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THE LIFE HISTORY OF CHROMASTRUM ALARIAE (JÓNSSON) PAPENFUSS (RHODOPHYTA, ACROCHAETIACEAE)

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SUMMARY

Field and culture observations are presented, related to the morphology and life history of *Chromastrum alariae* (Jónsson) Papenfuss in Europe. The life history of *C. alariae* corresponds with the general pattern of the genus *Chromastrum*, showing a combination of a gametophyte with a unicellular base, 1–3 erect axes, a relatively simply built carposporophyte, including 3–4 carposporangia, and a tetrasporophyte with a septately germinating spore and a multicellular base bearing numerous erect axes.

Gametophytes are monoecious. Pairs of spermatangia are formed on the cells of short branchlets, which bear on their top a carpogonium with a lateral trichogyne directed towards the spermatangia.

Influence of temperature and daylength was tested in strains from the Isle of Man and Brittany. Some differences between these strains were observed.

All stages in the life history have been detected in both the type material and herbarium material from Norway and Brittany.

The affinities of the gametophyte generation of *C. alariae*, *C. rhipidandrum* (Rosenvinge) Papenfuss and *C. kurogii* (Lee et Lindstrom) nov. comb. are discussed.

1. INTRODUCTION

Chromastrum alariae has been described by JÓNSSON (1901) as *Chantransia alariae*. Jónsson found the small red seaweed in 1897 growing on *Alaria esculenta* in the Hvammsfjördur, SW-Iceland. As JÓNSSON (1901) stated, the same species had been found earlier in western Norway by Rosenvinge in 1885, in Maine (USA) by Collins in 1894 and by Børgesen in the Faroes in 1895. Since then, the species has been reported in other parts of the north Atlantic Ocean. The specimens have exclusively been found on *Alaria*.

The species under consideration has been placed in the following genera: *Chantransia* (JÓNSSON 1901), *Acrochaetium* (BORNET 1904), *Kylinia* (KYLIN 1944), *Chromastrum* (PAPENFUSS 1945) and *Audouinella* (WOELKERLING 1973). In my opinion, following PAPENFUSS (1945) and STEGENGA & MULDER (1979), this species must be placed in the genus *Chromastrum*, because of the occurrence in the cells of a stellate chloroplast with a central pyrenoid.

The plants described as *C. alariae* all possessed a one-celled holdfast, a fact which led STEGENGA & MULDER (1979) to the conclusion that these plants represent the gametophyte generation. Since previous studies reported that, for this species, only asexual reproduction by means of monospores occurs, this previously mentioned hypothesis had to be proved.

In the present study material from the Isle of Man and Brittany was cultured in order to elucidate the life history of *C. alariae* by applying standard culture techniques including different temperature-daylength combinations.

Herbarium material, including the type material, has also been studied in order to evaluate the results obtained in culture.

2. MATERIALS AND METHODS

Plants of *Chromastrum alariae* were collected and taken into culture from two localities:

a. Great Britain, Isle of Man, Port Erin, the breakwater near the Marine Biological Station; 26-X-1980.

A few plants representing the gametophyte (588) and one plant representing the tetrasporophyte (635) of *C. alariae*, both from phylloids of *Alaria esculenta* growing in the upper sublittoral.

b. France, Brittany, Ile de Sieck, Golhédec; 27-IX-1981.

Many plants, both gametophytes and tetrasporophytes (669, 670), from one phylloid of *Alaria esculenta*, growing in the upper sublittoral. Part of the material was preserved in 4% formalin for morphological study and part was taken into culture.

Numbers in parentheses indicate serial numbers of isolates, in store at the Biologisch Laboratorium, Vrije Universiteit, Amsterdam.

Plants were grown in plastic petri dishes (9 cm diameter), containing c. 20 ml medium. The culture medium, an enriched seawater according to PROVASOLI (1968), was usually changed every two weeks, in some cases the medium was not changed for 2–4 months.

The cultures were kept under 12°C, neutral day (12 h light/12 h dark) conditions, which appeared to be suitable conditions to complete the life history. In order to study reproductive capacity and morphological variability, both gametophytes and tetrasporophytes were cultured at various temperatures (4, 8, 12, 16, 20°C) and daylengths (8, 12 or 16 h light in 24 h, indicated as SD (short day), ND (neutral day) and LD (long day) respectively).

Irradiance in the experiments varied from 11 to 40 μ E $m^{-2}sec^{-1}$, illumination with cool white fluorescent light (Philips 33).

Herbarium material from several localities was studied:

a. France, Brittany, westcoast, Trémazan; 2-VI-1977; as *Acrochaetium alariae* (AVU), collected by H. Stegenga, I. Mol and M. J. van Wissen.
b. Norway, southcoast, Vest Agder, Hille (near Mandal); 14-VII-1967; as *Acrochaetium alariae*, collected by P. Svendsen.
c. Norway, westcoast, Hordaland, Lyroddane (municipality of Sund); 30-VIII-1966; as *Acrochaetium alariae*, collected by P. Svendsen.
d. Iceland, southwest, Hvammsfjördur; 28-VI-1897; as *Chantransia alariae*; holotype (C, Jónsson 597).

Abbreviations for the herbaria are according to the Index Herbariorum (HOLMGREN et al. 1981). The Norwegian material was obtained from the Biological Station of Bergen University at Blomsterdalen.

3. MORPHOLOGY OF FIELD-COLLECTED MATERIAL

3.1. The gametophyte

3.1.1. Isle of Man (*fig. 1*)

Plants had a unicellular base from which 2–3 erect filaments arose; diameter of the basal cell was c. 11 μm. The erect filaments attained a length of about 300 μm, diameter of the filaments was 7–10 μm, cell length 12–20 μm. Branching was scarce. Observations exclusively revealed rather short, mostly secund branches (1–5 cells long) with terminal and lateral monosporangia. Monosporangia measured 10–12 × 13–16 μm. Other reproductive structures were not observed.

3.1.2. Brittany, Ile de Sieck (*figs. 3–7, 61*)

The unicellular base (diameter 11–15 μm) was sometimes provided with a thick wall, forming a flat hyaline foot on the substrate (up to 5 μm broad). 1–3 erect filaments were given off by the basal cell, attaining a length of 400–600 μm. Indeterminate laterals were scarce. Short branches occurred, often bearing monosporangia. The diameter of the filaments was (7–)9–11.5 μm, near the base up to 12.5 μm, cell length in the main axes 11–20 μm, near the base rather constant, c. 12 μm. Monosporangia were not very numerous and were found on the main axes and laterals in pedicellate, sessile or terminal positions. Monosporangia measured 8.5–11(13.5) × (10)13–17(20) μm. Both indeterminate laterals and monosporangia were also found in opposite positions.

On a minority of the plants sexual reproduction was observed (*figs. 4–6, 61*). Carpogonia were found terminally on short branches (1–3 cells long) and measured 5.5–7 × 6–10 μm and were provided with a short lateral or subapical trichogyne (length 4–6 μm). On the cells of the same short axes the spermatangia were found, mostly two per cell. The spermatangia measured 3–4 × 3–5 μm. The trichogynes were directed towards the spermatangia.

The carposporophytes included 3–4 carposporangia, which measured 10.5–12.5 × 14–17(19) μm (*fig. 6*). On one occasion a structure was found which could be called a carpotetrasporangium (or rather a "carpobisporangium") (*fig. 7*).

3.2. The tetrasporophyte

3.2.1. Isle of Man (*fig. 2*)

Only one plant was found, drawn and taken into culture. In the basal part of the plant the original spore was still visible, divided into 4 cells (the structure measured 15 × 22.5 μm). From each of these 4 cells one short, unbranched, prostrate filament originated, diameter 5–7 μm, with cells somewhat longer than

broad. From the prostrate filaments a number of short, unbranched, erect filaments originated, each terminated by a monosporangium. Cells of the erect filaments had a diameter of 7.5–9 μm and were somewhat longer than broad. Monosporangia measured c. 11 × 15 μm.

3.2.2. Brittany, Ile de Sieck (*figs. 8–13, 60*)
Many tetrasporophytes were found, although in lower abundance than the gametophytes. A number of different germination patterns was observed. Usually the original spore was divided in two cells, which together measured 10–14 × 11–18 μm (*figs. 8, 12, 60*). In some cases 3 cells were formed ((9)11.5–14 × (14) 16–20 μm) (*fig. 9*) or 4 cells (14–18 × 18–23 μm) (*fig. 10*) and in very few cases the spore (diameter c. 12 μm) remained undivided and immediately gave rise to prostrate and erect filaments (*figs. 11, 13*). Each of the cells of the (septately divided) spore gave rise to one (or two) creeping filaments (diameter 5–9 μm, cell length 7–15 μm).

The erect filaments originated from the original spore and/or other cells of the prostrate system. The erect filaments attained a length of c. 480 μm and were hardly branched. In the basal parts of the erect filaments cells measured 6.5–9 × 8–14 μm, higher up 8–9(11) × 11–23 μm.

Monosporangia were found in most cases 1 or 2 on a stalk cell, but also sessile and terminal on the axes; they measured (8.5)10–12 × 13.5–18.5 μm. Tetrasporangia were scarce, usually found in terminal positions; they were cruciately divided and measured c. 15 × 20 μm (*fig. 13*).

4. LIFE HISTORY IN CULTURE

At first all strains were cultured under 12 °C ND conditions, which turned out to be favourable conditions for *C. alariae* to grow well and to complete the life history in all strains. In chapter 4.1 and 4.2 primarily the results are given obtained with the strains from the Isle of Man (588, 635) under 12 °C ND; differences between the strains from Man and Brittany (669, 670) are indicated.

4.1. The gametophyte (*figs. 14–39, 81*)
A spore sticks to the substrate (i.e. the plastic wall of the petridish), forms a cell wall and germinates in unipolar fashion. The spore may increase in diameter (from 10–14 μm growing up to 20 μm) and form a thick cell wall (up to 13 μm); sometimes the basal cell (original spore) is somewhat flattened (*fig. 81*). A minority of the plants forms a rather thick, mostly flat foot, up to 10 μm (*figs. 15, 16, 31–33*).

From the one-celled base 1 to 3 erect filaments arise, often not simultaneously. The filaments are often somewhat adpressed to the substrate. The filaments attain a length of about 450 μm in the strains from Man, 700 μm in the strains from Brittany.

Unicellular hairs are very rare and are only formed in very old cultures (2–4 months), in which the culture medium has not been changed. The hairs can attain a length of 220 μm (*fig. 35*).

Cells near the base often become barrel-shaped in older plants, especially in the Man-strains (*figs. 15, 31, 32*), diameter 13–18 (20) μm, length of the first cells near the base 12–18 μm; cell length in the main axes is generally bigger in the middle and top of the plant: (17)20–35(40) μm; diameter in the middle of the filaments 7.5–11(14) μm. The cells contain a stellate chloroplast with a central pyrenoid, some cells contain 2 pyrenoids (*figs. 31, 32*).

Asexual reproduction: Monosporangia are formed on the main axes and laterals, in many cases (1)2–3 on a stalk cell, but sessile or terminal positions can also be occupied (*figs. 15, 16, 30, 31, 38, 81*).

The monosporangia of the Man-strains are usually longer than those from Brittany: 10–12.5(14) × (15)18–20 μm (Man), 10–14 × 11–16.5 μm (Brittany).

The spores are liberated through an apical rupture of the sporangium wall; internal proliferation occurs frequently, as may be the case in all sporangia in the life history.

Sexual reproduction: Spermatangia and carpogonia are formed on short branches (1–3 cells long). At first 2–3 spermatangia are formed on the cells of the branchlet or on small stalk cells; the spermatangia measure 3–4 × 4–5 μm. The terminal cell of the branchlet develops into a carpogonium by forming a subapical-lateral, short trichogyne (maximum length 9–14 μm) directed towards the spermatangia and (thus) towards the main axis. Carpogonia measure (7.5)9–11 × (10)13–14(15) μm in the strains from Man, being somewhat shorter in the strains from Brittany: 10–12 μm (*figs. 17–21, 36–38, 81*). Sometimes more carpogonia are formed on the same branchlet (*fig. 21*). In most cases the carpogonium seems to be fertilized by a spermatium from one of the spermatangia on the same branchlet as the carpogonium.

After fertilization the carpogonium elongates and either divides transversally or remains undivided. In either case the resulting structure gives rise to (3–)4 sessile carposporangia (*figs. 22–25, 39*). Carposporangia measure 11–13(16) × 17–21 μm in the strains from Man, 11–12.5 × 15–22.5 μm in the strains from Brittany.

The carpospores render the tetrasporophyte.

4.2. The tetrasporophyte (*figs. 27, 40–58, 81*)

A spore germinates septately to form a two-celled structure which remains visible during the development of the plant (*figs. 27, 40, 41, 45, 48, 51, 81*). Each of the two resulting cells usually gives off one or two prostrate filaments. In some instances a second division results in a 3–4 celled structure (*figs. 40, 52*) or the spore remains undivided and gives directly rise to prostrate and erect filaments (*figs. 42, 44, 53, 54*).

The prostrate filaments may remain unbranched, short or long (up to 550 μm), but in some cases they branch rather intensively to form a kind of cell plate (*fig. 48*). The cells of the prostrate system measure 5–9 × 10–35 μm.

Cells of the original spore and the creeping filaments may bear one or two erect filaments, which may attain a length of c. 500 μm (sometimes 800 μm in the strains from Brittany). The erect filaments are usually not intensively branched; branching is often irregular and may be alternate, secund or opposite. Filament diameter is (7)8–11(12.5) μm, cell length 20–35 μm, near the base often shorter (c. 15 μm) than in the middle of the filament.

Each cell contains a stellate chloroplast with a central pyrenoid; sometimes 2 pyrenoids per cell can be found, especially in older cells.

Monosporangia occur often on a stalk cell (1–3 together) or sessile, also in opposite positions (*fig. 46*). On the prostrate filaments often typical short erect axes occur, which bear a number of monosporangia (*fig. 47*). Monosporangia measure (10)12–16 × (15)17–22(24) μm in the Man-strains; they are smaller in the Brittany-strains: 11–13 × (11.5)14–17(18) μm.

Occasionally a part of an amoeboid spore is pinched off (*figs. 56–58*).

Under suitable conditions tetrasporangia are practically the only reproductive structures to be formed and can be found in the same places on the plant as monosporangia (*figs. 43, 49, 50, 55*). Their division is cruciate, first division transversal. Tetrasporangia measure (15–)17–20 × (19)22–29 μm in the Man-strains, often somewhat broader and shorter in the strains from Brittany: (17)20–22 × (19)22–26 μm. The diameter of free tetraspores varies from 11 to 14 μm.

Unicellular hairs are very rare and only formed in old cultures.

The life history of *C. alariae* is summarized in *fig. 81*.

4.3. Growth and reproduction under different temperature-day-length regimes

Both generations in all strains grow well and reproduce by monospores in the temperature range 4–16 °C (SD, ND or LD). Under 20 °C LD or SD conditions growth of the gametophyte is very slow and aberrant, the cell contents becomes vacuolate, the chloroplast grows pale and asexual reproduction is practically absent. Gametophytes of the Man-strains die under 23 °C ND conditions. Tetrasporophytes in all strains die under 20 °C conditions.

The formation of sexual organs and tetrasporangia, on gametophytes and tetrasporophytes respectively, is influenced by temperature and/or daylength; see *table 1*.

Formation of sexual organs and fertilization occur from 8 °C until 16 °C, especially under SD conditions. Occasionally some spermatangia and/or carpogonia are formed under 4 °C SD or 20 °C SD/LD, but no fertilization was observed under these circumstances.

Short (maximal length 4 μm), terminal trichogynes, a deviation from the normal position, were found twice in old cultures, under 16 °C ND (Man) and 20 °C LD (Brittany) conditions respectively.

Table 1. Sexual reproduction and tetrasporangia formation under different temperature-daylength regimes.

temp. (°C)	daylength	Gametophyte sexual reproduction		Tetrasporophyte tetrasporangia formation	
		Man	Brittany	Man	Brittany
4	SD	s	s, c	+	+
4	ND	−	−	−	+
4	LD	−	−	++	++
8	SD	++	?	−	+
8	LD	−	−	++	++
12	SD	++	++	−	++
12	ND	++	++	+	+
12	LD	−	−	+	++
16	SD	++	++	−	−
16	ND	+	+	−	−
16	LD	−	+	−	−
20	SD	s	dead	dead	dead
20	LD	−	c	dead	dead

−: absent; +: present (carpogonia, spermatangia and carposporangia in the case of gametophytes); ++: abundant; s: spermatangia; c: carpogonia; ?: unknown

Overall morphology is hardly influenced by the different temperature-daylength regimes.

Cell length in the gametophytes is influenced by daylength (not by temperature); cells in the main axes under SD or ND conditions do not become longer than 35–40 μm, under LD conditions cells may attain a length of 50–60 μm (observed both in the strains from Man and Brittany).

Only in the Man-strains a comparable effect occurs in the erect filaments of the tetrasporophyte, but only at higher temperatures: under LD conditions (at 12°C or higher) cells can become as long as 55 μm, in other conditions cells do not exceed a length of c. 35 μm (as is the case in all experimental conditions for the Brittany-strains).

Other parameters (cell diameter, dimensions of reproductive structures etc.) are hardly influenced by temperature and/or daylength.

5. MORPHOLOGY OF HERBARIUM MATERIAL, INCLUDING THE TYPE MATERIAL

The main reason for examining material from several other sites, including the type from Iceland, was to investigate whether sexual reproduction and/or tetrasporophytes occurred at those localities at the time of collecting; overall morphology and dimensions were also considered (*figs. 59, 62–80*). Results are summarized in *table 2*.

Table 2. Data obtained from examination of herbarium material of *C. alariae*, including the type material.

	Norway		France	Type
locality:	Hille	Lyroddane	Trémazan	SW-Iceland
Gametophyte				
no. erect axes	1–3	(1)2–3	1–2	1–2(3)
max. height	300–470	400	500–700	500–700
cell diameter				
below	7.5–17	8–17	(6.5)9–21	11–22
above	(5)7–8	(6)8–13	(6)9–11	(6)9–12(15)
cell length				
below	15–20	14–19	12–20	20–40
above	24–50	22–40	(20)30–55	24–55
monosporangia				
diameter	8–8.5	8–11	8.5–11	(7.5)10.5–12.5
length	12–17	12–17	(11)12.5–15	15–20
carpogonia			–	
diameter	4.5–6	9		5–7.5
length	5.5–7	9–11		(6)7.5–11.5
trichogyne				
length	4	5–9		4–5
spermatangia			–	
diameter	3	3–3.5		3–4.5
length	4	3–3.5		3.5–6
carposporangia			–	
diameter	10	11–13		11–15
length	16–18	17–21		20–24
Tetrasporophyte			–	
germination-pattern				
no. cells	(1)2(3,4)	(1)2(3,4)		2
prostrate axes				–
cell diameter	5–12	5–9		
cell length	6–9	9–16		
erect axes				
max. length	c. 200	400		>200
cell diameter	7–8(11)	7–9(11)		7.5–9.5
cell length	15–26	18–31		17–28
monosporangia	–	–		–
tetrasporangia	–			
diameter		13–14		17–20
length		17.5–20		27–30

All dimensions in μm; –: absent

In the Norwegian material many tetrasporophytes were present among the gametophytes with sexual stages (*figs. 71–80*). In the material from Trémazan only gametophytes with monosporangia were found (*fig. 70*).

In the type material only one plant, with tetrasporangia, was found which could represent the tetrasporophyte of *C. alariae* (*fig. 63, 69*). Sexual stages could also be detected on the gametophytes in the type material.

The *gametophytes* always had a single basal cell, sometimes provided with a thick wall (up to 3.5 μm) and/or a thick, flat foot (up to 9 μm broad). The erect axes were often somewhat obliquely placed on the basal cell, a feature which could be seen best when only one axis was developed (*fig. 59*).

The development and position of the reproductive organs were comparable with those found in the strains from Man and Brittany (Ile de Sieck) (*figs. 64–68, 70–74*).

The basal parts of the *tetrasporophytes* were often poorly developed (*figs. 69, 75–79*). Only in the material from Lyroddane (Norway) the prostrate filaments attained a length of c. 120 μm. In nearly all plants the original spore germination pattern was still visible: in most cases two cells from which prostrate and/or erect filaments originated (*figs. 69, 75*).

Sometimes a three- or four-celled germination pattern was visible (*figs. 76–79*), only in a few instances the spore remained undivided.

Monosporangia have not been observed, only a few tetrasporangia on the erect axes in the material from Lyroddane (*fig. 80*) and the type material (*figs. 63, 69*).

Branching of the plants was in all cases rather scarce and irregular, only rather intensive in relation to the occurrence of reproductive organs (*fig. 70*).

Hairs have not been observed.

6. DISCUSSION

6.1. The gametophyte

Sexual reproduction has not been reported earlier for *C. alariae*, although present in material now deposited in herbaria and even in the type material (this paper). WOELKERLING (1973) examined the type material, but he did not report sexual reproduction. This is probably due to the particular morphology of the carpogonium with a (short) trichogyne not apically formed on the carpogonium, but laterally or subapically. The lateral position of the trichogyne is rather exceptional within the Rhodophyta, but known to occur in another member of the Acrochaetiaceae, *Audouinella kurogii* Lee et Lindstrom (LEE & LINDSTROM 1979) and in the case of *intercalary* carpogonia lateral trichogynes do occur in *Rhodochorton purpureum* (WEST 1969).

The trichogyne is always directed towards spermatangia and thus enhancing the change of fertilization: the spermatia may stick to the adjacent trichogyne, immediately after their release. This could be advantageous in the environments where these species are found. Both *C. alariae* and *A. kurogii* occur in highly exposed localities where the released spermatia are easily washed away.

The reason why carposporophytes have never been reported might be found in the great resemblance of the carposporophytes, including only 3–4 carposporangia, and the rather common clusters of up to 3 monosporangia on a stalk

cell. In this study, including material from France, Great Britain, Norway and Iceland (type) monosporangia never exceeded a length of 20 μm, carposporangia sometimes did. Probably all reports of monosporangia being longer than 20 μm in fact referred to carposporangia (JÓNSSON 1901, LEVRING 1937, TAYLOR 1957, DIXON & IRVINE 1977).

Dimensions of vegetative cells are quite variable in *C. alariae*, cells often being comparatively broad and short near the base, narrower and longer in the middle and top of the plant. These observations agree with earlier reports (e.g. JÓNSSON 1901). Dimensions of reproductive structures are also rather variable (e.g. *table 2*).

Comparing field collected plants with cultured plants we see that in culture, plants often become somewhat bigger and more branched, especially opposite branching becomes more usual. Dimensions of monosporangia, carpogonia and carposporangia in culture can exceed those in the field.

In culture, cells become considerably longer under long day conditions than under neutral or short days. This result agrees with the field situation; cells in the field collected plants from Brittany (Ile de Sieck) and the Isle of Man (neutral-short day) did not exceed a length of c. 20 μm, whereas cells in the herbarium material (*table* 2), all collected from June to August (long day) were as long as 40–55 μm. Several other species of *Chromastrum* have shown the same long day effect (STEGENGA & VROMAN 1976, STEGENGA & BORSJE 1977, STEGENGA & MULDER 1979).

In culture, sexual reproduction and carposporophytes can be found on plants grown under neutral day and especially under short day conditions (8–16°C). Only in the Brittany strains sexual reproduction was found under 16°C, long day conditions (*table 1*). The requirement of short days for sexual reproduction in culture seems to be contradictory to some findings in the herbarium material. Both the Norwegian and the type material were collected under long day conditions (June-August), yet sexual reproduction was present. On the other hand, plants from the Isle of Man (although very few) were collected under short day conditions (end of October) and nò sexual reproduction was found on these plants. The results obtained with the field collected and herbarium material from Brittany (Trémazan and Ile de Sieck) fit in with those obtained in culture.

Hairs have only been observed in some very old cultures, perhaps they were formed as a reaction to the possible depletion of the culture medium. There are reports of unicellular hairs in *C. alariae* (e.g. JÓNSSON 1901, TAYLOR 1957, DIXON & IRVINE 1977), but they seem to be relatively scarce. This can be illustrated by the fact that both WOELKERLING (1973) and myself were not able to trace hairs in the type material in which JÓNSSON (1901) had seen them.

C. alariae has exclusively been found on *Alaria*. This host selectivity has led JAASUND (1965) to suggest that the cementing substance to fix the basal cell of *C. alariae* on its substrate is probably produced by the basal cell in the presence of some chemical component only yielded by *Alaria*. Our culture experiments have shown that spores, in the absence of *Alaria*, are able to attach to an inert

substrate as plastic and may form a thick mucous foot as well. The reason why *C. alariae* can be found only on *Alaria* remains unknown.

C. alariae is widely distributed in the cold temperature region (MICHANEK 1979) of the North Atlantic Ocean, correlated with the distribution of its host *Alaria*. The species has been reported from New England (COLLINS 1906, WOELKERLING 1973), Nova Scotia (ERSKINE 1956, EDELSTEIN et al. 1969, WILSON et al. 1979) and Newfoundland (SOUTH & HOOPER 1980) in North America and from Iceland (JÓNSSON 1901, MUNDA 1978, 1980), Faroes (BØRGESEN 1902), Norway (KYLIN 1910, LEVRING 1937, JAASUND 1965, JORDE 1966) and the British Isles (DIXON & IRVINE 1977, GUIRY 1978, WILKINSON 1979) in Europe. According to DIXON & IRVINE (1977) *C. alariae* can be found in Greenland, but LUND (1959) and PEDERSEN (1976) do not mention the species. Our collections from Brittany seem to represent the first report of *C. alariae* from France.

Most collections were made from spring until fall, but plants were also found in December (SOUTH & HOOPER 1980) and February (WOELKERLING 1973).

From our culture experiments it has become clear that *C. alariae* is not able to grow in water warmer than 20 °C (*table 1*), a temperature hardly ever encountered by the species in its distribution area.

The distribution of *C. alariae* at a particular locality is rather peculiar. Some *Alaria* phylloids can be almost completely covered with C. alariae, while most *Alaria* specimens of the same population are completely devoid of the small red epiphyte. The red coloured *Alaria* phylloids, which are relatively very rare, have led some authors to the somewhat misleading remark that *C. alariae* is "common" in a particular region (e.g. JORDE 1966).

Some authors have synonymized *C. alariae* with *C. rhipidandrum* (WOELKERLING 1973, Rueness 1977). WOELKERLING (1973) examined both the type specimens of *C. alariae* and *C. rhipidandrum*. Although he found differences, for instance he mentioned that cells of *C. alariae* were often much broader near the base (up to 18 μm) than in *C. rhipidandrum* (up to 13 μm), he considered them conspecific. Apart from the larger dimensions in *C. alariae* more differences between the two species can be put forward. Plants of *C. rhipidandrum* are in most cases unisexual. *C. rhipidandrum* bears in sexual state "normal" bottle shaped carpogonia with a terminal trichogyne and spermatangia in rather intricate, branched clusters (e.g. ROSENVINGE 1909). The carposporophyte includes more carposporangia in *C. rhipidandrum* than in *C. alariae* (ROSENVINGE 1909, STEGENGA & MULDER 1979). Moreover, the tetrasporophyte of *C. rhipidandrum*, known as *C. virgatulum*, is quite different from the tetrasporophyte of *C. alariae* (BORSJE 1973, STEGENGA & MULDER 1979).

Audouinella kurogii and *C. alariae* are probably more closely related. In the cells of *A. kurogii* Lee et Lindstrom (LEE & LINDSTROM 1979) one stellate chloroplast with a central pyrenoid is present. Therefore in my opinion the species belongs to the genus *Chromastrum*, and a new combination is proposed: *Chromastrum kurogii* (Lee et Lindstrom) *nov. comb.* (*Audouinella kurogii* Lee et Lindstrom, Jap. J. Phycol. **27**, 115–122, 1979).

The sexual organs and carposporophyte structure in *C. kurogii* (Lee et Lindstrom) nov. comb. are almost the same as in *C. alariae*. However, enough differences exist between the two species to keep them apart. In *C. kurogii* the very big basal cell lies endophytic in the substrate, i.e. *Constantinea rosa-marina* and gives off 4–6 erect filaments (in *C. alariae* 1–3), the cells in the erect filaments are much smaller than in *C. alariae* and the monosporangia are very small in *C. kurogii* (c. 5 μm).

6.2. The tetrasporophyte

From this study it has become clear that in most cases the tetrasporophyte generation is also present, although often in lower numbers, among the gametophytes of *C. alariae*. In the field they have been overlooked so far, probably because the erect parts of gametophytes and tetrasporophytes are hardly distinguishable, neither based on overall morphology nor based on dimensions of vegetative cells or monosporangia. So when plants do not bear sexual organs or tetrasporangia and if one does not know the morphology of the basal part of a plant, it is not possible to discriminate between a tetrasporophyte or gametophyte.

The germination pattern of the tetrasporophyte is rather variable, as observed both in field collected and cultured specimens, and not as constant as has been reported for other *Chromastrum* species (e.g. STEGENGA & MULDER 1979). The occasionally observed aseptate germination is rather exceptional in the tetrasporophyte of a *Chromastrum* species and thus far only known to occur, although also rarely, in *C. collopodum* (STEGENGA & MULDER 1979). In the cultures where I found aseptate germinations I often saw that relatively large parts of just liberated spores were pinched off. It is not known whether there exists a causal relation between the loss of a part of a spore and the aseptate germination. The loss of small parts of a spore has been reported for *Acrochaetium proskaueri* (WEST 1972) and *A. pectinatum* (WEST 1968).

Plants in culture are usually better developed and more branched than the field collected plants; especially the prostrate part is more extensive and cells in the prostrate system are usually much longer.

Dimensions of sporangia in culture were sometimes different from the field collected specimens: monosporangia became bigger in the Man strains, while in the Brittany strains no difference could be detected. In the Brittany strains tetrasporangia became bigger than in the field collected specimens.

In vegetative state, the tetrasporophytes of the Man strains are completely comparable with those in the strains from Brittany, but the monosporangia of the Man strains are often considerably bigger than in the Brittany strains, while the tetrasporangia in the Brittany strains are often broader and shorter than in the strains from Man.

The dimensions of the tetrasporangia found in the type material are comparable with those found in culture in the Man strains, whereas the tetrasporangia found in the Norwegian material, collected at Lyroddane are comparatively small.

The formation of tetrasporangia is influenced by temperature and daylength (*table 1*). Tetrasporangia are only formed in culture from 4–12 °C in all strains tested, in the strains from Man tetrasporangia are most abundant under long day conditions, while in the strains from Brittany the influence of daylength is less clear.

The occurrence of tetrasporangia in field collected tetrasporophytes from Brittany (Ile de Sieck), growing at the time of collecting under c. 17 °C neutral day conditions, does not agree with the findings in culture, i.e. absence of tetrasporangia above 12 °C.

In the course of my field and culture work on the genus *Chromastrum* I found tetrasporophytes of *C. alariae* only on *Alaria esculenta*, so it seems that the tetrasporophyte generation is also confined to one substrate only.

Together with *Chantransia alariae*, JÓNSSON (1901) described another new member of the Acrochaetiaceae, *Rhodochorton repens*, which also grew on *Alaria esculenta*. *R. repens* was characterized by having a prostrate system with erect axes, with a length up to 1 mm (diameter 8–13 μm, cells being 2–3(5) times as long as broad), bearing only tetrasporangia (14–17 × 20–27 μm). Jónsson was not sure which type of chloroplast was present in the cells. To quote: "The colour of this plant I cannot describe, as I have only got it preserved in alcohol, and on account of its bad condition I am not sure of the shape of the chromatophore, but it seems to be one parietal plate".

Considering the dimensions *R. repens* could represent the tetrasporophyte of *C. alariae*, but in absence of observations on the type material and thus its chloroplast, the status of *R. repens* Jónsson remains uncertain.

6.3. The life history

C. alariae has shown to possess a diplobiontic life history consisting of morphologically dissimilar generations. This result shows a great deal of similarity to comparable studies on other *Chromastrum* species. Borsje and Stegenga et al. have found diplobiontic life histories in *C. virgatulum* (BORSJE 1973), *C. catenulatum* (STEGENGA & VROMAN 1976), *C. hallandicum* (STEGENGA & BORSJE 1977), *C. reductum* (STEGENGA & VAN WISSEN 1979), *C. collopodum* and *C. moniliforme* (STEGENGA & MULDER 1979).

All above mentioned species have a life history with an alternation of a gametophyte with a unicellular base, one or more erect axes, a relatively simple carposporophyte and a tetrasporophyte with a septately germinating spore and a multicellular base.

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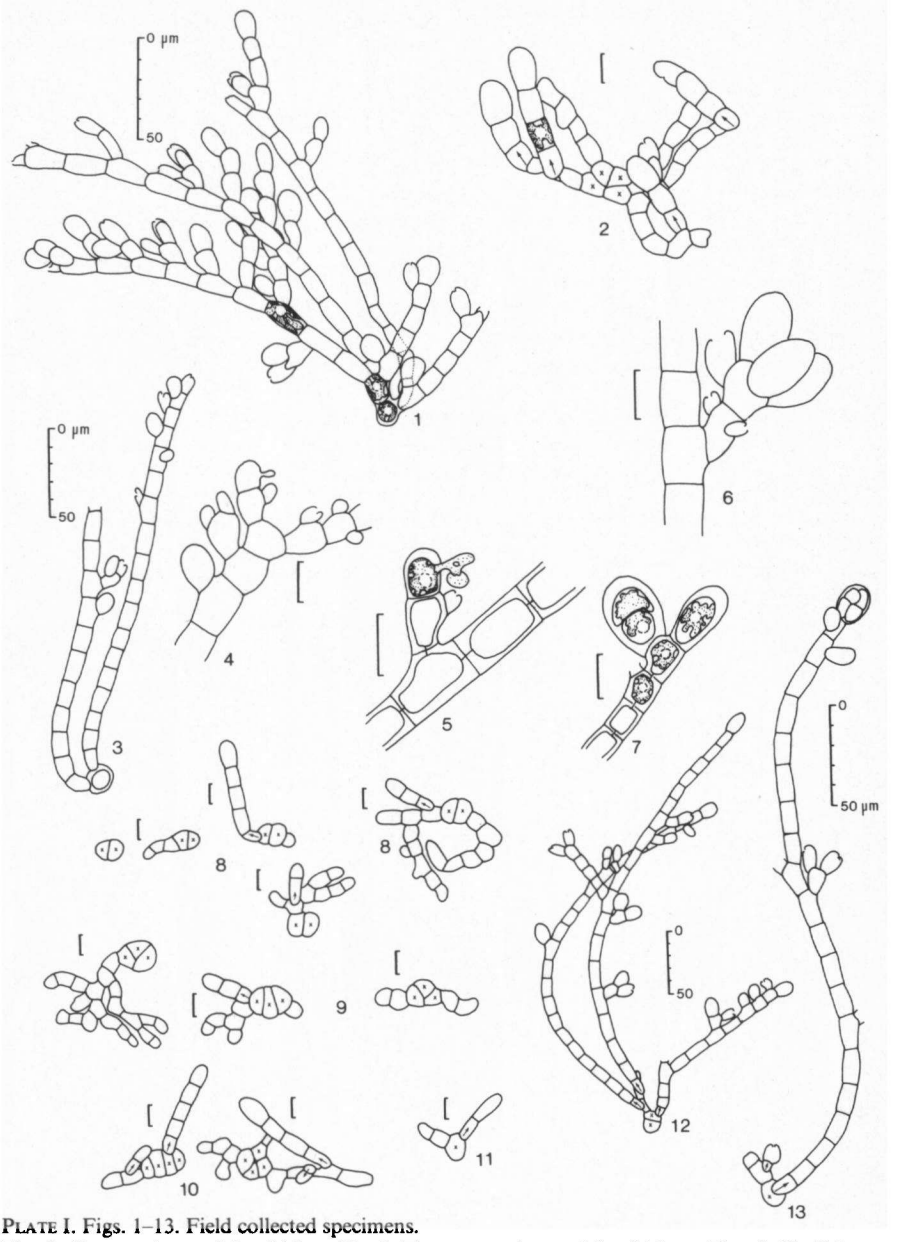

PLATE I. Figs. 1–13. Field collected specimens.

Fig. 1. Gametophyte – Isle of Man, Fig. 2. Tetrasporophyte – Isle of Man, Figs. 3–13. Brittany (Ile de Sieck), Figs. 3–7. Gametophyte, Fig. 3. Monosporangial plant, Fig. 4. Carpogonium, spermatangia, Fig. 5. Fertilization, Fig. 6. Mature carposporophyte, Fig. 7. Carpotetrasporangium, Figs. 8–13. Tetrasporophyte, Figs. 8–11. Germlings, Fig. 12. Monosporangial plant, Fig. 13. Plant with monosporangia and tetrasporangium.

Scale bar represents 10 µm, if not stated otherwise.

Arrow indicates base of erect filament, × indicates cell of original germination pattern.

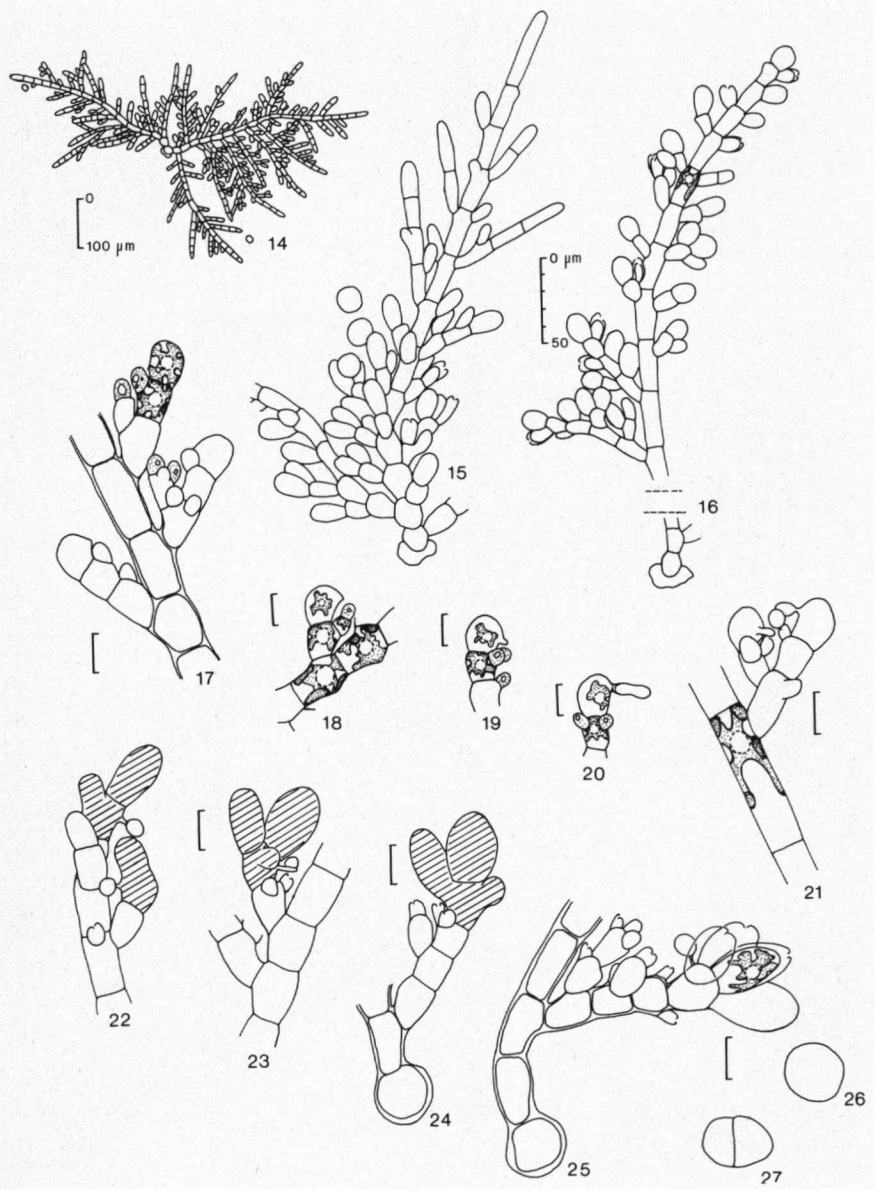

PLATE II. Figs. 14–27. Gametophyte and sexual reproduction in culture.
Figs. 14, 17–27. Strain 588, 12 °C, ND, Fig. 15. Strain 635, 4 °C, ND, Fig. 16. Strain 670, 12 °C, ND.
Figs. 14–16. Monosporangial plants (fig. 16. only basal part and top of the plant), Figs. 17–21. Spermatangia and carpogonia, Figs. 22–25. Developmental stages of carposporophyte, Fig. 26. Free carpospore, Fig. 27. Germination of carpospore.
Scale bar represents 10 µm, if not stated otherwise.

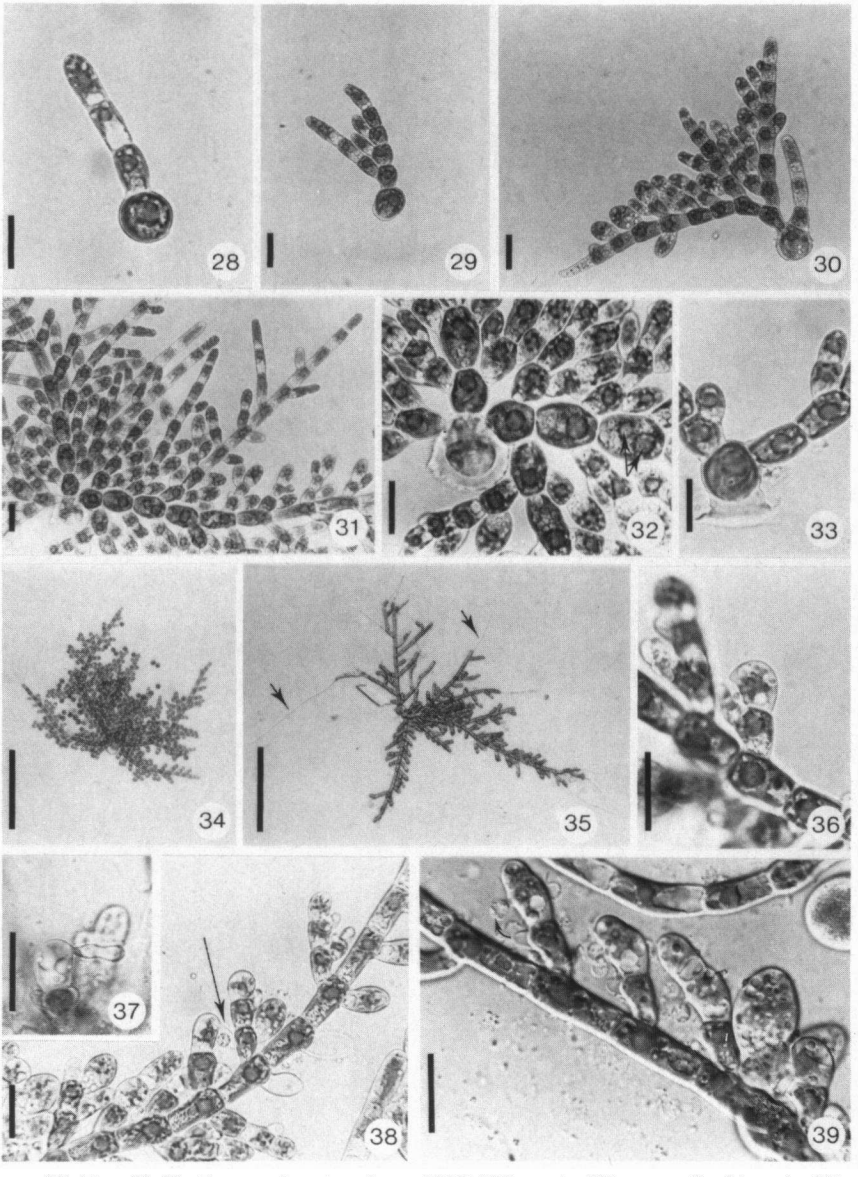

PLATE III. Figs. 28–39. Gametophyte in culture, 12°C, ND; strain 588, except fig. 34 strain 670. Figs. 28, 29. Germlings, Fig. 30. Young, monosporangial plant, Fig. 31. Older, monosporangial plant, Fig. 32. Detail of fig. 31, note thick foot and two pyrenoids in one cell (arrows), Fig. 33. Base with thick foot, Fig. 34. Monosporangial plant, Fig. 35. Old plant with hairs (e.g. arrows), Fig. 36. Young carpogonium, Fig. 37. Mature carpogonium, Fig. 38. Fertilization (arrow), Fig. 39. Developmental stages of carposporophyte (arrow indicates probable way of spermatium). Scale bar represents 20 μm, except in fig. 34, 35 200 μm.

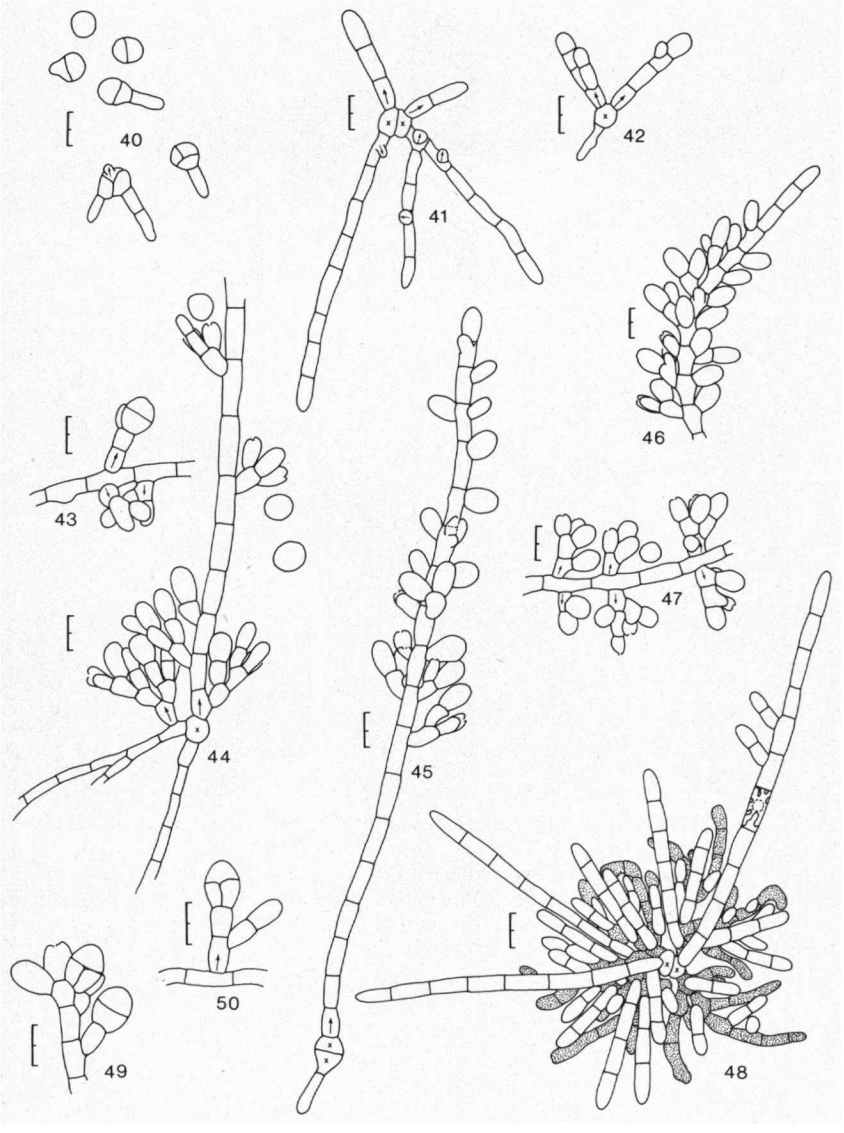

PLATE IV. Figs. 40–50. Tetrasporophyte in culture.
Figs. 40, 41 (16°C, KD), 45, 48–50 (12°C, ND): strain 588, Figs. 44 (12°C, ND), 46 (10°C, ND): strain 635, Figs. 42, 43, 47 (12°C, ND): strain 670.
Fig. 40. Germinating spores, Fig. 41, 42. Germlings, Fig. 43. Tetrasporangium, Figs. 44, 45. Monosporangial plants, Fig. 46. Erect axis with monosporangia, Fig. 47. Monosporangia on short erect axes, Fig. 48. Plant with compact prostrate part, Fig. 49, 50. Tetrasporangia.
Scale bar represents 20 μm, divided in two.
Arrow indicates base of erect filament, x indicates cell of original germination pattern.

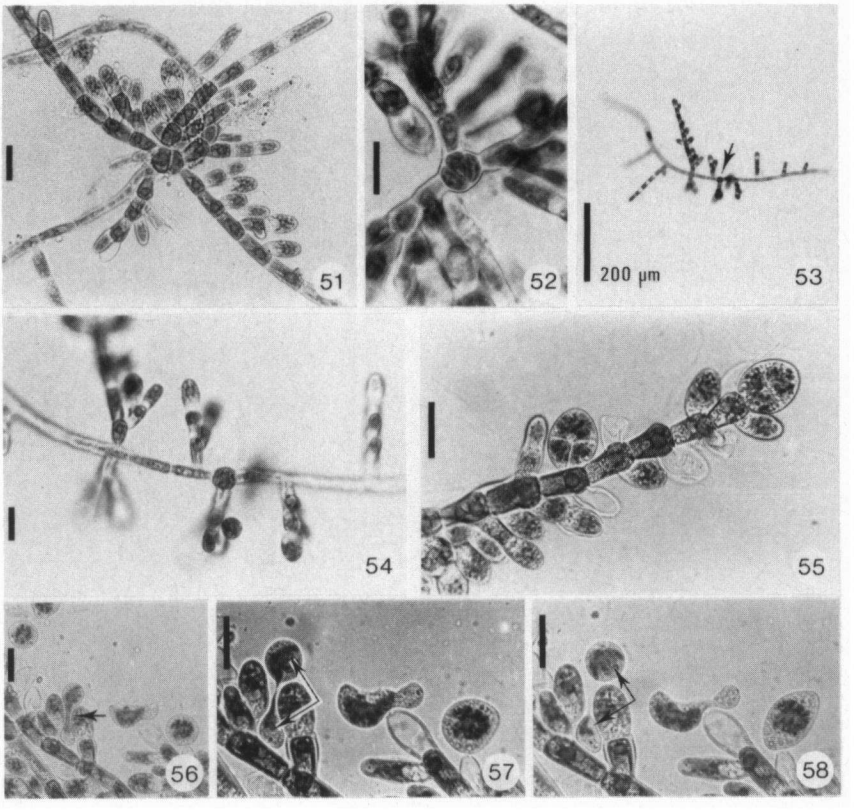

PLATE V. Figs. 51–58. Tetrasporophyte in culture (12 °C, ND), Figs. 51–54, 56–58: strain 588, Fig. 55: strain 635.
Figs. 51–53. Monosporangial plants with different germination patterns (arrow in fig. 53 indicates original spore), Fig. 54. Detail from fig. 53, Fig. 55. Tetrasporangia, Figs. 56–58. Amoeboid spores, a part of a monospore being pinched off (arrows).
Scale bar represents 20 µm, if not stated otherwise.

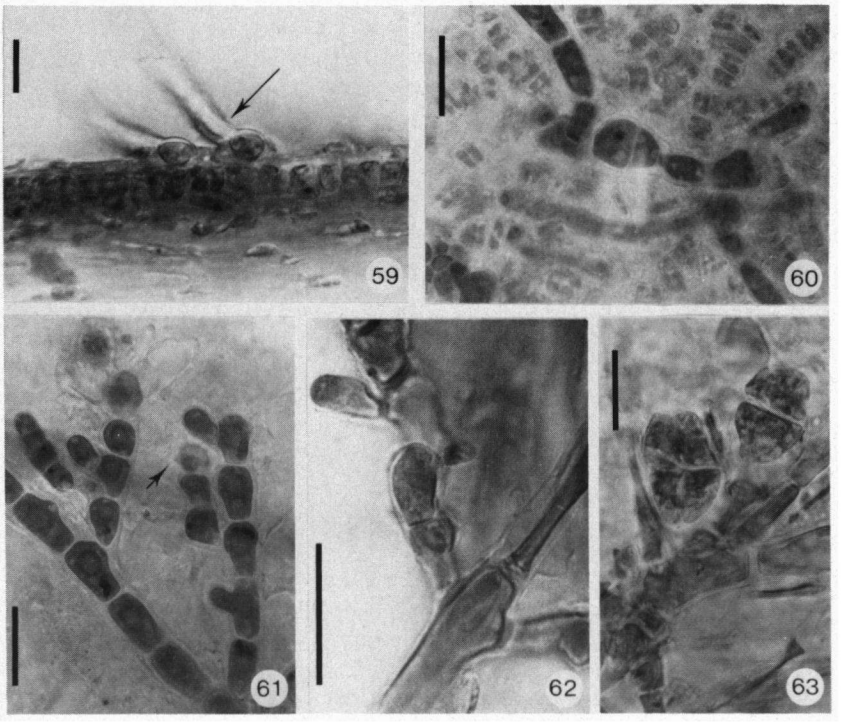

PLATE VI. Figs. 59–63. Field collected, herbarium and type material.
Fig. 59. Cross section of *Alaria esculenta*, note two basal cells of gametophytes with erect axis (arrow) (Brittany, Trémazan), Fig. 60. Tetrasporophyte with two-celled germination pattern (Brittany, Ile de Sieck), Fig. 61. Young carpogonium (arrow) (Ile de Sieck), Fig. 62. Carpogonium (type material), Fig. 63. Tetrasporangia (type material).
Scale bar represents 20 μm.

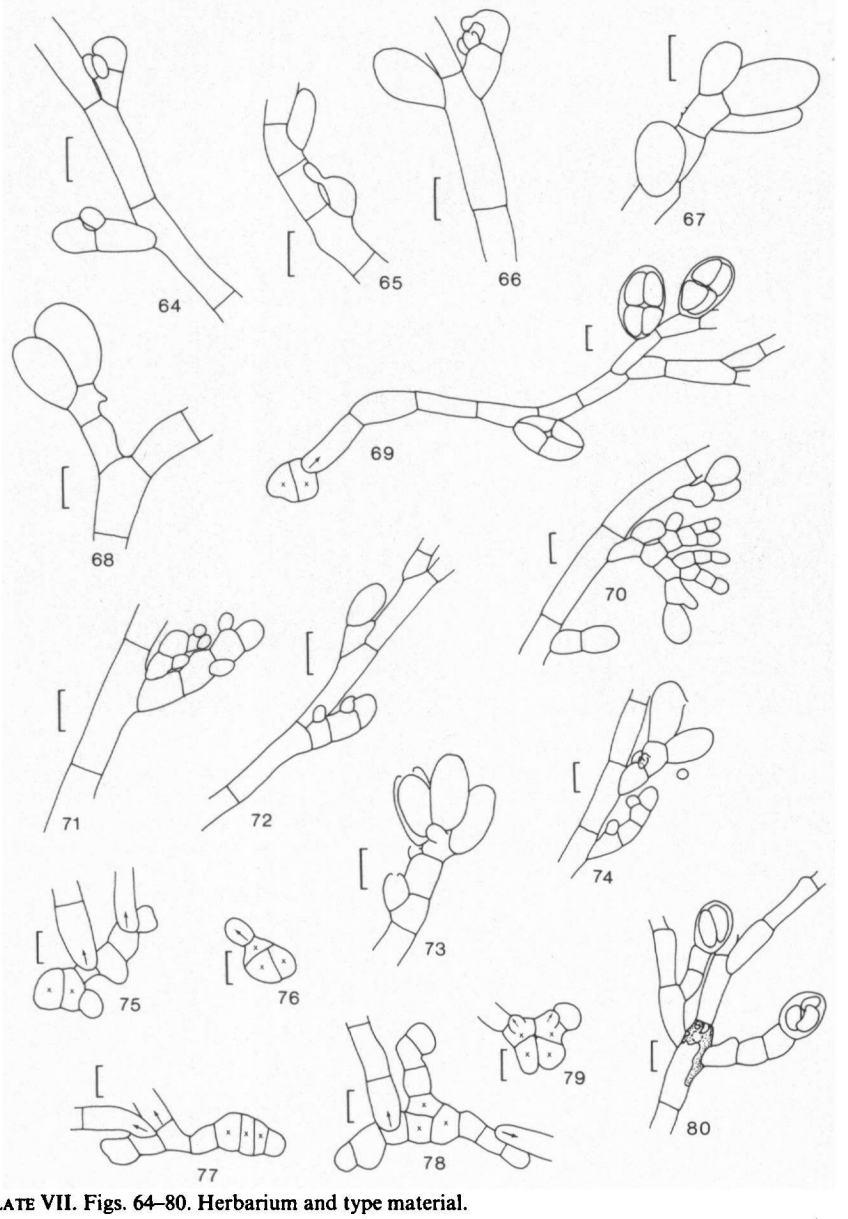

PLATE VII. Figs. 64–80. Herbarium and type material.
Figs. 64–69. Type material, Figs. 64–66. Carpogonia, spermatangia, Figs. 67, 68. Carposporophytes, Fig. 69. Tetrasporangia, Fig. 70. Monosporangia (Brittany, Trémazan), Fig. 71, 72. Spermatangia, carpogonia (Norway, Hille), Fig. 73. Carposporophyte (Norway, Hille), Fig. 74. Spermatangia, carpogonia, carposporophyte (Norway, Lyroddane), Figs. 75–79. Germination patterns of tetrasporophyte (Norway, Hille), Fig. 80. Tetrasporangia (Norway, Lyroddane).
Scale bar represents 10 μm. Arrow indicates base of erect axis, x indicates cell of original germination pattern.

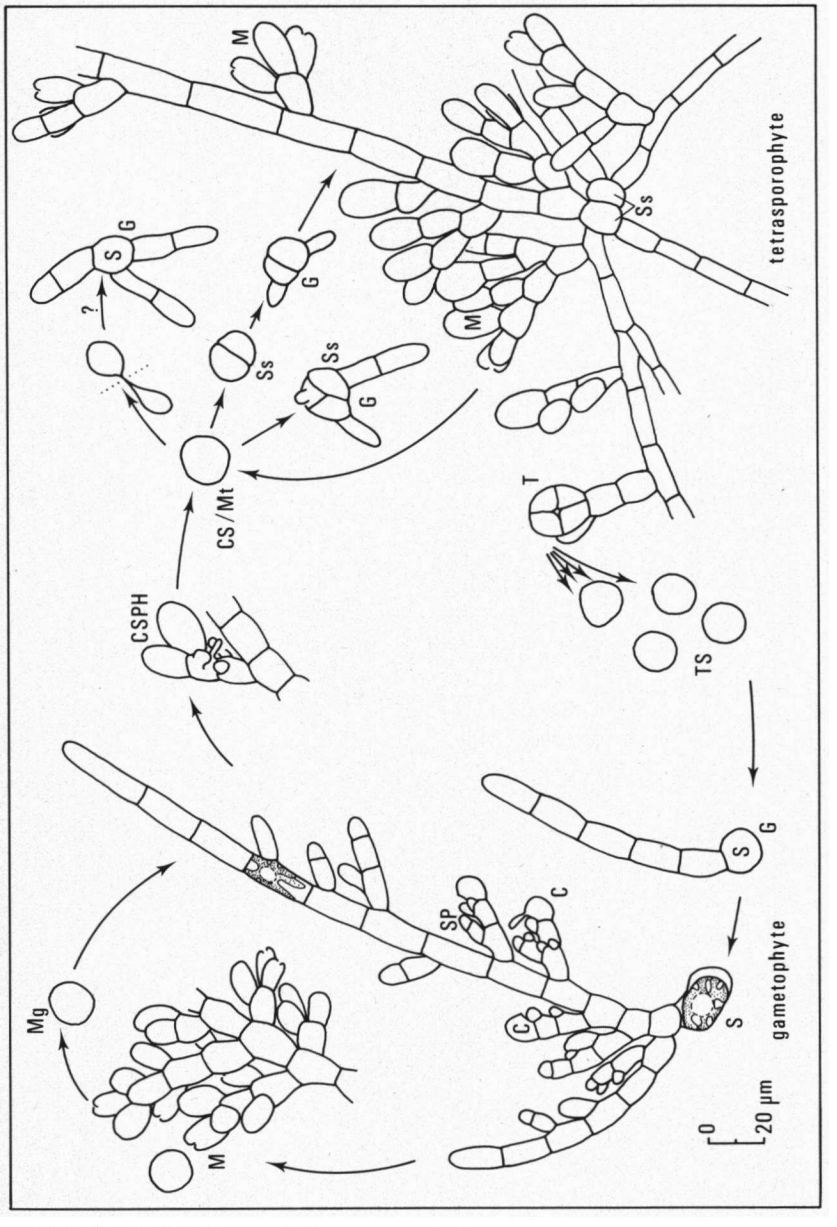

PLATE VIII. Fig. 81. Life history of *Chromastrum alariae*.
Legend: C = carpogonium, CS = carpospore, CSPH = carposporophyte (young), G = germling (either generation), M = monosporangium (either generation), Mg = monospore (gametophyte), Mt = monospore (tetrasporophyte), S = original spore – persistent, SP = spermatangium, Ss = original spore – septate, T = tetrasporangium, TS = tetraspore.