Florideophyceae)

- *Pyropia leucosticta*, on the herbarium sheet under the name *Porphyra leucosticte*, is a representative of the small class Bangiophyceae. As most of the red algae in this book belong to the class of Florideophyceae and only the *Porphyra* and *Pyropia* species belong to the Bangiophyceae, here it is necessary to give some information about the higher taxonomic level. The phylum red algae can be divided into four subphyla that end with the suffix "-phytina". Some of them have more than one class:

- The **Cyanidiophytina** contain only one class, the **Cyanidiophyceae**. Here the genera of the hot and acidic springs *Cyanidium* and *Galdieria* belong to. As unicellular algae they are not found in a herbarium. The class only contains 7 species.

- The **Rhodellophytina** are composed of three classes: The **Porphiridiophyceae** (13 species) and the **Rhodellophyceae** (6 species) only contain unicellular algae. In the **Stylonematophyceae** (41 species) there are also filamentous members that are so tiny that they also are not found in herbaria.

- The **Metarhodophytina** only contain one class, the **Compsopogonophyceae** (75 species) which for example contains macroscopic algae of the genus *Compsopogon*. Two major orders with macroscopic algae are included: The Compsopogonales (10 species) and the Erythropeltales (64 species). The specimen shown has a length of about 10 cm.



Pyropia leucosticta

(Thuret) Neefus & J.Brodie in Sutherland et al.

Red algae (Florideophyceae)

- Continuation of left page

- The **Eurhodophytina** contain two classes, the **Bangiophyceae** to which *Pyropia* and *Porphyra* belong and the **Florideophyceae** to which the bulk of the other red algae in this book belong.

- The **Bangiophyceae** contain only 190 species and only three genera are of greater interest: The genus *Bangia* (18 species), the genus *Porphyra* (71 species) and the genus *Pyropia* (64 species). There are further 15 genera that are poor in species number.

- The **Florideophyceae** contain 6798 species. These are more than 95 % of the red algae. There are a lot of orders in the Florideophyceae:

  - Acrochaetiales (248 species)
  - Batrachospermales (261 species)
  - Ceramiales (2631 species)
  - Corallinales (602 species)
  - Gigartinales (905 species)
  - Gracilariales (247 species)
  - Nemaliales (277 species)
  - Rhodymeniales (393 species)

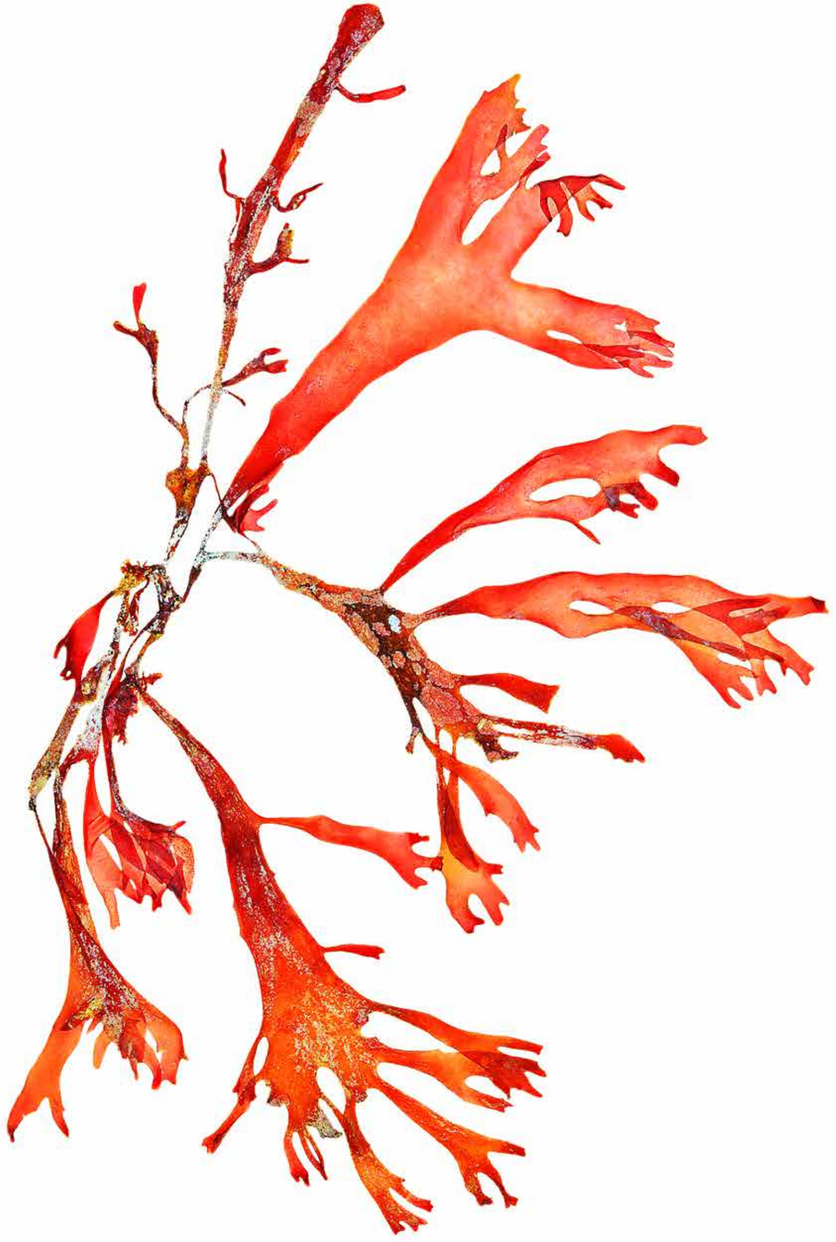
- There are much more orders with less species in the Florideophyceae. The numbers and systematics are achieved by Algaebase. In older textbooks the systematics can be different. *Pyropia* (see headline) is one of the algae with the highest value in food industry (see text of *Porphyra umbilicalis* and *Porphyra linearis*). The specimen shown has a length of about 6 cm.

Gracilaria foliifera

(Forsskål) Børgesen

Red algae (Florideophyceae)

Gracilaria foliifera is a red alga with a flat ribbon-like thallus that is irregularly subdichotomously branched. As a red alga it has rhodoplasts which are different from the chloroplasts and the plastids of the brown algae. There is only chlorophyll a in the plastids and no chlorophyll b as in green algae and no chlorophyll c as in brown algae. Accessory pigments are phycoerythrin and phycocyanin which are arranged in phycobilisomes. In brown algae the typical accessory pigment is fucoxanthin. Looking at the ultrastructure of the plastids, in red algae the photosynthetic lamellae are singular, in brown algae they are ever in stacks of three and in the green algae thee or more. Looking at the envelope if the plastids, the rhodoplasts of the re algae and the chloroplasts of the green algae are surrounded by two membranes, those of the brown algae by four. And looking to the reserve polysaccharides produced by photosynthesis, in the red algae it is floridean starch which is deposited extraplastidial as small grains in the cytoplasm. In the green algae it is also starch, deposited as larger grains in the chloroplasts. And in the brown algae it is no starch but chrysolaminaran which is deposited extraplastidial in vacuoles. Thus the three macroalgal groups can also be distinguished by the structure of the plastids and their storage products. The specimen of *Gracilaria* shown has a length of about 15 cm.



Fucus cottonii

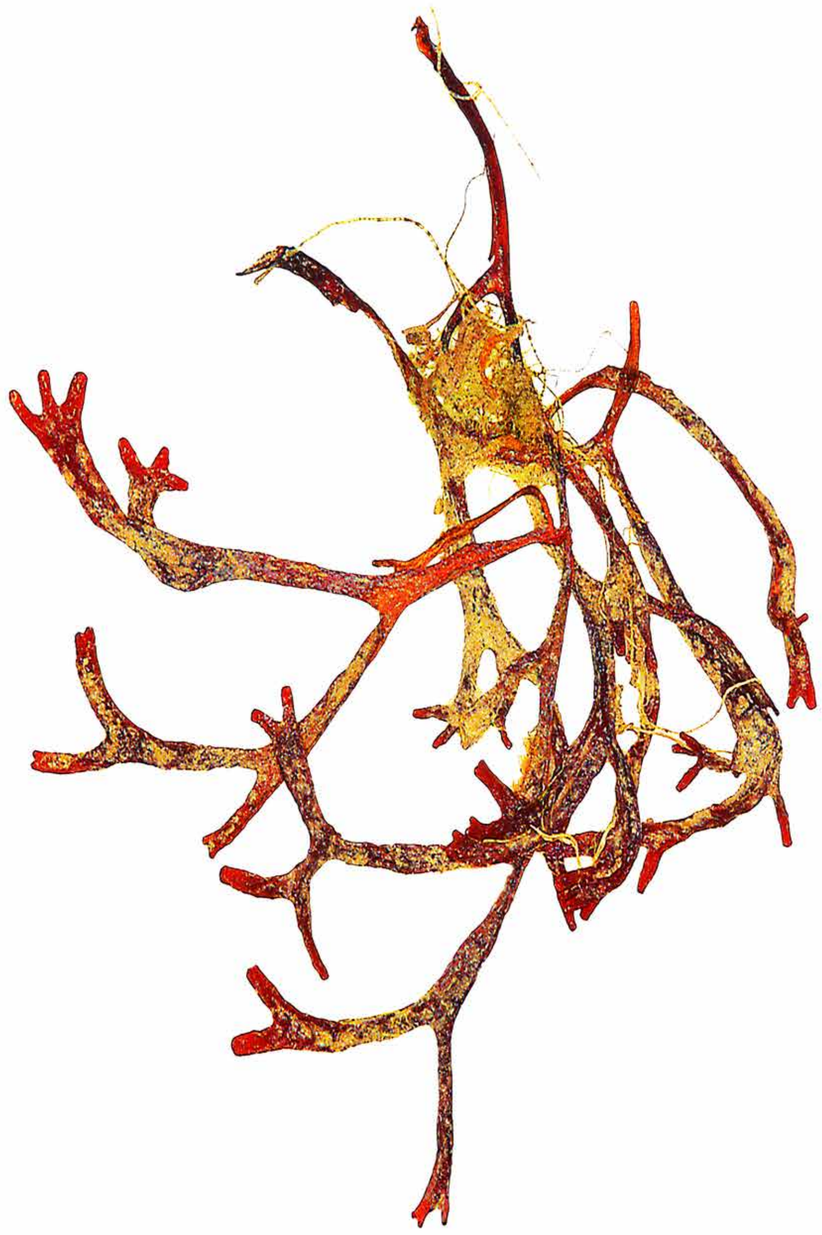
W. J. Wynne & Magne

Brown algae (Phaeophyceae)

Fucus cottonii is a typical species of the salt marshes. Saltmarshes are habitats that can be found worldwide where the coast is flat, the sedimentation rate is higher than the erosion rate, and where the power of waves is weak enough also in time of storm tides. In these habitats a special fauna and flora is found. *Aster tripolium*, *Halimione portulacoides*, *Salicornia europaea* and *Salsola kali* are some plant species, adapted to the conditions of salt marshes. The stresses against which plants and algae have to be adapted are:

- Flooding of the habitat with seawater.
- Wave action in the time of storm tides.
- High salinity in periods of drought.
- Low salinity in longer periods of rain.
- High light conditions. And more.

There are also a lot of algae that are adapted to salt marsh conditions: *Bostrychia scorpioides*, *Ulva* species of the *Enteromorpha morphotype*, *Fucus cottonii*, diverse *Cyanobacteria* and diatoms and the Xanthophycean alga *Vaucheria*. The specimen shown has a length of about 10 cm.



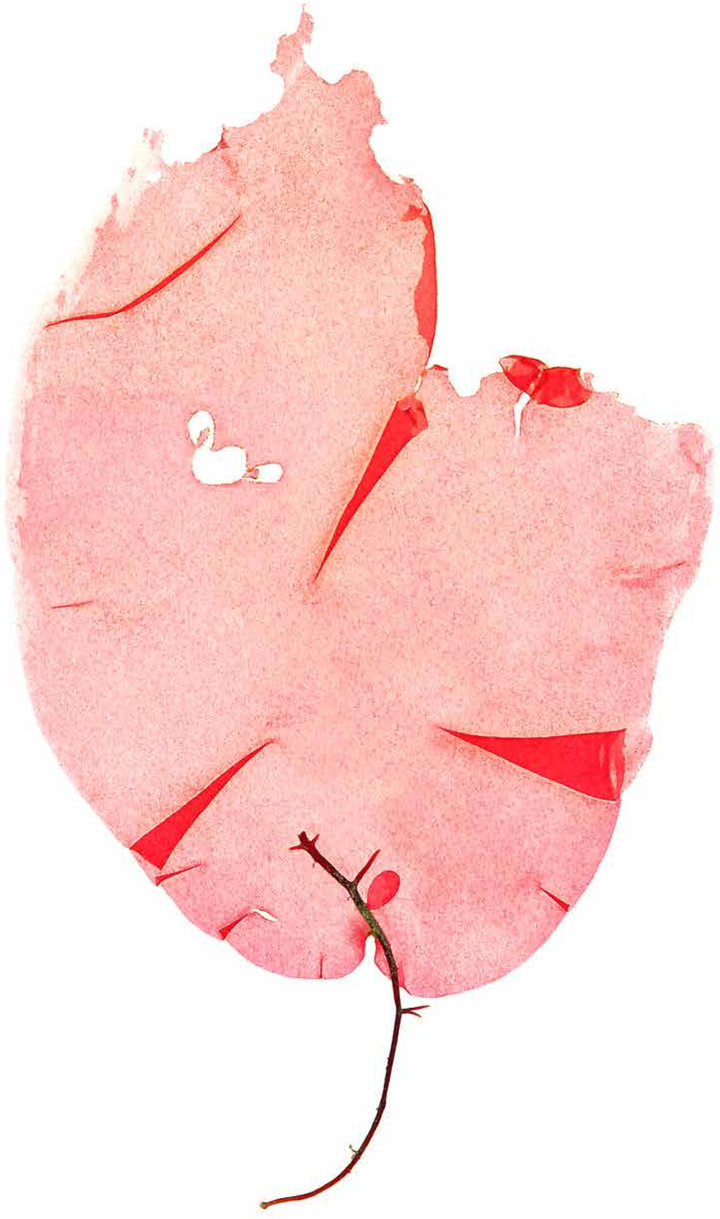
Pyropia leucosticta

(Thuret) Neefus & J. Brodie in Sutherland et al.

Red algae (Florideophyceae)

Looking on *Pyropia leucosticta*, the former "*Porphyra leucosticta*", the similarity of the thallus to that of *Ulva lactuca* is striking: a flat thallus with two layers of cells, looking like a blade of salad. The only difference seems to be the colour. Is it the colour alone which allows us the allocation to two different classes? But there are a lot of other differences when looking closer. In *Ulva* the reproduction, sexually as well as asexually, is done by flagellated zoospores. In *Pyropia* and in all the other red algae there are never flagellated stages. Even the male gametes, the spermatia, don't have flagella. And, as described in another text, *Ulva* has an isomorphic life cycle where sporophyte and gametophyte look identical. In *Pyropia* the life cycle is strongly heteromorphic. Here the sporophyte is a tiny branched filament growing in the shells of mussels, so different to the leaf-like thallus of *Pyropia*, that it was described earlier as an own genus *Conchocelis*. In *Ulva* the starch is enclosed in the chloroplast, whereas it is stored in the cytoplasm in all red algae. Looking on the ultrastructural level, the thylakoids in red algae are singular lamellae with phycobilisomes, whereas they are stacked and without phycobilisomes in *Ulva* and the green algae.

Pyropia is a member of Bangiophyceae in contrast to most of the other red algae in this book. 64 species worldwide belong to this genus. The specimen shown has a length of about 15 cm.



Scytosiphon lomentaria

(Lyngbye) Link

Brown algae (Phaeophyceae)

Scytosiphon lomentaria is a brown alga with a thallus that does not look like a blade. It is a long light brown tube of up to 40 cm length arising from a crustose thallus on the ground. In larger specimens the thallus is periodically flattened. On the *Lomentaria*-like thallus only plurilocular sporangia are known. But it is reported that on the crustose thallus from which the tubular thalli arise, also unilocular sporangia are formed. In higher plants flat leafs represent the main type of photosynthetic organs. This is also the case in most of the thalli of red and brown algae. But also in higher plants leafs occur that look like the thalli of *Scytosiphon*. In the genus *Allium* for example such green round leafs can be found in onion and chives. And, returning to the algae, also among red algae we can find such tubular terete thalli, for example in *Dumontia incrassata*. In all these cases the photosynthetic surface is reduced. But probably the amount of light is sufficient for effective photosynthesis at the places, where they grow. In the brown algae the photosynthetic surface is further reduced, for instance in *Colpomenia peregrina* which resembles *Scytosiphon lomentaria*, a member of the Scytosiphonaceae.

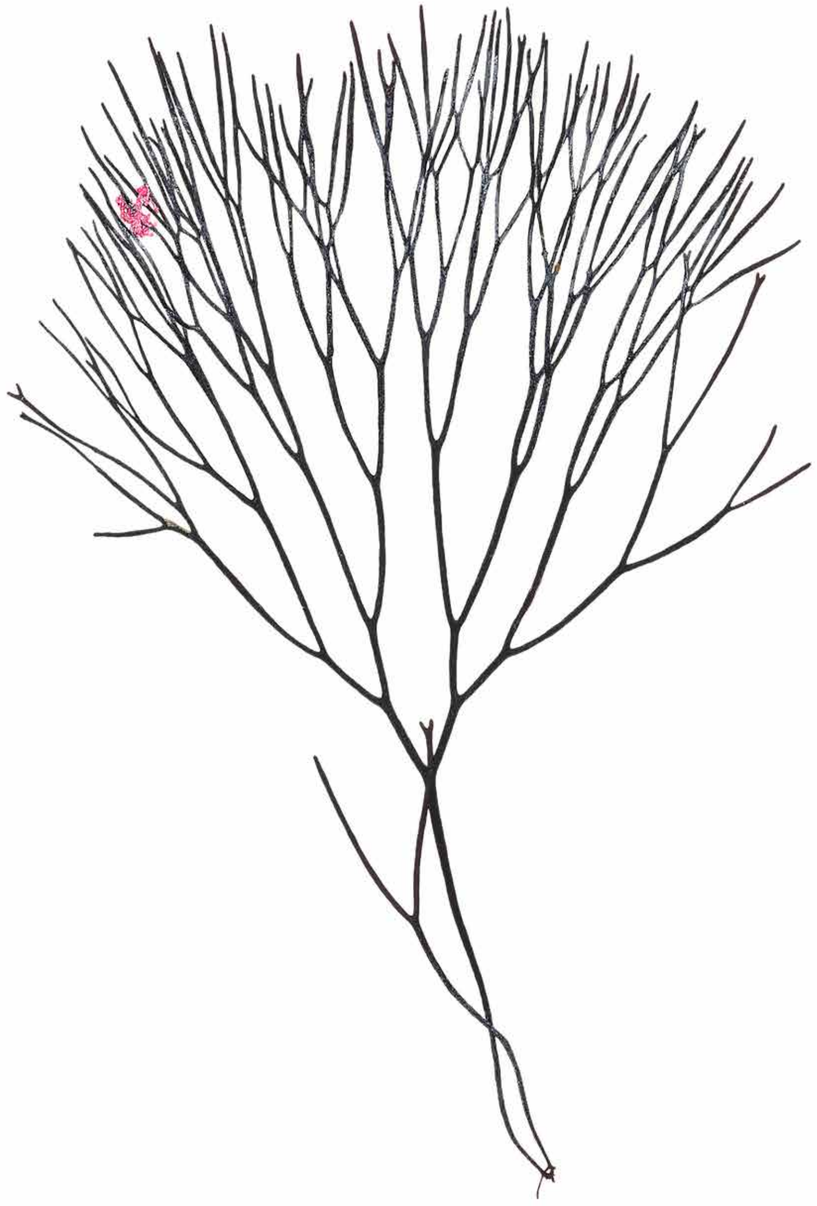
Seven species are included in the genus *Scytosiphon* worldwide. The genus belongs to the order Ectocarpales. The specimen shown has a length of about20 cm.

Furcellaria lumbricalis

(Hudson) J. V. Lamouroux

Red algae (Florideophyceae)

In F*urcellaria lumbricalis* the thallus has no blade-like structure as in many other red algae. The plant is rather a three dimensional system of solid dichotomous branches. The plant is anchored on the substrate with a branched holdfast, from which more than one plant can arise. This is an essential difference to *Polyides rotundus*, a species easy to confuse with *Furcellaria*. *Polyides* is attached with a disc. The plant starts from the rhizoid with a long "stem", which is then building a crown like that of a tree. The "tree" reaches a height of 20 cm. In cross sections a central part of hyphae-like filaments is seen, surrounded by large storage cells and assimilatory filaments vertical to the surface. The plant is brownish to blackish and not red as would be expected from a red alga. The gametophytes are dioecious; tetrasporophyte and gametophytes are isomorphic. Male gametophytes form their spermatangia on the surface of terminal thickened branches. Carpogonia and carposporophytes are developed within the thallus. The release of the carpospores happens by disintegration of the surrounding cells. Also the tetraspores are embedded in the thallus. The plants are found in the lowermost eulittoral and the upper sublittoral. The species has a European distribution. The specimen shown has a length of about 15 cm.



Dilsea carnosa

(Schmidel) Kuntze

Red algae (Florideophyceae)

Dilsea carnosa is one of the larger red algae characterized by its deep red colour and the fleshy thallus blade. In microscopical cross sections the central medulla is composed of filamentous hyphae like cells. The outermost layers are radial series of small cells that contain rhodoplasts. Here photosynthesis takes place. A layer of larger cells, possibly responsible for storage, is found between the photosynthetic layer and medulla. There is no complete analogy between the thallus of *Dilsea* and the leaf of a higher plant. Storage of photosynthetic products in higher plants is normally not in the leaf. But in *Dilsea* the "leaf" is nearly the complete plant. The gametophytes are dioecious. Spermatangia are in larger sori near the margin. Carpogonia and carposporophytes within the blade near the margin. Cystocarps are without ostiolum. The tetrasporophyte is isomorphic to the gametophytes. And also here the tetrasporangia are in groups near the margins of the thallus. The specimen shown has a length of about 20cm.

Only six species belong to the genus. *Dilsea edulis*, the former name of *Dilsea carnosa* it the type species. *Dilsea carnosa* is a species occurring only in the North Eastern Atlantic from the Arctic region to Portugal. It is a species of the upper sublittoral.

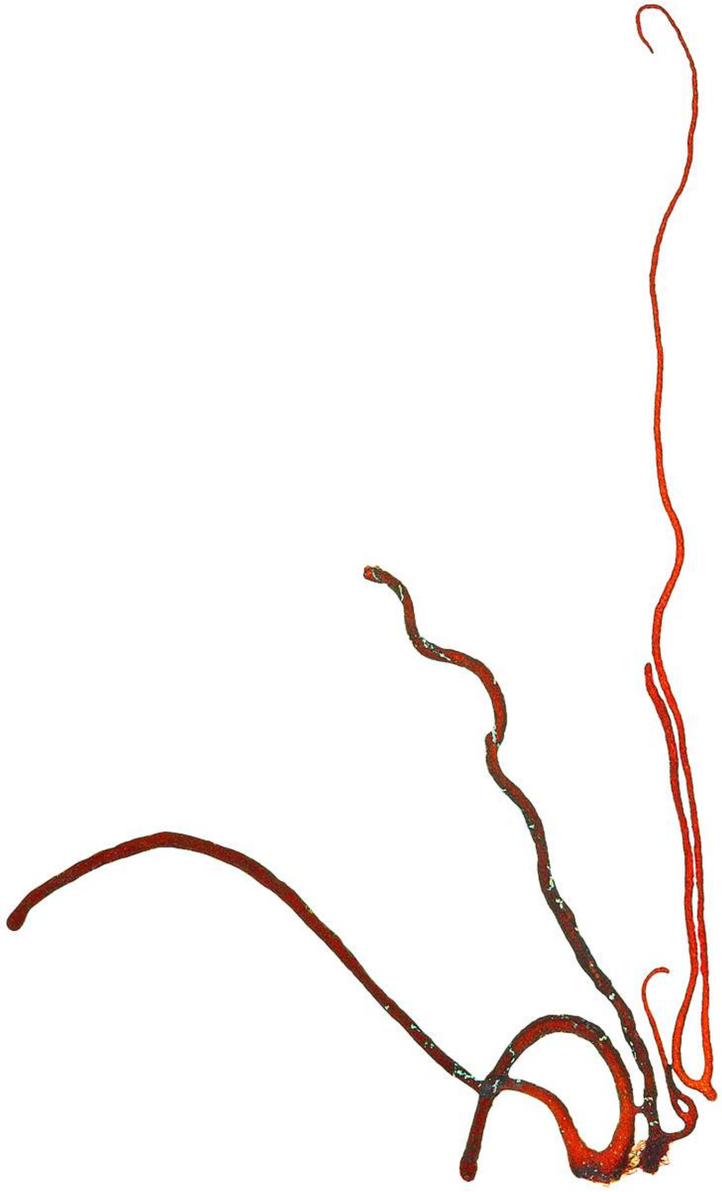
Mesogloia vermiculata

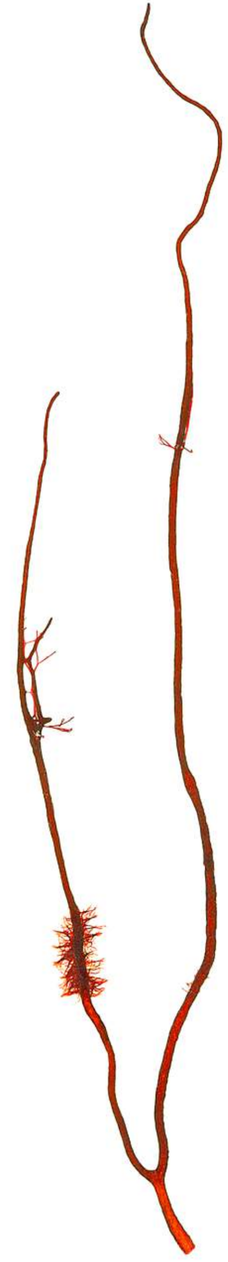
(smith) s. F. Gray

Brown algae (Phaeophyceae)

Mesogloia vermiculata is a brown alga with an irregularly branched thallus of up to 20 cm length. The cylindrical thallus is terete in cross section and feels gelatinous. It is attached to the substrate with a small disc-like holdfast. In the centre of the thallus are whitish filaments, from which thin brownish filaments arise to the surface. The assimilating brown filaments are embedded in mucilage. At the basis of the brown assimilating filaments unilocular sporangia can be formed. Plurilocular sporangia were not found. It is said that there is a change between the *Mesogloia*- like sporophyte and a microscopic gametophyte, which looks like the brown algal genus *Streblonema*. But sexual reproduction has not been verified until now. It is assumed that there are more life cycles with *Streblonema*- like gametophytes, where the sporophytes are not correlated.

Mesogloia is a member of the family Chordariaceae and the order Ectocarpales. *Mesogloia vermiculata* occurs in Europe in the Atlantic and the Mediterranean. It also occurs at the Atlantic Islands and in Chile. The specimen shown has a length of about 15 cm.





chapter 6
Root, stem, leaf – analogies in the morphology of algae

Mesogloia vermiculata

(smith) s. F. Gray

Brown algae (Phaeophyceae)

Mesogloia vermiculata is a brown alga of the order Ectocarpales. Members of Ectocarpales normally have thalli that are uniseriate and mostly branched. Although *Mesogloia* appears to be a tissue-like thallus, but in principle it is uniseriate. So it matches the typical structure of Ectocarpales. With 761 species Ectocarpales is the largest order of the Phaeophyceae (2038 species) and accounts for 37 % of the brown algae. Although in classical systematics it was considered the most primitive group of the brown algae, it was proved by molecular phylogeny that it is a sister group of the Laminariales. Thus it must be considered a highly developed group. The Dictyotales and some other groups are more basal in the modern systematics. There are four families of the Ectocarpales with higher species numbers:

The first family is that of Chordariaceae, to which Mesogloia belongs. It comprises a surprisingly high number of 111 different genera.

The second family is that of Ectocarpaceae with 104 species, containing 7 genera. *Ectocarpus* is by far the most species-rich one of this family with 96 members.

The third is the family Acinetosporaceae with 92 species.

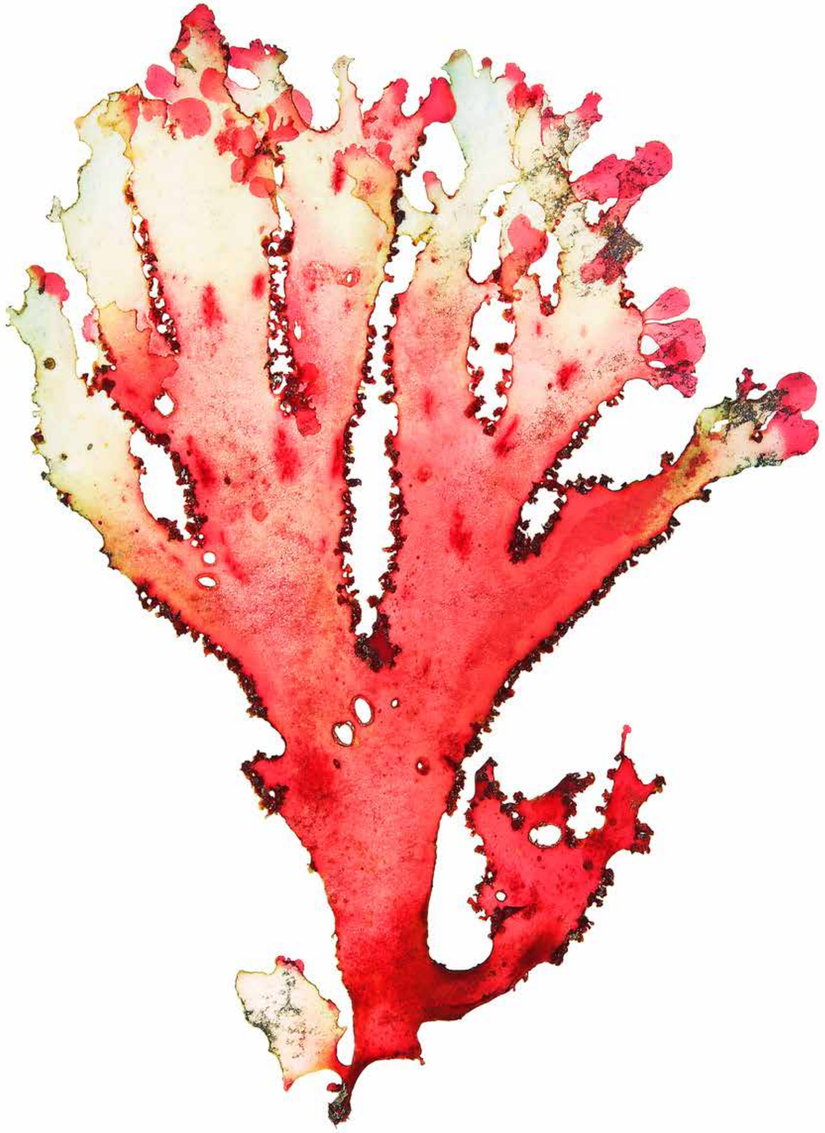
And the fourth is the family Scytosiphonaceae with 54 species. *Scytosiphon* and *Colpomenia* are present in this book. The specimen shown has a length of about 15 cm.

Callophyllis laciniata

(Hudson) Kützing

Red algae (Florideophyceae)

Callophyllis laciniata is a red alga with a flat thallus that is branched dichotomously or pseudodichotomously. It is fixed with a small disc and a short stalk to solid substrates. The general structure of the thallus is multiaxial. In microscopical cross-sections the central part consists of large isodiametric storage cells; the cells at the surface are smaller and contain the rhodoplasts. The gametophytes are dioecious; tetrasporophyte and gametophyte are isomorphic. The spermatangia are scattered over the thallus and arranged in sori. The carpogonia and the carposporophytes are at lateral lobes and are embedded in the thallus. Female thalli look crowded at their margin when fertile. The specimen shown appears to be a female one. The cystocarps are ca 500 µm in diameter and open by more than one pore. Tetrasporangia are found distributed over the thallus of the tetrasporophyte. The species occurs in the sublittoral on stipes of *Laminaria hyperborea* and on rocks till a depth of more than 30 m. It is found in Europe, the Atlantic Islands, Morocco, but also in Brazil and Chile. The genus contains 61 species. It is assigned to the family Kallymeniaceae and the order Gigartinales. The species can be easily confused with a lot of leaf-like red algae, especially with *Cryptopleura ramosa*. The closely related *Callophyllis cristata* has ribbon-like thallus lobes that are narrower than those of *Callophyllis laciniata*. The specimen shown has a length of about 15 cm.



Palmaria palmata

(Linnaeus) F. Weber & D. Mohr

Red algae (Florideophyceae)

In *Palmaria palmata* the female gametophyte was unknown for a long time. This was surprising, because male plants were known and also tetrasporophytes were found regularly. Therefore it was obvious that sexual reproduction must exist and one had to search for a female gametophyte that doesn´t look like *Palmaria*. And it was verified that the female gametophyte is a small plantlet with a one-celled carpogonia. And it was surprising that after fertilization no carposporophyte develops but the zygote directly develops to a tetrasporophyte. And this overgrows the small female plantlet. So it is no wonder that the female plant was never found. Critical viewing of the developmental cycles of algae therefore promises new scientific knowledge. So when in *Asparagopsis armata* the tetrasporophyte was unknown, the proposition was a tetrasporophyte which looks totally different from the gametophytes, so different that it was described as a different genus *Falkenbergia*. A similar pair of two red algal species that are in truth two generations of one species is *Bonnemaisonia hamifera* (Gametophyte) and *Trailliella intricata* (Sporophyte). Similar cases are also known for green algae and brown algae. In the green algae one example is well known: The sporophyte *Derbesia marina* and the gametophyte *Halicystis ovalis*. And similar heteromorphic cycles also occur in numerous brown algae, for example the pair *Scytosiphon/Ralfsia*. The specimen shown has a length of about 25 cm.

Heterosiphonia plumosa

(J. Ellis) Batters

Red algae (Florideophyceae)

Heterosiphonia plumosa is a red alga that forms thalli of up to 30 cm length. The uniaxial thallus has a central filament that is corticated by up to 10 pericentral cells, only the very terminal branches are without this cortex. The thallus so looks segmented in its younger parts. In older parts the thallus is surrounded by an additional cortication that is not segmented but consists of isodiametric cells. The thallus consists of a main axis and smaller lateral branches that are more or less in one plane. These lateral branches are standing alternate. The plant is dioecious. Gametophytes and tetrasporophyte are isomorphic. Spermatangia are in cone-like structures at the basis of younger lateral branches. Also the carpogonia and the carposporophyte are more or less at the basis of terminal branches. Carposporophytes are large, up to 1000 µm long and surrounded by a pericarp. Carpospores are released through an ostiolum. Tetrasporangia are also formed at younger branches arranged in rows.

The plants are found in sublittoral till to a depth of more than 30 m. They are also found in low-tide rock pools. The plants are found in the Eastern Atlantic and in the Mediterranean Sea. According to Algaebase the genus *Heterosiphonia* consists of 32 species. It is a member of the family Dasyaceae in the order Ceramiales. The specimen shown has a length of about 20 cm.

Hypoglossum hypoglossoides

(Stackhouse) Collins & Hervey

Red algae (Florideophyceae)

Hypoglossum hypoglossoides is a species of the family Delesseriaceae. Like other members of the family it forms phylloids that are like those of higher pants: A lanceolate blade with a midrib. Visible lateral veins are missing. Unlike higher plants new blades can grow from the midrib of old blades. The blades have a cylindrical stipe. The whole thallus can reach a length of 30 cm. As in all Delesseriaceae the general construction of the thallus is uniaxial. Gametophytes are dioecious and are isomorphic to the tetrasporophyte. Spermatangia are in groups next to the midrib. They are found on both faces of the blade. On the female plants the carpogonia and carposporophytes are located on younger leafs. They are surrounded by a pericarp that is open by a pore. The tetrasporophytes bear sporangia that are arranged in sori on both sides of the rib. So we have a triphasic isomorphic life cycle typical for most red algae: gametophyte, carposporophyte and tetrasporophyte. *Hypoglossum hypoglossoides*, on the herbarium sheet named with its former name *Hypoglossum woodwardii*, is a plant of the sublittoral found on rocks as well as on the stipes of *Laminaria hyperborea*. It is found on both sides of the Atlantic, also in the Mediterranean and the Atlantic islands. In the field it can be confused with *Apoglossum ruscifolium* which in contrast to *Hypoglossum hypoglossoides* has visible lateral veins. The specimen shown has a length of about 20 cm.

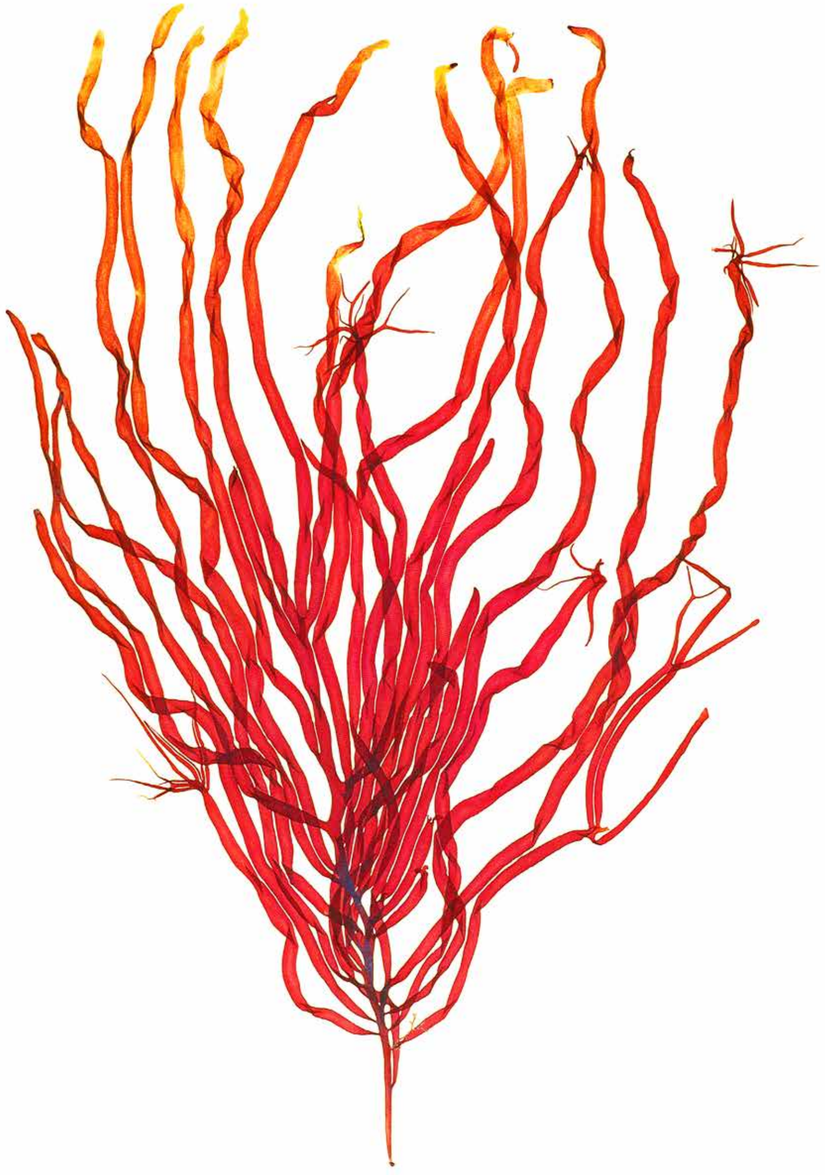
Dumontia contorta

(S.G.Gmelin) Ruprecht

Red algae (Florideophyceae)

Dumontia contorta is a red alga which can be easily recognized by its irregular branched tubular thallus of ca. 1 cm width and ca. 20-25 cm length. The colour is brownish red. The plant arises from a small disc-like thallus which presumably is persistent over the year. The typical erect thallus from which *Dumontia* can be recognized comes in late autumn and can be found until summer. Then the erect thallus disappears. The gametophytes and the tetrasporophytes are isomorphic. The plant is dioecious, so that spermatangia and carpogonia are found on different plants. Spermatangia stand in pairs on the surface of the male plant. They are arranged in sori. On the female plant the carpogonia are on the surface and after fertilization a carposporophyte is developing, in which all cells are carposporangia. The carposporophyte is not surrounded by a layer of sterile cells.

The plant is found from the upper eulittoral to the upper sublittoral, growing attached to rocks. It can be also found in intertidal rock pools. The regions of distribution are the North Atlantic and North Pacific reaching in the south to the Azores. *Dumontia contorta* is used as food in Japan. *Dumontia incrassata* is the old name of this species and this is the name found on the herbarium sheet. It is the type species of the genus. Five species are included in the genus. According to Algaebase the genus has its own family Dumontiaceae in the order Gigartinales. The specimen shown has a length of about 25 cm.



Calliblepharis ciliata

(Hudson) Kutzing

Red algae (Florideophyceae)

At the end of vegetation period *Calliblepharis ciliata* detaches from the ground and is often found in the drift. Depending on the phase of the thallus, carpospores or tetraspores are yet present and can be distributed. But also spores from other algae can settle on the surface of the drifting thallus. It seems as if the thallus is "infected" by a crustose red alga. Deduced from size and colour it might be *Melobesia sp.*, a crustose red alga normally growing on sea grasses but also occurring on red algae. With growing age of a thallusthe chance is higher that other organisms settle on their surface. Some smaller filamentous red algae are nearly exclusively found as epiphytes on older algae. And it is not only red algae which can establish. So on old *Fucus serratus* plants different Bryozoan species and genera can establish. These are multicellular animals that can be easily seen when they grow in colonies. And *Fucus serratus* appears to be most attractive for *Pylaiella littoralis*, an Ectocarpalean alga which is forming large tufts on the surface of especially this species. And also other small filamentous genera of brown algae exist that are specialized settlers:

Elachista fucicola is growing always on Fucus.

Herponema velutinum is found nearly exclusively on *Himanthalia elongata*.

And the endophytic green alga *Acrochaete geniculata* is growing obligate in *Ulva rigida*. The specimen shown has a length of about 20 cm.

Phycodrys rubens

(Linnaeus) Batters

Red algae (Florideophyceae)

Phycodrys rubens is a member of the family Delesseriaceae and has the thallus-organization typical of this family: The plant is fixed to the substrate by a disc, from which one or more stipes arise. At the end of the stipes are phylloids that are similar to leafs of higher plants. A central vein and lateral veins are easy to be recognized. Because of the lobed margin of the phylloids this species has the popular name "Sea Oak". The plant reaches a length of 20 cm. The general structure is of the uniaxial type having a main axis and lateral branches in one plane. They stick to one another forming a blade.

The gametophytes are dioecious. In male plants the spermatangia are typically on small lateral lobes. Also the carpogonia and later the carposporophytes may be on separate lateral lobes or on the normal blade. Carpogonia and the carposporophyte are surrounded by sterile tissue, which is open to the surrounding water by a pore, the so called "ostiolum".

The tetrasporophyte is isomorphic to the gametophytes. Here tetrasporangia are formed on the normal blade or also on lateral outgrowths.

Worldwide there are 25 species in the genus *Phycodrys*. *Phycodrys rubens* is an Atlantic species, but also occurs in Alaska and Kamchatka. It is restricted to the subtidal kelp forests and below to a depth of 27 m and frequently occurring on the stipes of *Laminaria*. The specimen shown has a length of about 25 cm.

Delesseria sanguinea

(Hudson) J.V. Lamouroux

Red algae (Florideophyceae)

Delesseria sanguinea is the plant from which the name of the family Delesseriaceae derives. The principal structure of the thallus is the same as described for *Phycodrys rubens* (left page): stipes, blades with visible veins, uniaxial structure. The blades in this species are not lobed as in *Phycodrys rubens*.

All reproductive structures are on outgrowths that arise from the midrib of a blade. This happens frequently when the lamina of older blades have disappeared by destruction. The gametophytes are dioecious. In the male plant the spermatangial outgrowths are on blades with persistent lamina. In female plants and on the tetrasporophyte the reproductive outgrowths are found on midribs without lamina.

The species is perennial and new blades are produced in winter. They occur in the sublittoral up to 30 m dethp but also on the stipes of *Laminaria*. Adult plants cannot be confused with other red algae.

In the genus *Delesseria* 268 species were described, but according to Algaebase only 8 species are valid. *Delesseria sanguinea* is the type species of the genus. The distribution is in the Northeast Atlantic reaching Iceland in the North. The specimen shown has a length of about 15 cm.

Himanthalia elongata

(Linnaeus) S.F. Gray

Brown algae (Phaeophyceae)

Himanthalia elongata is a member of the brown algae order Fucales. In the Fucales different developmental lines can be observed in regard to following features:

- Their general size
- The design of receptacles
- The number of eggs per oogonium
- dioecious or monoecious
- The development of pneumatocysts
- The type of branching
- Their place in vertical zonation

Himanthalia reaches a length of more than 5 m. Most of the thallus is functional a receptacle but also responsible for photosynthesis. When cutting the receptacle, the conceptacles are either male, bearing antheridia, or female, bearing oogonia. The branching of *Himanthalia elongata* is strongly dichotomous, as can be easily deduced from the picture. *Himanthalia* is an alga of the low tide level in eulittoral and a constituent of the kelp forest at subtidal level. According to Algaebase, the genus *Himanthalia* is monotypic with only one species worldwide.

In the headline additional to the name of the algae, authors are specified which have described the species. In the case of *Himanthalia elongata* (Linnaeus) S.F. Gray, Carl von Linné was the first. Carl von Linné (1707-1778) was the inventor of the binary nomenclature. Since his scientific work (Systema naturae, Genera plantarum…) plants and animals have to be denominated with a generic name, in our case "Himanthalia", and an epitheton, in our case "elongata". Linné gave a simplified system of the lower plants in which nearly all marine macroalgae were assigned to the genus "*Fucus*". So also our *Himanthalia elongata* was named "*Fucus elongatus*" by Linné. As also in taxonomy there is progress in knowledge, the name of our organism was changed several times (from Algaebase):

- *Fucus loreus* Linnaeus 1767
- *Fucus pruniformis* Gunnerus 1772
- *Ulva tomentosa* (Hudson) De Candolle 1805
- *Funicularius tuberculatus* Roussel 1806
- *Himanthalia lorea* (Linnaeus) Lyngbye 1819
- *Himanthalia elongata* var. *inaequalis* S.F. Gray 1821

As S.F. Gray was the last person who changed the taxonomic name, his name is given without brackets. The year of the taxonomical change is indicated.

Ascophyllum nodosum

(Linnaeus) Le Jolis

Brown algae (Phaeophyceae)

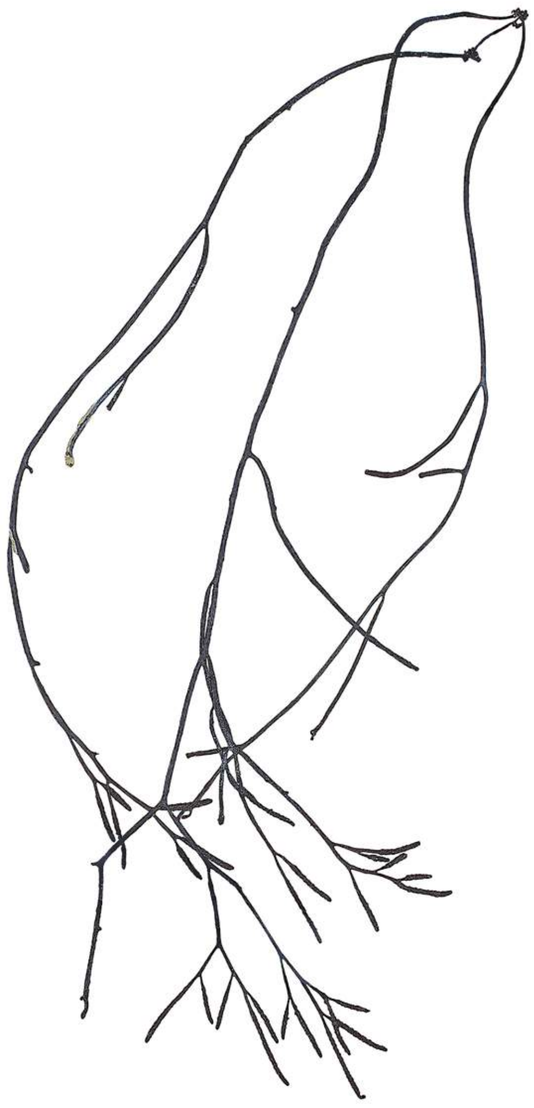
Ascophyllum nodosum is a thallus of medium size reaching a length of 1.5 m. Conceptacles are located lateral on side branches in the axil of small serrations. There are female and separately male thalli, i.e. the species is dioecious. When fertile, male thalli can be distinguished from female ones by the orange colour of the receptacles. In female conceptacles four eggs develop in one oogonium. *Ascophyllum* is easily recognized by the large pneumatocysts, gas bladders that give the plants buoyancy so that they can be erect in the water at high tide condition. Only one of the gas bladders is built per year on a branch. They can grow during the years to a length of 5 cm. *Ascophyllum* is growing more or less with main axes. In some areas also a growth type that is nearly dichotomous can be observed. In upper eulittoral the species can occur in great bulks. So the algae can easily be collected for alginate production. In spite of the very different shape, the next relative of *Ascophyllum* is *Pelvetia canaliculata*. In this small plant of 10 cm length the receptacles are at the end of the main axis, the branching is dichotomous, the plant is monoecious and pneumatocysts are missing. The number of eggs in the oogonium is two. There is an interesting common feature pointing to a near relationship between *Ascophyllum* and *Pelvetia*: In both species a symbiotic fungus, *Mycosphaerella ascophylli*, is growing. The specimen shown has a length of ca. 25 cm.

Bifurcaria bifurcata

R. Ross

Brown algae (Phaeophyceae)

Bifurcaria bifurcata is a relatively small plant of less than 30 cm length. The thallus is terete and has no leaf-like structures. The branching of the thallus is dichotomous as is indicated by the name *Bifurcaria*. The receptacles are located at the ends of the branches and are recognized by the ostioli of the conceptacles that are visible as small dots. The plant is monoecious, but the conceptacles are unisexual. At the basis of the receptacle the conceptacles are female, containing only oogonia. At the top there are male conceptacles presenting only antheridia. The oogonia contain only one egg. So in the oogenesis during meiosis all but one of the nuclei disintegrates. Pneumatocysts which are present in other species of the order Fucales are missing in this species. *Bifurcaria bifurcata* is found at the low tide level and in the sublittoral; it is also very characteristic for the rock pools which keep filled with water under low tide conditions. The species is brown to yellowish in nature. When drying out for example in a herbarium the specimens are getting dark brown to black. *Bifurcaria* is a member of the family Sargassaceae. The genus contains only two species. One of them has a Pacific distribution. The other, *Bifurcaria bifurcata* is occurring from Brittany to Morocco. The specimen shown has a length of ca. 20 cm.

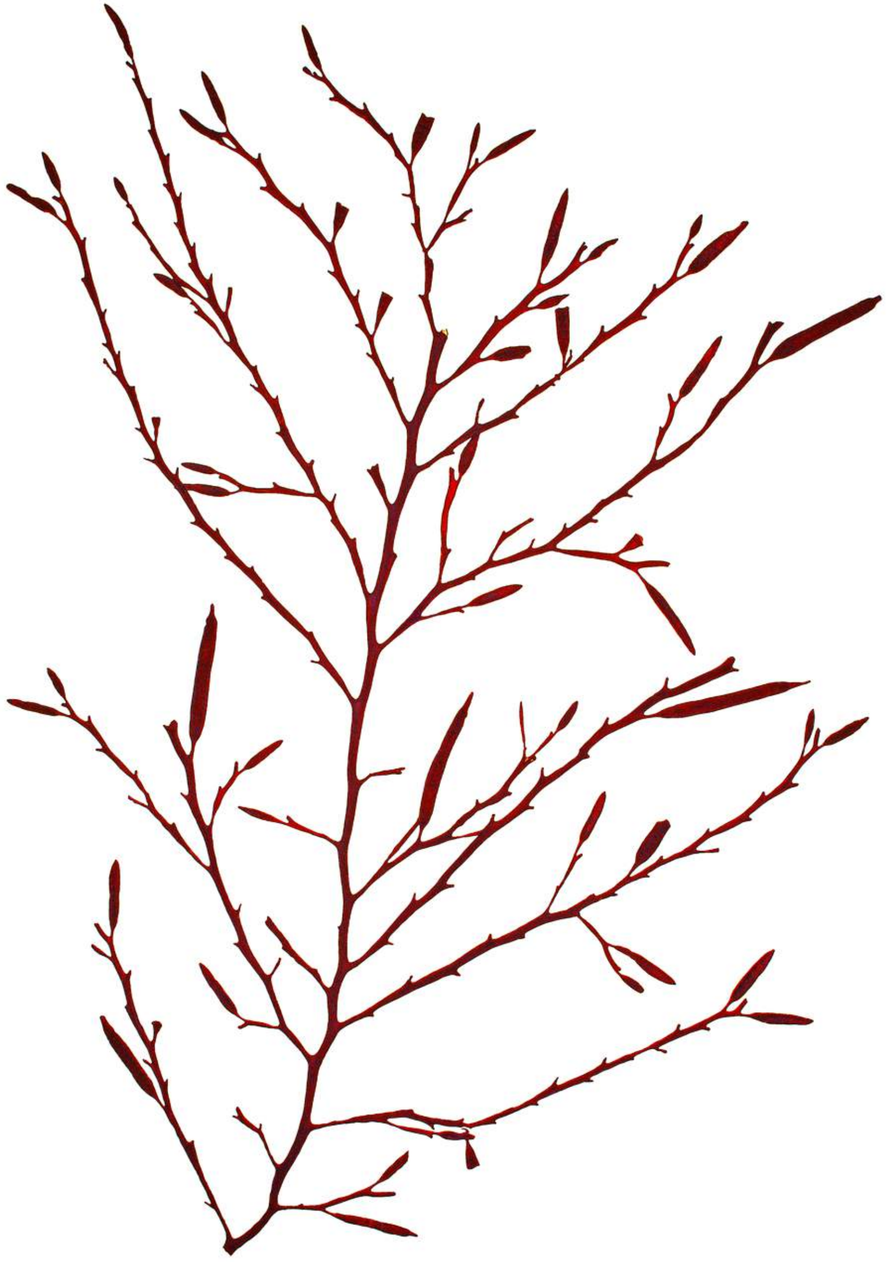


Halidrys siliquosa

(Linnaeus) Lyngbye

Brown algae (Phaeophyceae)

Halidrys siliquosa is a large plant of the order Fucales reaching a length of 1.5 m. In cross section the thallus is flattened and all branches are in one plane. Receptacles are found at the tips of the long thalli, but here arranged laterally to the main axis. They are silique-like and are containing oogonia and antheridia in one conceptacle. So the plant is monoecious. The thallus is branched anisotomous, so that a main axis is visible. In the oogonium most probably there is only one egg. The plant can grow upright in the water, as it has a lot of lateral pneumatocysts. Similar to the receptacles they are silique-like. The pneumatocysts are chambered, which is not due to receptacles. *Halidrys siliquosa* is a plant of the subtidal zone, where it grows in the kelp forest. *Halidrys siliquosa* is the type species of the genus, which contains only two species. It is distributed from the Baltic Sea till Spain in the south. It has a common name: Sea oak; in German: Seeeiche. In the order Fucales there are two larger and some small families that contain only few species. One of the species. rich families is that Fucaceae (75 species). The other one is the family Sargassaceae (502 species). *Halidrys siliquosa* is a species of the Sargassaceae. The specimen shown has a length of about 25 cm.



Fucus vesiculosus

Linnaeus

Brown algae (Phaeophyceae)

Fucus vesiculosus is the most frequent species of this genus in Europe. As the other larger species, it is not exceeding a length of 80 cm. Some of the *Fucus* species are much smaller. So *Fucus muscoides* is reaching a length of only 5 cm. The receptacles in the genus *Fucus* are normally at the end of the dichotomously branched thalli. In most cases the thalli are dioecious, but for example in *Fucus spiralis* oogonia and antheridia are found in one and the same conceptacle. So this species is monoecious. Looking at the oogonium, in all *Fucus* species eight eggs are developed. So after meiosis mitosis takes place. Pneumatocysts are missing in most *Fucus* species. But in *Fucus vesiculosus* they are present. This species has a midrib. The pneumatocysts are on both sides of this midrib. Also in some varieties of *Fucus spiralis* thallus vesicles filled with gas can be observed. The *Fucus* thalli normally are dichotomously branched, but also anisotomy can be observed in some species. This means that one of the two branches is dominant, but no obvious main axis is developed. *Fucus spiralis* is a species of the uppermost eulittoral, *Fucus vesiculosus* and *Fucus serratus* are found a little bit lower in the eulittoral. *Fucus ceranoides* is a species of the estuaries, whereas *Fucus muscoides* is a species occurring in the salt marshes. The specimen shown has a length of about 20 cm.

Sargassum muticum

(Yendo) Fensholt

Brown algae (Phaeophyceae)

Sargassum muticum is one of the largest species in the order Fucales. Its thalli reach a length of more than 5 m. The axis grows monopodial and the side branches are subordinate. The receptacles appear at the end of the thalli in the axis of side branches. The plant is monoecious, so male and female reproductive structures are on the same plant. But in one conceptacle either antheridia or oogonia are found and not both in one. Interestingly the eggs are not released from the conceptacle. The zygote develops on the mother plant to an embryo, that is released later. Perhaps this protection on the mother plant is the reason why this invasive plant is so successful in Europe. *Sargassum muticum* is easily recognized because of its size, and it is the only species in which small globose pneumatocysts are present, that are located lateral and are shortly stalked. Gas bladders on stalks are also present in most of the other species of this genus, that do not occur in Europe. More than 350 species exist. Most of these species have a tropical distribution and grow fixed to a substrate. Two species of *Sargassum* are free floating and not attached to a substrate: *Sargassum natans* and *Sargassum fluitans*. In these species only vegetative reproduction by fragmentation is known. The specimen shown has a length of about 20 cm.

Sargassum muticum

(Yendo) Fensholt

Brown algae (Phaeophyceae)

With more than 350 species it may be difficult to distinguish all the species of *Sargassum*. Surely, in Europe we don't expect additional *Sargassum* species, because most species are adapted to tropical climate. When researching in Algaebase, some of the features that can be different in the 350 species are listed:

- The thallus length (10 to 200 cm, in *Sargassum muticum* up to 500 cm).
- The number of stipes arising from the basal disc (one or a few).
- The primary branches arising from these stipes can be distichously or radially.
- Primary branches terete, angular, 3-sided or compressed.
- Pneumatocysts ovoid, globose or apiculate.
- Branchlets leaf-like or not.
- Leaf-like branchlets entire or serrate/dentate.
- Thallus monoecious or dioecious.
- Receptacles unisexual or bisexual.
- Receptacles in axils or on ramuli.
- Receptacle solitary or in clusters.
- Conceptacles unisexual or bisexual.
- Thallus free floating or attached.

Not all features of *Sargassum* are given. A combination of all these characters allows the differentiation of the more than 350 species. The specimen shown has a length of about 30 cm.

Bostrychia scorpioides

(Hudson) Montagne

Red algae (Florideophyceae)

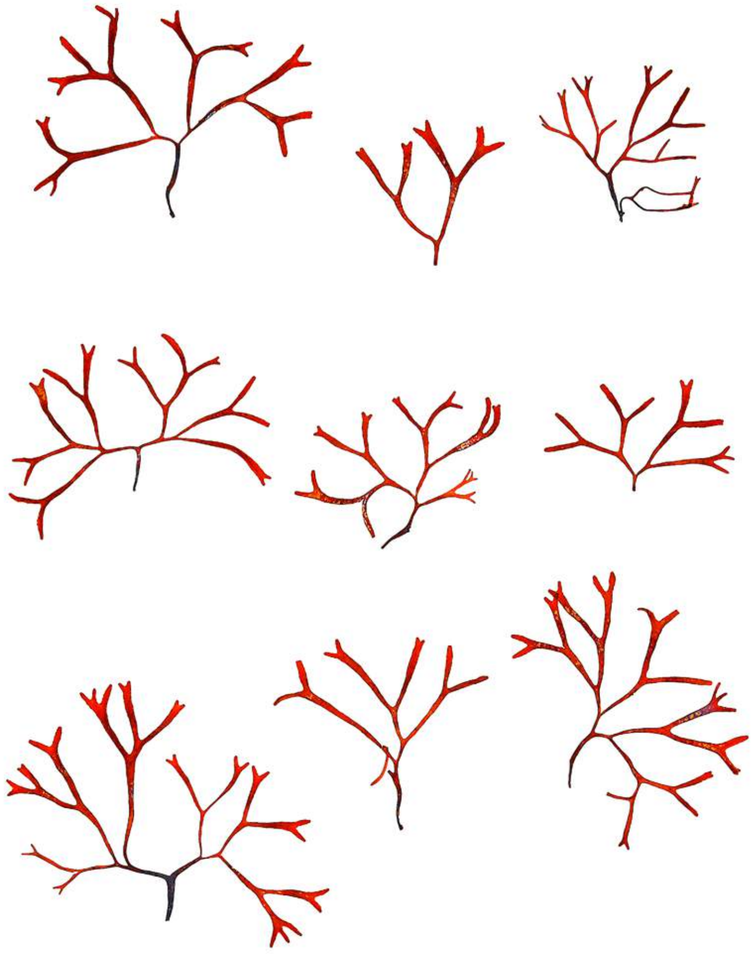
- *Bostrychia scorpioides* is a species of the salt meadows and is found regularly where *Halimione portulacoides* is growing. It is well adapted to conditions of this habitat:
- The ground of the saltmarshes is warp, composed of very small particles.
- The habitat is flooded only in the time of highest tide. This means that there are only a few days in a month where seawater is present.
- As a consequence *Bostrychia* must be adapted to varying salt conditions.
- When a dry period is following after flooding, high salt concentrations and drought must be tolerated.
- On the other hand, when it is raining heavily, the alga is exposed to freshwater conditions and also this kind of low-salt-stress must be tolerated.
- In winter frost periods must be survived. These are completely different conditions compared to the algae that are flooded daily or are growing at the subtidal level.
- That's why there are only a few specialists adapted to the conditions of salt marshes. Equally there is a special flora of higher plants in saltmarshes. Among the algae cyanobacteria are well adapted, as they don't have vacuoles which would make them sensitive to salt stress. But also halotolerant *Vaucheria* (Xanthophyceae) species and some diatoms are tolerant to changing salt conditions. The specimens shown have a length of ca. 5 cm.

Fucus ceranoides

Linnaeus

Brown algae (Phaeophyceae)

- *Fucus ceranoides* is a brown alga that is found in estuaries regularly. In estuaries freshwater of a river is mixed with seawater and therefore there is a lower salt concentration than in pure seawater. Also this species must be more tolerant to differing salt concentrations than the marine members of the genus, *Fucus spiralis*, *Fucus vesiculosus* and *Fucus serratus*. In *Fucus ceranoides* pneumatocysts which are found in *Fucus vesiculosus* are missing. But instead of these long inflations of the thallus can occur on both sides of the midrib. In principle, the adaptatios of the brackish forms are somewhat similar to those of the saltmarshes but in the estuaries flooding is more frequent. There are some other *Fucus* species occurring in the estuaries:
- The dioecious *Fucus lutarius* which is mostly not fixed to hard material.
- *Fucus distichus* with narrow ribbon-like thalli, without pneumatocysts and with a distinctive midrib.
- Also on the mud in the estuaries halotolerant species of *Vaucheria* are frequent.
- Another *Fucus*, the very tiny *Fucus cottonii*, is occurring at special locations: in saltmarshes near to small saltwater pools, but also in the estuaries.
- The specimens shown have a length of ca. 5 cm.



Dictyopteris polypodioides

(A. P. DC Candolle) J. V. Lamouroux

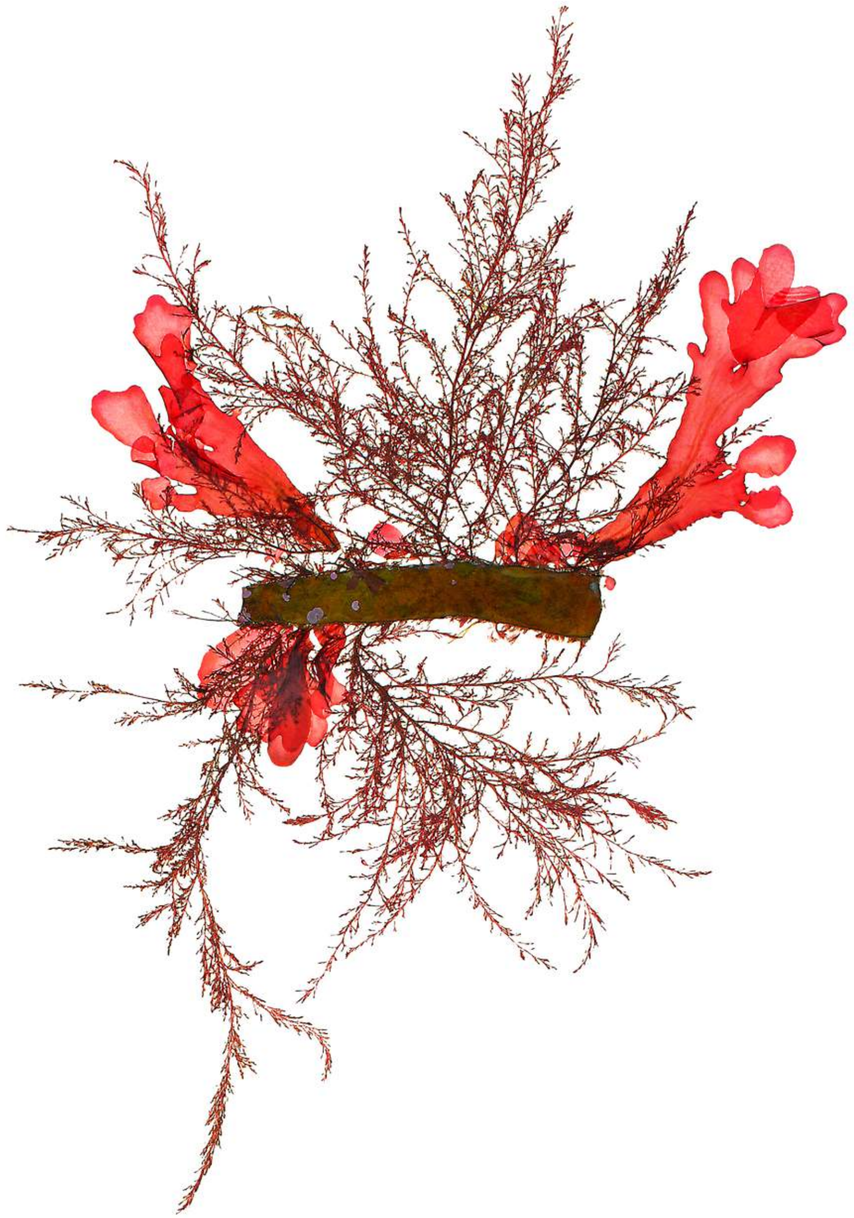
Brown algae (Phaeophyceae)

Dictyopteris polypodioides is a member of the brown algal family Dictyotaceae and the order Dictyotales. The plant has a ribbon-like brownish to yellowish thallus and can reach a length of 30 cm and a width of 1.5 cm. *Dictyopteris* differs from *Dictyota dichotoma* by its subdichotomous branching and its distinctive midrib. But like *Dictyota dichotoma* the life cycle is isomorphic. The gametophytes are dioecious bearing spermatangia arranged in large whitish sori and oogonia scattered over the female thallus. The type of fertilization in *Dictyopteris polypodioides* is oogamy, i.e. flagellated spermatozoids are released from the antheridia; they are attracted by the oogonia which excrete a pheromone.

The resulting zygote grows into a sporophyte which looks identical to the gametophytes. Characteristic for the Dictyotales are the meiosporangia in which four unflagellated spores are produced during meiosis. In analogy to the building of spores inred algae they are called "tetrasporangia".

The plant is occurring under warm temperate conditions attached with a disc on rocks. It is found in the sublittoral up to a depth of 40 m. It occurs worldwide under appropriate conditions.

Due to its midrib *Dictyopteris polypodioides* cań t be confused with other brown algal species. The specimen shown has a length of ca. 15 cm.



Callithamnion tetragonum

(Withering) S. F. Gray

Red algae (Florideophyceae)

Callithamnion tetragonum is a red alga growing with uniseriate branched filaments as in all members of this genus. The cells are multinucleate in contrast to those in the genus *Aglaothamnion*. The thallus can reach a length of 10 cm. Species differentiation in *Callithamnion* is possible using diameters of the main filament, the design of the terminal branchlets and the design of the terminal cell. Growth happens by the division of apical cells. In *Callithamnion tetragonum* the thallus arises as a single main filament from an attaching disc. The filament is richly branched. Basal branches are longer than the terminal ones. The outline of the plant can therefore be triangular. The apical cell (8 µm) is much smaller than the basal ones that can reach 1000 µm in diameter.

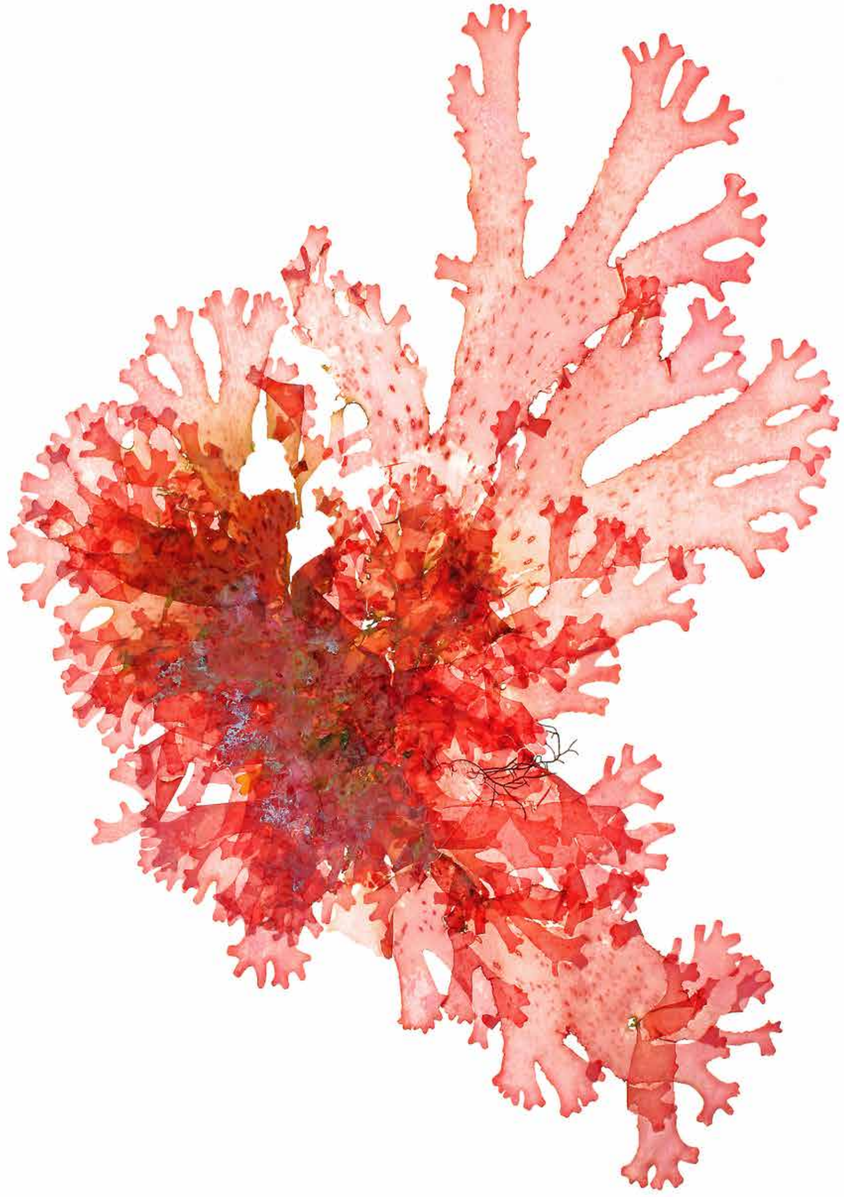
In *Callithamnion* the gametophytes are monoecious. The spermatangial branches bear clusters of spermatangia on their upper face. The carpogonia are on lateral branches. The carposporophyte is not surrounded by a pericarp. The tetrasporophyte and the gametophyte are isomorphic. Tetrasporangia are arising from terminal branches. The species is growing typically epiphytic on other algae in the sublittoral or in intertidal rock pools. Actually 88 species of the genus *Callithamnion* are accepted in Algaebase. It occurs in the Northern Atlantic and in the Mediterranean Sea. The specimen shown has a length of about 20 cm.

Apoglossum ruscifolium

(Turner) J. Agardh

Red algae (Florideophyceae)

Apoglossum ruscifolium is a species of the family Delesseriaceae. Members of this family are found frequently in the herbaria, because the family is species-rich (453 species according to Algaebase) and contains the most impressing species of macroalgae at all. That's why in this book a lot species of Delesseriaceae are found: *Phycodrys*, *Hypoglossum*, *Apoglossum*, *Delesseria*, *Membranoptera*, *Polyneura*, *Cryptopleura* and *Nitophyllum*. This is only 50 % of the genera of Delesseriaceae in Europe. When collecting data for this book, two pairs of species arrested attention: *Apoglossum ruscifolium/Apoglossocolax pusillum* and the pair *Erythroglossum laciniatum/Asterocolax erythroglossi*. They are interesting, because they are closely related species where the one partner is a parasite of the other. *Apoglossocolax* is parasitic on *Apoglossum*, *Asterocolax* is parasitic on *Erythroglossum*. In both species the rhizoids grow in the host tissue, penetrate the cell walls and suck out nutrients from the host. *Apoglossocolax* is said to be a hemiparasite, *Asterocolax* to be a parasite. In both cases a pale red colour is described, so that a rest of photosynthesis is active in both species. Then the relationship should be hemiparasitic. May be that *Asterocolax* has gone a step further to holoparasitism. A holoparasite should be colourless and get the complete nutrients from the host. A relationship, where the parasite is close to the host, is called "adelphoparasitism", which means "parasitism on the brother". The specimen shown has a length of about 20 cm.



Nitophyllum punctatum

(Stackhouse) Greville

Red algae (Florideophyceae)

Nitophyllum punctatum is a red alga of the family Delesseriaceae. The red thalli have the form of a salad blade and are dichotomously lobed at the margin. Also ribbon-like thalli with clear dichotomous branching occur. They adhere to the ground with a small holdfast and sit on a short stalk. In contrast to other Delesseriaceae there are intercalary meristems allowing the characteristic growth of the blade. The gametophytes are dioecious. The spermatangia are arranged in elliptical sori at both faces of the thallus. The carpogonia and later the carposporophytes are arranged pairwise at both faces of the thallus. On the tetrasporophyte also the sporangia are arranged in sori. All the reproductive structures are scattered uniformly over the thallus and the sori are visible as dark red dots. This is the reason for the epitheton "punctatum". Confusion is possible with *Polyneura bonnemaisonii*, which has the same outline. But this species has very distinctive veins in the basal part of the blade. Confusion is also possible with *Cryptopleura ramosa*. Here the tetrasporangial sori are found on lateral outgrowths.

Nitophyllum punctatum is the type species of the genus *Nitophyllum*, a genus which contains 33 species worldwide. *Nitophyllum punctatum* has a worldwide distribution. It is a plant of the sublittoral and the kelp forest also occurring in rock pools. The specimen shown has a length of about 20 cm.

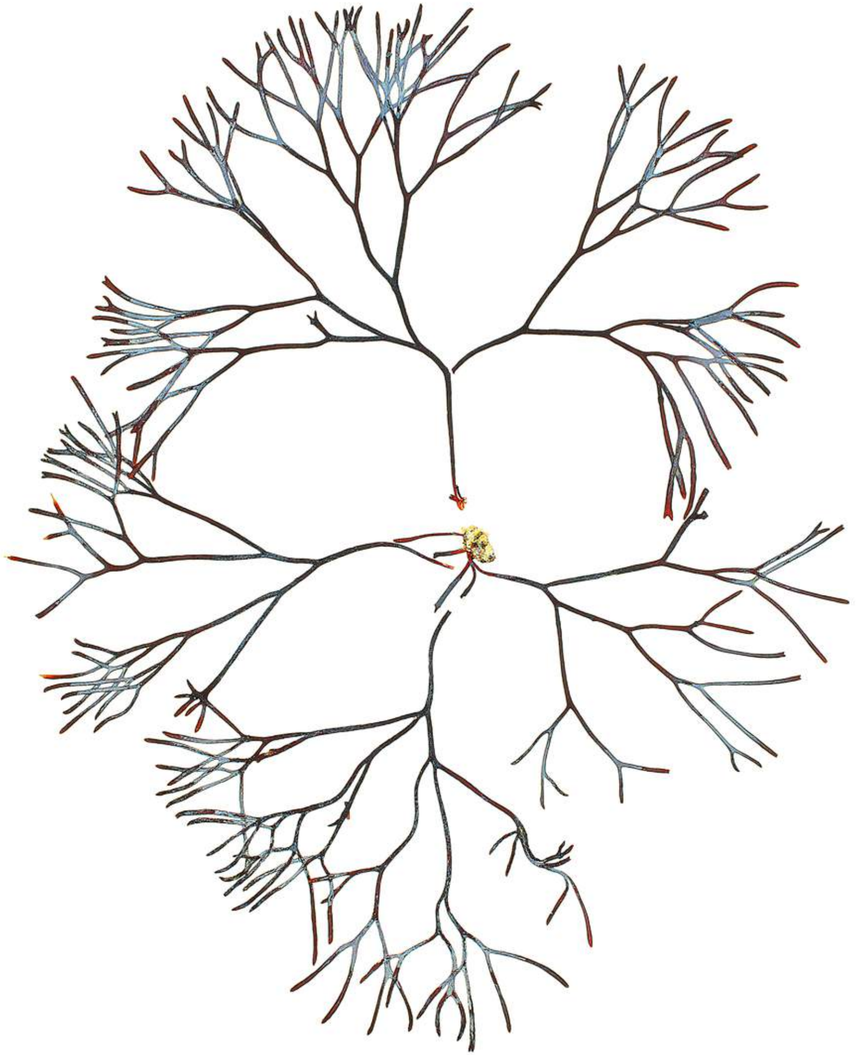
Polyides rotundus

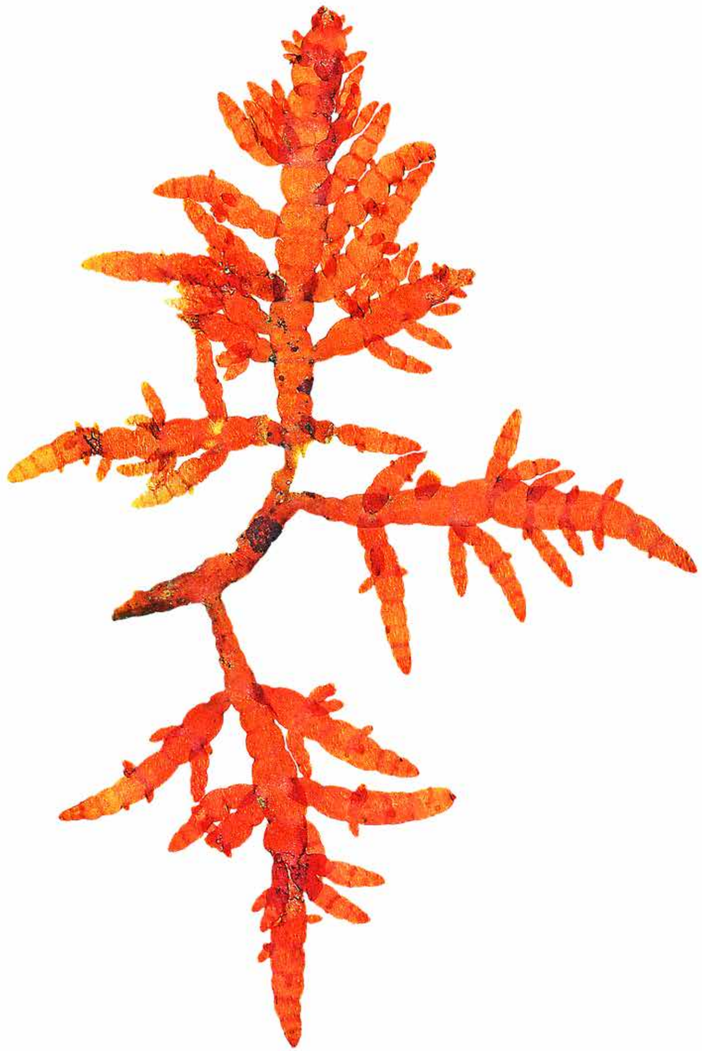
(Hudson) Gaillon

Red algae (Florideophyceae)

Polyides rotundus is a red alga with a thin thread-like thallus which is branched dichotomously thus giving the plant the shape of a tree. The thread-like thallus grows from a disc-shaped holdfast. The whole plant feels cartilaginous. Its colour is dark red to black. The plant can reach a length of 20 cm and the diameter of the threads can reach 2 mm. The general structure of the thallus is multiaxial. So no main axis is found in cross-sections. Central filaments are parallel to the longitudinal axis; from the centre filaments bend outwards so that the red coloured tips of the filaments are vertical to the surface. Gametophytes are dioecious; tetrasporophytes and gametophytes are isomorphic. Spermatangia are found on the surfaces of the terminal branches; carposporophytes often are arranged in large patches, tetrasporangia in sori. The plants of *Polyides rotundus* can be easily confused with *Furcellaria lumbricalis*. *Furcellaria* has an acute thallus tip; that of *Polyides rotundus* is rounded (name!). At the basis *Furcellaria* arises from a branched holdfast; thalli of *Polyides* arise from a disc-like basis.

The plants of *Polyides rotundus* are found in the lower eulittoral and in sublittoral. The species is found in the North Atlantic region. *Polyides* is a monotypic genus. The specimen shown has a length of about 20 cm.





Champia parvula

(C. Agardh) Harvey

Red algae (Florideophyceae)

Champia parvula is a rather small alga that is segmented. The thallus is hollow and the visible segments are separated by septa. The general construction of the thallus is multiaxial. The thallus reaches a length of 10 cm and is branched irregularly with alternate to opposite ramuli. The gametophytes are dioecious. The tetrasporophytes are isomorphic to the gametophytes. The spermatangia are arranged in sori surrounding the segments. Sometimes more than one segment bear the spermatangia. Carpogonia buildcarposporophytes after fertilization that are surrounded by a sterile envelope, the pericarp. Carpospores can leave the pericarp by a pore. The tetraspores are embedded in the cortex of the tetrasporophyte. *Champia parvula* is a plant of the sublittoral and is sometimes also found in rock pools.

Champia parvula can be confused with *Chylocladia verticillata* which is of similar construction. In *Champia parvula* the ultimate branchlets rarely stand in whorls and maximally three in one whorl. In *Chylocladia* whorls normally have more than three. The length/width relation of a segment in *Champia* is less than two; in Chylocladia it is always more than two.

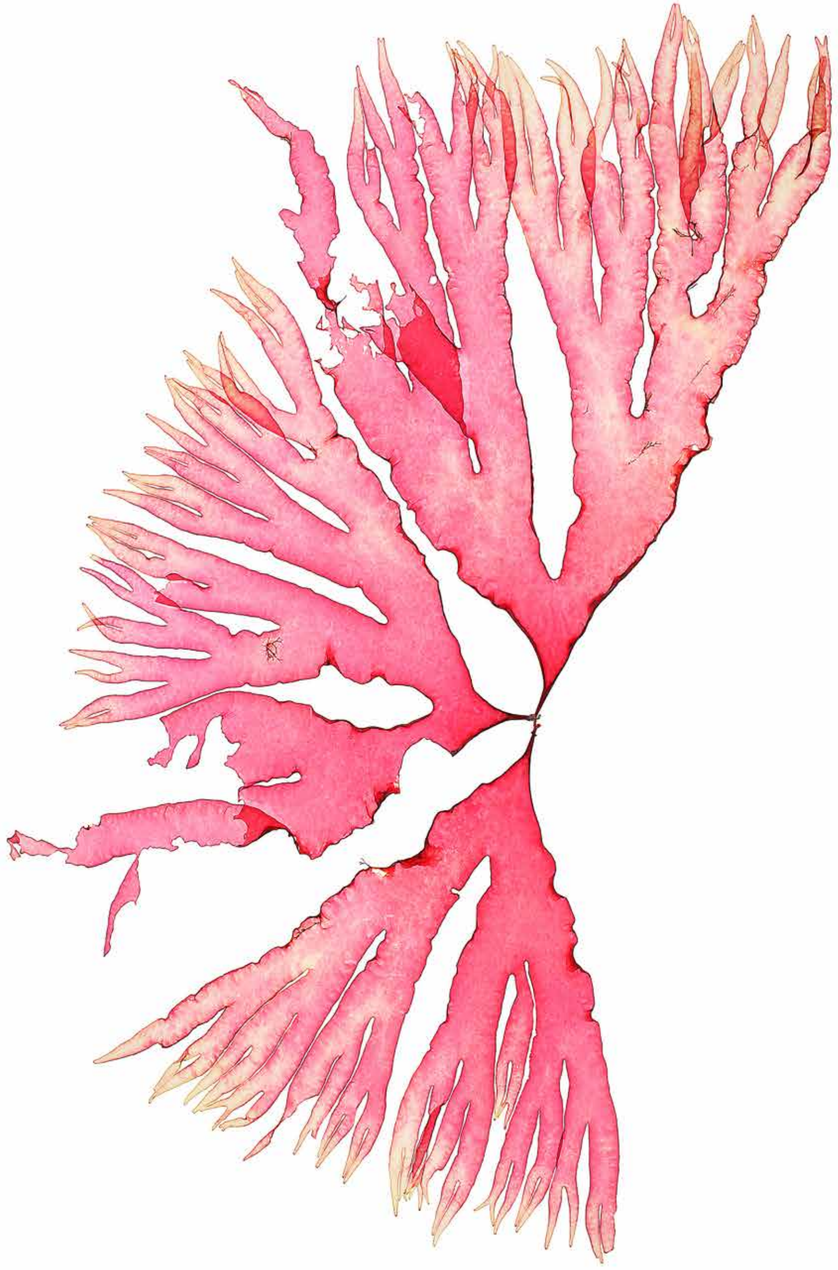
Champia is a genus containing 36 species. *Champia parvula* has a worldwide distribution. The genus is building its own family, the Champiaceae which belongs to the order Rhodymeniales. The specimen shown has a length of about 10 cm.

Itonoa marginifera

(J.Agardh) Masuda & Guiry

Red algae (Florideophyceae)

Itonoa marginifera is a red alga that is known to most phycologists as *Platoma marginifera*. It has a leaf- like thallus of ca. 25 cm length which is 4-5- fold dichotomously divided into lanceolate lobes. The terminal lobes have acute tips. The whole plant feels thick and lubricous. In cross sections through the blade the multiaxial central part is visible. In the outer parts of the blade filaments are vertical to the surface, each separated from the neighbouring branches by mucilage. And they are red in colour due to their rhodoplasts. The gametophytes are monoecious, so spermatangia and carpogonia are found on the same plant. Spermatangia are not easy to see as they are not in groups and are built by cortical cells. Also the carpogonia are somewhat hidden in the gelatinous cortex. After fertilization the resulting carposporophyte is very small. All cells of the carposporophyte develop to carpospores. The carposporophyte is not surrounded by a pericarp. Tetrasporophytes were unknown for a long time (see next page). *Itonoa marginifera* is a species which is very rarely found in rock pools. This species is only known from Europe, Morocco and the Atlantic Islands. The specimen shown has a length of about 20 cm.



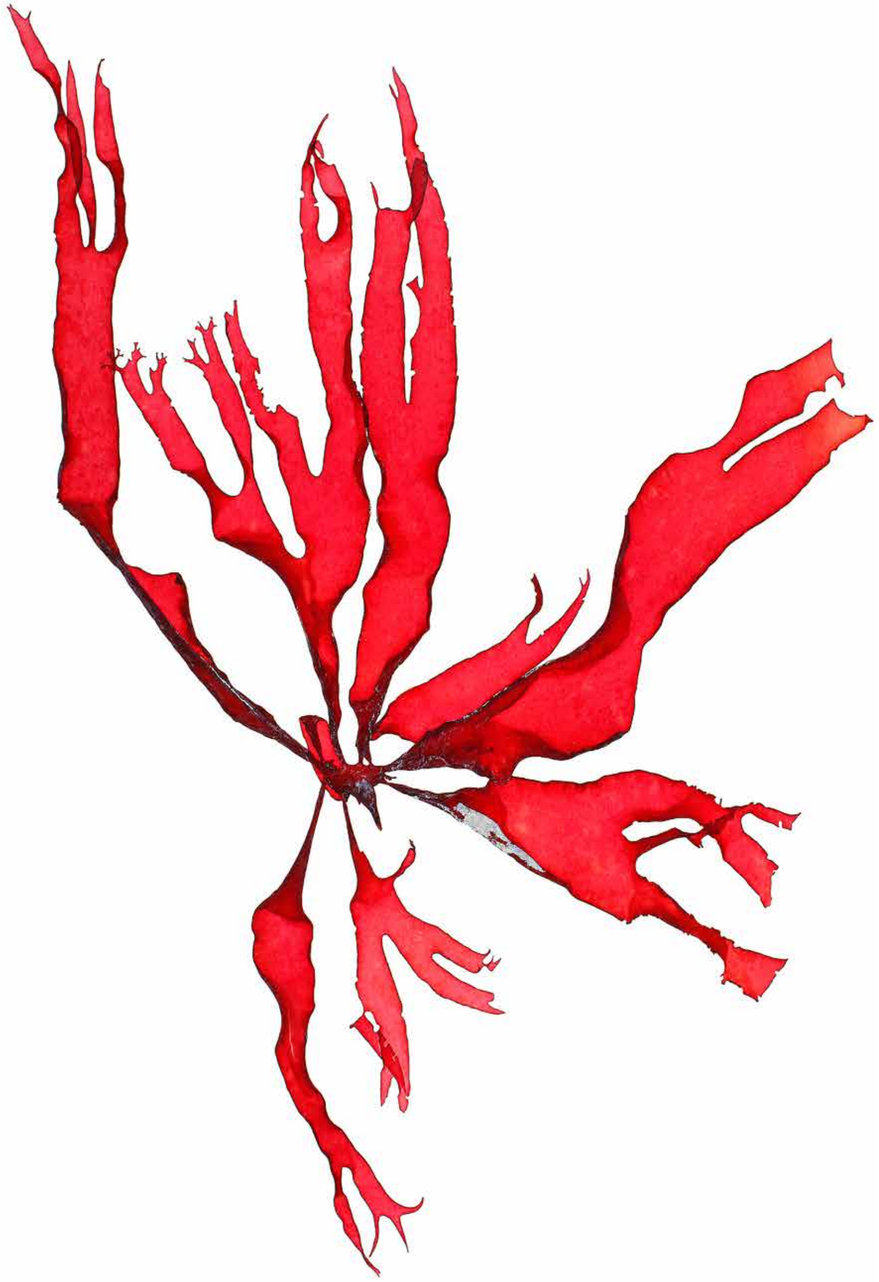
Itonoa marginifera

(J.Agardh) Masuda & Guiry

Red algae (Florideophyceae)

Itonoa marginifera has been identified by the collector of this specimen as *Platoma marginifera*. This was the state of the art when Prof. Grau collected the plan in the 1970ies. It was later re-examined and due to the development of carpogonium and the carposporophyte a new genus "*Itonoa*" was defined. Differences were great enough to assign it to another red algal family: From the Schizymeniaceae, to which Platoma belongs, to the Nemastomataceae.

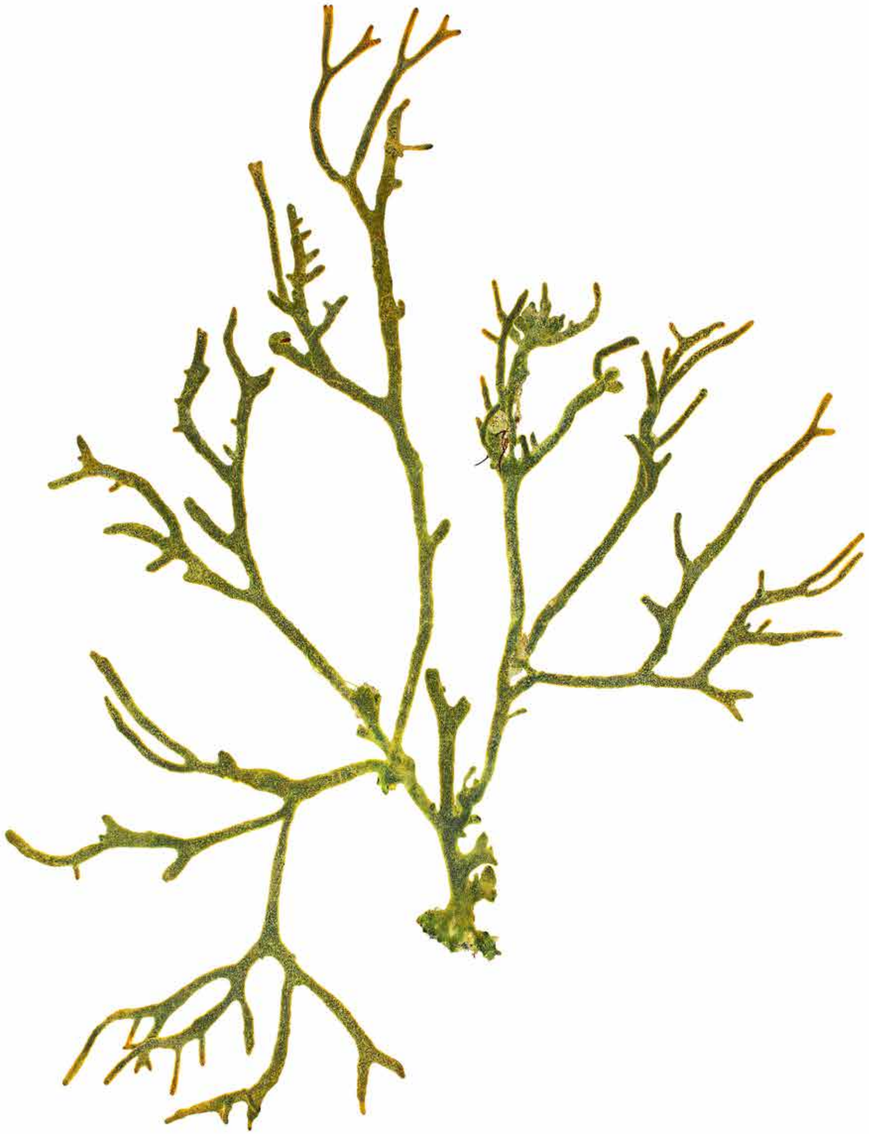
There was an open gap in the life cycle of *Itonoa marginifera*. The tetrasporophyte was unknown. Cultivation experiments could show that germinating carpospores developed to a branched filamentous plant that is completely different from the gametophyte. It s a pity, but tetrasporangia were not yet found. It is the question of finding suitable culture conditions under which tetrasporangia are formed. Otherwise you have to find a plant in nature with tetrasporangia and isolate spores, from which *Itonoa* gametophytes arise. So it seems that in *Itonoa* a type of life cycle exists in which gametophyte and tetrasporophyte are strongly heteromorphic. This type of life cycle is relatively rare; but we find it in *Asparagopsis armata* where the tetrasporophyte was so different that it was described as a completely different genus *Falkenbergia*. The specimen shown has a length of about 20 cm.



Codium sp.

Green algae (Chlorophyta, Ulvophyceae)

Codium is a genus of the green algae which is characterized by thick dichotomously branched thalli that are terete in cross section. This is true for all the specimens depicted in this book. There are also morphotypes in the genus that form green balls of 20 cm diameter or spongy mats that creep over the substrate. In the cross sections of the branched thalli it is visible that the thallus is built by siphonous green filaments; this means that no cross walls exist in the filaments and that there are a lot of nuclei and chloroplasts in a long filamentous cell. In the centre of the branches filaments run parallel to the axis. Then they turn outwards so that the green tips are vertical to the surface of the thallus. These green ends are separated from the rest of the thallus by a ring-like thickening of the cell wall; they are called "utriculus". Their function is photosynthesis. The only portions that are separated completely from the siphonous thallus are reproductive cells which are gametangia. When life cycles of *Codium* were investigated, it was revealed that the thallus is diploid and only the gametes arising by meiosis are haploid. So *Codium* is an example for a diplontic life cycle. The plants are dioecious. The gametes of the two sexes are biflagellate, the female gamete being larger than the male one. Such a fertilization type is called anisogamy. The specimen shown has a length of about 20 cm.



Codium sp.

Green algae (Chlorophyta, Ulvophyceae)

Sometimes *Codium* species are difficult to identify. This is the case in our two specimens where identification is only possible with cross sections of the thallus. It must be determined, if the ends of the utriculi are mucronate (with a small acute tip) or blunt. This was not done by the collectors. It is most probable that they were mucronate as in the most frequent species *Codium fragile*. This could be examined also with the dried specimen of a herbarium. Only a small portion of the thallus must be rewetted and prepared for the microscope. The dichotomously branched species *Codium tomentosum* and *Codium fragile* are species of the sublittoral but they are also found in rock pools in the intertidal zone.

The two other European species of this genus are *Codium adhaerens* and *Codium bursa*. *Codium adhaerens* creeps over rocks and builds a green spongy carpet of up to 1 m^2. It is typically found at the lowermost eulittoral and in the sublittoral. *Codium bursa* is the ball-shaped species which is rarely found in the Northern part of Europe but more frequently in the Mediterranean. It occurs till a depth of 10 m and more.

According to Algaebase there are 142 accepted species worldwide. The specimen shown has a length of about 20 cm.

Cystoseira sp.

Brown algae (Phaeophyceae)

- *Cystoseira* is a brown algal genus frequently found in rock pool. These are water bodies that are completely filled with sea water during high tide and don't fall dry during low tide. In these habitats we have special conditions:

- They are permanently filled with water.
- At least at low tide they have high light conditions.
- In summer the water of rock pools can heat up.
- When it rains during low tides the salt concentration decreases.
- There is no to low wave action during low tide.

- There we can find a lot of species that are normally inhabitants of the sublittoral. This is the "normal" habitat which is permanently flooded. If one wants to find species of the sublittoral on field excursions, rock pools can be a substitute for this habitat, because no excursion group goes into the water. In rock pools one can find the following genera that are rarely or never found in the intertidal zone:

- *Codium*
- *Corallina*
- *Lithothamnion*, *Lithophyllum* and other *Corallinaceae*
- *Bifurcaria*
- *Bryopsis*, a rare siphonous green alga
- *Cystoseira*, different species

- The specimen shown has a length of about 25 cm.

Bifurcaria bifurcata

R. Ross

Brown algae (Phaeophyceae)

- Also *Bifurcaria bifurcata* is a species frequently found in rock pools. Such rock pools are rather diverse in regard to the algal vegetation.

- In the upper eulittoral we find rock pools that are flat. Here the temperature is strongly fluctuant and also the salt concentration due to rain or drought. In these habitats only a few species survive. They are rich in Ulva sp. (the former *Enteromorpha*) and also some *Corallina* and *Lithophyllum sp.* can be found.

- At the uppermost eulittoral and the supralitoral level there are rather small rock pools where the exchange of seawater is rare, temperature and salinity can be even more variable. Here the waterbodies are often turbid. One has to use the microscope to see that there are flagellates of the green algal genera *Pyramimonas* and *Tetraselmis* and a lot of other flagellate algae. And often in such mini rock pools a heterotrophic dinoflagellate, *Oxyrrhis marina*, is found which can live as a predator on the flagellate algae.

- Descending to the low tide level, the rock pools are often deeper and their water is more frequently exchanged. The conditions are similar to those of the sublittoral. Here, although we are yet in the eulittoral we can find algae of the sublittoral. The specimen shown has a length of about 20 cm.

Laminaria digitata

(Hudson) J.V. Lamouroux

Brown algae (Phaeophyceae)

Laminaria digitata is found at the lowermost eulittoral and the sublittoral. It also can be found in deep and large rock pools in the lower intertidal zone. In the sublittoral it is one of the species forming the kelp forest. This kelp forest is composed mainly of brown algae. In Brittany and the British Isles these vegetation building species are:

- *Laminaria digitata*
- *Laminaria hyperborea*
- *Saccorhiza polyschides*
- *Himanthalia elongata*
- *Chorda filum*
- *Halidrys siliquosa*
- *Laminaria ochroleuca*
- *Saccharina latissima*
- *Alaria esculenta*
- *Desmarestia viridis*
- *Desmarestia aculeata*

.... and others. Regarding other regions of the world, kelp forests also exist but there are other species and genera not occurring in Europe.

At the pacific coast:
- *Macrocystis pyriformis*
- *Nereocystis luetkeana*

At the south African coast:
- *Ecklonia maxima*
- *Laminaria pallida*

A lot of epiphytic red algae are characteristic for the kelp forest. The specimen shown has a length of about 25 cm.

Saccharina latissima

(Linnaeus) C.E. Lane, C. Mayes, Druehl & G.W. Saunders

Brown algae (Phaeophyceae)

Saccharina latissima is a member of the order "Laminariales". Since Carl von Linné's rules of binominal nomenclature scientists try to arrange the species according to their natural phylogeny. For this purpose higher categories (genera, families, orders, subclasses and classes) were created. These artificial groups should reflect the natural phylogeny when phylogenetic analyses show that groups are monophyletic. So the brown algae – the Phaeophyceae – are a monophyletic group. Molecular analyses revealed the following groups (simplified, only orders mentioned in this book are included):

Class: Phaeophyceae

- Subclass: Discosporangiophycidae
- Subclass: Ishigeophycidae
- Subclass: Dictyotophycidae
  - Dictyotales
  - Sphacelariales
- Subclass: Fucophycidae
  - Desmarestiales
  - Laminariales
  - Ectocarpales
  - Fucales

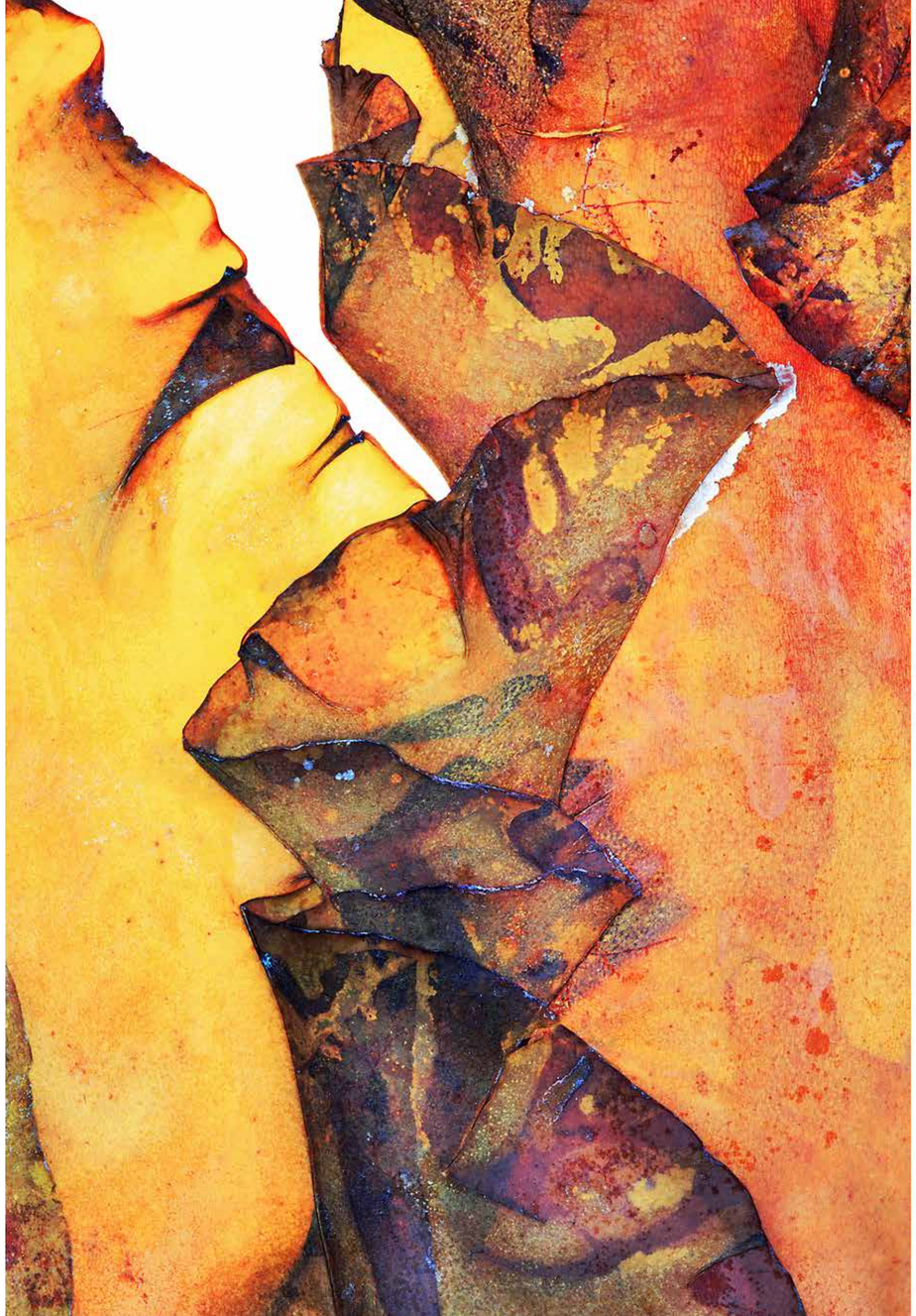
There are 18 orders of brown algae in modern literature. In order to visualize the phylogenetic relationships, dendrogams are used. When analysing such trees it becomes obvious that a lot of additional categories are needed and that a system with orders, subclasses and classes is only a coarse instrument. Only six of the 18 orders of brown algae are mentioned in this book. The specimen shown has a length of about 10 cm.

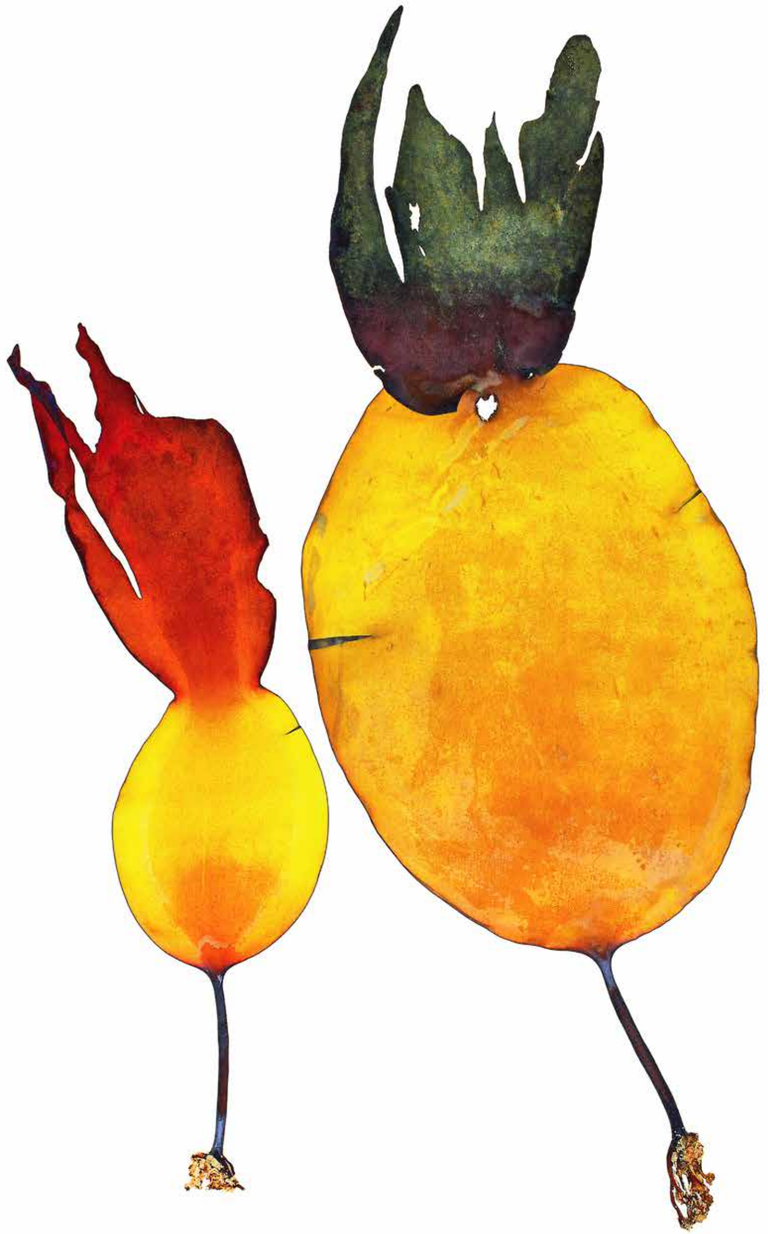
Saccharina latissima

(Linnaeus) C.E. Lane, C. Mayes, Druehl & G.W. Saunders

Brown algae (Phaeophyceae)

Saccharina latissima is one of the largest brown algae in Europe. In winter this plant loses its blade and begins to produce a new phylloid in spring. A meristem at the tip of the cauloid is activated and produces the tissue for the new blade. This mode of phylloid regeneration is true also for the genera *Laminaria* and *Saccorhiza*. Often this meristem already gets active even when the old blade is not yet removed. This type of active tissue is called intercalary meristem. Intercalary meristems are not only found in the complex thalli of Laminariales. Also in the filamentous thalli of *Ectocarpus* intercalary meristemoids are responsible for the growth of the thallus. In other cases exclusively apical cells are responsible for growth. In the brown alga *Sphacelaria* a large apical cell is producing continuously segmental cells towards the basis. These cells then elongate. They produce a cortex of peripheral cells by periclinal cell divisions. These periclinal cells are as long as the central cell. So a real three dimensional tissue is produced. Apical cells in filamentous algae are not rare in the algae. *Cladophora*, *Chara* and most red algae are growing with apical cells. Also in the case of the brown alga *Dictyota* an apical cell is responsible for the growth. Segmental cells produced by the apical cell are able to perform some additional divisions to build up the ribbon like thallus. And in the brown alga *Fucus* the growth is starting with an apical cell but this cell is later on surrounded by meristematic cells that are responsible for further growth. The specimen shown has a length of about 10 cm.





Laminaria digitata

(Hudson) J.V. Lamouroux

Brown algae (Phaeophyceae)

Laminaria digitata is easily recognized be the dark flexuous cauloid. *Laminaria hyperborea*, occurring in the same locations has a thick upright stalk which is not flexible and light brownish in colour. The phylloid in adult plants can reach a length of 1.5 m. Every year in late winter the phylloid is replaced. At the basis of the old leaf a meristematic zone is getting active, producing the leaf for the next year. The old leaf keeps connected to the new one until it is torn off by the winter and spring storms. Initially the new leaf is undivided. Later on the leaf is divided in its typical way. The form of this division is like a hand with its fingers and therefore called "digitate". And this is the epitheton of this *Laminaria* "*digitata*". In summer to autumn on the thallus irregular dark zones are developing. Surveying cross-sections of these zones in the microscope, one can see the sporangia of *Laminaria* which are long cylindrical. These are the cells in which the meiosis takes place. After the meiosis three mitoses are performed so that 32 spores are released. These biflagellate spores are genetically different and they grow out to tiny male or female gametophytes. As in all species of the Laminariales they are few-celled and only short living. They release eggs or sperms and the zygotes grow out to new *Laminaria* sporophytes. The specimen shown has a length of about 25 cm.

Macrocystis pyrifera

(Linnaeus) C. Agardh

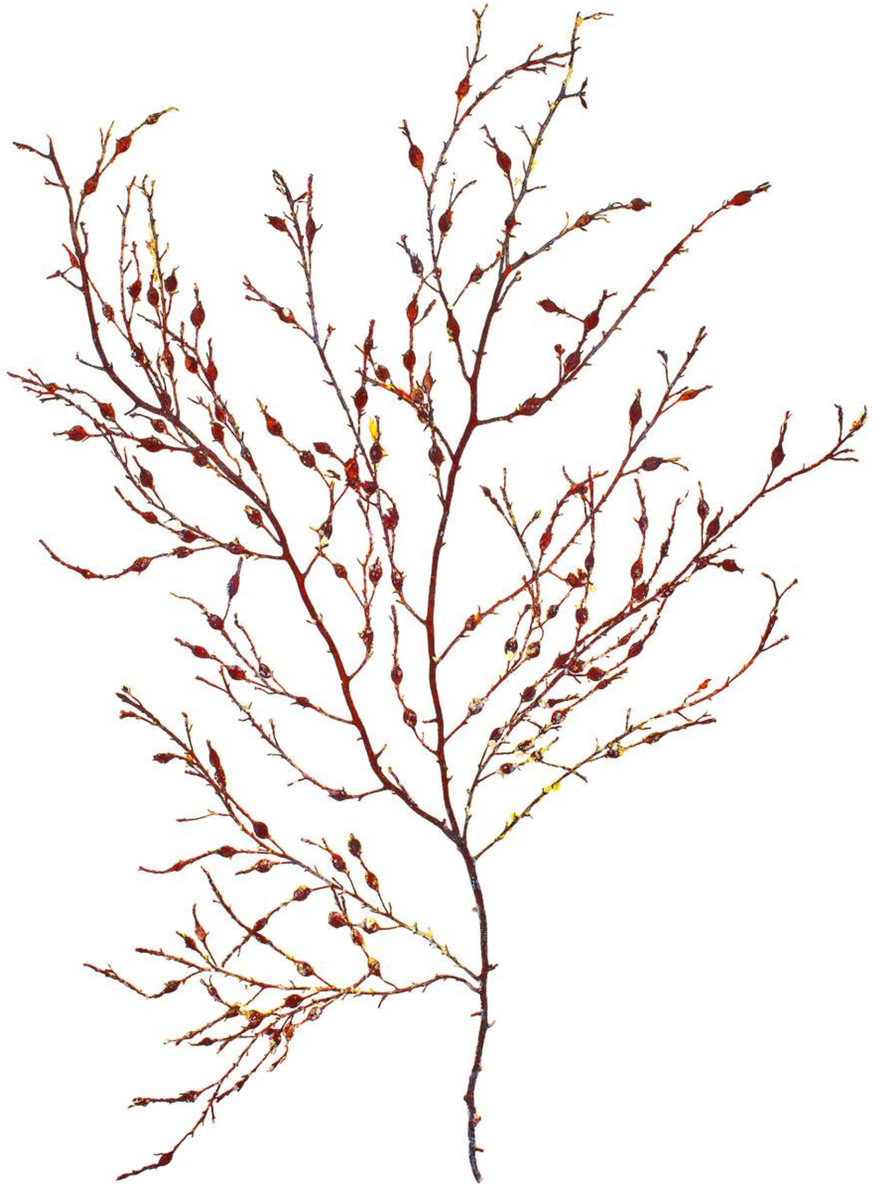
Brown algae (Phaeophyceae)

With a maximum length of 45 m *Macrocystis pyrifera* is the largest alga worldwide. It is an alga that is occurring at the Pacific coasts of North and South America, the South Atlantic and Australia. Growing in a depth of 6-20 m, the plant has developed pneumatocysts filled with gas to get buoyancy and to grow erect in the water. These pneumatocysts are pear-shaped which explains the scientific name "*pyrifera*" which means "bearing pears". The alga is attached with a strong holdfast ("rhizoid") on rocks. The cauloid is long and thin and in regular distances phylloids are developed. The pear-shaped gas bladders are at the basis of these phylloids. *Macrocystis* is harvested in industrial extent to extract alginates from the plant material. Alginates are of great value in food industry. In spite of its completely different habit this species belongs to the order of Laminariales. This is reflected in its life cycle: A very large diploid sporophyte produces haploid spores that grow out to very tiny, few-celled heterothallic gametophytes that release eggs or spermatozoids. The zygotes grow to a new sporophyte. *Macrocystis* is monotypic which means that *Macrocystis pyrifera* is the only member of the genus. Of similar size but different in morphology is *Nereocystis luetkeana*. Here only one large pneumatocyst is responsible for buoyancy. *Nereocystis luetkeana* is also a species of the Laminariales and a monotypic species.

Cystoseira sp.:
Linnaeus

Brown algae (Phaeophyceae)

Like Fucus, *Cystoseira* is a genus of the order Fucales. *Cystoseira* belongs to the family Sargassaceae. The thallus is irregularly branched, in cross section flat or terete. It is attached to the ground with a small disc. The thalli normally not exceed 70 cm in length. Pneumatocysts, if present, are globose to ovoid inflations in the centre of the cauloid. Because of the buoyancy of these pneumatocysts the thalli grow upright in the water. The differentiation of species in this genus is not easy because of the plasticity in morphology and the difficult delineation of correlated species. This may be the reason why the species above was only identified as *Cystoseira sp.* As all members of the Fucales, *Cystoseira* has receptacles. These are located at the end of ramuli. They contain oogonia and antheridia. The oogonia contain only one egg. Most species are occurring near to the low tide mark or in rock pools. Some species show intensive iridescence in the sunlight. Differentiation of species is possible by the size of the thallus, the form of the leaf-like appendixes at the main axis, the form of pneumatocysts and the iridescence. According to Algaebase the genus contains 42 species. Members of the genus *Cystoseira* are distributed worldwide. The specimen shown has a length of ca. 25 cm.



Cystoseira sp.:
Linnaeus

Brown algae (Phaeophyceae)

Some *Cystoseira* species from the European seashores:

Cystoseira tamariscifolia: This is a species where the thalli show strong iridescence in the sun under water. The branchlets of the thallus somewhat resemble those of the higher plant Tamarix; older phycologists know the species under the name "*Cystoseira ericoides*"; in this nomenclature the name refers to the habit of the genus *Erica*, the heather.

Cystoseira montagnei: Here the thallus is richly branched; the branches are inflated at their basis; the pneumatocysts are below the axils of the branches.

Cystoseira foeniculacea: This rare plant is not iridescent; its surface is rough because there are a lot of spines on their surface. The receptacles are sometimes divided. The name "foeniculacea" refers to the scientific name of the fennel, "*Foeniculum*".

Cystoseira baccata: Also not iridescent; the surface being smooth and not rough like in *Cystoseira foeniculacea*. It is probably the most frequent species on our seashores. The species can reach a length of 90 cm.

The specimen shown has a length of about 25 cm.

Ascophyllum nodosum

(Linnaeus) Le Jolis

Brown algae (Phaeophyceae)

On the seashores of Central Europe *Ascophyllum nodosum* is the species with the largest pneumatocysts. Like Fucus vesiculosus it is occurring in the upper eulittoral and must resist the same salt- and heat-stress. *Ascophyllum nodosum* is easy to recognize by its large pneumatocysts that are located in the middle of the ribbon-like thallus. The massive thallus has a length of up to 70 cm and doesn´t have a midrib. The pneumatocysts start with a small size of 1 cm length; in older thalli they can grow to a length of 7 cm and a diameter of 3 cm. In contrast to Fucus which is dichotomously branched, *Ascophyllum* has a distinctive main axis and subordinate side branches. In Fucus the receptacles are developing at the end of main branches, in *Ascophyllum* at the ends of the side branches. *Ascophyllum* is a dioecious plant; male plants are recognized by the orange colour of the receptacles; the female receptacles stay brownish to greenish. The thalli of *Ascophyllum* are frequently "infected" by a specific red alga *Vertebrata lanosa*, a genus which is similar to *Polysiphonia*. This species in former times indeed was named "*Polysiphonia lanosa*". It is never found on other algae than *Ascophyllum*. The display detail shown has a length of ca. 15 cm.

Sargassum muticum

(Yendo) Fensholt

Brown algae (Phaeophyceae)

Sargassum muticum is a species which is not native in Europe. It was first seen in 1973 at the Isle of Wight and presumably occurred some years before at the coasts of Brittany. It is an invasive species introduced from Japan possibly with the ballast water of ships.

The thalli, normally 2-3 m long, can reach in some cases a length of 10 m. The cauloids are cord-like and carry a lot of lateral phylloids. This species, a member of the order Fucales is shown here as a plant, which has special pneumatocysts. These are beside the branchlets of the plant, on small stalks and have a diameter of 2-4 mm. Although very small, the mass of these gas bladders gives the plant buoyancy so that they stand upright in the water at high tide.

As a fucalean alga *Sargassum muticum* has receptacles that appear in the axils of side branches. The species is monoecious so that male and female gametes are produced on the same plant. Male gametes are released from the receptacle whereas eggs stay in the oogonium. The zygotes develop to a new sporophyte and are released from the mother plant as young seedlings. The specimen shown has a length of about 15 cm.

Dilsea carnosa

(Schmidel) Kuntze

Red algae (Florideophyceae)

Dilsea carnosa is a red alga with one of the largest thalli. The thallus is leaf-like and attached with a short stalk. The length is about 50 cm, the width ca. 20 cm. It is a very tough thallus which is up to 1 mm thick. The species is found at the low tide level and also in the subtidal region to a depth of more than 20 m. The thallus construction is of the multiaxial type so that no main axis is visible. Gametophytic generation and tetrasporophyte are isomorphic. Male and female plants exist, i.e. the species is dioecious. The plants are fertile in the winter half year.

Similar to *Palmaria palmata* that is collected as "Dulse" in Brittany, also *Dilsea carnosa* is collected as nutrition. The old name "*Dilsea edulis*" where the Latin term "edulis" means "eatable" reflects the use as nutrition.

Dilsea carnosa is occurring in the Northeast of the Atlantic. The genus *Dilsea* belongs to the family Dumontiaceae and the order Gigartinales. According to Algaebase the genus contains six accepted species. A genus "*Neodilsea*" also containing six species was separated from *Dilsea* in the middle of the last century. The specimen shown has a length of ca. 30 cm.

Bostrychia scorpioides

(Hudson) Montagne

Red algae (Florideophyceae)

Bostrychia scorpioides is one of the smaller species of red algae. The smallest species in fact are the unicellular species like *Porphyridium* or *Cyanidioschyzon*. Also among the filamentous red algae there are some smaller species, but they are so small that they are rarely found in herbaria. So *Bostrychia* was chosen as the example of a very small red algae. Because of its small size more specimens were sticked to the sheet. *Bostrychia scorpioides* is a red alga which is regularly found in salt meadows at the upper limit of high tide. It is growing especially on the sea purslane (*Halimione portulacoides*). The name "*scorpioides*" refers to the ends of the thalli that are incurved like the tail of a scorpion. The gametophytes are isomorphic and heterothallic, tetrasporophyte and gametophyte are isomorphic.

Bostrychia scorpioides belongs to the large order Ceramiales (2638 species) and to the large family Rhodomelaceae (1054 species). The genus *Bostrychia* itself contains 38 species. The first *Bostrychia* species ever described was *Bostrychia scorpioides* so that this European species is the type species of the genus.

The specimen shown has a length of ca. 5 cm.

Ulva sp.:

Green algae (Chlorophyta, Ulvophyceae)

Ulva sp. is one of the larger species on the European seashore. The thallus can reach a length of more than 30 cm. It is attached to the substrate with a small disc and sitting on a small stalk. It resembles a great green leaf with entire margin of ovoid to round shape. There are no structures on the "leaf" like veins etc. The thallus is two cell layers thick and all cells are like one another. Experiments have shown that *Ulva* has an isomorphic life cycle: Gametophyte and sporophyte look identical. When in nature thalli are found the margins of which are white instead of green, they are in reproduction. They are often seen in small ponds at the time of low tide and the water is greenish from the flagellate cells that are released by the thallus. Cells of the sporophyte are quadriflagellate and are therefore zoospores. These zoospores have undergone meiosis before their release. After germination haploid gametophytes arise. The flagellate cells that later arise from the haploid gametophytes are gametes which pairwise can fuse and so built a diploid zygote. This again develops to a new sporophyte. This type of isomorphic life cycle is characteristic for all *Ulva* species including the old genus *Enteromorpha* which was added to the genus *Ulva* in the last decades. Gametes that don't have a difference in form and size are isogametes. According to Algaebase the genus *Ulva* comprises 128 species. The specimen shown has a length of about 25 cm.

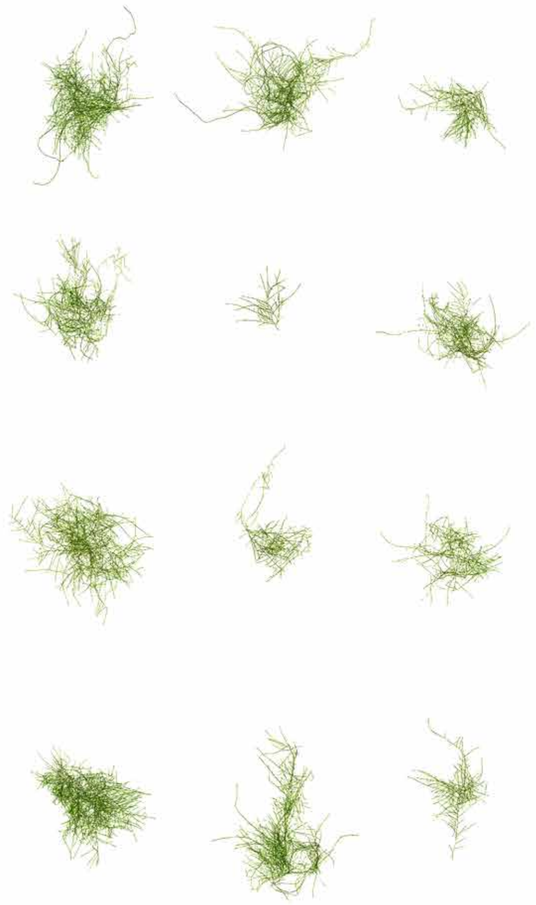
Cladophora sp.:

Green algae (Chlorophyta, Ulvophyceae)

Although *Cladophora* species can reach a length of more than 10 cm, it is chosen as an example of small green algae. This is because the single filaments are small in size (see herbarium sheet on the left). There are smaller filamentous green algae but these are too delicate for a herbarium. And there is a bulk of unicellular species in the green algae. Specimens of unicellular algae are chemically fixed in tubes and/or a drawing and/or a microscopical photograph is deposited in a museum. The best way to document such a species is to deposit a living strain of a species in an algal culture collection. This allows further scientific work with the alga in the future.

Cladophora is a uniseriate branched filamentous green alga with large cells. These cells bear a lot of nuclei and chloroplasts. This type of organization is called "siphonocladous". It is one of the genera that occur in marine and freshwater habitats. For the marine species isomorphic life cycles could be shown. This is not the case in the freshwater representatives of the genus. According to Algaebase 216 species are in the genus *Cladophora*. They build an own family (Cladophoraceae) and order (Cladophorales). The class in which Cladophorales and other orders are united is named after the genus on the left page "Ulvophyceae".

The specimens shown have a length of ca. 5 cm.



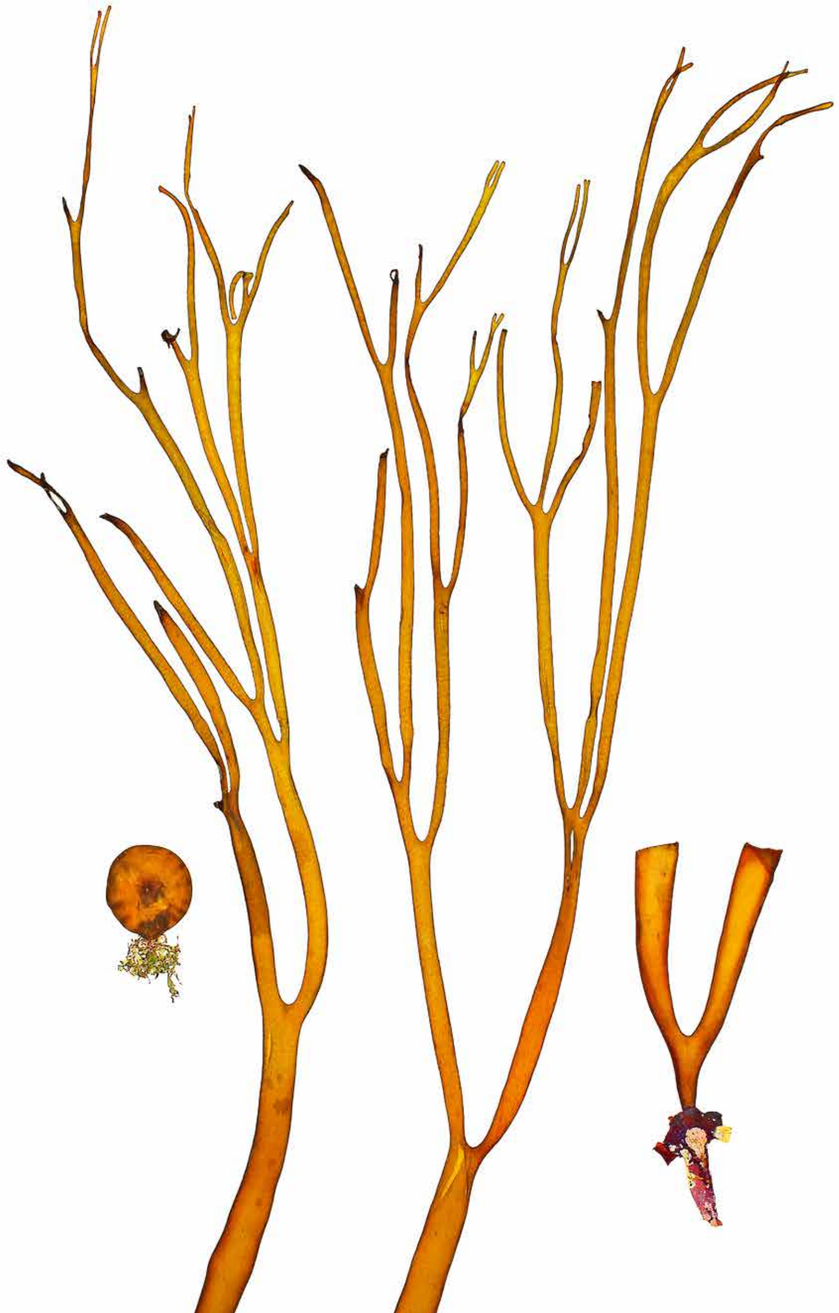
Himanthalia elongata

(Linnaeus) S.F. Gray

Brown algae (Phaeophyceae)

Himanthalia elongata is one of the larger native brown algae in our seashores. On field excursions in Brittany we found thalli of 8 m length. The normal size is 2-4 m. In the last decades another invasive species with large size (> 5 m) has come to our flora: *Sargassum muticum*. The over 40 m -genera Macrocystis and Nereocystis are not occurring in Europe.

The thallus of *Himanthalia*, when germinating out of a zygote, looks like a small greenish spinning top of 3 cm diameter. But then the receptacles are growing out, two ribbon-like brownish bands that branch repeatedly in a dichotomous way. As growth takes place over the year, the thalli can reach an enormous length. On the bands later on dark brownish dot are seen which are the conceptacles. So the complete thallus, except the initial "spinning top" is a receptacle which is carrying out also the photosynthesis of the thallus additional to the reproduction. *Himanthalia elongata* is monotypic, the only member of the genus and the family Himanthaliaceae. The presence of a receptacle is indicative for the order of Fucales to which *Himanthalia* belongs. *Himanthalia elongata* is restricted to the Northeast Atlantic region.



Sphacelaria sp.

Brown algae (Phaeophyceae)

Sphacelaria sp. is one of the smaller genera in the brown algae reaching a length of about 5 cm in our region. The thalli are filamentous and grow with an apical cell. The descendants of a few cells behind the apical cell build a cortex around the central filament performing anticlinal divisions. So the size of the central cell is visible in the pattern of the pericentral cells.

In cases examined *Sphacelaria* has an isomorphic life cycle with alternating of gametophyte and sporophyte. The gametophytes are mostly monoecious and anisogamic; female macrogametes and male microgametes are formed. Additionally female gametes that could not fuse with microgametes can behave like spores and regenerate gametophytes. In some species propagules are built, triangular thallus-portions that are easily released from the mother plant and grow out to new plants. This type of vegetative (clonal) propagation enhances the success of plants which are once established in a habitat.

42 species are accepted in the genus *Sphacelaria* worldwide according to Algaebase. Together with other genera they constitute the family Sphacelariaceae and the order Sphacelariales. The specimen shown has a length of about 2 cm.

Porphyra umbilicalis

Kutzing

Red algae (Florideophyceae)

Porphyra umbilicalis belongs to the Bangiophyceae, a group of red algae that is different from the Florideophyceae which contain most of the red algal species (>95%) worldwide. The Bangiophyceae contribute for only 2.6 % of the red algae. The life cycle of *Porphyra* is strongly heteromorphic: The large leaf-like thalli are the gametophytes that can be dioecious or monoecious. Parts of the thallus perform intracellular divisions and a lot of male gametes that are not flagellated (spermatia) are released. These spermatia stick on the thallus and female cells (eggs) are fertilized by them. The resulting zygote performs intracellular division so that as the result of one fertilization large amounts of diploid cells are released. In analogy to the Florideophyceae these zygotospores are called by some authors as "carpospores". They are germinating on the shells of mussels to the sporophytic phase which is completely different from the leafy gametophytic phase. This phase was in former times described as a different genus "*Conchocelis*". Only when culture experiments had been performed the *Conchocelis* phase could be identified as a stage in the life cycle of *Porphyra*. This diploid sporophytic phase ends when in special sporangia conchospores are formed by meiotic division. From these conchospores gametophytes arise again. From the gametophytic phase also spores can be released that regenerate the gametophyte in a clonal way. The life cycles of different *Porphyra* species are similar. The specimen shown has a length of ca. 20 cm.

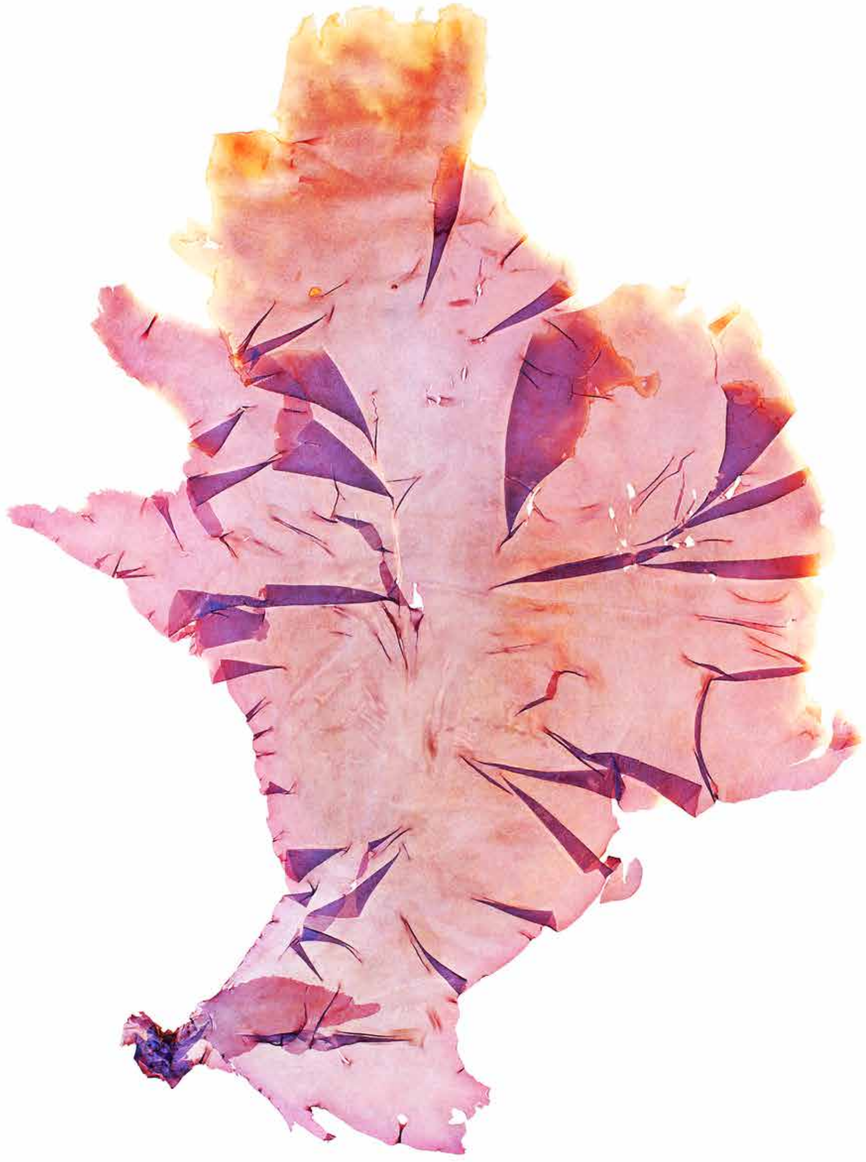
Porphyra linearis

Greville

Red algae (Florideophyceae)

Porphyra linearis is another species or variety in the Bangiophyceae. Two species of the genus Pyropia, formerly accounted to the genus *Porphyra*, are *Pyropia yezoensis* and *Pyropia tenera*. These species are cultivated in aquafarms in Korea and Japan in large extent as "nori" which is used as the outer cover of the modern seafood "sushi". Sushi, in former times a delicious food only in Japan can be ordered today in each city of the world. Therefore there is a great market for nori, the major component of this food. So it was very helpful that the life cycle of *Porphyra* was elucidated. Today the nets on which the Nori plants are cultivated are inoculated with the *Conchocelis* spores and then brought to the aquafarms, where the *Pyropia* species are allowed to grow. They can be harvested several times a year.

The genera *Porphyra* and *Pyropia* belong to the family Bangiaceae and the order Bangiales. The genus *Porphyra* comprises 71 species, the genus *Pyropia* 64. In both genera the sporophytic phase is a *Conchocelis* stage, formerly an own genus. Another genus of the Bangiales is *Bangia*, from which the names of the family Bangiaceae, the order Bangiales and the class Bangiophyceae are derived: *Bangia* comprises 18 species worldwide. Members of this genus can also occur in the freshwater. The specimen of *Porphyra* linearis shown has a length of ca. 20 cm.



Palmaria palmata

(Linnaeus) F. Weber & D. Mohr

Red algae (Florideophyceae)

Palmaria palmata is one of the most frequently collected algae for vegetarian seafood cooking. In Brittany it can be bought as fresh material as well as in a drought form under the name "dulse". Irish people collect *Palmaria* under the name "dillisk". It contains all minerals and trace elements needed for human nutrition including high amounts of iron and vitamin B6. It is rich in proteins and dietary fibres. It can be used directly for salads or in its drought form for flavouring soups and seafood. Recipes for the use of dulse are found in the internet and in cookbooks. Searching for algae that are used in human nutrition, one can find some species:

- *Ulva lactuca* (right page)
- *Palmaria palmata* (this text)
- *Undaria pinnatifida*, a brown alga of the order Laminariales, eaten as "Wakame" in Japan
- *Alaria esculenta*, a brown alga of the order Laminariales, eaten in Iceland, Scotland, Ireland
- *Dilsea carnosa*, a red alga, not proposed for eating anymore
- *Chondrus crispus*, a European red alga
- *Saccharina japonica*, a brown alga of the order Laminariales, eaten as "Kombu" in East Asia
- *Pyropia yezoensis* and *P. tenera*, red algae eaten as "Nori"
- *Himanthalia elongata*, a brown alga of the order Fucales, eaten in Europe as "spaghetti de la mer"

This list is far away from being complete.

Ulva lactuca

Linnaeus

Green algae (Chlorophyta, Ulvophyceae)

Ulva lactuca, a very common species in the North Atlantic region, is used as seafood for a long time. It can be used as fresh "leaf" in the salad or dried in form of shredded particles. The latter is used to flavour soups or seafood. The algae are normally not cultivated but rather collected on the seashore as sea lettuce. The dried variant can be bought in seafood shops in coastal regions and due to its durability also ordered by mail.

Ulva is containing considerable amounts of magnesium, calcium, and the vitamins A, B12 and C. There are a lot of other elements in *Ulva* including trace elements. A lot of recipes can be obtained by the internet and from special cookbooks. *Ulva* can also be used as a substitute for nori in sushi recipes. And also other species like *Ulva intestinalis*, the former *Enteromorpha intestinalis*, can be eaten like *Ulva lactuca*.

Ulva has also contributed a little bit to the negative image of algae in the public view. When algae pests occur in the coastal regions, it is often the genus *Ulva* which can grow over-abundantly. That's because under nutrient rich conditions almost every cell of the thallus can build a new thallus. So, when agriculture is spilling a lot of nutrient into the groundwater and rivers and these nutrients reach the sea the algal boom of *Ulva* can be predicted. Thus algal pests are ever man-made problems. The specimen shown has a length of about 30 cm.

Agarum clathratum

Dumortier

Brown algae (Phaeophyceae)

Agarum clathratum is a species occurring in the arctic sea for example in Greenland, Alaska and Kamchatka. It is well adapted to arctic climate and growth is optimal below 10 °C. High temperatures inhibit the formation of gametes so that the arctic distribution of this species can be explained by these adaptations. *Agarum clathratum* is a species of the order Laminariales. It is fixed with a holdfast of branched "rhizoids". The cauloid reaches a length of 30 cm, the phylloid up to 1 m. This phylloid has a distinctive median rib. The most evident character of *Agarum clathratum* is the number of round holes in the phylloid that reach a diameter of 2 cm. The species occurs at the low-tide mark and reaches a depth of at least 15 m. As a member of Laminariales it has a life cycle similar to that of *Laminaria*. The dominant phase of the life cycle is the sporophyte and the sporangial sori are found at the edges of the phylloid. The genus *Agarum* contains 6 subarctic species not occurring in Europe There are some other non-European genera of the Laminariales:

Ecklonia is distributed in the southern hemisphere. Species reach a length of 15 m.Also *Lessonia* is a genus of the southern hemisphere. They are main contributors to the kelp forests. *Postelsia* occurs in the North-eastern Pacific. The small sporophytes (60 cm) release unflagellated spores. *Eisenia bicyclis*, a pacific species, is eaten as "Arame" in Japan.

For the large algae *Macrocystis* and *Nereocystis* see the page of Macrocystis.

The specimen of *Agarum* shown has a length of about 25 cm.

Gelidium pusillum

(Stackhouse) Le Jolis

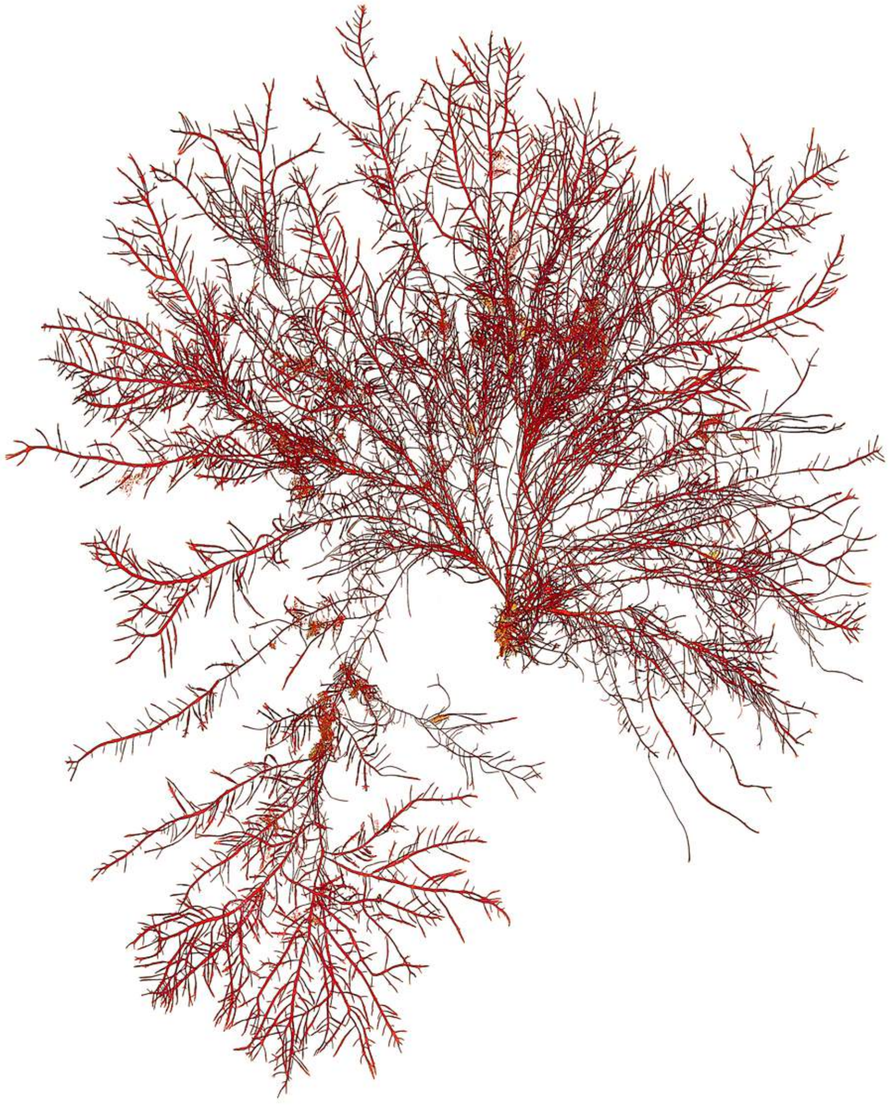
Red algae (Florideophyceae)

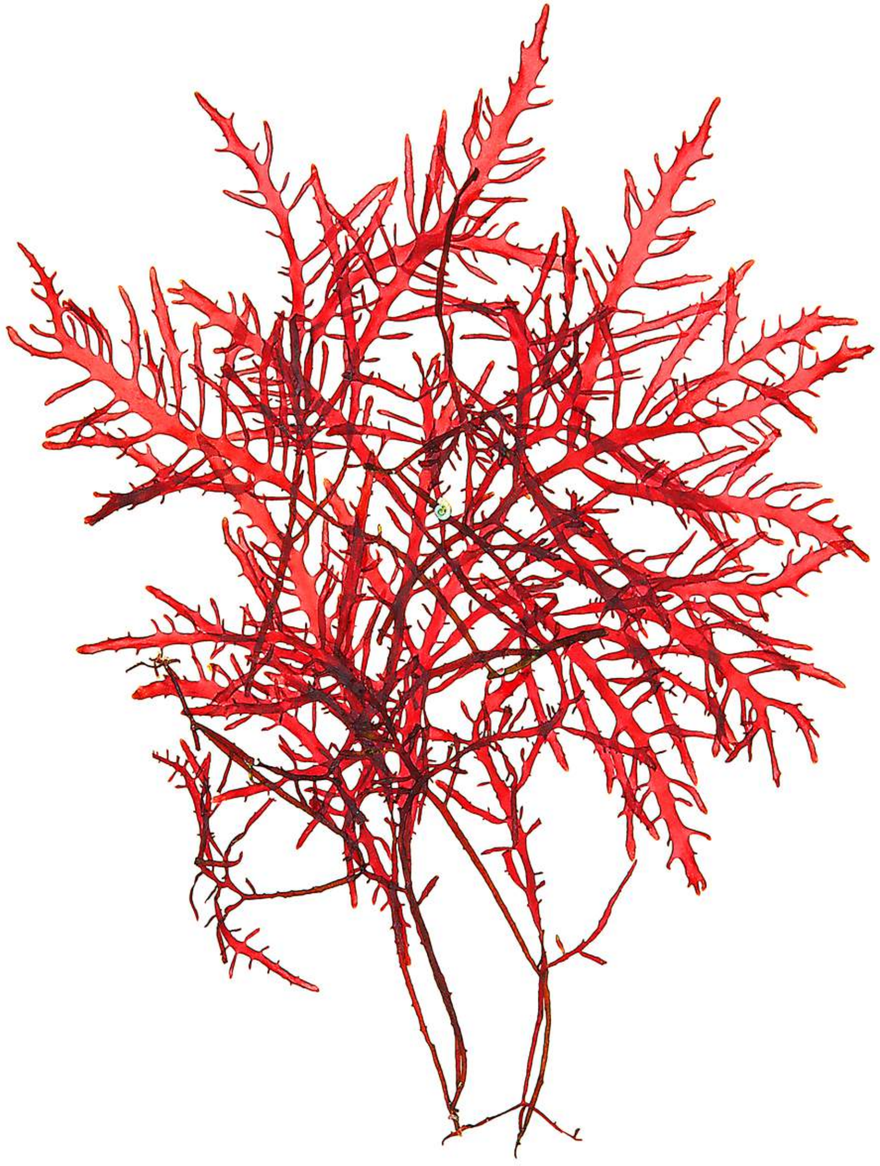
Gelidium pusillum is one of the red algae that are called "agarophytes". These are species or genera from which agar can be extracted. Some genera well known for a high concentration of agarose and agaropectine in the cell walls are *Gracilaria*, *Gigartina*, *Phyllophora*, *Ceramium* and *Chondrus*.

Agar is capable to solidify liquid media and 1% and less are enough to form a solid culture medium. Such solid media are needed in microbiology as well as for algae or sterile higher plants. And gels of a purified fraction, the agarose, are used worldwide to separate nucleic acids in electrophoresis.

Agar is used in East Asian cookery for a longer time for soups and sweets. Also in Europe Agar is used for the production of ice cream, marmalade and glaze. In recent times it is used as an adequate vegetarian alternative for gelatine which is produced from cartilage and bones of animals. As agar cannot be digested, it can be used in diets as an appetite suppressant or in medicine as a laxative.

Normally agarophytes are not cultivated but are collected from free nature. There is a lot of other agarophytes in the red algae that can be used for agar production.





Gelidium spinosum

(S. G. Gmelin, P. C. Silva)

Red algae (Florideophyceae)

Gelidium spinosum is another species of the large genus *Gelidium* which comprises 134 accepted species according to Algaebase. From the genus name also the family name Gelidiaceae and the name of the order Gelidiales derived. In *Gelidium* the thallus lobes are flattened and they are feathery branched in one plane. The consistency of the thallus is cartilaginous and the colour mostly deep red to nearly blackish. The genus can be confused with *Pterocladia* and *Gelidiella*. For the differentiation of the genera light microscopy is necessary. The structure of the thallus is uniaxial. As far as known the life cycle is similar to most other red algae; tetrasporophyte and gametophyte are isomorphic. The distribution of the genus is cold to tropical seashores, not occurring in Arctic and Antarctic zones.

Gelidium pusillum (left page) only builds small thalli of 2 cm length. Its distribution is worldwide in moderate to tropical climates on rocks in the upper tidal zone.

Gelidium spinosum (former name *Gelidium latifolium*) builds thalli of 10 cm length and the lobes are getting broader towards their tips. Also this species has a worldwide distribution in moderate to subtropical climate and is a plant of the mid eulittoral. The specimen shown has a length of about 10 cm.

saccharina latissima

(Linnaeus) C. E. Lane, C. Mayes, Druehl & G. W. Saunders

Brown algae (Phaeophyceae)

Unlike in the red algae, in brown algae the alginates are main components of the cell wall. They are polymers of guluronic acid and mannuronic acid. In brown algal cell walls they are responsible for stability and flexibility of the thallus. The main sources for alginate extraction are members of the order Laminariales (*Laminaria*, *Saccharina*, *Ecklonia*, *Macrocystis*, *Lessonia*), but also members of the order Fucales (*Ascophyllum*, *Durvillea*). The material is harvested by ships with subaquatic mowing machines. Later it is transported to alginate facilities where the material is washed, homogenized and then fractionated by different physical and chemical methods. In absence of calcium alginates are viscose; when calcium is added the molecules interconnect and the alginates become gel-like. Alginates are included in numerous foods, in bakery products, sauces, mayonnaise, dietary and light-products, ice cream and many more products. It is also used in cosmetics to stabilize unguents and creams. Also in medicine alginates are used in surgery and dentistry.

Saccharina latissima (former *Laminaria saccharina*) is one of the Laminariales that are harvested for alginate extraction. When harvested from European coasts, there is no differentiation which *Laminaria* species is collected. The specimen shown has a length of about 25 cm.

Laminaria digitata

(Hudson) J. V. Lamouroux

Brown algae (Phaeophyceae)

Laminaria digitata can be easily distinguished from *Laminaria hyperborea* by its thin, blackish and flexible cauloid. There are a lot of more species of Laminariales in Europe and related regions, many of which are used as source for alginates or for food:

- *Alaria esculenta*
- *Ecklonia biruncinata* (Canary Islands)
- Ecklonia muratii (Canary Islands)
- *Undaria pinnatifida* (Native in NW Pacific; invasive in Europe)
- *Chorda filum* (Native in Europe)
- *Halosiphon tomentosus* (Native in Europe, Stschapoviales now)
- *Laminaria digitata* (Native in Europe)
- *Laminaria hyperborea* (Native in Europe)
- *Saccharina japonica* (introduced from East Asia)
- Saccharina nigripes (Scandinavia, Greenland, Iceland
- *Laminaria ochroleuca* (Native in Europe)
- *Laminaria rodriguezii* (Native in the Mediterranean)
- *Saccharina latissima* (Native in Europe)
- *Laminaria solidungula* (Native in Greenland, Spitsbergen)
- *Phyllariopsis brevipes* (Native in Europe, Mediterranean, Atlantic up to France; Tilopteridales now)
- *Phyllariopsis purpurascens* (Native in Europe, Mediterranean, Atlantic up to Portugal; Tilopteridales now)

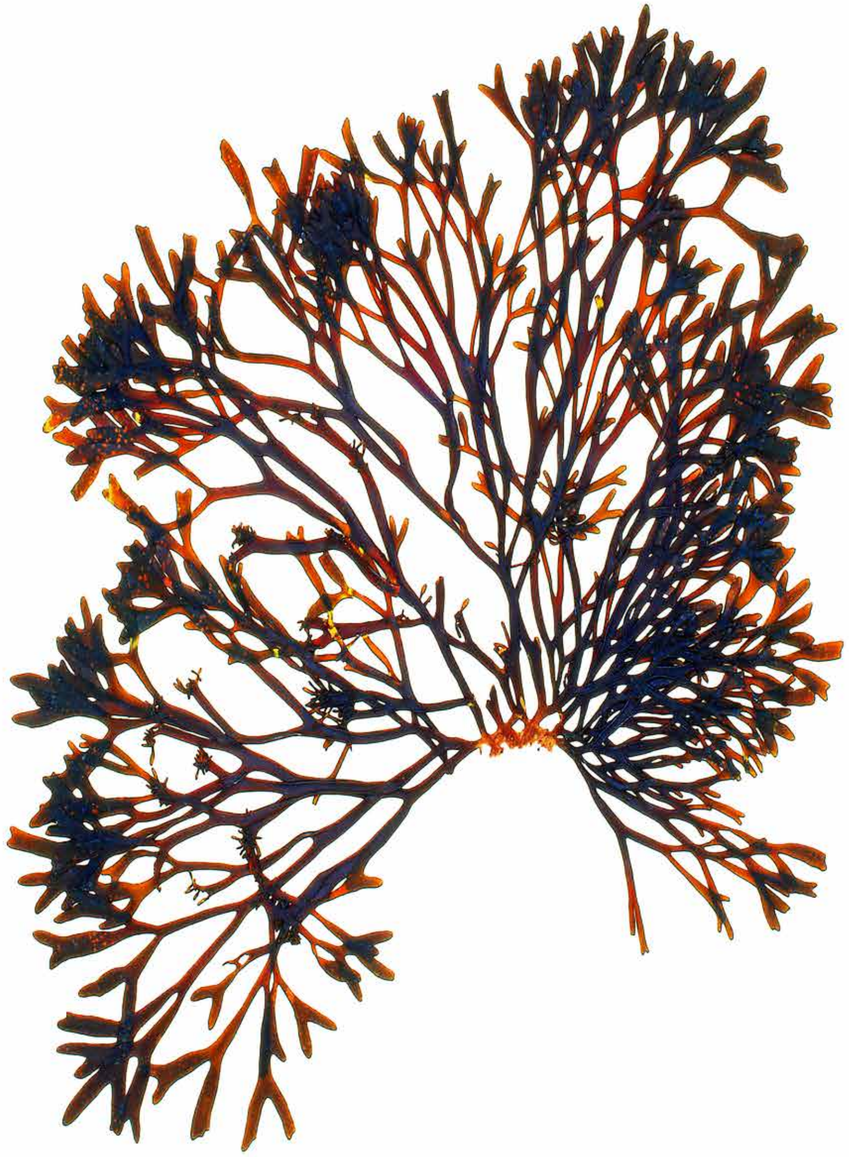
Source: Costello et al.: European Register of Marine Species; Paris 2001. The specimen shown has a length of about 25 cm.

Pelvetia canaliculata

(Linnaeus) Decaisne & Thuret

Brown algae (Phaeophyceae)

Pelvetia canaliculata is the brown alga occurring at the uppermost eulittoral next to the supralittoral. The supralittoral is the habitat directly above the maximum high tide line and is covered with seawater only under extreme conditions: When highest tide and strong storms occur at the same time. Organisms of this habitat have to tolerate some extreme conditions: Salt stress; freshwater (rain); extreme drought when the habitat is sunny and there is no rain for a longer time; frost in the winter; predation by animals. At the rocky shores of Europe, the supralitoral has identical composition: The rocks are blackish by bluegreen algae and by lichens that contain bluegreen algae. Two lichens, exclusively found in the supralitoral, predominate: *Verrucaria maura*, a black crustose lichen containing cyanobacteria as phycobionts and *Lichina pygmaea*, also containing bluegreen algae as symbiont. Additionally also the shrub-like lichen *Ramalina siliquosa* is almost exclusively found in the supralitoral. A lot of other greyish or yellow to orange crustose lichens are found a little bit above the *Verrucaria maura*- and the *Lichina pygmaea* zone. Some animals are specialized to feed in the supralittoral. So the snails *Littorina littoralis* and *Eurydice sp.* are frequently found in this zone although normally feeding also in the uppermost eulittoral. Also the isopods of the genera *Armadillidium* and *Porcellio* feed in the supralitoral. The specimen shown has a length of about 15 cm.



Ascophyllum nodosum

(Linnaeus) Le Jolis

Brown algae (Phaeophyceae)

In *Ascophyllum nodosum* and other species of the order Fucales, especially in the genus *Fucus*, the reproduction biology was investigated intensively. In order to reach best fertilization the release of the gametes must be synchronized. The *Fucus* plants have a sensor to determine the water motion in their environment. It makes sense to release the gametes when the sea is calm. Under these conditions the chance is enhanced that eggs and spermatozoids meet. Additionally, the eggs release a pheromone that attracts the spermatozoids and so again enhances the possibility of fertilization. This attractant is called "fucoserraten" according to *Fucus serratus*, from which this pheromone was prepared for the first time. As this pheromone is not species-specific, a cell-cell cognition mechanism exists to ensure that the fusion is with the right partner. In *Fucus* the result of the gamete-fusion, the zygote, is sinking rapidly to the ground and starts cell divisions: The first cell division decides that the basal cell will develop to the holdfast and the upper cell to the photosynthetically active thallus.

The pheromones of brown algae are well investigated: There is a lot of chemical attractants in the different groups that are named after the organism from which it was isolated: ectocarpene (*Ectocarpus*); hormosirene (*Hormosira*); dictyotene (*Dictyota*); desmarestene (*Desmaretia*); lamoxirene (*Laminaria*); finavarrene (*Ascophyllum nodosum*). The specimen shown has a length of ca. 30 cm.

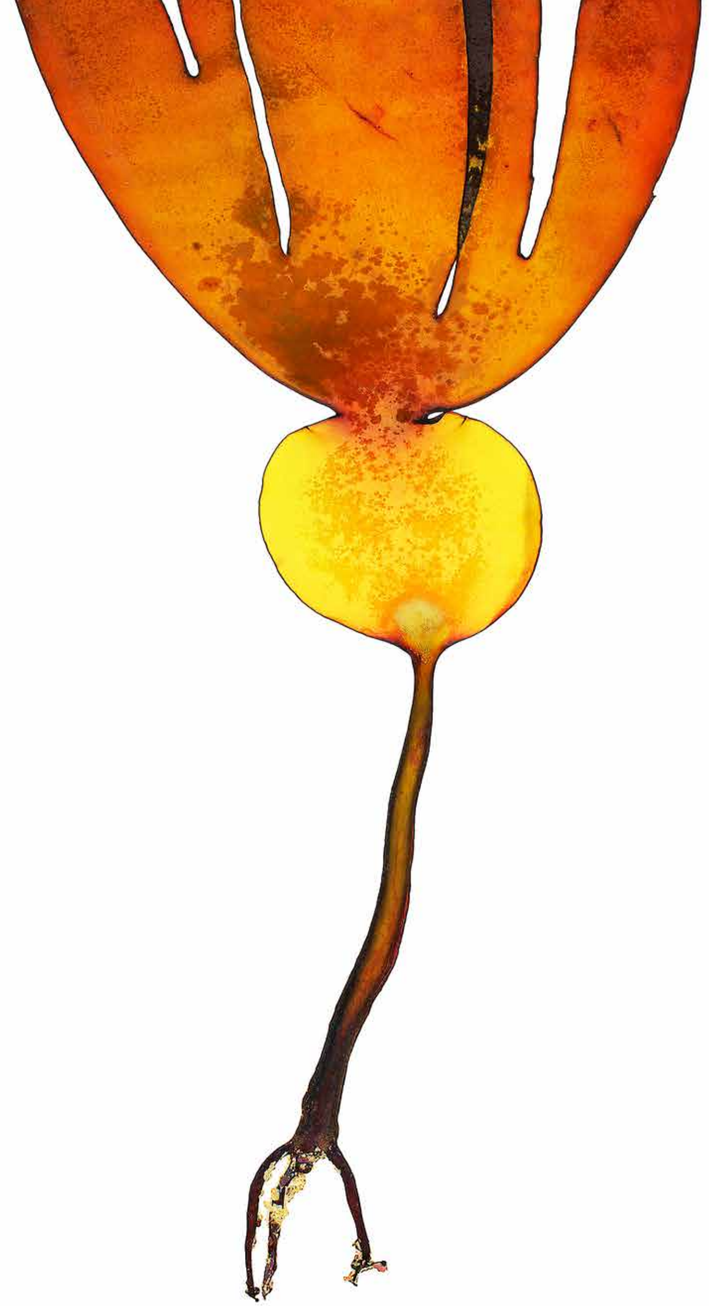
Laminaria hyperborea

(Gunnerus) Foslie

Brown algae (Phaeophyceae)

In *Laminaria hyperborea* and other species of the order Laminariales a special cell type was found which strongly resemble the sieve elements of higher plants. This type of cells is found in the cauloids and also in the phylloids. The cells are very long and look like the hyphae of fungi. They are expanded at their ends and connected to a neighbouring filament. As this expansion at the end looks like a trumpet, the elements are called "trumpet hyphae". At the trumpet like contact zone of the two cells there is a perforated plate like the sieve plates in higher plants. And the function of the plates and the trumpet hyphae seems to be the same as in higher plants: The transport of organic compounds that have been produced in photosynthesis.

In a cross-section of a phylloid the trumpet hyphae are located in the centre of the blade, followed by cells of parenchymatic character that are presumably storage cells. Near to the surface the cells are getting small and they contain a lot of brown plastids. This is the layer where the photosynthesis takes place. In the cauloid the trumpet hyphae are in the centre and are oriented parallel to the length axis. They are surrounded by parenchymatic storage tissue. The cauloid and the rhizoids are the locations where the reserve products are stored for the formation of the new blade which replaces the old one at the end of winter. The specimen shown has a length of about 25 cm.



Alaria esculenta

(Linnaeus) Greville 1830

Brown algae (Phaeophyceae)

In the headline additional to the name of the algae, authors are noted who have described the species. In the case of *Alaria esculenta* (Linnaeus) Greville, Carl von Linné was the first. Carl von Linné (1707-1778) was the inventor of binary nomenclature. Since his scientific work (Systema naturae, Genera plantarum…) plants and animals have to be denominated with a generic name, in our case "*Alaria*", and an epitheton, in our case "*esculenta*". Linné created a simplified system of the lower plants in which nearly all marine macroalgae were assigned to the genus "*Fucus*". So also our Alaria esculenta was named "*Fucus esculentus*" by Linné. As also in taxonomy there is progress in knowledge, the name of our organism was changed several times (data from Algaebase):

- Fucus esculentus
  Linnaeus 1767
- Ceramium esculentum
  (Linnaeus) Stackhouse 1797
- Musaefolia esculenta
  (Linnaeus) Stackhouse 1809
- Orgyia esculenta
  (Linnaeus) Stackhouse 1816
- Laminaria esculenta
  (Linnaeus) C.Agardh 1817
- Phasgonon esculentum
  (Linnaeus) S.F.Gray 1821
- Agarum esculentum
  (Linnaeus) Bory 1826
- Podopteris esculentum
  (Linnaeus) De la Pylaie 1830
- Alaria esculenta
  (Linnaeus) Greville 1830

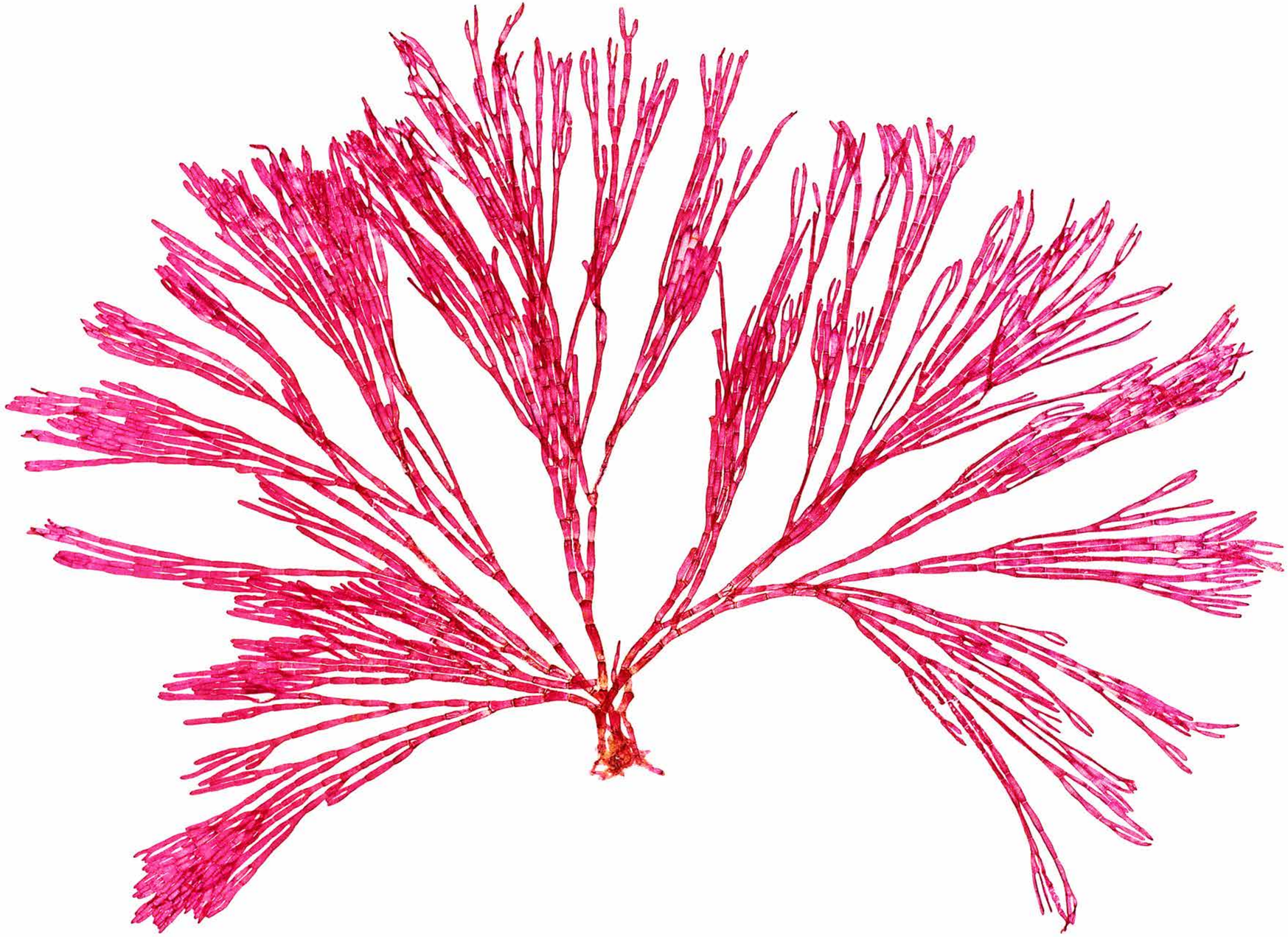
As Greville was the last person, who changed the taxonomic name, his name is given without brackets. The year of the taxonomical change is indicated.

Bornetia secundiflora

(J. agardh) Thuret

Red algae (Florideophyceae)

Bornetia secundiflora is a red alga of the family Ceramiaceae and the order Ceramiales. It builds filamentous thalli of up to 20 cm length. The tuft of filaments is coming from a holdfast that is built from interweaved rhizoids. The filaments are uniseriate and are not corticated. The large cylindrical cells have a diameter of up to 850 µm and a length of 3-4 mm. They are therefore visible with the naked eye. The cells are multinucleate and contain numerous discoid rhodoplasts. Older cells can form rhizoid that can secondarily fix to the substrate.



chapter 12
Physiological adaptations – algae are adapted to ecological niches

Bornetia secundiflora

(J. agardh) Thuret

Red algae (Florideophyceae)

The species is dioecious; tetrasporophytes are isomorphic to the gametophytes. Spermatangia are formed in heads in the axils of branches. Carpogonia and carposporophyte are surrounded by incurved basal branches. It is reported that reproductive structures of *Bornetia secundiflora* were never seen in England. But in the Mediterranean they occur.

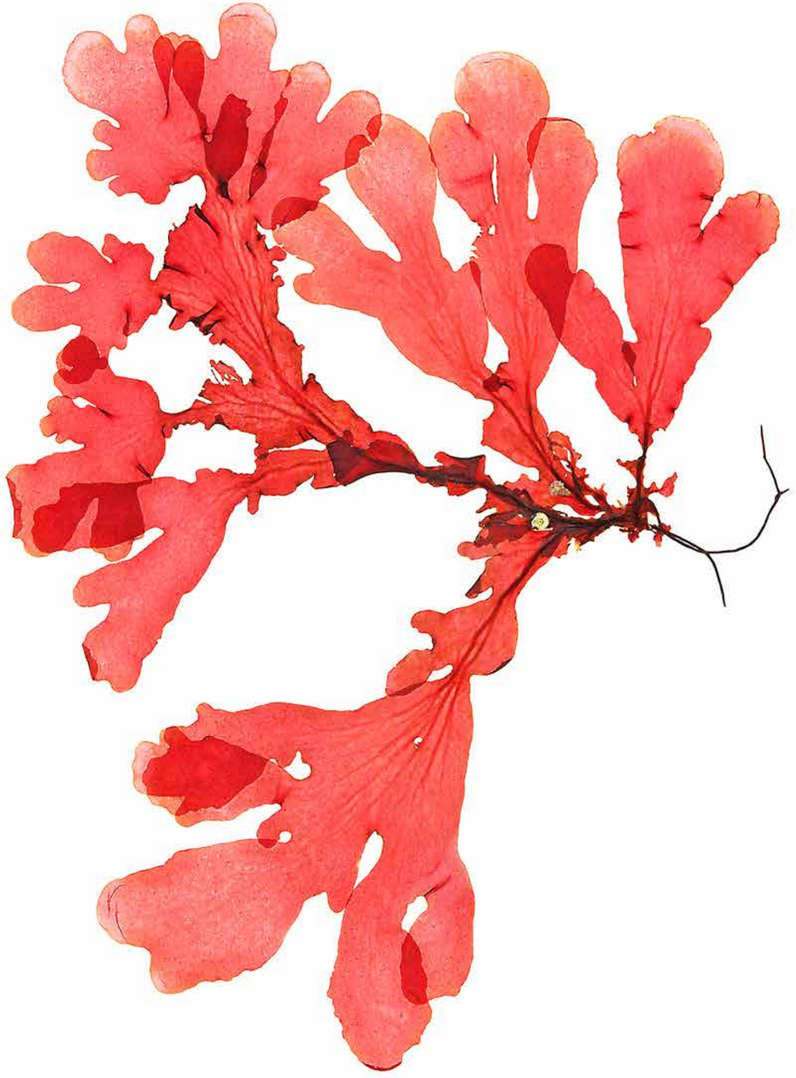
Five species are included in the genus *Bornetia*. *Bornetia secundiflora* is the type species of the genus and is occurring in the Northeast Atlantic and in the Mediterranean. The specimen shown has a length of ca. 10 cm.

Polyneura bonnemaisonii

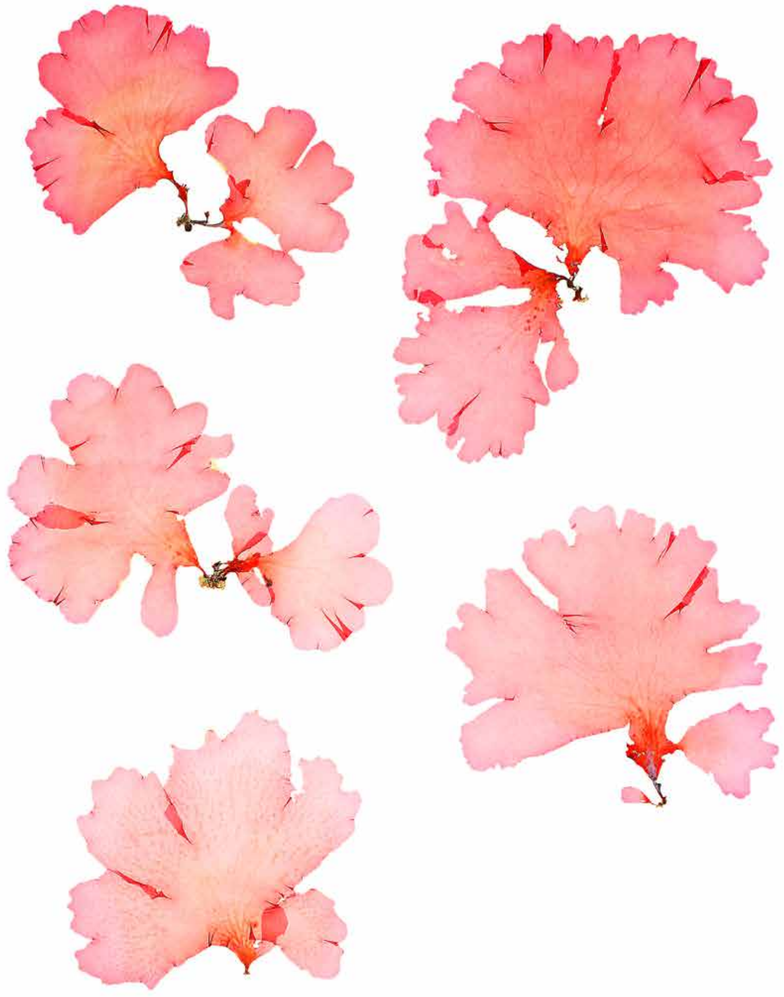
(C.Agardh) Maggs & Hommersand

Red algae (Florideophyceae)

Polyneura bonnemaisonii is a member of the family Delesseriaceae. The thallus is a lobed blade fixed to the substrate by a disc-shaped holdfast and a stalk. This holdfast can have outgrowths that allow the formation of new thalli. The young thallus grows by the activity of an apical cell. In older thalli intercalary meristems are activated resulting in the habit of the adult plant. The blades are monostromatic in the beginning. Later they get up to four layers thick. The genus is called "*Polyneura*" because of the many veins at the basis of the blade. They are not like those in *Delesseria* where they are arranged with a central vein and subordinate lateral veins, but more branched sympodially. The dioecious gametophytes and the tetrasporophyte are isomorphic. Spermatangia, carpogonia, carposporophytes and tetrasporangia are developing radially between the veins. Carposporophytes are surrounded by a pericarp that is open to the surrounding water by a pore (ostiolum). 6 species are accepted in the genus *Polyneura*. *Polyneura bonnemaisonii* is, under its old name *Polyneura hillae*, the type species of the genus. *Polyneura hilliae* was also the name on the herbarium sheet and is regarded as a synonym of *P. bonnemaisonii*. *Polyneura bonnemaisonii* is probably a European species. As most members of the Delesseriaceae it is a species of the subtidal zone occurring also in rock pools of the lower eulittoral. It also can be found on stipes of *Laminaria* in the kelp forest. The specimen shown has a length of about 15 cm.



chapter 12
Physiological adaptations – algae are adapted to ecological niches



Polyneura bonnemaisonii

(C.Agardh) Maggs & Hommersand

Red algae (Florideophyceae)

Polyneura bonnemaisonii can be confused with *Erythroglossum laciniatum*, *Nitophyllum punctatum* and *Haraldiophyllum bonnemaisonii*. For the differentiation of these species the following criteria are used:

- The existence and the design of veining.
- The size and arrangement of the reproductive structures.
- The mode of branching.

A lot of specimens of Delesseriaceae are mentioned in this book. But when searching data for the text of this book it came out that even in Europe there are a lot of genera of Delesseriaceae missing in the four herbaria evaluated for this book:

- *Erythroglossum laciniatum* (1 species)
- *Haraldiophyllum bonnemaisonii* (1 species)
- *Drachiella* (3 species)
- *Gonomophyllum buffhamii* (1 species)
- *Acrosorium venulosum* (1 species)
- *Radicilingua thysanorhizans* (1 species)

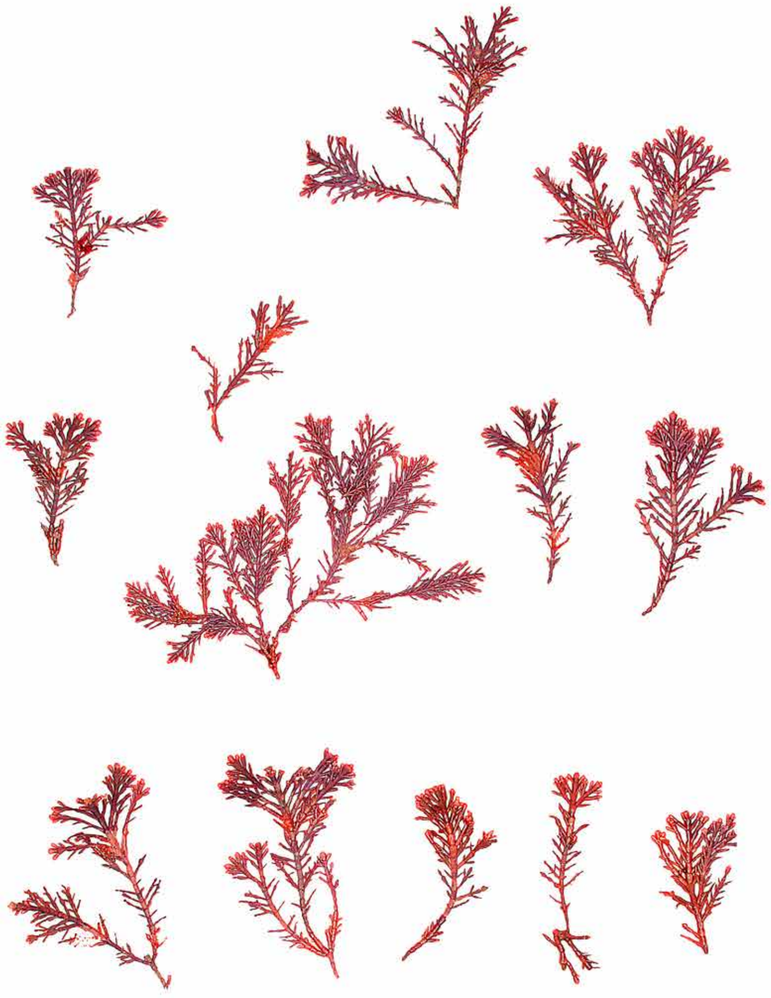
The specimen shown has a length of about 10 cm.

Ellisolandia elongata

(J. Ellis & Solander) K. R. Hind & G. W. Saunders

Red algae (Florideophyceae)

Ellisolandia elongata is much better known to phycologists under the former name *Corallina mediterranea*. The name has changed first into *Corallina elongata* according to nomenclatural rules. Then it had to be changed after molecular studies in the last years to the genus *Ellisolandia*. The species is one of the many lime-incrusted red algae: Calcium carbonate is deposited into the cells in the periphery of the thallus. This incrustation protects the algae against mechanical stress. But it also prevents the alga to be eaten by snails and other predators. The alga is branched in a pinnate way. It can reach a length of 20 cm, but is normally much smaller; the single specimens on the herbarium sheet are about 5 cm. In order to give certain flexibility there are nodes which are not incrusted so that the whole plant has a geniculate habit. The plant has a bright pink colour due to the lime. Gametophytes are dioecious and they are isomorphic to the tetrasporophyte. The reproductive structures are hidden in conceptacles with an ostiolum. Conceptacles are found at the main axis and at the ends of branches. *Ellisolandia elongata* is a plant frequently found in intertidal rock pools as well as on rocks in the lower eulittoral and the upper sublittoral. The species appears to be of East and West Atlantic distribution with a focal point in the Mediterranean. The genus *Corallina*, to which *Ellisolandia* once belonged, contains 33 species. *Ellisolandia*, after being separated from *Corallina*, is a monotypic species. The specimen shown has a length of about 5 cm.



Amphiroa bowerbankii

Harvey 1849

Red algae (Florideophyceae)

Amphiroa bowerbankii is also one of the lime-incrusted genera of the family Corallinaceae. It is a genus of tropical distribution. With a thallus size of 20 cm this herbarium specimen is much larger than *Ellisolandia elongata*. In contrast to *Ellisolandia* and *Corallina* where a distinct monopodial axis is visible, in *Amphiroa* the branching is sympodial. The geniculate structure of the thallus is easily confirmed, because the nodes that are not calcified are blackish in colour. There is a lot of biodiversity in the family of Corallinaceae with its 495 species. Generally two morphotypes can be distinguished:

The geniculate type: *Ellisolandia elongata* and *Amphiroa bowerbankii* belong to this type. All the species of this type show a regular change of incrusted and non-incrusted regions (nodes and internodes). In Europe there are four genera of this type: *Corallina*, *Ellisolandia*, *Jania* and *Haliptilon*.

The second type is the non-geniculate type. Here the complete thallus is mostly blade-like and grows as a crust on the surface of stones. The following European genera belong to this morphotype. *Titanoderma*, *Lithophyllum*, *Hydroltihon*, *Pneophyllum*, *Leptophytum*, *Exilicrusta*, Lithothamnion, *Melobesia*, *Mesophyllum*, *Phymatolithon*.

Corallinaceae are mostly found in rock pools and the upper sublittoral. There is also a habitat in the deep sublittoral, the so called maerl, where the living lime-incrusted algae *Lithothamnion corallinoides*, *Phymatolithon calcareum* and *Lithothamnion glaciale* form a sediment.

Codium sp.

Green algae (Chlorophyta, Ulvophyceae)

- *Codium*, the genus of the green algae which is characterized by large thalli composed of interwoven siphonous filaments, has 143 species according to Algaebase. But only a few of them are found in Europe. So only five species are found in the "Seaweeds of the British Isles":

- *Codium adhaerens*
- *Codium bursa*
- *Codium fragile*
- *Codium tomentosum*
- *Codium vermilaria*

- Regarding the Mediterranean region, there are six species in the book "Guide des algues des mer d'Europe":

- *Codium bursa*
- *Codium coralloides*
- *Codium effusum*
- *Codium fragile*
- *Codium vermilaria*
- *Codium decorticatum*

- The comparison of the two lists shows that there is only an overlap of three species: *C. bursa*, *C. fragile* and *C. vermilaria*.

- Checking Algaebase where the distribution of species is well documented one can find that the species of both lists occur in the Mediterranean region, but not vice versa. This is an indication that the species are probably adapted to warmer climate. The fact that the bulk of the 143 species are not found in Europe is due to the fact that most species of *Codium* have a narrow geographic range. The specimen shown has a length of about 20 cm.

Halimeda tuna

(J. Ellis & Solander)

Green algae (Chlorophyta, Ulvophyceae)

- *Halimeda* is one of the most important algae making up the reefs in subtropical and tropical regions. The thallus is segmented: Calcified disc-like segments are alternating with the non-calcified hinges. The plants are growing upright and the segmented thalli can be branched. They are anchored in the substrate by rhizoids or with a bulb. In the microscope the thallus consists of interwoven siphonous filaments. Depending on the grade of calcification the plant can look green to grey. There is a lot of 45 species worldwide that can be distinguished by size (few cm to 100 cm), the form of the thallus segments (round disc, triangular, cylindrical…), the grade and mode of branching. Looking on the distribution of the species, only six of them are more or less worldwide distributed, among them *Halimeda tuna*. The rest of them have a very local distribution.

- The genus is separated into five sections:
- Section Rhipsalis (8 species)
- Section Opuntia (8 species)
- Section Halimeda (13 species)
- Section Micronesicae (3 species)
- Section Crypticae (1 species)

- *Halimeda tuna* is the type species of the genus. Traditional botanists know it under its old name "*Halimeda opuntia*". This name hints at the habit which is similar to an Opuntia cactus. The specimen shown has a length of ca. 15 cm.

Flabellia petiolata

(Turra) Nizamuddin

Green algae (Chlorophyta, Ulvophyceae)

The thallus of *Flabellia petiolata* is a tissue-like frond which is fan-shaped and reaches a length of 10 cm. It is composed of siphonous interwoven filaments. The thallus is anchored in the substrate by rhizoidal filaments. The fan-shaped blade is connected to the ground rhizoids by a short stalk. Stalk and blade are lime-incrusted. Vegetative propagation is possible by the formation of new thalli from the rhizoidal mat. Sexual reproduction is holocarpic. This means that the whole thallus is used up for the production of gametes. The life cycle was not examined completely but it can be speculated that it is diplontic and similar to those of the closely related *Codium* and *Halimeda*. *Flabellia petiolata* is a monotypic species. Older phycologists know it under the old name *Udotea petiolata*. This is also the name on the herbarium sheet. *Udotea* is a genus containing 35 species very similar to our *Flabellia petiolata*, occurring predominantly in tropical reefs and contributing much to the biomass of the reefs.

Flabellia is a member of the family Udoteaceae which belongs to the order Bryopsidales. Other genera of the Bryopsidales handeled in this book are:

- *Codium*
- *Halimeda*
- *Caulerpa*

The specimen shown has a length of ca. 10cm.

Acetabularia mediterranea

J. V. Lamouroux

Green algae (Chlorophyta, Ulvophyceae)

Acetabularia mediterranea is a siphonous green alga of a very special architecture and life cycle. In the life stage seen on the herbarium sheet the thallus is composed of a rhizoid, a stalk and an umbrella-like hat. Cell biologists regard this as a single cell because no cross wall exists. And in this stage only one diploid nucleus is present in the rhizoid. Then meiosis is performed and afterwards a lot of mitoses. The resulting thousands of haploid nuclei begin to migrate through the cytoplasm into the chambers of the umbrella. The chambers are then separated from the stalk by a wall and cysts are formed containing one nucleus and a portion of cytoplasm. These cysts are later released from the chamber and open by a lid. Each cyst releases one gamete. After fusion of two gametes the diploid zygote sinks to the ground and grows out to a new *Acetabularia* plant. But before building a new umbrella there is a period of vegetative growth. A stalk is arising from the rhizoid with whorls of green branches. This vegetative plantlet is quite different from the fertile plantlet, which we see on the left. In this vegetative phase only one diploid nucleus exists in the basal rhizoid. The fact that the nucleus is clearly separated from the rest of the thallus was the basis for experiments in which the influence of the nucleus on the morphology could be proven. Twelve accepted species are listed in Algaebase. *Acetabularia* is a member of the order Dasycladales and has a more tropical distribution. The specimen shown has a length of about 5 cm.

Jania sagittata

(J.V. Lamouroux) Blainville

Red algae (Florideophyceae)

Jania sagittata is a member of the family Corallinaceae. On the herbarium sheet the specimen is called "*Cheilosporum sagittatum*". When looking into Algaebase, the genus *Cheilosporum* doesn't exist anymore and must be called *Jania*. So *Jania sagittata* is the right name. The specimen was collected in Natal/South Africa. This matches with the distribution of the species according to the literature. The species seems to be restricted to the southern hemisphere. As a member of the family Corallinaceae, *Jania* is one of the species that are incrusted with lime. And, as clearly can be seen, it is an example for the geniculate type of this family. Gametophytes are dioecious or rarely monoecious. Gametophytes and tetrasporophytes are isomorphic. All reproductive structures are in conceptacles.

The genus *Jania* contains 48 species of which only very few are known from Europe. The centres of diversity in the genus *Jania* are clearly the tropical and subtropical regions.

Other genera of the articulate morphotypes of Corallinaceae are:

- *Corallina* (32 species)
- *Arthrocardia* (10 species)
- *Bossiella* (14 species)

And some other genera poor in species.

Some species of *Corallina* occur in the European seaweed flora. The specimen shown has a length of about 20 cm.

Amphiroa bowerbankii

Harvey 1849

Red algae (Florideophyceae)

Amphiroa bowerbankii is also one of the lime-incrusted genera of the family Corallinaceae. Searching in Algaebase for the distribution of the species, for *Amphiroa bowerbankii* the following locations are given: Sri Lanka, Taiwan, Indonesia. On the Herbarium sheet of Prof. Grau is written: South Africa – Natal. So Herbarium specimens can be used to elaborate distribution maps of certain species. In our case it is a location which was not yet registered in Algaebase. Looking on the distribution of other species of *Amphiroa*, selected by chance, one can see different distribution patterns, from worldwide distribution to very local distribution in tropical and subtropical regions:

- *Amphiroa anceps*:
  Taiwan, China, Australia, Galapagos, Kenya (worldwide)
- *Amphiroa capensis*:
  South Africa (local distribution)
- *Amphiroa fragilissima*:
  France, Italy, Taiwan, Cap Verde Islands, Florida, Bangladesh (worldwide)

- *Amphiroa minutissima*:
  Costa Rica (local distribution)
- *Amphiroa taylorii*:
  Mexico (local distribution)
- *Amphiroa zonalis*:
  Korea (local distribution)

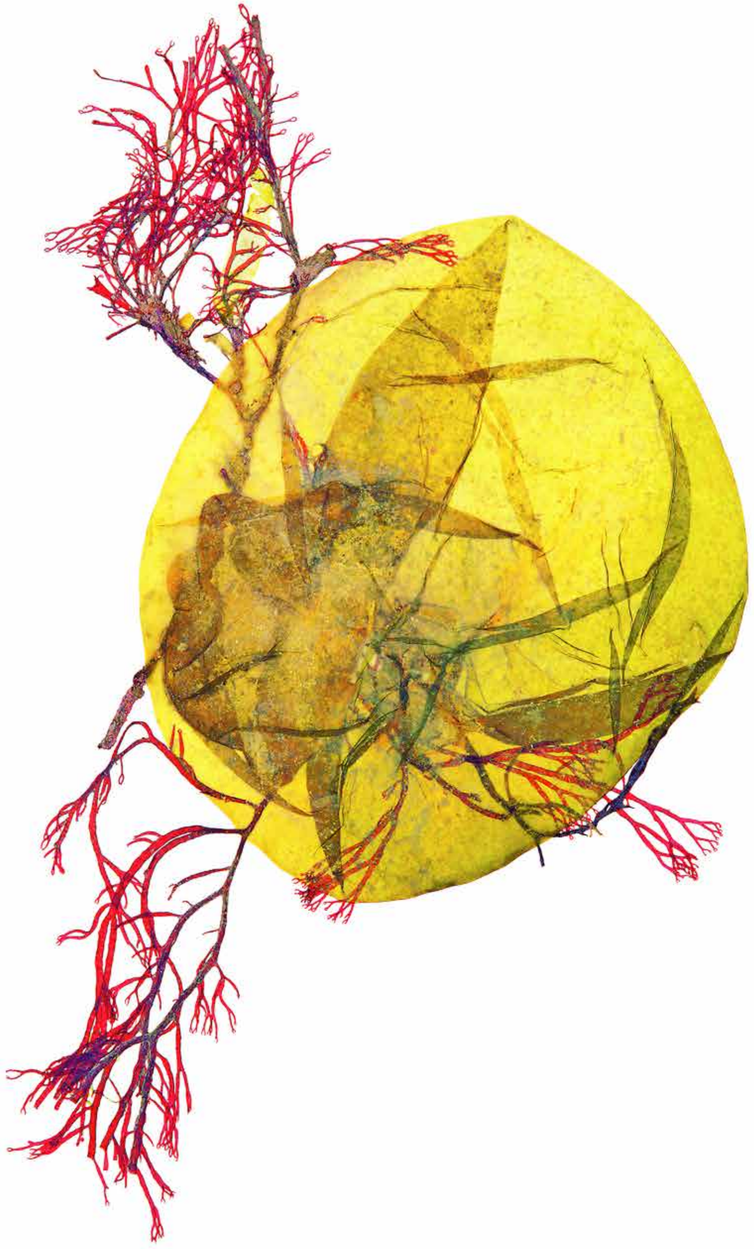
The specimen shown has a length of about 15 cm.

Colpomenia peregrina

sauvageau

Brown algae (Phaeophyceae)

Colpomenia peregrina is known to be a neophyte in our seaweed algal flora. A neophyte is defined as a plant which is not native in our flora. The plants were introduced by human activities like travelling with ships or active introduction for cultivation. In the case of *Colpomenia peregrina* the species was introduced with American oysters which were cultivated in France. The species is said to have distributed over Europe by natural propagation. The species was found first in 1907. Higher plants are classified as neophytes and archaeophytes this means plants that were introduced a long time ago. The limit between neophyte and archaeophyte is the year 1492, the discovery of America. The difference between neophyte and archaeophyte is not applied to the algae because nothing is known about the distribution of algae before 1492. Among the neophytes, plant ecologists differentiate between invasive and non-invasive species. The non-invasive species don't have a great influence on the natural composition of the flora, but the invasive species can displace or finally extinct native plant species. In the case of *Colpomenia peregrina* there is a tendency to classify it as an invasive species. But there is no alga known which was extinct recently by the competition with *Colpomenia peregrina*. The specimen shown has a length of about 6 cm.



chapter 4
Neophytic algae – some new algae are aggressive invaders to our flora

Colpomenia peregrina

sauvageau

Brown algae (Phaeophyceae)

Colpomenia peregrina is not the only species of the genus introduced to Europa. *Colpomenia sinuosa* was introduced some 60 years earlier to Spain from which it distributed over Europe. But *Colpomenia peregrina* is not viewed as an invasive species because the competition with other species is moderate. Possibly both *Colpomenia* species were introduced from the Pacific Ocean by oysters. The genus *Colpomenia* belongs to the family Scytosiphonaceae and to the order Ectocarpales.

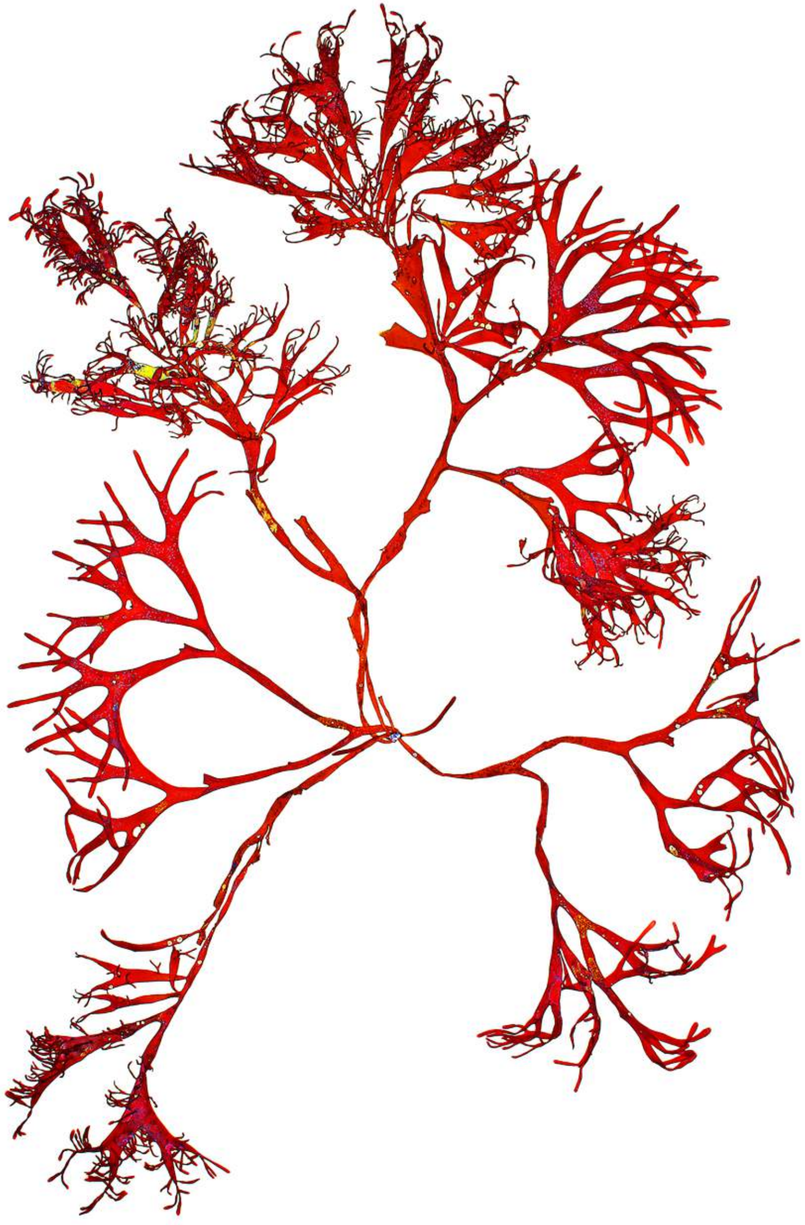
Another brown algal genus, *Undaria pinnatifida*, not shown in this book, is invading our seaweed flora in the last decades. It is a species consumed in Japan as an edible alga under the name "Wakame". It is thought to be one of the most invasive algae in Europe and other regions in the world and seems to be able to eradicate other species. It was introduced in Europe and cultivated in the sea as a crop. It is a brown alga of the order Laminariales. As in *Alaria esculenta* the sporangial sori are on separate lobes. Neophytic algae can come to their new locations by purpose import (e.g. for cultivation), by incidental import (e.g. with oysters) or accidentally (e.g. growing on the outside of ships or in ballast water of ships). Also animals (Shanghai hairy crab, zebra mussel) have been imported in this way. The specimen of *Colpomenia* shown has a length of ca. 6 cm.

Mastocarpus stellatus

(stackhouse) Guiry in Guiry, J.a. West, D.-H. Kim & Masuda

Red algae (Florideophyceae)

Mastocarpus stellatus is a species of worldwide distribution and therefore is not a good example for a neophytic or invasive algae. Nevertheless it was not a native plant on the small German Island Helgoland until 1980. Then it was introduced artificially for an experiment and in the following years it behaved like an invasive plant. Ecological niches were occupied and the old inhabitants of these niches were displaced. Perhaps the missing of species specific enemies and parasites was the reason for this competitive fitness of this species. The similar species *Chondrus crispus* can be distinguished from *Mastocarpus* by its flat margin which is incurred in *Mastocarpus*. Female plants are easily recognized by the cystocarps the margin of which is protruding when getting older. *Chondrus crispus* as well as *Mastocarpus stellatus* are collected for the production of Agar. On the herbarium sheets the plants are labelled as "*Gigartina stellata*" which is an old name. Today *Gigartina* and *Chondrus* are genera of the family Gigartinaceae whereas *Mastocarpus* is assigned to the family Phyllophoraceae. Both families belong to the order Gigartinales. The genus *Chondrus* contains 13 species, *Gigartina* 41 species, *Mastocarpus* 15 species. The specimen shown has a length of ca. 15 cm.

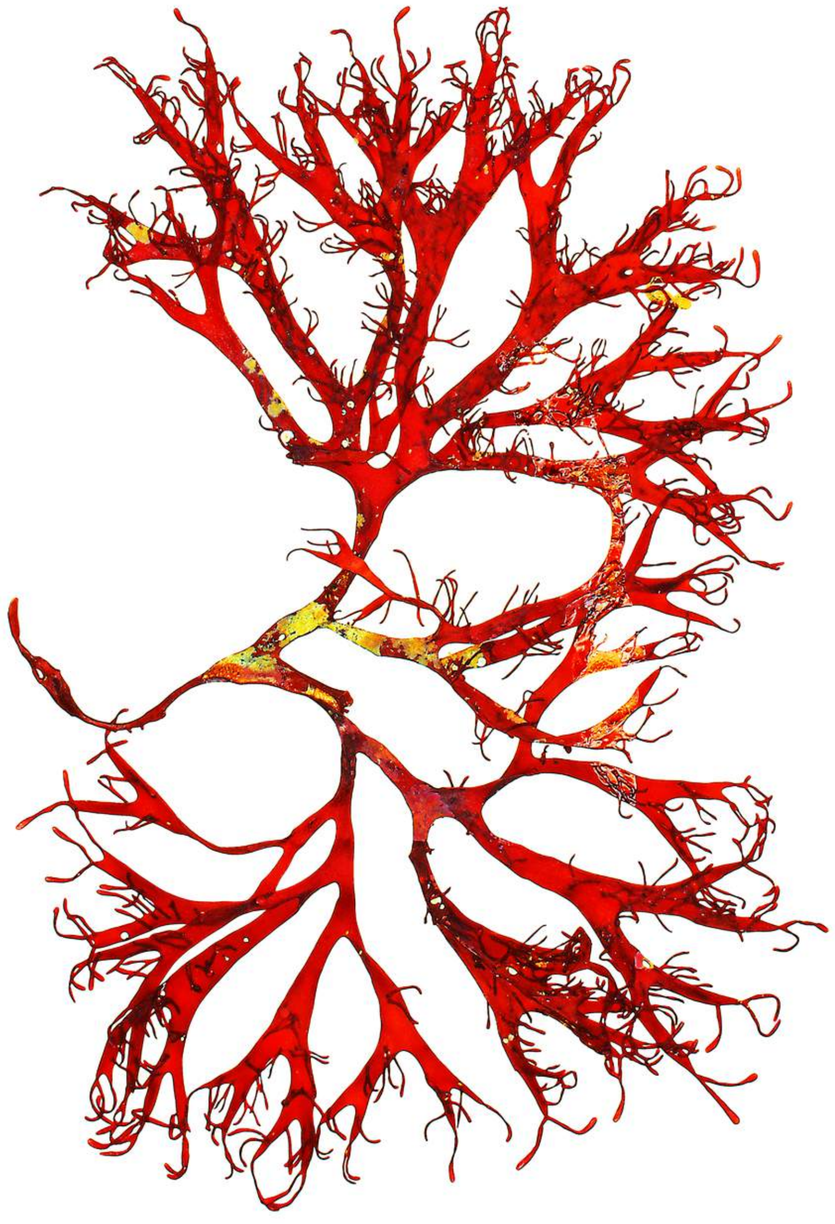


Mastocarpus stellatus

(stackhouse) Guiry in Guiry, J.a. West, D.-H. Kim & Masuda

Red algae (Florideophyceae)

Comparing the life cycle of *Mastocarpus stellatus* and *Chondrus crispus* differences are evident. In *Chondrus crispus* female and male gametophytes are more or less identical and the tetrasporophyte is isomorphic to the gametophytes. So far the life cycle is similar to most other red algae in this book. *Gigartina*, to which *Mastocarpus* was assigned for a long time, has a similar life cycle. In *Mastocarpus* the male and female gametophyte can be distinguished without microscope, because the carposporophytes are in the papillae that grow out to tube-like appendages on older female plants. On the male plants these appendages are missing. For a long time it was thought that a tetrasporophyte is missing in the life cycle of *Mastocarpus stellatus*. Now it is clear that a plant for long thought to be an own genus called "*Petrocelis*", which grows as a blackish-red crust on solid substrates, is the tetrasporophyte of *Mastocarpus*. Tetraspores grow out to new *Mastocarpus* plants. The tetrasporophyte is now called "Petrocelis-phase". It is not clear, if the other *Mastocarpus* species have the same type of life cycle. In the three genera mentioned here the thallus structure is multiaxial. The specimen shown has a length of about 15 cm.



Sargassum muticum

(Yendo) Fensholt

Brown algae (Phaeophyceae)

Sargassum muticum is a neophytic brown alga that originally comes from the Japanese Sea. It was found in the USA in 1944. In England it was found first in 1976. The European distribution is now from Norway to Spain. At German coasts the plant was found first in 1988. The species is clearly invasive occupying habitats that were occupied by other species before. Interestingly the thalli in Japan reach a length of ca. 3 m, but in Europe they can get more than 10 m long. This is probably due to the fact that there are no enemies or parasites that are specialized on this plant. So a length is reached that never occurs at the native locations. As the whole plant bears pneumatocysts it is always floating. The alga reduces the light needed for photosynthesis of the algae growing on the ground. So plants of the same habitat like *Laminaria saccharina* and *Himanthalia elongata* can die due to the lack of light.

When complete plants detach from the ground this is an enormous biomass rotting on the shore. The species is also a problem for swimmers and motor boats.

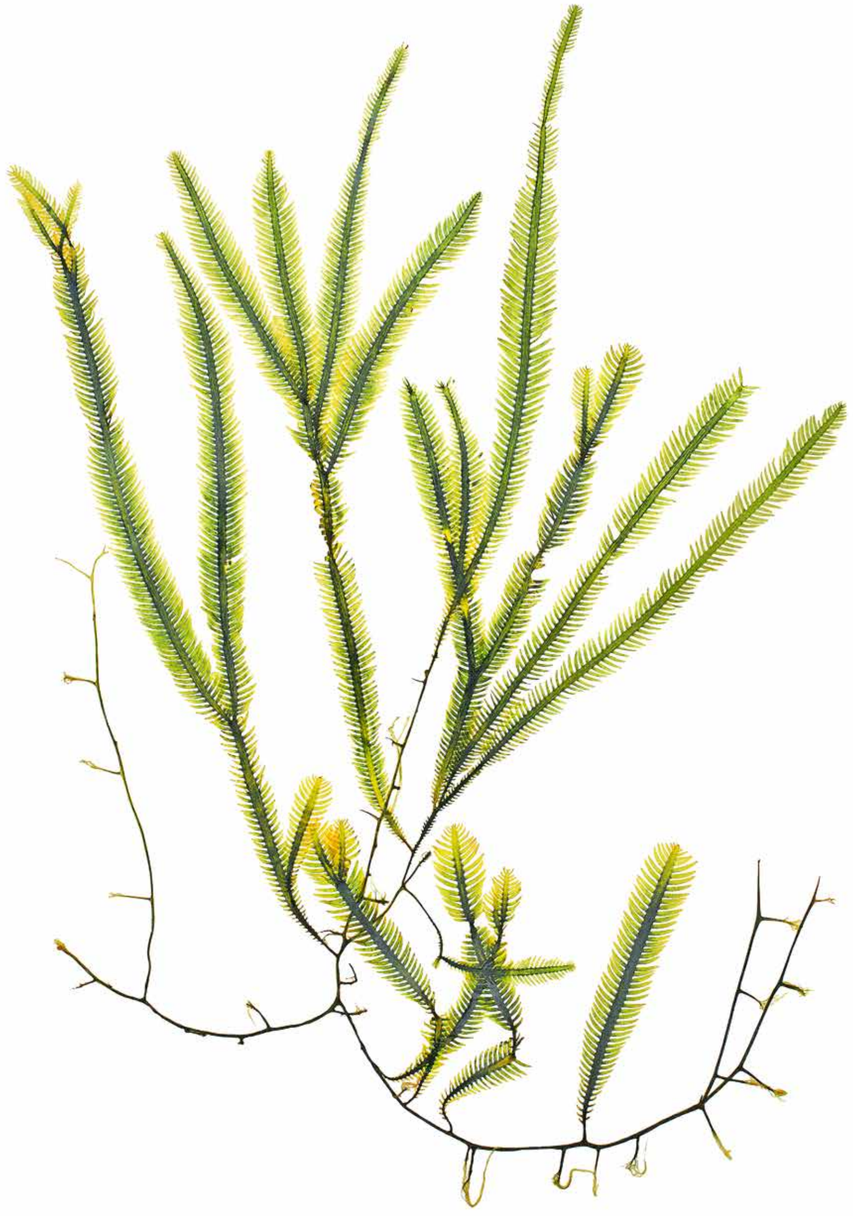
Sargassum muticum is a member of the order Fucales and builds an own family Sargassaceae. The specimen shown has a length of about 15 cm.

Caulerpa taxifolia

(M. Vahl) C. Agardh

Green algae (Chlorophyta, Ulvophyceae)

Caulerpa taxifolia is a species which is known as "killer alga" in the Mediterranean Sea. It is of Indo-Pacific origin and has possibly arrived in the Mediterranean Sea via the Oceanographic Museum of Monaco. Here it was found first in 1984. From here the species invaded the complete Mediterranean Sea in a relatively short time. It was shown that the alga is clonal and that it is identical to a strain developed in the "Wilhelma Zoo and Botanical Garden" in Stuttgart/Germany which is tolerant to lower temperature. From Stuttgart the alga was transferred to Monaco. Normally members of the genus *Caulerpa* are sensitive to lower temperatures and are of strict tropical distribution but the strain from Stuttgart could grow in the Mediterranean Sea. When searching for algae in a warm seawater aquarium different *Caulerpa* species are offered by aquarium-trade, among them *Caulerpa taxifolia*. *Caulerpa* species are similar to higher plants having rootlike rhizoids, shootlike cauloids and leaflike phylloids. They can grow on sandy locations as well as on rocks. And growth is fast, ca. 1 cm per day. Sexual reproduction is not possible in the Mediterranean strain because only male gametes are produced. Thus only vegetative propagation is possible. But because of the fast growth anchors of boats, fisher nets and similar things can be settled and a new colonization of locations far away is possible. The specimen shown has a length of ca. 25 cm.



chapter 13
Cultivated – some macroalgae can be grown in aquaria

Caulerpa taxifolia

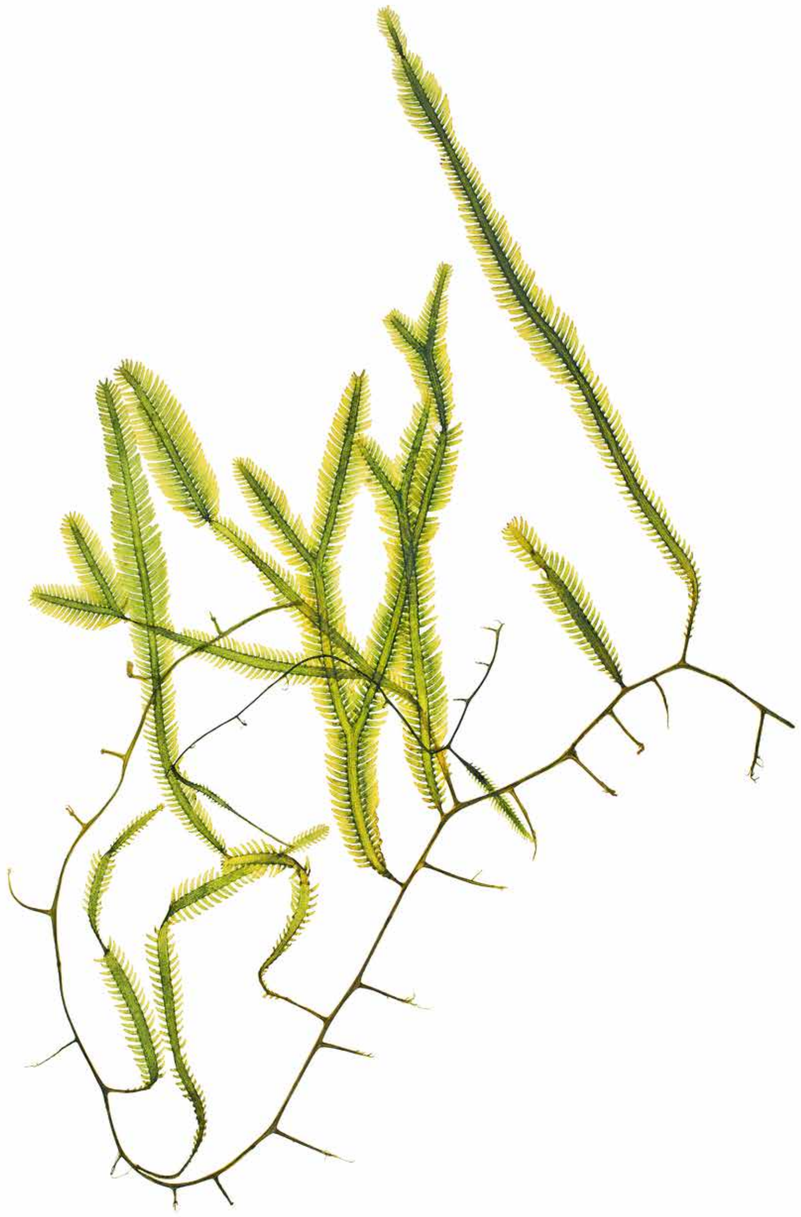
(M. Vahl) C. Agardh

Green algae (Chlorophyta, Ulvophyceae)

Caulerpa taxifolia is one of the nicest species of the genus *Caulerpa*. The name "*taxifolia*" means that the phylloids look like branches of *Taxus*, the yew. But as nice as it is, the plant is toxic by a substance that is enriched in the thallus. As often the name of the toxin derives from the genus where it was found: Caulerpicin. By the way: *Taxus*, responsible for the species name of *Caulerpa taxifolia* is one of the most toxic higher plants. And the poison in this plant is: Taxin.

The thallus of *Caulerpa* is on the first view like the tissue of a higher plant. But when looking with the microscope, one can see that there are interwoven filaments that give stability to the thallus. And a closer look shows that the filaments are siphonous and that there are no crosswalls in the filaments. This type of thallus structure can also be seen in the green algal genera of *Codium*, *Halimeda* and *Udotea*. Interestingly all these genera belong to the same order Bryopsidales. But the four genera belong to four different families: Caulerpaceae, Codiaceae, Halimedaceae and Udoteaceae.

Caulerpa is the only genus in the family of Caulerpaceae. 97 species of this genus exist worldwide and only a very few of them are cultivated in our seawater aquaria. The specimen shown has a length of about 20 cm.



Caulerpa prolifera

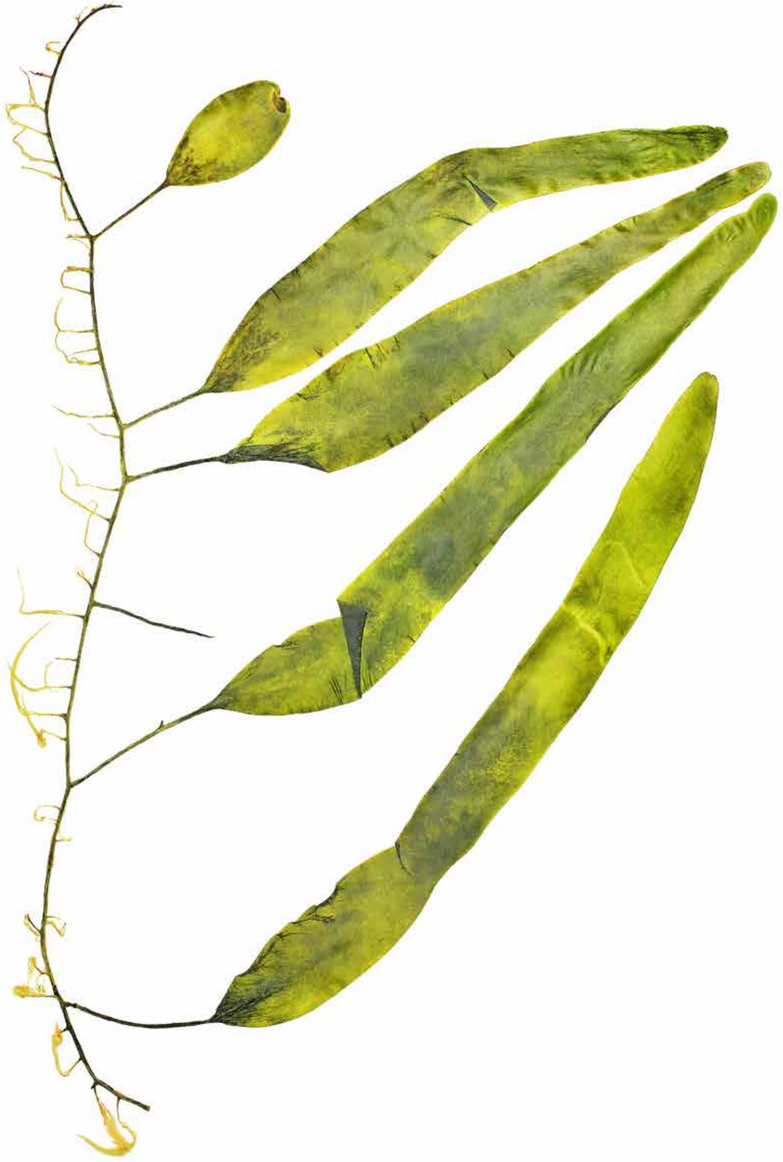
(Forsskål) J.V. Lamouroux

Green algae (Chlorophyta, Ulvophyceae)

Caulerpa prolifera is another *Caulerpa* species which is used in aquaria. In contrast to *Caulerpa taxifolia* the phylloid is entire and not pinnatifid. But the general thallus construction is as in all *Caulerpa* species: rhizoids, cauloids and phylloids. And the thallus is siphonous when viewed with the microscope. From the cauloids, but also from the phylloids new "shoots" are arising. This process of building new cauloids is called "proliferation" and so the species name *Caulerpa prolifera* can be explained.

The phylloids are rounded at the end and are at the basal side gradually tapering into a stalk of 2-3 cm length. This is a species which is distributed worldwide in subtropical and tropical regions, native also in the Mediterranean Sea. Here it is found in lagoons in shallow water and also between the seagrass *Posidonia*.

The horizontal cauloids are also, in analogy to similar structures in the higher plants, called "stolons". An example of higher plants building stolons is strawberry. The phylloids of *Caulerpa prolifera* can reach a length of 15 cm and a width of 3 cm. A single plant can cover some square meters. When searching for macroalgae that can be used for a seawater aquarium, often a mixture of *Caulerpa* and *Chaeteomorpha* is offered: *Caulerpa prolifera* is among them and the specimens shown on both pages are from such an offer. The specimen shown has a length of ca. 20 cm.



Caulerpa prolifera

(Forsskål) J.V. Lamouroux

Green algae (Chlorophyta, Ulvophyceae)

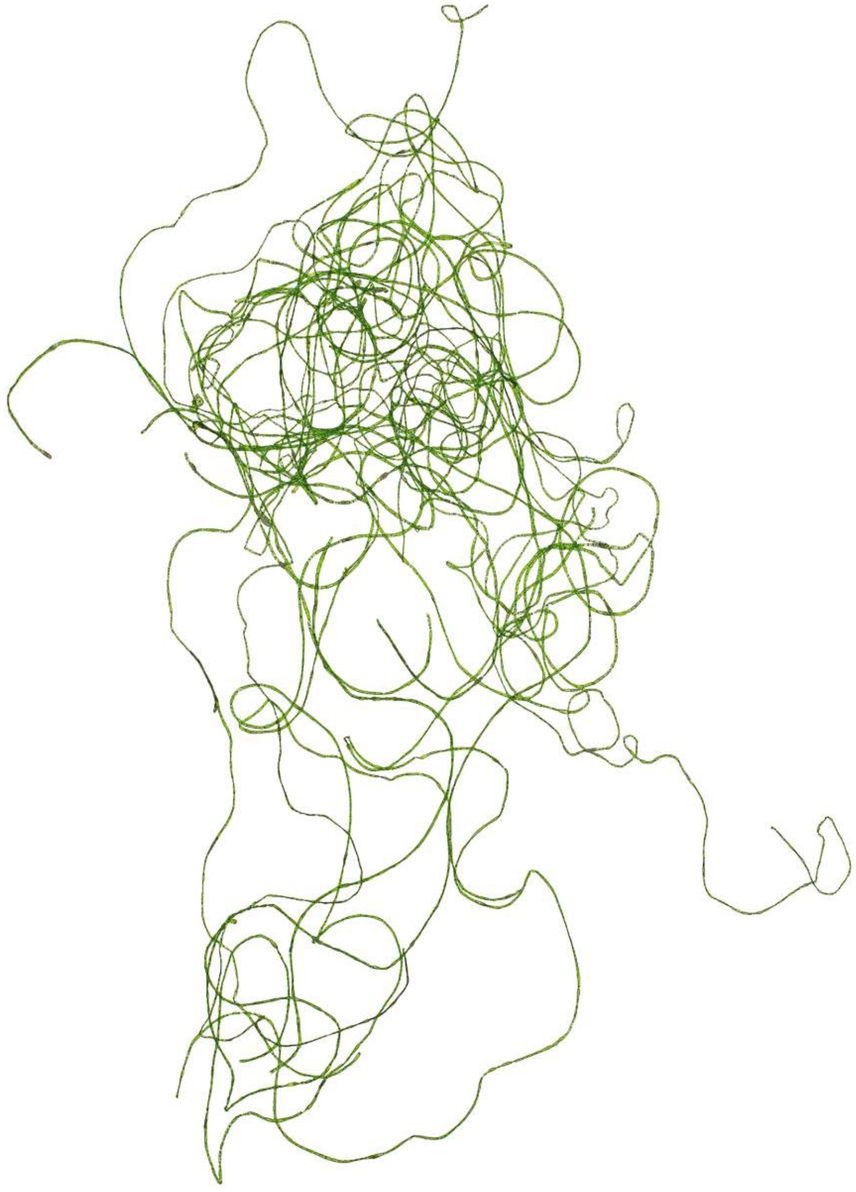
The normal thallus of *Caulerpa prolifera* is up to 15 cm in length. There is a smaller strain where the phylloids have only a length of 3-4 cm. It is surely more applicable for smaller aquaria. The genus *Caulerpa* is known to cell biologists for the phenomenon of kleptoplastidy. There is a group of snails called "*Saccoglossa*", especially the genus "*Elysia*" that suck out the filaments of *Caulerpa* and digest the cytoplasm, but not the Chloroplasts. These are transported to the skin of the snail and are maintained over a long period. The snail gets green and, when sun exposed, uses the photosynthetic products of the algal chloroplasts. The snails, *Elysia chlorotica* and *Elysia crispata*, can then sustain a longer period without food. But after a longer time the plastids can't be held and new *Caulerpa* plants must be sucked out. This kind of kleptoplastidy is also known between *Vaucheria litorea* and the saccoglossan snail *Elysia viridis*, a system well established for the investigation of kleptoplastdy. And a similar process is known also from dinoflagellates of the genus *Nusuttodinium* where algae of the genus *Chroomonas* are taken up and their plastids are held in the dinoflagellate for a longer period. Kleptoplastidy is not a symbiosis, because the plastids don't survive this process and are taken up again and again. But perhaps the snails are on the right way and we have real photosynthetic snails in some million years. The specimen shown has a length of about 20 cm.

Chaetomorpha linum

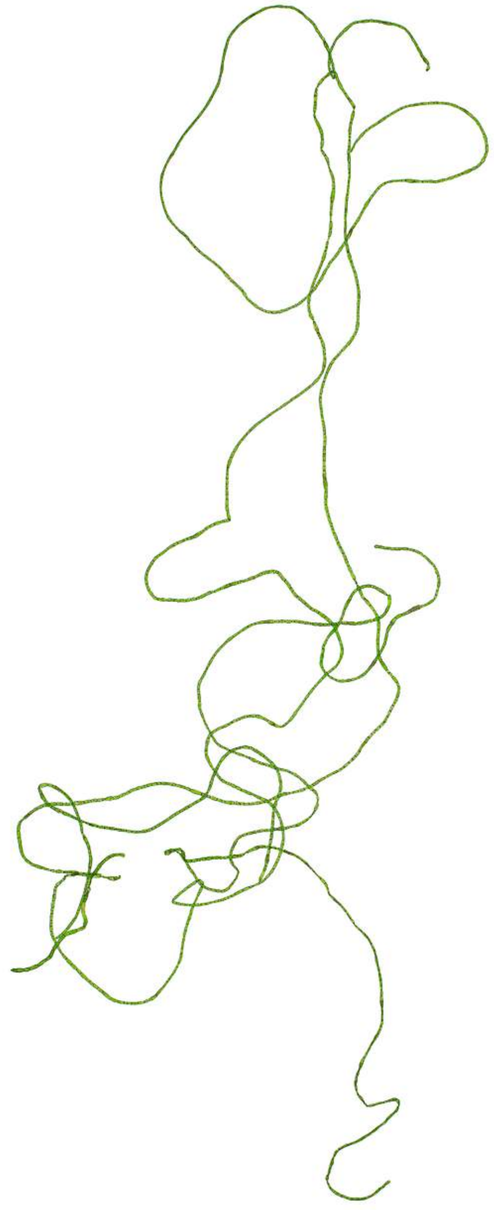
(O. F. Müller) Kützing

Green algae (Chlorophyta, Ulvophyceae)

Chaetomorpha linum is among the algae which are offered for marine aquaria. When found in nature it can grow like a ball, kept in this form by the steady wave action. Or it can grow as an attached filament. When held in an aquarium where wave action is missing they grow as a tangle of irregular filaments. The irregular arrangement of the filaments is a result of the intercalary division of cells which leads to an incurved growth of the filaments. The filaments are very broad. Their diameter can reach 500 µm and more. The reproduction can be by the fragmentation of the filament but also by the release of quadriflagellate zoospores from the diploid sporophyte. These zoospores are haploid, thus they have undergone meiosis prior to their release. The resulting gametophytes are male and female, i.e. the species is dioecious. Gametophytes and sporophyte are isomorphic. Gametophytes later develop gametangia in which biflagellate gametes are formed. The gametes are of the same size and fertilization is therefore isogamic. A new sporophyte is growing from the zygote. So this is a typical isomorphic and diplohaplontic life cycle. This type of life cycle is also found in marine *Cladophora* species. *Chaetomorpha* and *Cladophora* belong to the same family, the Cladophoraceae. The specimen shown has a length of ca. 20 cm.



chapter 13
Cultivated – some macroalgae can be grown in aquaria



Chaetomorpha linum

(O. F. Müller) Kützing

Green algae (Chlorophyta, Ulvophyceae)

Chaetomorpha is characterized by the always unbranched filaments which can have an unusual size: In the European flora species with a diameter of more than 1000 µm are occurring. The large cells are multinucleate and the number of nuclei is correlated to the size of the cell. The chloroplast is parietal and perforated containing numerous pyrenoids. The cells are more or less quadratic to rectangular.

The genus *Chaetomorpha* contains 68 species predominately in marine habitats.

The genus belongs to the class of Ulvophyceae and here to the order Cladophorales (473 species) with the following families:

- Anadyomenaceae (31 species)
- Boodleaceae (35 species)
- Cladophoraceae (328 species)
- Pithophoraceae (35 species)
- Siphonocladaceae (28 species)
- Valoniaceae 13 Species

The most species- rich family of Cladophoraceae (328 species) contains the following genera (genera with less than 10 species let off):

- *Acrocladus* (19 species)
- *Chaetomorpha* (68 species)
- *Cladophora* 196 species
- *Rhizoclonium* (34 species)

The specimen shown has a length of about 20 cm.

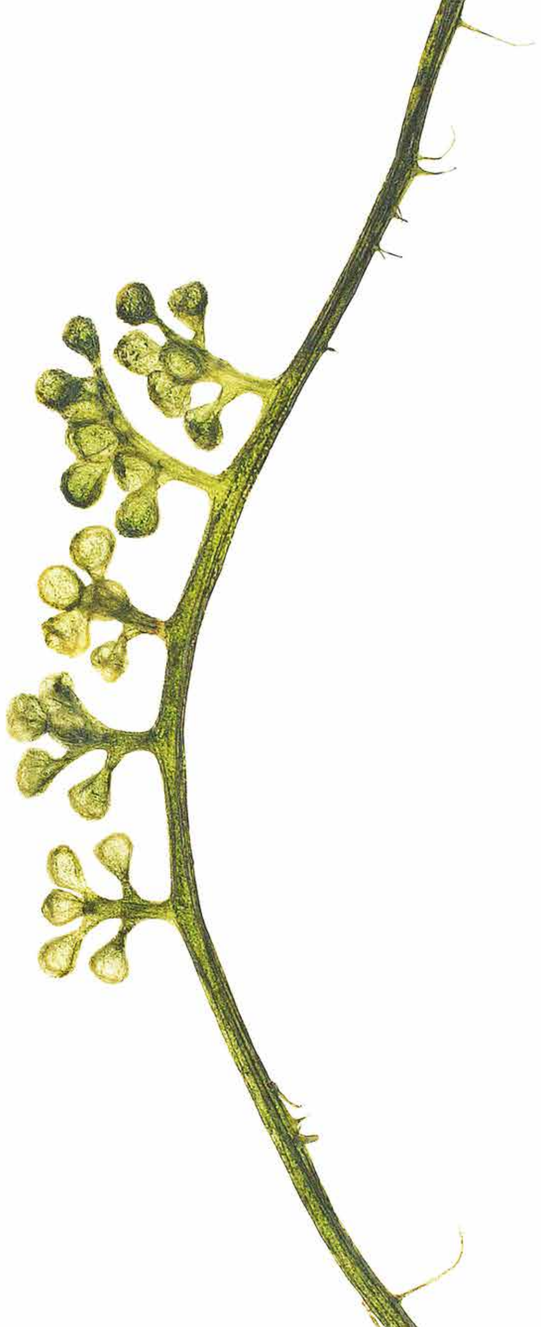
Caulerpa lentillifera

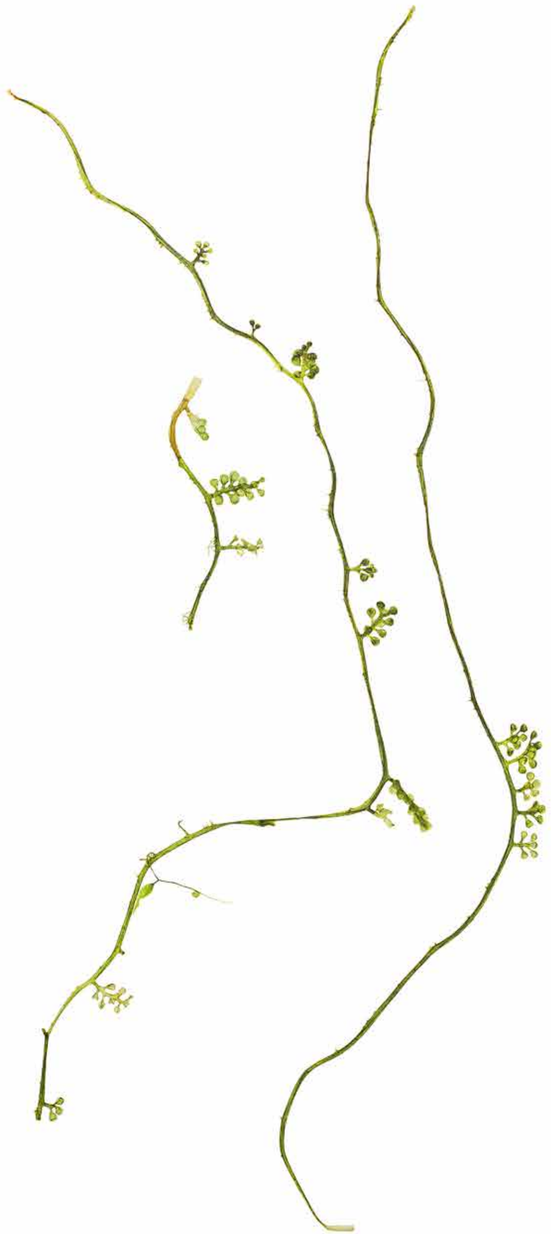
J. Agardh

Green algae (Chlorophyta, Ulvophyceae)

Caulerpa lentillifera is one of the marine macroalgae frequently offered for the use in aquaria. It is distributed in the Indian Ocean and the Pacific. In contrast to *Caulerpa taxifolia* it is not toxic. On the Philippines it is cultivated as an edible alga used for example as salad.

For a long time *Caulerpa* has been an object of biological research. So the regeneration of the siphonous thallus, which is in principle a single cell, was studied. With a simple trick, by pressure, the building of crosswalls in the siphonous is possible. Pieces of a phylloid can be cut of and the regeneration of such pieces can be observed: Regeneration starts at the basal end of the fragment by forming rhizoids; then above the rhizoids cauloids are formed and at the upper end of the phylloid-fragment buds for the formation of new phylloids arise. If one cuts off such a bud for phylloid formation, at the basis again rhizoids appear. Cutting off a fragment with rhizoids, new buds for the formation of phylloids develop at the upper side. As it was known from higher plants also in the alga Caulerpa phytohormones (auxins) are involved in the process of thallus regeneration. In earlier times it was thought that *Caulerpa* only propagates by thallus fragments what could be seen frequently in natural habitats. This is in principle what is also seen in the laboratory: Nearly every fragment of a *Caulerpa* thallus can develop to a new plant. The specimen shown has a length of about 8 cm.





Caulerpa lentillifera

J. Agardh

Green algae (Chlorophyta, Ulvophyceae)

Caulerpa lentillifera has a phylloid that looks like a bunch of grapes. In contrast the phylloids of *Caulerpa prolifera* look like an undivided leaf of a higher plant and that of *Caulerpa taxifolia* like a twig of Taxus.

In *Caulerpa* also sexual reproduction was investigated. The different species can be monoecious or dioecious. It is thought that the life cycle is diplontic and the meiosis is performed during the formation of gametes. The gametogenesis is holocarpic, this means that the complete thallus is used up during the formation of the gametes. It was described that there is no separation of the plasma portions prior to gametogenesis, as it is described in other siphonous species, e.g. *Vaucheria*. This is possibly due to the holocarpic reproduction of *Caulerpa*. The gametes are extruded through papillae at the surface of the thallus as a gelatinous mass. They are unequal in size. Thus the fertilization type is anisogamy. The fusion of gametes and the behaviour of the zygote have not been described. If the species is monoecious, as is the case in the invasive species *Caulerpa taxifolia* and *Caulerpa racemosa*, male and female gametes are formed at different parts of the same thallus. In the Mediterranean species *Caulerpa prolifera* male and female gametes are formed on different plants; this plant is dioecious. The specimen shown has a length of about 20 cm.

Glossary

Akinete Thick walled resting cell of algae derived from a vegetative cell

Algabase Database for taxonomical and distributional information: www.algaebase.org/

Anisogametes Motile gametes of unequal size

Anisogamy Fusion of motile gametes of unequal size

Anisotomous Branching with a dominant and a subdominant branch

Antheridium Male gametangium producing flagellated gametes

Apical cell Initial cell at the tip of an axis which divides

Auxiliary cell Cell taking up the diploid nucleus of the carpogonium after fertilization and giving rise to the carposporophyte

Axial filament Central filament of an axis

Bacillariophyceae Algal class of the Heterokontophyta, diatoms

Benthic Living on the ground of a waterbody

Bangiophyceae Red algal class to which *Bangia*, *Porphyra* and *Pyropia* belong

Benthos Community of organisms living on the ground of a waterbody

Biflagellate Bearing two flagella (spores, vegetative cells or gametes)

Blade Thallus part resembling a leaf of higher plants

Carpogonium Female gametangium of red algae

Carposporangium Sporangium formed by the carposporophyte

Carposporophyte Generation arising from the fertilization of the carpogonium in red algae

Cartilaginous Feeling like cartilage

Ceramiales Order of the red algae with *Ceramium* as name-giving genus

Cauloid Stem-like "organ" in macroalgae

Chloroplast Photosynthetic organelle of the green algae

Chantransia phase Diploid stage in the life cycle of *Batrachospermum* and *Lemanea*

Chrysophyceae Algal class of the Heterokontophyta, Gold algae Haptophyceae and the large group of diatoms (Bacillariophyceae)

Coccoid Organization level of unflagellated unicellular cells or multicellular colonies

Conceptacle Cavity in which gametangia are formed

Corallinales Order of the red algae with *Corallina* as name-giving genus

Cortex Outer layer of an axis, usually small celled

Corticated With a cortex

Cruciate Division planes in a tetrasporangium perpendicular to one another

Crust Thallus which is creeping over the substrate

Cryptophyceae Algal class, containing a nucleomorph

Cyanobacterium Procaryotic group of algae

Cystocarp Carposporophyte with surrounding gametophytic tissue

Desmarestiales Order of the brown algae with *Desmarestia* as name-giving genus

Dictyotales Order of the brown algae with *Dictyota* as name-giving genus

Dichotomous Forked with two equal branches

Dioecious Female and male gametangia on different thalli

Dinophyceae Algal class, photoautotrophic dinoflagellates

Diploid Containing double of the haploid chromosome number

Diplontic Life cycle in which all cells are diploid with the exception of the gametes

Distichous Branches in opposite rows

Ecorticate Witout a cortex

Ectocarpales Order of the brown algae with *Ectocarpus* as name-giving genus

Egg Unflagellated female gamete

Endocytobiosis Symbiotic association where an organism lives in a cell

Endosymbiosis Symbiotic association where one organism lives in another

Epilithic Living on stones

Epiphytic Living on plants/algae

Epitheton The name following the genus name, characterizing a species

Eulittoral The benthic zone between high tide mark and low tide mark

Fertile Capable of forming gametes

Flagellate Cell bearing flagella

Flagellum Whip-like outgrowth of a cell, organ for locomotion

Fucales Order of the brown algae with *Fucus* as name-giving genus

Florideophyceae Class where most of the macroscopic red algae belong to

Fucoxanthin Brown pigment characteristic for brown algae and Heterokontophyta

Gametangium A cell in which gametes are produced

Gamete A sexual cell

Gametophyte A phase in life cycle producing gametes

Gigartinales Order of the red algae with *Gigartina* as name-giving genus

Haploid With a single set of chromosomes

Haptophyceae Algal Class, characterized by a haptonema

Haplont, haplontic Type of life cycle where all stages but the zygote are haploid

Hemiparasitic Living from substances of a host, additionally capable to perform own photosynthesis

Heteromeric In Lichens: when there is a distinct algal layer (mostly green algae) in the lichen thallus

Hetermorphic Having different morphological from in a life cycle

Heterophasic In life cycles: Different ploidy in different generations

Heterotrichous In filamentous algae, when morphologically different creeping and upright filaments are developed

Heterotrophic Using organic carbon for growth

Holdfast Attachment organ of an alga

Homoeomeric If there is no distinct algal layer in the cross-section of a lichen; usually bluegreen algae like *Nostoc* are predominant.

Homophasic In life cycles: Identical ploidy in different generations

Intercalary Occurring between basis and top of a plant

Intertidal between low tide mark and high tide mark

Intracellular Inside of a cell

Isodiametric Cells having approximately the same length and width

Isogametes Gametes having the same morphology and size

Isogamous Gametes having the same morphology and size

Isomorphic Generations having the same morphology and size

Laminariales Order of the brown algae with *Laminaria* as name-giving genus

Kelp forest Association of macroalgae in the sublittoral

Life cycle The changes occurring between a stage one generation and the next generation

Macroalga Alga that can be seen without microscope

Meiosis Division in which the chromosome number is halved

Meiospores Spores formed under meiosis

Meristem Tissue in which cells are dividing, causing growth of the thallus

Microalga Alga that can be seen only with a microscope

Midrib Thickened tissue in the length axis of a blade

Mitosis division of replicated chromosomes into two nuclei

Monadoid Organization level of flagellated unicellular cells or multicellular colonies

Monoecious Female and male gametangia on one and the same plant

Monopodial Main axis of the thallus is strongly dominant

Monosporangium Sporangium in which only one spore is formed

Monostromatic Composed of one cell layer

Mucilaginous Slimy

Multiaxial In red algae: Centre of the thallus built by many axes of equal value

Multinucleate Cell containing many nuclei

Node, Nodium Point in the length axis where two cells/ segments are joint together

Oogamous, Oogamy Fertilization of an egg cell

Oogonium Female gametangium containing an egg

Organelle Intracellular compartment, surrounded by a membrane performing a special function

Ostiolum Aperture of a conceptacle (brown algae) or a cystocarp (red algae)

Paramylon Reserve carbon hydrate of the Euglenophyceae, β1/3 Glucan

Parenchyma Tissue of isodiametric cells

Pericarp Gametophytic tissue surrounding the carposporophyte

Phaeophyceae Algal class, brown algae

Pericentrals Cells around the main axis in red algae of the uniaxial type

Pheromone Specific chemical attractant for gametes

Phycobilins Pigment group of bluegreen algae, red algae and Cryptphpyceae

Phycobilisome Structure in which the phycobilins are arranged in bluegreen algae and red algae, visible only in electron microscope

Phycoerytrhin Red Pigment ofbBluegreen algae, red algae and Cryptphpyceae

Phycocayanin Blue Pigment of bluegreen algae, red algae and Cryptphpyceae

Phycologist Scientist working with algae

Phycology Biology of algae

Pit connection Pore between red algal cells, closed with a plug

Phylloid Leaf-like "organ" in macroalgae

Plastid Photosynthetic organelle

Plectenchymatic Thallus of interwoven filaments giving the impression of a tissue

Plurilocular Containing many loculi (in the reproduction of brown algae)

Pneumatocyst Organ filled with gas in the thallus of brown algae

Polyploid Containing more than two haploid sets of chromosomes

Proliferation Vegetative growth producing new thallus parts

Pseudodichotomous Branching with two unequal axes

Pseudoparenchyma Parenchyma-like "tissue" resulting from the aggregation of filaments

Pyrenoid Microscopical dot in plastids compound of Rubisco

Ramulus Little twig

Quadriflagellate With four flagella

Receptacle Assembly of numerous conceptacles in the thalli of Fucaceae

Rhizoid Unicellular or multicellular outgrowth at the basis, attaching the thallus to the ground

Rhodoplast Photosynthetic organelle in the red algae

Secondary pit connection Pit connection developed secondarily between mature cells in red algae

Siphonous, Siphonaceous Thallus without cross walls

Sorus, Sori Groups of gametangia or sporangia

Spermatangial branch Branch on which spermatangia are developed (red algae)

Spermatangium Cell releasing a spermatium

Spermatium Male gamete of red algae, never bearing flagella

Spermtozoid Flagellated male gamete

Sphacelariales Order of the brown algae with *Sphacelaria* as name-giving genus

Sporangium Cell releasing spores

Spore Asexual cells growing out to new plants, flagellated or non-flagellated

Sporophyte Asexual plant producing spores

Sublittoral Part of the littoral covered by water also at low-tide conditions

Substratum Material on which the plants grow

Subtide, Subtidal Part of the littoral covered by water also at low-tide conditions

Supralittoral Part of the littoral not covered by water at high-tide conditions

Symbiosis Permanent interaction between two different species which can be mutualistic, commensalistic or parasitic

Sympodial Basal axes are predominant, no main axis is existent

Terete Round in cross section

Tetrasporangium Sporangium in which four unflagellated spores are formed by meiosis

Tetraspore One of the four spores in a tetrasporangium

Tetrasporophyte Diploid plant on which tetrasporangia are formed

Thallus Plant body which doesń t have roots, shoots and leafs as higher plants

Taxon Taxonomic unit of any hierarchical level (species, genus, family, order ...)

Trichogyne Filamentous outgrowth of a carpogonium

Triphasic Life cycle with three different generations

Uniaxial Thallus is built by one central axis

Whorl More than two branches at one node

Zoosporangium Sporangium releasing flagellated spores

Zoospore Flagellated spore

Zygote Diploid cell resulting from fertilization

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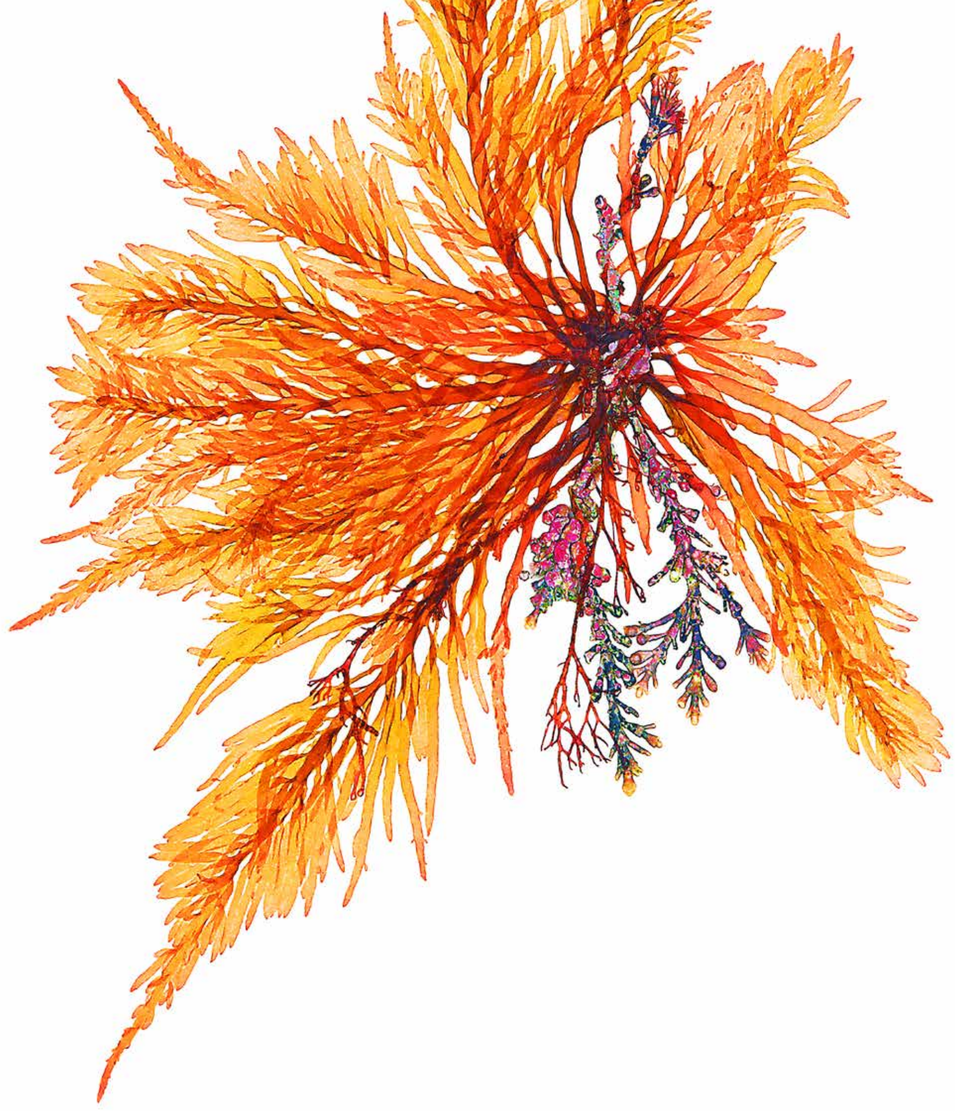

Literature

collectors of the algae

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6	*Desmarestia ligulata*	Grau
7	*Desmarestia ligulata*	Grau
8	*Dictyota dichotoma*	Linne von Berg
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10	*Desmarestia ligulata*	Grau
11	*Dictyota dichotoma*	Linne von Berg
12	*Gastroclonium ovatum*	Dietrich
13	*Hypoglossum hypoglossoides*	Santarius
14	*Osmundea pinnatifida*	Dietrich
15	*Cryptopleura ramosa*	Santarius
16	*Chaetomorpha aerea*	Santarius
17	*Ulva flexuosa*	Santarius
18	*Ulva linza*	Linne von Berg
19	*Ulva*	Santarius
20	*Ulva*	Santarius
22	*Fucus vesiculosus*	Linne von Berg
23	Dictyopteris	Linne von Berg
24	*Calliblepharis jubata*	Dietrich
25	*Polysiphonia elongata*	Dietrich
26	*Calliblepharis ciliata*	Grau
27	*Calliblepharis ciliata*	Grau
28	*Calliblepharis jubata*	Linne von Berg
29	*Calliblepharis jubata*	Santarius
30	*Plocamium*	Grau
31	*Halurus equisetifolius*	Grau
32	*Phyllophora*	Santarius
33	*Chondrus crispus*	Santarius
34	*Plocamium*	Santarius
35	*Plocamium*	Santarius
36	*Plocamium*	Santarius
37	*Plocamium*	Santarius
38	*Acrosiphonia spinescens*	Santarius
39	*Halimeda*	Grau
40	*Acrochaetium secundatum*	Linne von Berg
41	*Halimeda*	Linne von Berg
42	*Colpomenia*	Dietrich
43	*Saccharina latissima*	Linne von Berg
44	*Asparagopsis armata*	Dietrich
45	*Asparagopsis armata*	Dietrich
46	*Asparagopsis armata*	Grau
47	*Asparagopsis armata*	Grau
48	*Polysiphonia stricta*	Linne von Berg
49	*Ceramium virgatum*	Santarius
50	*Polysiphonia*	Dietrich
51	*Vertebrata*	Dietrich
52	*Nitophyllum punctatum*	Santarius
53	*Gracilariopsis*	Santarius
54	*Gracilariopsis*	Linne von Berg
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66	*Taonia*	Grau
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68	*Alaria esculenta*	Linne von Berg
69	*Alaria esculenta*	Linne von Berg
70	*Halidrys siliquosa*	Linne von Berg
71	*Ascophyllum*	Santarius
72	*Colpomenia*	Santarius
73	*Scytosiphon lomentaria*	Linne von Berg
74	*Colpomenia*	Santarius
75	*Scytosiphon lomentaria*	Linne von Berg
76	*Pelvetia*	Dietrich
77	*Pelvetia*	Santarius
78	*Fucus spiralis*	Santarius
79	*Ascophyllum*	Linne von Berg
80	*Fucus vesiculosus*	Dietrich
81	*Fucus serratus*	Dietrich
82	*Himanthalia*	Dietrich
83	*Himanthalia*	Santarius
84	*Saccharina*	Dietrich
85	*Laminaria*	Santarius
86	*Phycodrys rubens*	Dietrich
87	*Plumaria*	Santarius
88	*Apoglossum*	Linne von Berg
89	*Palmaria*	Linne von Berg
90	*Callithamnion*	Santarius
91	*Callithamnion*	Santarius
92	*Chondracanthus*	Grau
93	*Chondracanthus*	Grau
94	*Palmaria*	Linne von Berg
95	*Phyllophora*	Santarius
96	*Phyllophora*	Dietrich
97	*Palmaria*	Santarius
98	*Lomentaria articulata*	Santarius
99	*Callophyllis laciniata*	Linne von Berg
100	*Lomentaria articulata*	Linne von Berg
101	*Lomentaria clavellosa*	Dietrich
102	*Membranoptera alata*	Linne von Berg
103	*Ceramium*	Dietrich
104	*Ceramium*	Santarius
105	*Ceramium*	Linne von Berg
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107	*Laminaria digitata*	Linne von Berg
108	*Fucus serratus*	Linne von Berg
109	*Padina*	Linne von Berg
110	*Pelvetia*	Linne von Berg
111	*Cystoseira*	Linne von Berg
112	*Pyropia*	Linne von Berg
113	*Pyropia*	Linne von Berg
114	*Gracilaria*	Linne von Berg
115	*Fucus*	Linne von Berg
116	*Pyropia*	Linne von Berg
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119	*Dilsea*	Linne von Berg

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124	*Heterosiphonia*	Linne von Berg
125	*Hypoglossum hypoglossoides*	Santarius
126	*Dumontia*	Linne von Berg
127	*Calliblepharis ciliata*	Santarius
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134	*Halidrys siliquosa*	Santarius
135	*Fucus vesiculosus*	Dietrich
136	*Sargassum*	Linne von Berg
137	*Sargassum*	Linne von Berg
138	*Bostrychia scorpioides*	Dietrich
139	*Fucus ceranoides*	Santarius
140	*Dictyopteris*	Linne von Berg
141	*Callithamnion*	Dietrich
142	*Apoglossum*	Dietrich
143	*Nitophyllum punctatum*	Dietrich
144	*Polyides*	Dietrich
145	*Champia*	Dietrich
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150	*Cystoseira*	Dietrich
151	*Bifurcaria*	Dietrich
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154	*Saccharina*	Linne von Berg
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158	*Cystoseira*	Santarius
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167	*Porphyra umbilicalis*	Dietrich
168	*Porphyra linearis*	Santarius
169	*Palmaria*	Linne von Berg
170	*Ulva lactuca*	Linne von Berg
171	*Agarum*	Grau
172	*Agarum*	Grau
174	*Gelidium*	Santarius
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189	*Halimeda*	Linne von Berg
190	*Flabellia*	Linne von Berg
191	*Acetabularia mediterranea*	Linne von Berg
192	*Cheilosporum*	Grau
193	*Amphiroa*	Grau
194	*Colpomenia*	Santarius
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196	*Mastocarpus stellatus*	Santarius
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203	*Chaetomorpha*	Linne von Berg
204	*Chaetomorpha*	Linne von Berg
205	*Caulerpa*	Linne von Berg
206	*Caulerpa*	Linne von Berg

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Linne von Berg 2): Dr. Karl-Heinz Linne von Berg, *12.02.1953; scientist at the University of Cologne; Dr. Gerlinde Linne von Berg; *20.10.1956; teacher, Kall/ Eifel.

Santarius 1): Prof. Dr. Kurt Adolf Santarius, *23.11.1933; Full Professor for Ecology; Heinrich-Heine University, Düsseldorf, retired.

1): The herbaria of Dr. Dietrich, Prof. Grau and Prof. Santarius are deposited in the "Botanische Staatssammlung München"; Curator: Dr. Dagmar Triebel.

2): The joint herbarium of Dr. Gerlinde and Dr. Karl-Heinz Linne von Berg is deposited in the University of Cologne and is used for teaching.