

STUDIES ON THE ERYTHROPELTIDACEAE (RHODOPHYCEAE-BANGIOPHYCIDAE)

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SUMMARY

From culture studies it appears that the species of *Erythrocladia* and *Erythrotrichia* have a great morphological variability. The delimitation of the species has been studied. In the genus *Erythrocladia* two species are recognized, in *Erythrotrichia* three, and in *Porphyropsis* two.

In cultures of *Erythrotrichia carnea* a conchocelis stage was found; its morphological structure is similar to that of the conchocelis thalli as described for *Bangia* and *Porphyra*. The mode of spore formation in the conchocelis thalli is, however, different; in *Erythrotrichia* monospores were formed whereas in *Bangia* and *Porphyra* only neutral spores are known.

Cell-fusions were observed in filaments of *Erythrotrichia carnea*; this could indicate the occurrence of sexual reproduction. There is a striking agreement with the observations made by Flint and Magne on *Kyliniella* and *Rhodochaete* respectively.

Besides a preliminary scheme of the life-cycle of *Erythrotrichia carnea*, information on distribution, cytology, development, and asexual reproduction of all species is given.

INTRODUCTION

This study was begun as a revision of the Dutch species of the *Erythropeltidaceae* but it soon became obvious that a more extensive revision was necessary and so a revision of the entire family has been attempted.

The bibliography is as complete as possible; this was particularly necessary for the compilation of the distribution records of the species.

MATERIAL AND METHODS

Culture studies were made of several species of *Erythrocladia* and *Erythrotrichia* and, for purposes of comparison, also of species of *Bangia*, *Goniotrichum*, and *Asterocytis*.

The morphological variability of these species was studied in cultures growing under different circumstances: temperature 4°, 12°, and 20° C., with and without aeration, different culture solutions, and by varying light intensity and photoperiod. Most of the cultures were exposed to a 16 h. photoperiod day.

The normal culture solution used was an enriched Erdschreiber: $\frac{1}{3}$ litre of soil, steamed together with $\frac{2}{3}$ litre of sea water for 3 hours; after filtration per 500 ml of this extract 0.2 g K_2HPO_4 and 1.0 g KNO_3 was added. Of this rough Erdschreiber 50 ml was added to 950 ml of sea water and boiled for 3 hours. The pH was adjusted at 7.5.

Parts of filaments of *Erythrotrichia* and *Erythrocladia* were pulled with a thin wolfram needle through a seawater-agar plate (2, 2.5, or 3 %) to remove diatoms, small algae, etc. The cleaned filaments were cut in several parts and the fragments were placed in sterilized test tubes filled with culture solution. The test tubes were placed in the culture rooms and exposed to a 16 hours day and 8 hours night rhythm. The culture solution was renewed if necessary. Later several subcultures of each culture were made in the same way.

Herbarium material studied consisted mainly of dried specimens present in the following collections: Rijksherbarium, Leyden; herbarium of the Nederlands Instituut voor Onderzoek der Zee, Den Helder; herbarium of the Koninklijke Nederlandse Botanische Vereniging kept at the Rijksherbarium, Leyden; herbarium of the Rijksuniversiteit of Groningen. Further some material from the herbaria of Kew and Copenhagen has been studied.

The measurements given in the descriptions and figures are taken from living specimens, unless the contrary is stated.

ERYTHROPELTIDACEAE

Thallus erect, filamentous, ribbon-shaped, or foliaceous, often with an extended basal attachment organ, or consisting of several filaments creeping in or on other algae and hydroids. Chromatophore either stellate, central, with a distinct pyrenoid, or band- or bowl-shaped, parietal, without a distinct pyrenoid. Sexual reproduction incompletely known; a shell-boring conchocelis stage sometimes present. Asexual reproduction by monospores.

Type genus: *Erythropeltis* Schmitz 1896.

KEY TO THE GENERA *)

- 1 a. Thallus consisting of filaments creeping in or on cell-walls of other algae and on hydroids, sometimes forming a disc or a cushion. Chromatophore parietal 1. *Erythrocladia*
- b. Thallus consisting of erect filaments often with a basal disc, or sometimes consisting only of a basal disc. Chromatophore central, stellate 2. *Erythrotrichia*
- c. Thallus consisting of erect filaments or monostromatic blades, attached to the substratum by hyaline protuberances of a great number of basal cells. Chromatophore central, stellate 3. *Porphyropsis*

1. ERYTHROCLADIA

Rosenvinge, The marine Algae of Denmark 1 (1909) 71. — *Rhodorus* Geitler, Arch. Protist. 69 (1930) 615.

Thallus consisting of several branched filaments; very regular, forming a monostromatic disc, or irregular, forming a polystromatic cushion or a monostromatic network (fig. 1a, b, c). Cells smaller than in *Erythrotrichia* and purplish-red, length about 5—15 μ , width 5—10 μ . Chromatophore parietal, band- or bowl-shaped, without a distinct pyrenoid. Asexual reproduction by monospores, sexual reproduction unknown. Pit connections never seen.

Type species: *E. irregularis* Rosenv.

By culture it became clear that the species are very variable and that the form of the plant is influenced by the substratum. Nichols and Lisant (1967) found the same. *Erythrocladia* was cultured on glass, mica, calcite (inside of oyster-shells), hairs, and cotton fibres.

*) I was not able to study *Smithora* Hollenberg 1959 in extenso. However, this genus is so different in every aspect that it cannot be maintained in the *Erythropeltidaceae*.

The endcell of a creeping filament becomes distally retuse giving a bicuspidate appearance to the cell. After some time it divides longitudinally and the daughter cells also divide longitudinally from the distal end. So a dichotomous appearance is established.

Older cells not in the margin of the disc form monospores of about $5\ \mu$ in diameter. The monospores often divide a few times so forming a kind of 'palmella' stage (fig. 2), showing a great resemblance to *Rhodorus marinus* Geitler. This 'species' was once seen in a sea water culture (Geitler 1930, p. 615). Sometimes a group of 'Rhodorus' cells remained attached to the mother plant (fig. 3).

The germination of the monospores is very irregular (fig. 4).

The genus *Colacodictyon* Feldmann 1955 (p. 23—28) (= *Colaconema* Batters, 1896, p. 8, *pro parte*) seems to be closely related to several species of *Erythrocladia*, viz. *E. recondita*, *E. vagabunda*, *E. endophloea*, and *E. pinnata*. A detailed study of the mode of spore-formation in all these species is wanted. Feldmann stated that *Colacodictyon* has neutral spores (entire content of a cell liberated as a spore), whereas *Erythrocladia* has monospores (only part of the cell content liberated as a spore).

KEY TO THE SPECIES

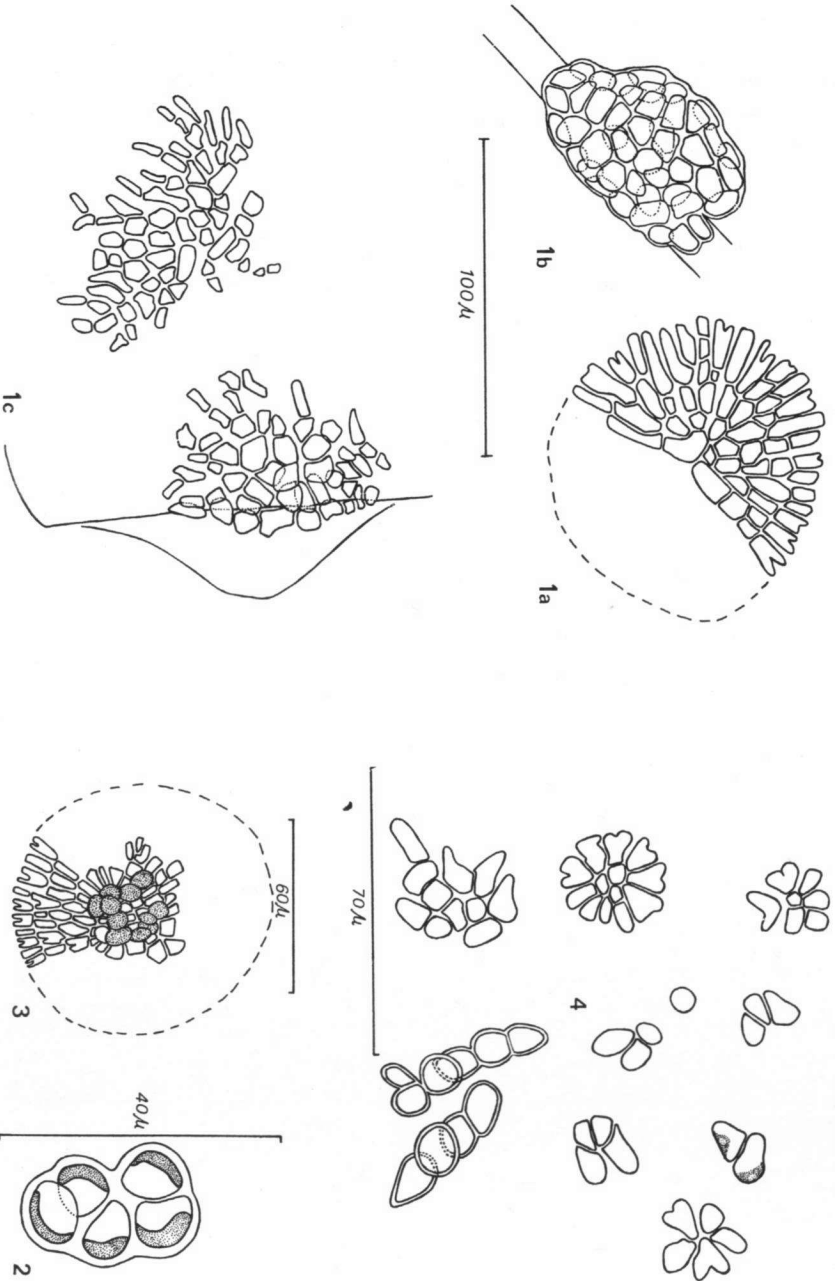
- 1 a. Filaments creeping on various substrates, forming a closed disc or a polystromatic cushion. **1. *E. irregularis***
 b. Filaments creeping in or partly on cell-walls of other algae, forming a very open network. **2. *E. endophloea***

1. *Erythrocladia irregularis* Rosenvinge, 1909, p. 72—73; Svedelius, 1911, p. 217—218; De Toni, 1924, p. 17; Kylin, 1925, p. 9; Dawson, 1944, p. 251; Kylin, 1944, p. 7; Smith, 1944, p. 166; Doty, 1947, p. 159; Hollenberg, 1948, p. 156; Dawson, 1953, p. 5; Sundene, 1953, p. 178; Zinova, 1955, p. 47; Levring, 1960, p. 28; Lee, 1965, p. 67. — *E. subintegra* Rosenvinge, 1909, p. 73—75; Børgesen, 1915, p. 7—9; Collins & Hervey, 1917, p. 95; Weber-van Bosse, 1921, p. 188; De Toni, 1924, p. 18; Hamel, 1924, p. 7; Kylin, 1925, p. 9; Printz, 1926, p. 54; Taylor, 1928, p. 132; Dangeard, 1934, p. 251; Feldmann, 1939, p. 256; Kylin, 1941, p. 3; Taylor, 1942, p. 74—75; Smith, 1944, p. 166; Dawson, 1944, p. 251; Dawson, 1945, p. 65; Doty, 1947, p. 159; Hollenberg, 1948, p. 156; Dawson, 1953, p. 5—6; Sundene, 1953, p. 179; Feldmann, 1954, p. 256; Zinova, 1955, p. 47; Van den Hoek, 1958, p. 210; Den Hartog, 1959, p. 166; Levring, 1960, p. 28—29; Lee, 1965, p. 67; Jorde, 1966, p. 50. — *E. polystromatica* Dangeard, 1932, p. 145; Waern, 1952, p. 180—182; Zinova, 1955, p. 48. — *E. ectozoica* Dawson, 1953, p. 4—5.

Distribution: Probably cosmopolitan. It is known from the west coasts of North and South America (Washington, Oregon, California, Mexico, Chile), the east coast of North America (Florida, Bermuda, the Antilles), Europe (from Trondheim Fjord south to the Mediterranean), and Asia (Hongkong, Indonesia).

Distribution in the Netherlands: In the Province of Zeeland it has been found in the following localities: Schouwen-Duiveland (Zierikzee, Kistersinlaag); Noord-Beveland (Wissekerke, Katse Hoek); Zuid-Beveland (Kanaal door Zuid-Beveland near Postbrug, Sas van Goes, Wemeldinge); Walcheren (Vlissingen, Nolledijk). Further there is allochthonous material from Katwijk.

Notes: Culture experiments showed that *Erythrocladia irregularis*, *E. subintegra*, and *E. polystromatica* are only forms of one species. Only the fact by itself, that *E. ectozoica* is growing on hydroids is not sufficient for it to be regarded as a separate species. I found *E. irregularis* commonly on hydroids.



Erythrocladia irregularis Rosem. — Fig. 1. Several forms of thallus. — Fig. 2. 'Palmella' stage. — Fig. 3. Sporulating thallus with adhering spores. — Fig. 4. Several forms of young stages.

2. *Erythrocladia endophloea* Howe, 1914, p. 81; De Toni, 1924, p. 18. — *E. recondita* Howe & Hoyt, 1916, p. 112—115; De Toni, 1924, p. 18. — *E. vagabunda* Howe & Hoyt, 1916, p. 115.

Distribution: The species is known from Peru and the eastern coast of the U.S.A. (North Carolina).

Note: From a study of the literature it is obvious that *Erythrocladia endophloea*, *E. recondita*, and *E. vagabunda* are synonymous.

DOUBTFUL SPECIES

It was not possible to study material of the following taxa.

Erythrocladia insignis Laing, 1928, p. 56—59.

Erythrocladia laurenciae Børgesen, 1924, p. 270—271.

Erythrocladia pinnata Taylor, 1942, p. 58.

Erythrocladia vagans Børgesen, 1924, p. 269—270.

It is quite probable that these taxa are not good species.

EXCLUDED

Erythrocladia chaetomorpha Tanaka & Pham-Hoang Ho, 1962, p. 32—33.

E. chaetomorpha possesses 'hairs' and therefore must be considered to be an *Acrochaetium* species of which the correct name is: *Acrochaetium chaetomorpha* (Tanaka & Pham-Hoang Ho) Heerebout, *nov. comb.*

2. ERYTHROTRICHIA

J. E. Areschoug, *Nova Acta Soc. Sci. Upsal. ser. 2*, 14 (1850) 435, *nom. conserv.* — *Ceramicola* Oersted, *Region. Mar.* (1844) 42. — *Porphyrostromium* Trevisan, *Algh. Cocc.* (1848) 100. — *Erythropeltis* Schmitz, in Engler-Prantl, *Nat. Pfl. Fam.* 1, 2 (1896) 313.

Areschoug included in the genus *Erythrotrichia* both *Ceramicola* Oersted and *Goniotrichum* Kützing (*Phycologia generalis*, 1843, p. 244, Leipzig). If the name had not been conserved *Erythrotrichia* would be a superfluous name for the older name *Goniotrichum* Kützing. Both *Ceramicola* and *Porphyrostromium* are *nomina rejicienda*. (See Drew & Ross, 1965, p. 95—97).

Thallus erect, filamentous or ribbon-shaped, often with a disc- or cushion-shaped attachment organ. Filamentous thallus branched or unbranched, monosiphonous or polysiphonous. Ribbon-shaped thallus always monostromatic; unbranched. Cells larger than in *Erythrocladia* and brick red, length about 7—25 μ , width 10—20 μ . Chromatophore stellate, with a distinct pyrenoid. Asexual reproduction by monospores; life cycle with a conchocelis stage. Pit connection never seen.

Type species: *Erythrotrichia ceramicola* (Lyngb.) Aresch.

Vegetative features

a. Attachment organ:

Most authors have followed Berthold (1882), distinguishing in their keys two kinds of attachment organ: the filaments being attached by lobes of the lowermost cell (fig. 5) or by a primary discoid thallus (fig. 8). It proved difficult to maintain this division. Several species were described with 'rhizines' or 'rhizoids', being cells formed by the basal cell (fig. 6a, b). Other species were described with still other types of attachment, e.g.: 'short, creeping, uniseriate filament', 'basal creeping portion of the frond filamen-

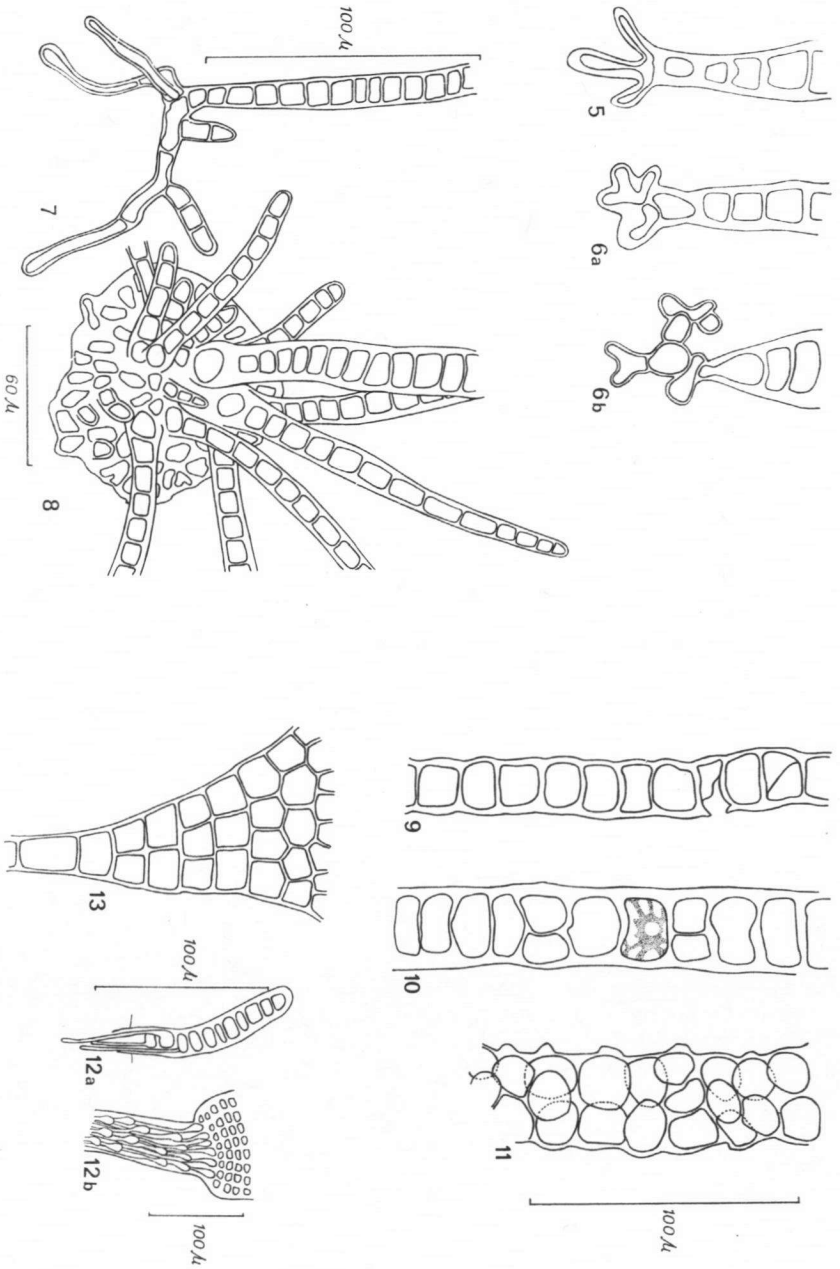


Fig. 5—8. Various kinds of attachment organs of *Erythrotrichia carnea* (Dillw.) J. Ag. — Fig. 9—11. Various kinds of filaments of *Erythrotrichia carnea* (Dillw.) J. Ag. — Fig. 12. Mode of attachment of young (a) and old plants (b) of *Porphophysis vexillaris* (Mont.) Heerebout (after Hamel, 1929). — Fig. 13. Basal part of thallus of *Erythrotrichia boryana* (Mont.) Berthold.

tous', 'multicellular rhizoidal filaments, with secondary erect filaments' (fig. 7). In the specimens of *Erythrotrichia* collected from natural environments it was possible to find all transitions between lobed basal cell and basal disc with several erect filaments. These features were also found by culture experiments. The monospores of a specimen of *Erythrotrichia* with a lobed basal cell gave rise to small filaments which started with a lobed basal cell that grew into a disc bearing several erect filaments (fig. 8). In the same way the monospores of a specimen of *Erythrotrichia* with a basal disc gave rise to filaments with a lobed basal cell that grew into filaments with a basal disc.

First Berthold, and after him many other authors, called the basal disc 'primary', which means that first the disc is formed and after some time the erect filaments. Berthold made these observations in *Erythrotrichia boryana*. It was not possible to reproduce this in culture, but in the dried herbarium specimen of *Porphyra boryana* Montagne [= *E. boryana* (Mont.) Berthold] sent by Montagne to Kützing it was possible to find all stages, from a germinating spore growing out into a multicellular disc without filaments up to a multicellular disc with filaments. In Roscoff (France) I was able to collect these stages alive.

In culture the spores of *E. boryana* after germinating form not a monostromatic disc but small monosiphonous filaments; unfortunately they died after some days.

Several species are described with a cushion-like attachment organ; I did not find *Erythrotrichia* specimens with this kind of attachment organ and so it was not possible to reproduce this in culture and for that reason I cannot say whether this cushion is 'primary' or 'secondary'. Gardner (1927) described the origin of such a cushion as coming into existence in the same way as Berthold described for the origin of the primary basal disc of *E. boryana*, i.e. by repeated radial division of a spore. I believe a cushion-like base is just a special form of a basal disc. One species, *Erythrotrichia vexillaris* (Mont.) Hamel, is attached by hyaline protuberances, so it must be regarded as not belonging to the genus *Erythrotrichia*. I suggest that this species be removed from this genus and placed into *Porphyropsis*. Its correct name is *Porphyropsis vexillaris* (Mont.) Heerebout, *vide infra*.

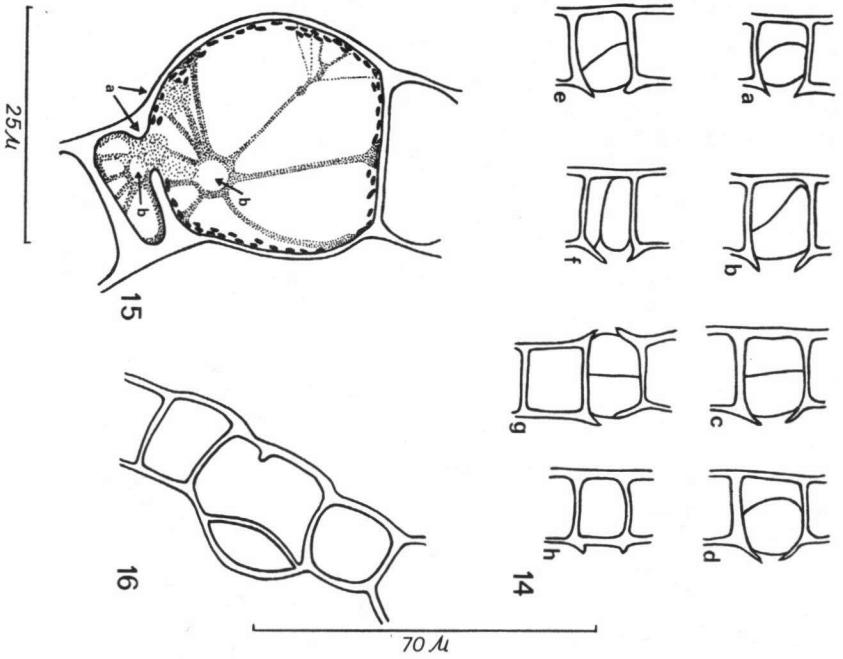
b. Form of the filament:

In Hamel's paper (1924), mainly based on the papers of Berthold (1882) and Batters (1900), the following features are used to distinguish the species of *Erythrotrichia*:

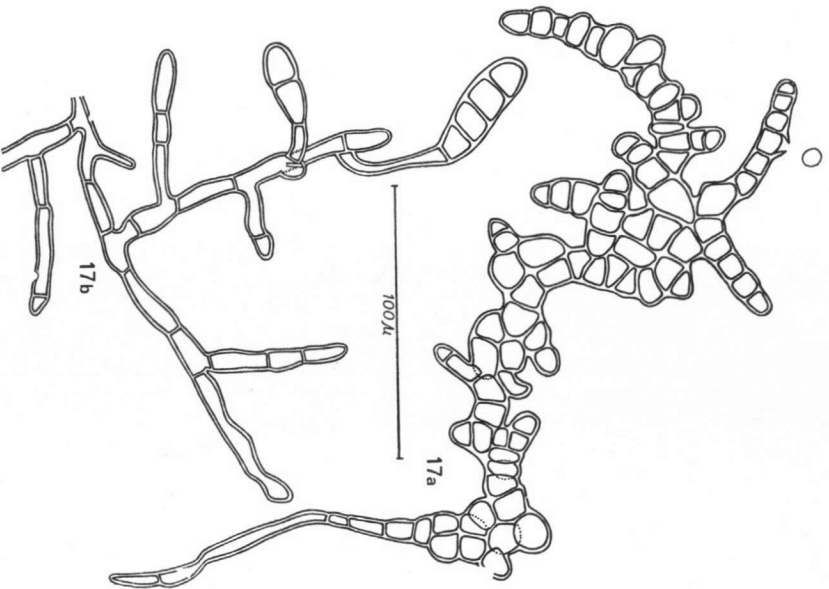
1. Frond consisting of one row of cells.
2. Frond consisting of one row of cells, but sometimes a few cells have divided longitudinally into two cells.
3. Frond, at least partly, consisting of more than one row of cells, forming a polysiphonous filament or a monostromatic blade.
4. Frond branched or unbranched.

Hamel (1924) stated that it is likely that *E. bertholdii*, possessing a frond of several rows of cells (fig. 11), passes in its development through a 'carnea' (fig. 9) and an 'investiens' (fig. 10) stage. In my cultures polysiphonous specimens of *Erythrotrichia*, after sporulation, gave rise to monosiphonous filaments, afterwards growing out into polysiphonous ones again. I was also able to obtain polysiphonous filaments in my cultures from monosiphonous forms collected in nature. So specimens with one or more rows of cells in the filament can be conspecific.

The arrangement of the cell rows is of taxonomic value, and it is possible to distinguish the species by this character. *E. boryana* has cell rows forming a monostromatic blade (fig. 13) and the other species have cell rows which can form a polysiphonous filament



Erythrorhiza carnea (Dillw.) J. Ag. — Fig. 14. Different methods of monospore formation. — Fig. 15. Cell fusion: a = nucleus, b = pyrenoid. — Fig. 16. First division after cell fusion. — Fig. 17. a. Conchoecelis stage with reduced sterile part and well-developed fertile part, producing monospores. b. Conchoecelis stage with well-developed sterile part, showing the formation of the so-called 'fertile plantlets'.



(fig. 11). Branching occurring in nearly all cultures is of no value in distinguishing the species. It is formed by a lateral division of a cell somewhere in the filament. After the division the original cell often becomes wedge-shaped.

c. Cell-structure:

The cells possess a central, stellate chromatophore with a clear pyrenoid; the branches of the chromatophore are often thickened at the end against the cell-wall (fig. 10). In *E. incrassata*, *E. japonica*, *E. tetraseriata*, *E. porphyroides*, *E. parksii*, *E. kylinii*, and *E. parietalis* the chromatophore is said to be band-shaped. If this is true it is perhaps better to place these species in a new genus, related to *Compsopogon* and *Rhodochaete*. But first it is necessary to examine the type specimens carefully.

There is no general agreement about the structure of the chromatophore in several *Erythrotrichia* species. Gardner (1927, p. 236) described *E. kylinii* with a band-shaped chromatophore. Kylin (1941, p. 3) found after careful examination a stellate chromatophore. The scanty material of *E. tetraseriata* present in the Rijksherbarium and correctly determined by E. Y. Dawson, possesses a stellate chromatophore, whereas Dawson (1953, p. 12) stated that it had a band-shaped chromatophore. Further, Gardner described a band-shaped chromatophore in *E. porphyroides* and Dawson found a stellate one.

Tseng and Chang (1955) showed that in the conchocelis-stage of *Porphyra*, in the creeping and boring long-celled part, a parietal, band-shaped chromatophore is present, whereas the so-called 'fertile plantlets' possess a central stellate chromatophore. They illustrated and described transitions between both forms of chromatophores. I could not find any indication of this feature in *Erythrotrichia*.

The length of the cells varies from 7 to 25 μ ; the width from 10 to 20 μ . The ratio length/width mostly varies between $\frac{3}{2}$ and $\frac{5}{2}$. Some authors state that in winter the cells of the filaments are shorter than in summer. In culture there was no clear difference between cell dimensions of filaments, growing at 4° or 20° C.

Generative features

a. Asexual reproduction:

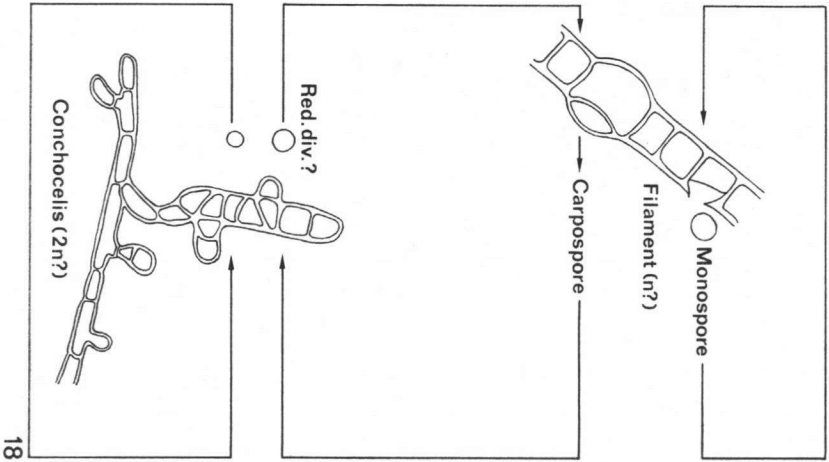
Asexual reproduction in *Erythrotrichia* is mentioned by many authors. I made the following observations in my cultures.

A monospore is formed by a vegetative cell, dividing into two daughter-cells of about equal size. One daughter-cell is liberated as a monospore (fig. 14a-f) of about 6-8 μ diameter; the other grows out to fill the empty cell part and can divide again. In one case I saw both daughter-cells becoming monospores (fig. 14g). The spore is liberated through a hole in the cell-wall; after liberation the hole is closed, after some time only the rim of the hole is visible (fig. 14h).

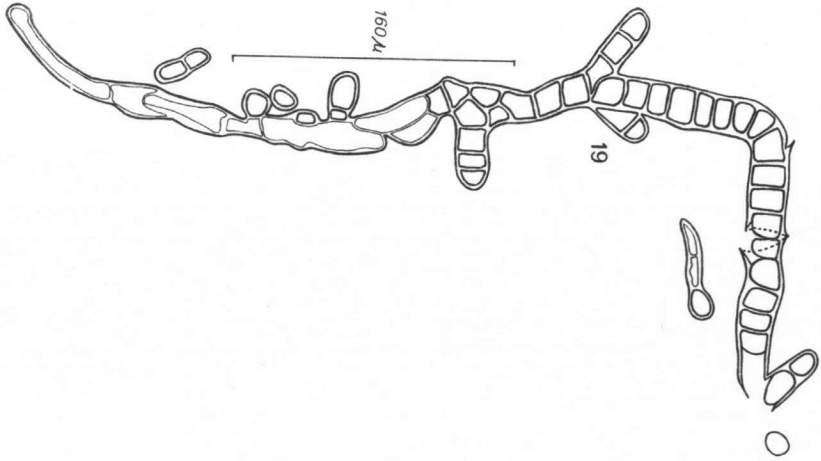
The monospore possesses a central, stellate chromatophore and much floridean starch. I did not see any amoeboid movements, supposed to be common in *Erythrotrichia* spores.

In culture the spores often remain attached to the surface of the filament, giving after germination a branched appearance to the filament. Levring (1955) found a similar phenomenon in specimens collected from natural environments. In order to prevent this attachment I made a culture in which the culture medium was kept in constant motion by aeration, but the spores adhered even more.

The spore germinates in about 10 days at 12° C and in about 8 days at 20° C, by dividing into two daughter-cells, one becoming the rhizoid (and later the discoid thallus), the other becoming the filament.



18



19

Fig. 18. Diagram of the life cycle of *Erythrotrichia carnea* (Dillw.) J. Ag. — Fig. 19. Thallus of *Erythrotrichia weiwitschii* (Rupr.) Barr. with apical and rhizoidal sporulation.

b. Sexual reproduction:

Berthold (1880, 1882) was the first who described sexual reproduction in *Erythrotrichia*. The spermatia are formed in exactly the same way as the monospores; they possess a central chromatophore and also show amoeboid movement. The only difference is that spermatia are smaller than monospores. The carpogonium consists just of one cell, not distinguishable in outward appearance from a vegetative cell. Berthold described the fertilization and illustrated it, showing a part of a filament on which, on one of the cells, a small cell is adherent. Drew was right in saying that it is not certain whether the small cell on the outside of the filament was establishing or losing contact. When the small cell is losing contact it is not fertilization but the forming of a spermatium.

Gardner (1927) described sexual reproduction in *E. parksii* var. *minor* but was not sure whether his interpretation of the facts was correct or not.

Baardseth (1941) observed two kinds of spores in *E. tristansensis*: monospores (8–10 μ) and spermatia (3–5 μ). Carpogonia were not found and he did not see fertilization.

Tanaka (1944) found that in *E. reflexa* the carpogonia often produce a hyaline protuberance. He did not see spermatia or fertilization.

In my cultures I was not able to find spermatia or carpogonia, but, as I found a conchocelis-stage, I presume that fertilization must have occurred, for in *Bangia* and *Porphyra* the conchocelis-stage probably originates from a fertilized carpospore.

Several times I observed cell-fusion in my cultures (fig. 15): a large, swollen cell fuses with a 'normal' cell, and after some enlargement the large cell divides in a special way. It is possible that this gives rise to a so-called 'intercalary sporangium', as occurs in *Bangia*. I saw only the first division of the large cell.

It is interesting to consider what Flint (1953) discovered in *Kyliniella*, a fresh-water representative of the *Bangiophycidae*. He found two types of sexual reproduction, one in which the spermatangium and the carpogonium have a 'positional relationship', the other without such a relationship. He wrote: 'In the first type two adnate cells developed respectively into one male and one female structure. The male structure lost pigmentation and turgidity, extended as a process through the sheath and gave rise to an unpigmented spermatium. In the meantime the adjoining cell developed into a greatly enlarged female structure. The spermatium was released in proximity to an apparently sensitised region of the enlarged cell and fertilization took place. Immediately following fertilization the spermatium was observed within the female structure. The fertilized cell subsequently became further enlarged, opaque and filled with granular material.' In the second type, the female structure is also enlarged, and possesses a kind of trichogyne. The spermatia become agglutinated to the terminal portion of this trichogyne.

The first type of sexual reproduction mentioned by Flint has a striking similarity with the cell fusion I observed; positional relationship and enlarging of the female structure.

Magne (1960) found in *Rhodochaete parvula* Thuret that after fertilization the carpospore is formed in a special way, the spore forming division resembles the division I saw in the large cells of *Erythrotrichia* (fig. 16). It would be interesting to know what kind of spore formation is present in the enlarged cells of *Kyliniella*.

The Conchocelis stage and life cycle diagram (fig. 18). In my cultures a growth, similar to the conchocelis stage of *Bangia* and *Porphyra* occurred spontaneously. It consisted of long-celled, creeping and boring filaments and of the so-called 'fertile plantlets', forming monospores (fig. 17). To be exact, I saw the formation of only two monospores.

I tried to stimulate it by decreasing and increasing the temperature and light, but without success.

In the literature concerning the conchocelis stage of *Porphyra* neutral spores are mentioned as occurring. There must be two kinds of spores, one reproducing the conchocelis stage and one giving rise to the filamentous stage. Because I found a reproducing conchocelis stage and monospores it is likely that the neutral spores form the filamentous stage and the monospores the conchocelis stage.

Since it is probable that the conchocelis stage occurs after fertilization it is important to know where the reduction-division takes place in the life cycle. Even over the economically important genus *Porphyra* there is no general agreement on this point. Ishikawa (1961), Dangeard (1927), and Tseng and Chang (1955) described the reduction division as occurring immediately after fertilization; Kurogi (1956), Yabu and Tokida (1963), and Kito (1966) found no reduction-division after fertilization.

In *Erythrotrichia* it is very difficult to distinguish chromosomes because of their very small size and of the fact that the equatorial plane is perpendicular to the plane of observation. Several times I stained the chromosomes but I was not able to count them.

In several cultures I used sterilized fragments of egg-shells and pieces of oyster-shells. Thin pieces from the inside of oyster-shells are somewhat transparent and so it was possible to observe the conchocelis filaments growing inside the shell. The egg-shells can be dissolved with aid of acetic acid or EDTA (Prud'homme van Reine and Van den Hoek, 1967) and after dissolution it is possible to study the boring filaments. There are indications that the use of acetic acid induces false pit connections (Dixon, 1963). Using EDTA it is possible to obtain the boring plant alive.

KEY TO THE SPECIES

- 1 a. Thallus consisting of rows of cells arranged in one plane, giving it a ribbon-shaped appearance. Nearly always with a basal disc, in young stages sometimes only a basal disc is present. 1. *E. boryana*
- b. Thallus mono- or polysiphonous, cell rows radially arranged 2
- 2 a. Thallus often attached by a basal disc or by small protuberances of the basal cell 2. *E. carnea*
- b. Thallus with a long, boring rhizoid, composed of hyaline cells, always growing on *Ralfsia* thalli attached to gastropods 3. *E. welwitschii*

1. *Erythrotrichia boryana* (Mont.) Berthold, 1882, p. 25; Hamel, 1924, p. 13; De Toni, 1924, p. 16; Dawson, 1953, p. 7. — *Porphyra boryana* Montagne, 1846, p. 150. — *E. discigera* Berthold, 1882, p. 25; Hamel, 1924, p. 6—7; Dangeard, 1932, p. 146; Kylin, 1937, p. 44; Feldmann, 1939, p. 252. — *Porphyrostromium boryi* Trevisan, 1848, p. 100. — *Erythropeltis discigera* (Berthold) Schmitz in Engler-Prantl, 1896, p. 6; Dawson, 1953, p. 6. — *E. polymorpha* Howe, 1914, p. 77—81; Setchell & Gardner, 1924, p. 741; Taylor, 1945, p. 132—133; Levring, 1960, p. 29. — *E. porphyroides* Gardner, 1927, p. 237; Dawson, 1953, p. 7—8. — *E. pulvinata* Gardner, 1927, p. 238; Smith, 1944, p. 164; Doty, 1947, p. 159; Hollenberg, 1948, p. 156; Dawson, 1948, p. 222—227; 1953, p. 11. — *E. tristaniensis* Baardseth, 1941, p. 33—36.

Distribution: Atlantic coast of France and Spain; Mediterranean. South Atlantic (Tristan da Cunha); west coast of America from Oregon (U.S.A.) to Chile; Galapagos Islands.

Distribution in the Netherlands: In the Rijksherbarium, Leyden, there is one dried specimen which was washed ashore on the island of Schouwen, which is probably *E. boryana*. Up to now it has not been found autochthonous further north than the Channel.

Note. Mainly as a result of literature study it became clear that *E. boryana*, *E. discigera*, *E. polymorpha*, *E. porphyroides*, *E. pulvinata*, and *E. tristansiensis* are synonymous.

2. *Erythrotrichia carnea* (Dillw.) J. Agardh, 1883, p. 15; Batters, 1902, p. 55; Rosenvinge, 1909, p. 67—68; Børgesen, 1915, p. 7; Collins & Hervey, 1917, p. 94; Hamel, 1924, p. 7—10; De Toni, 1924, p. 14—15; Printz, 1926, p. 52—53; Børgesen, 1927, p. 5—6; Taylor, 1928, p. 133; Newton, 1931, p. 242—243; Børgesen, 1932, p. 113; Dangeard, 1934, p. 250; Børgesen, 1935, p. 41; Levring, 1937, p. 79; Feldmann, 1939, p. 250—251; Børgesen, 1942, p. 6; Taylor, 1942, p. 76; Kylin, 1944, p. 8; Smith, 1944, p. 164; Tanaka, 1944, p. 92—93; Abbott, 1947, p. 200—201; Dangeard, 1949, p. 138; Tanaka, 1951, p. 97—99; Dawson, 1953, p. 10; Levring, 1953, p. 462; Sundene, 1953, p. 178—180; Levring, 1955, p. 409; Dawson, 1956, p. 44; 1957, p. 111; Taylor, 1957, p. 202—203; Den Hartog, 1959, p. 124, 145, 152, 159, 166, 171, 200, 203, 205, 211; Levring, 1960, p. 29; Abbott, 1961, p. 4; Dawson, 1963, p. 5; Jorde, 1966, p. 14, 50, 52; Dixon & West, 1967, p. 253—255. — *Conferva carnea* Dillwyn, 1807, p. 54; Kützing, 1849, p. 316. — *Conferva ceramicola* Lyngbye, 1819, p. 144. — *Ceramium ceramicola* (Lyngb.) C. Agardh, 1828, p. 155. — *Bangia ciliaris* Carmichel in Hooker, 1833, p. 316; Harvey, 1849, p. 218; Crouan, 1852, no. 392. — *Bangia ceramicola* (Lyngb.) Chauvin, 1842, p. 28—30; Harvey, 1849, p. 218, pl. 317; Ardissonne, 1866, p. 473; Hauck, 1885, p. 22. — *Ceramicola rubra* Oersted, 1844, p. 42. — *Bangia investiens* Zanardini, 1847, p. 68; Van den Bosch, 1853, p. 211—212; Kützing, 1869, p. 359; De Toni, 1897, p. 25. — *Porphyra bangiaeformis* Kützing, 1849, p. 691; 1869, p. 29. — *E. ceramicola* (Lyngb.) Areschoug, 1850, p. 435; Thuret in Le Jolis, 1880, p. 103; Farlow, 1881, p. 112—113; Berthold, 1882, p. 25; Kjellman, 1883, p. 193; Bornet, 1892, p. 259; De Toni, 1897, p. 24—25; Kylin, 1907, p. 107; Van Goor, 1923, p. 18. — *Bangia reflexa* Crouan, 1852, no. 394; Hauck, 1882, p. 22. — *Porphyra ceramicola* (Lyngb.) Crouan, 1867, p. 132. — *Callithammion simplex* Crouan, 1867, p. 134. — *Porphyra reflexa* (Crouan) Crouan, 1867, p. 132. — *Bangia caespitosa* Reinsch, 1875, p. 44. — *E. obscura* Berthold, 1882, p. 26; Hamel, 1924, p. 259; Børgesen, 1927, p. 6—8; Dangeard, 1932, p. 147; Feldmann, 1939, p. 252—253. — *E. ciliaris* Berthold, 1882, p. 25. — *E. investiens* (Zanardini) Bornet, 1892, p. 260; Cotton, 1912, p. 130—131; Van Goor, 1923, p. 18—19; Hamel, 1924, p. 14; Børgesen, 1927, p. 8; Feldmann, 1939, p. 251; Den Hartog, 1959, p. 23, 166, 205. — *E. reflexa* (Crouan) Thuret ex De Toni, 1897, p. 26; Hamel, 1924, p. 11—12; 1928, p. 168; Rosenvinge, 1931, p. 613; Dangeard, 1932, p. 149; Levring, 1937, p. 78; Feldmann, 1938, p. 251—252; Tanaka, 1944, p. 86—87; Sundene, 1953, p. 180; Den Hartog, 1959, p. 166; Dawson, 1963, p. 5; Zinova, 1967, p. 187—188. — *E. ciliaris* (Carmichel) Batters, 1900, p. 374, *nom. illeg., non* Berthold, 1882; Hamel, 1924, p. 18; Feldmann, 1939, p. 253—256; Dawson, 1953, p. 10—11. — *E. bertholdii* Batters, 1900, p. 375; Cotton, 1912, p. 130; Hamel, 1924, p. 10—11; De Toni, 1924, p. 16; Kylin, 1925, p. 8—9; Newton, 1931, p. 243; Dangeard, 1934, p. 250; Celan, 1938, p. 4—5; Zinova, 1967, p. 186—187. — *E. rhizoidea* Cleland, 1918, p. 144—145; De Toni, 1924, p. 16; Taylor, 1957, p. 202—203. — *E. kylinii* Gardner, 1927, p. 236. — *E. parksii* Gardner, 1927, p. 239. — *E. tetraseriata* Gardner, 1927, p. 240; Dawson, 1953, p. 12. — *E. californica* Kylin, 1941, p. 3—4; Smith, 1944, p. 165; Dawson, 1944, p. 252; 1953, p. 1—10. — *E. biseriata* Tanaka, 1944, p. 86—87; 1951, p. 99—100; Dawson, 1953, p. 7. — *E. ascendens* Dawson, 1953, p. 6. — *E. australis* Levring, 1953, p. 462—464. — *E. bangioides* Levring, 1955, p. 410.

Distribution: East Atlantic coast from the Trondheim Fjord to the Canary Islands, Mediterranean and Black Sea. West Atlantic coast from eastern Canada to the Caribbean

and Bermuda. Pacific coast of America from California to Chile. Hawaii, Galapagos Islands, Caroline Islands, Marshall Islands, New Zealand, Australia, Malay Archipelago, Japan. Indian Ocean: Mauritius, Bombay.

Distribution in the Netherlands: Waddenzee area: Den Helder (on a groyne and in the harbour), West Terschelling (harbour). Deltaic area: Schouwen-Duiveland (Westbout, Flaauwersinlaag, Zierikzee, De Val, Brouwershaven, Dreischor); Tholen (Strijenham, Gorishoek); Noord-Beveland (Wissekerke, Colijnsplaat, Kats, Katse Hoek); Zuid-Beveland (Sas van Goes, Kanaal van Goes, Kattendijke, Wemeldinge, Yerseke); Walcheren (Flushing, harbour and groynes).

3. *Erythrotrichia welwitschii* (Ruprecht) Batters, 1902, Suppl. p. 55; Cotton, 1912, p. 131; Hamel, 1924, p. 13—14; 1928, p. 168; Newton, 1931, p. 243; Smith, 1944, p. 163; Dangeard, 1949, p. 138—139; Drew, 1952, p. 50; Feldmann, 1954, p. 64; Boney, 1964, p. 327—331. — *Cruoria welwitschii* Ruprecht, 1856, p. 331—334; De Toni, 1897, p. 1687; 1924, p. 581. — *Callithamnion lepadicola* J. Agardh, 1876, p. 12. — *Rhodochorton lepadicola* (Ruprecht) De Toni, 1897, p. 1517; 1924, p. 529. — *Erythrotrichia elongata* Lami, 1938, p. 164—165.

Distribution: Ireland (Clare Island), South and East England, Atlantic coast of France and Spain, Morocco. The record given by Smith (1944) from Monterey Peninsula (California) is probably not correct. The species does not occur in the Netherlands.

Note. This species has been placed in the genus *Erythrotrichia*, although it shows some different features. Not only is there monospore formation, but apical sporulation also occurs by fracture of the filament, giving rise to neutral spores. The penetrating rhizoid also shows loosening of small cells which grow out into new plants ('budding'). Further it differs from the other species of *Erythrotrichia* by its highly specialized habitat; it occurs only on *Ralfsia* when this is attached to molluscs. However, I think it is better to maintain *E. welwitschii* in *Erythrotrichia* than to erect a new monotypic, closely related genus for it.

DOUBTFUL SPECIES

Erythrotrichia divaricata Schussnig, 1928, p. 164—165.

Erythrotrichia hunteri Gardner, 1936, p. 41—45.

Erythrotrichia incrassata Tanaka, 1944, p. 89—92.

Erythrotrichia japonica Tokida, 1938, p. 218—220.

Erythrotrichia parietalis Tanaka, 1952, p. 18; Dawson, 1954, p. 412; 1957, p. 111.

3. PORPHYROPSIS

Rosenvinge, *The marine Algae of Denmark* 1 (1909) 68.

Thallus foliaceous, monostromatic, consisting of many rows of regularly arranged cells, attached to the substratum by hyaline protuberances of several basal cells (as in *Bangia* and *Porphyra*). Chromatophore stellate with a distinct pyrenoid. Asexual reproduction by monospores, sexual reproduction unknown.

Type species: *P. coccinea* (J. Agardh) Rosenv.

Very little is known about the morphological variability and spore formation in this genus.

The foliaceous thallus is formed by lateral division of one row of cells or by bursting of a hollow cell-mass. The hollow cell-mass is probably homologous with the basal part of *Erythrotrichia*.

KEY TO THE SPECIES

- 1 a. Young plant forming a hollow cell-mass that bursts and grows out into a monostromatic thallus, usually several blades fixed to the substratum at one point 1. *P. coccinea*
 b. Young plant forming a monosiphonous filament, growing out by lateral division into a monostromatic thallus; only one blade fixed to the substratum at one point 2. *P. vexillaris*

1. *Porphyropsis coccinea* (J. Ag.) Rosenvinge, 1909, p. 69—71; Hamel, 1924, p. 19—20; Printz, 1926, p. 53—54; Newton, 1931, p. 244; Levring, 1937, p. 79; Kylin, 1944, p. 8; Sundene, 1953, p. 180; Feldmann, 1954, p. 64; Taylor, 1957, p. 205. — *Porphyra coccinea* J. Agardh, 1836, p. 6.

Distribution: Widely distributed in the northern Atlantic, along the west coasts of Norway and Sweden, Denmark, along the north-eastern and south coasts of Britain, Brittany, and along the north-eastern coast of the U.S.A.

2. *Porphyropsis vexillaris* (Montagne) Heerebout, *nov. comb.* — *Porphyra vexillaris* Montagne, 1856, p. 450. — *Erythrotrichia vexillaris* (Montagne) Hamel, 1929, p. 53—58; Taylor, 1942, p. 77. — *Bangia grateloupicola* Crouan in Mazé & Schramm, 1870—77, p. 93. — **Fig. 12.**

Distribution: Guadeloupe (Antilles).

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