Acta Bot. Neerl. 28(4/5), August 1979, p. 289–311

REMARKS ON THE AUDOUINELLA MICROSCOPICA (NÄG.) WOELKERLING COMPLEX, WITH A BRIEF SURVEY OF THE GENUS CHROMASTRUM PAPENFUSS (RHODOPHYTA, NEMALIALES)

H. STEGENGA and A. S. MULDER

Vakgroep Plantensystematiek, Vrije Universiteit, de Boelelaan 1087, 1081 HV Amsterdam

SUMMARY

Observations are presented on the life histories and morphological variability of Swedish material of *Chromastrum moniliforme* (Rosenvinge) Papenfuss and *Chromastrum collopodum* (Rosenvinge) Papenfuss. The life history of *C. moniliforme* fits in with the general pattern of the genus *Chromastrum*, showing a combination of a gametophyte with a unicellular base and a tetrasporophyte with a septately germinating spore and a multicellular base. The same holds true for *C. collopodum*, except that in the tetrasporophyte the germination is occasionally aseptate. It is concluded that the nature of variation between some members of the *Audouinella microscopica* (Näg.) Woelkerling complex is largely genotypic, and our work does not support the hypothesis of their conspecificity.

In addition, a brief survey is given of the genus *Chromastrum* Papenfuss, with an evaluation of most morphotaxonomic characters. Some 60 described species are presently thought to belong to this genus. A considerable reduction of this number must be anticipated for two reasons: first, generations of one life history have usually been described as two different systematic entities; second, morphologically similar species may prove conspecific, in view of the variability of some characters in culture. The genus *Chromastrum* is cosmopolitan, with probably a maximum diversity in the North Atlantic Ocean, and a low representation in tropical seas.

1. INTRODUCTION

The *Audouinella microscopica* (Näg.) Woelkerling complex was established in the present form when WOELKERLING (1972) concluded to conspecificity of 7 species of acrochaetioid algae, namely *Acrochaetium catenulatum* Howe, *Acrochaetium crassipes* Børgesen, *Acrochaetium compactum* Jao, *Acrochaetium microfilum* Jao, *Acrochaetium microscopicum* Nägeli, *Chantransia collopoda* Rosenvinge and *Chantransia moniliformis* Rosenvinge. This conclusion was based on comparative studies of types and material of New England and Australian populations.

Having recognized two species of this complex in isolates from the Swedish coast, we decided to study morphological variability of each, to determine the nature of the differences which apparently existed when these species were collected in the field. The species concerned are *Chantransia collopoda* and *C. moniliformis*.

Also, having recognized the species under consideration as belonging to the gametophytic part of the genus *Chromastrum* Papenfuss (sensu STEGENGA & VROMAN 1977), further studies of their life histories were made in order to obtain a more complete picture of this genus (cf. STEGENGA & BORSJE 1977). The name

Chromastrum will further on be applied to the relevant species, which in some cases has necessitated the use of new nomenclatural combinations.

Chromastrum collopodum is exclusively found on *Chordaria flagelliformis*, where the basal cell is attached to the apex of the assimilatory filaments of the substrate; the mucilaginous thickening of the basal cell wall, especially at the side attached to the substrate, is characteristic.

Chromastrum moniliforme has been recorded from more substrates. It is characterized by its barrel-shaped cells, while the basal cell does not deviate much in shape and size from the other vegetative cells.

The name *Chromastrum* in connection with a group of acrochaetioid algae was proposed by PAPENFUSS (1945), but has been in disuse since he (PAPENFUSS 1947) replaced it by *Kylinia*. It was reinstated by STEGENGA & VROMAN (1977), and connected with a special type of life history. Since several species have been studied experimentally now, we will give a brief survey of this genus, with a discussion of some morphotaxonomic characters used in species delimitation. The survey is provisional and does not claim completeness. Remarks on geographical distribution are necessarily of the same tentative nature.

2. MATERIALS AND METHODS

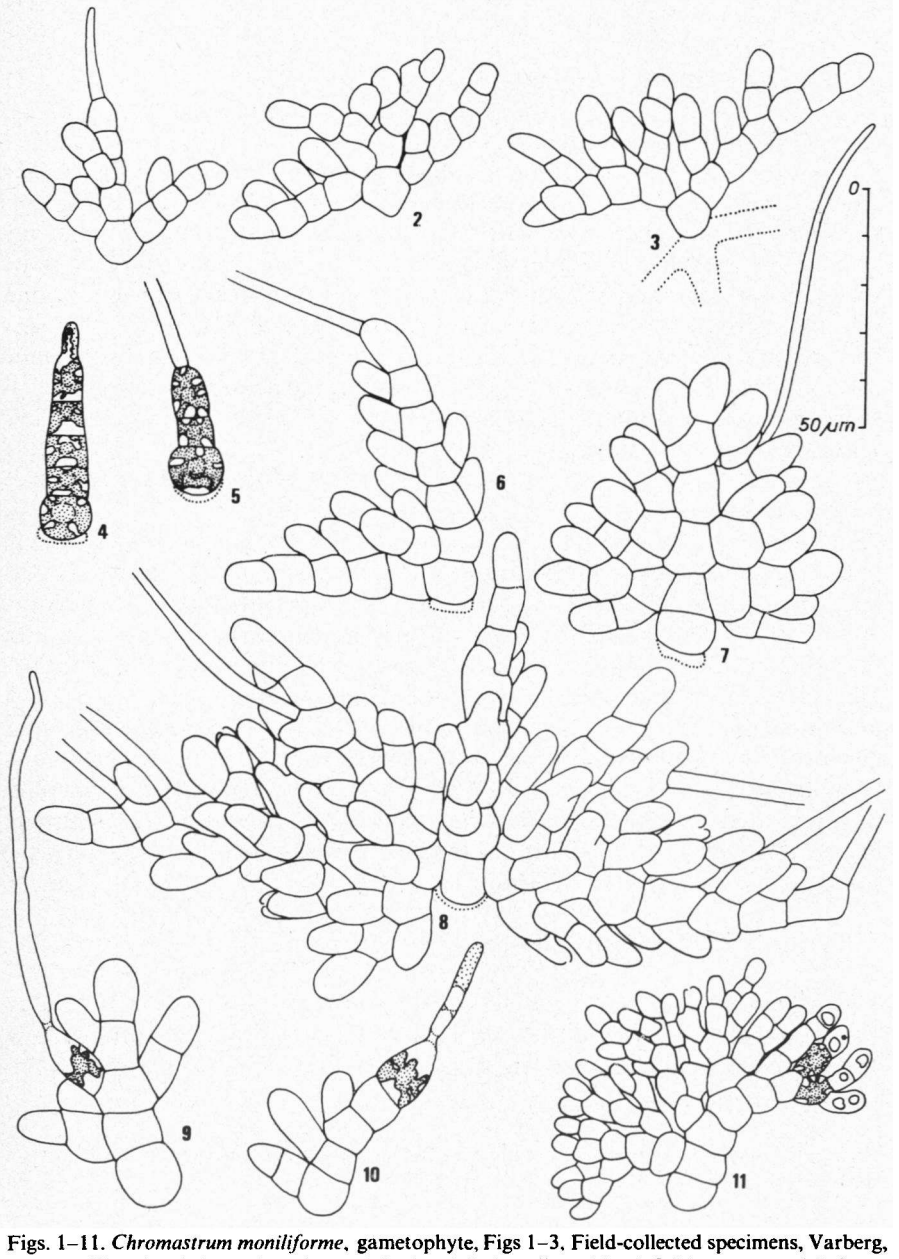
Material of *Chromastrum moniliforme* was collected 19-VI-1976 at Varberg (Halland) from *Ceramium* sp. (414) and *Polysiphonia* sp. The tetrasporophyte of this species, then identified as *Chromastrum humile*, was collected 3-VIII-1976 at Kristineberg (Bohuslän) from *Chorda tomentosa* (372) and *Ectocarpus* sp. (376, 424).

Material of *Chromastrum collopodum* was collected 5-VIII-1976 at Stora Testholmen, from *Chordaria flagelliformis* (392). Numbers in parentheses indicate serial numbers of isolates, in store at the Botanical Laboratory, Free University, Amsterdam.

Used culture methods were not different from those described in earlier studies on acrochaetioid algae (e.g. STEGENGA & VROMAN 1976). The culture medium, an enriched seawater according to PROVASOLI (1968), was changed every 2 weeks in the experiments. Plants were grown in plastic petri-dishes (9 cm diameter), with usually glass cover slips serving as a substrate for the plants.

Morphological variability of *C. moniliforme*, both gametophyte and tetrasporophyte, was studied in crossed gradients of light intensity (range: 125–4500 lx) and temperature (range: 2–30 °C) under a 12/12 daylength regime. Morphological variability and reproductive capacity of *C. collopodum* were studied by applying different temperatures (4, 8, 12, 16, 20 and 24 °C) and two different daylengths (8/16 and 16/8 photoperiods) while light intensity was kept at *c.* 1750 lx.

A study of the type material of *Chromastrum microscopicum* (Näg.) Papenfuss from Leiden (Herb. Lugd. Bat. 940 285 306) was made in order to shed some light on nomenclatural questions.



Figs. 1–11. *Chromastrum moniliforme*, gametophyte, Figs 1–3, Field-collected specimens, Varberg, 19 June 1976, Figs. 4–11. Cultured material, Figs. 4, 5. Germlings, Figs 6–8. Monosporangial plants. Figs. 9, 10. Carpogonia, Fig. 11. Spermatangia.

3. OBSERVATIONS

3.1 Field-collected material

3.1.1 *C. moniliforme (figs. 1–3).*

Plants are small, up to *c.* 60 μm high, and consist of 2–3 erect filaments, arising from a basal cell; diameter of the basal cell is *c.* 10 μm; diameter of the filaments is 7–8 μm, near the apex tapering to 5 μm. Cells are about as long as broad and somewhat barrel-shaped. Filaments are secundly branched; unicellular hairs are sometimes present. In our samples apparently only juvenile plants were present, since no reproductive structures, sexual or asexual, were found; this fact may also account for the somewhat smaller cell dimensions than in the original description by ROSENVINGE (1909). The tetrasporophyte was only recognized as such after culture studies had been performed; low abundance did not allow observations on wild material of this generation.

3.1.2 *C. collopodum (figs. 21–26).*

Plants reach a height of *c.* 100 μm, exclusive of hairs. The basal cell is 8–10 μm in diameter, on germination about isodiametric, later on more elongate; it possesses a thick foot of cementing substance, which usually forms a cap on the apical cells of the assimilatory filaments of *Chordaria flagelliformis*. 2–4 erect filaments are given off by the basal cell; cells are 5–7 μm in diameter, 8–13 μm long, the length/diameter ratio is 1.5–2. Branching is scarce. Hairs, up to 250 μm in length, are numerous on older specimens, but also may be the first cells to be given off by a germinating spore. Monosporangia are borne terminally and laterally on main axes; they measure *c.* 10 × 6 μm. Other reproductive structures were not observed. Cell dimensions, and especially cell diameter, fall somewhat below values given by ROSENVINGE (1898) and WOELKERLING (1972). Only the gametophyte was found in the field.

3.2 Morphology and life history in culture

3.2.1 *C. moniliforme (figs. 4–20, 39, 40; table 1)*

The gametophyte *(figs. 4–8, 39, 40; table 1)*. Experiments under different conditions were done with clones 376, 414 and 424. Growth of the gametophyte is

Table 1. *C. moniliforme*, interclonal variation. Values (in μm) show variation in cell dimensions of plants grown at 8 and 16°C, short, neutral and long day. t = tetrasporophyte.

strain	376–♂	424–♀	376–t	414–t	424–t
cell length	7.3–10.8	6.5–11.0	6.7–12.2	7.5–12.7	7.9–11.8
cell diameter	6.9–10.2	7.1– 9.6	6.1–10.8	6.2–10.4	6.1–10.6
monosporangial length	10.5–13.8	10.8–13.8	11.3–12.8	10.4–12.5	10.5–13.1
monosp. diameter	7.3– 9.0	6.7– 9.6	6.5– 7.7	6.5– 7.9	6.8– 7.8

limited to about 7–10 cells in height because of terminal monosporangium formation after that stage. The growth optimum is 15°C, but it continues for a longer time at low temperature, so that after 4 weeks plants of maximum height are found at 8°C *(fig. 39)*. Spore germination and growth take place in a temperature range of 2–26°C.

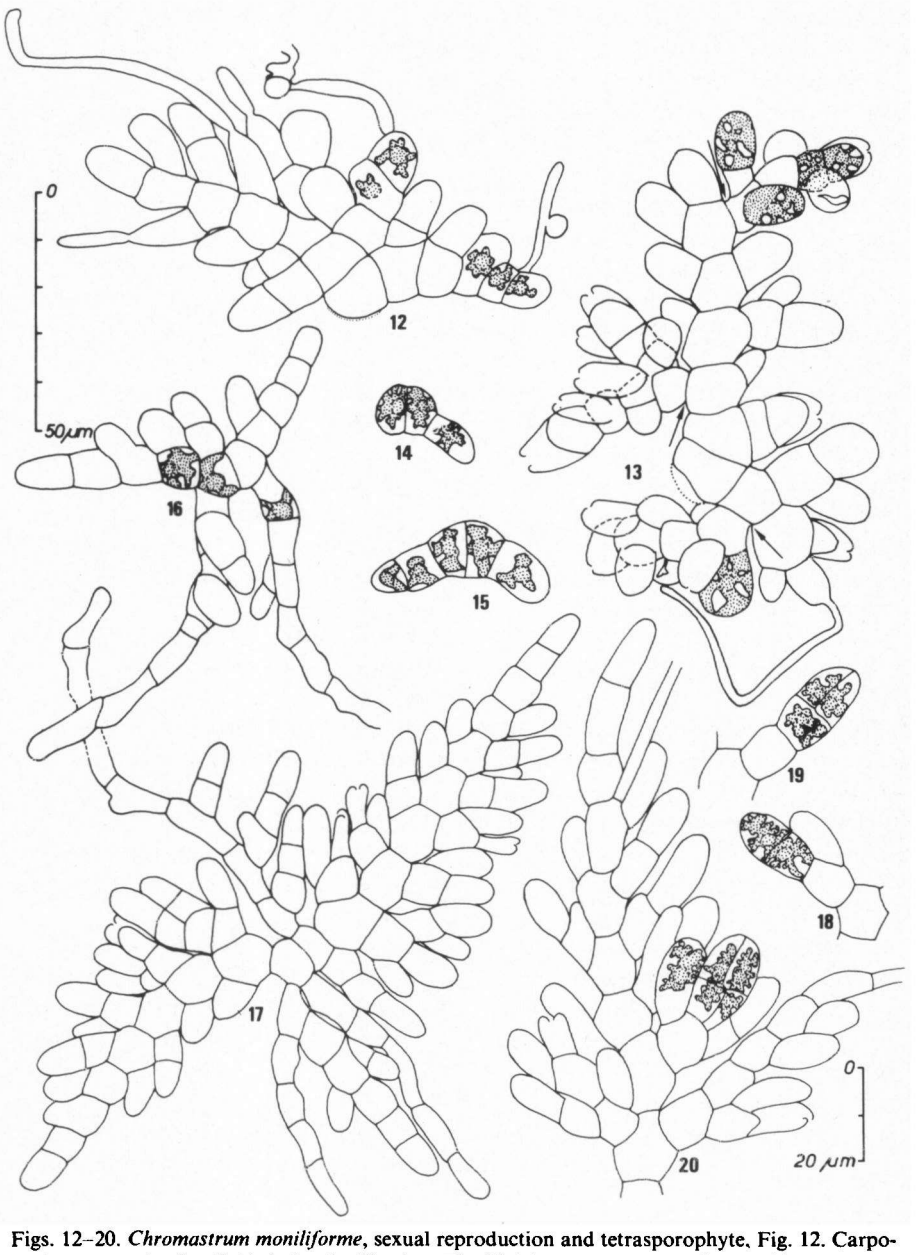
Diameter of the basal cell is 8.5–11.5 (12.5) μm. The number of erect filaments is 1–3 (4), the highest numbers occurring under low temperatures (2–15°C). Filament diameter is (7)8–11 μm in the middle of mature plants, tapering to 5.5–7.5 μm at the apex; it is not notably influenced by light or temperature (the low values found at 2°C most likely reflect the immaturity of the plants; cell diameter apparently increases during the growth period). Cell length is 6–11(12) μm, and reaches maximum values at low temperature and high light intensity *(fig. 40)*. Branching of the main filaments is secund, later opposite, and in much branched specimens up to 4 laterals per cell, placed in a whorl, are finally ›rmed. Branching frequency and pattern appear to be especially sensitive to culture density; in high density branching frequency will be low. This rule also applies to individual plants: in older specimens branching frequency will gradually decrease because of increasing 'intrinsical density'. Hairs are most abundant under a combination of low temperature and high light intensity; they measure up to 250 μm. Monosporangia, terminal and lateral on main axes and branches, measure (8)10–13(15.5) × (6)7–9(10.5) μm, attaining maximum length at 15°C; the diameter was fairly uniform in the tested range of culture conditions.

Sexual reproduction *(figs. 9–13)*. Gametangia were formed at a temperature of 16°C, while for light conditions short day or low light intensity was required. Plants appeared to be largely unisexual. Spermatangia (clone 376) are formed singly or with 2 or 3 together, terminally on branches of acropetally diminishing diameter. Spermatangia measure *c.* 6 × 4 μm. Carpogonia (clone 424) take a terminal or lateral position on the main axes; they measure *c.* 12 × 6.5 μm, trichogynes are up to 100 μm long and 2.5 μm in diameter.

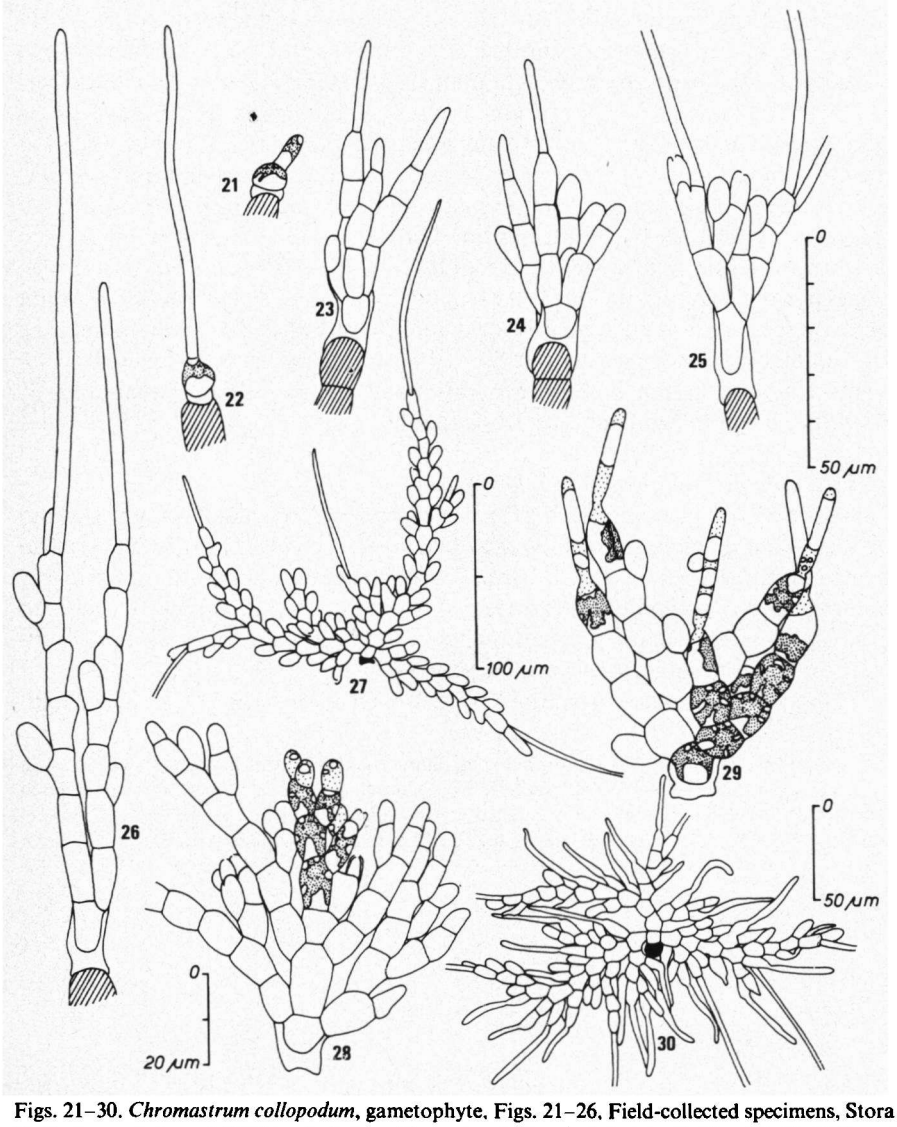
Carposporophytes were formed in aerated cultures of ♀ and ♂ gametophytes. As a rule the fertilized carpogonium undergoes 2 transverse divisions. After this the lowermost cells may each form a one or two-celled branchlet. Finally each cell of the carposporophyte develops 1–3 carposporangia. Mature carposporangia measure *c.* 12 × 10 μm.

The tetrasporophyte *(figs. 14–20, 39, 40: table 1)*. The tetrasporophyte, like the gametophyte, survived and formed monosporangia in a temperature range of 2–26°C, but died at 30°C. Carpospores (and also tetrasporophytic monospores) germinate septately, dividing into two equal halves. From both resulting cells one or two prostrate filaments arise. Both the original spore and the prostrate filaments give off erect axes. The divided spore is 10–13.5 μm in largest diameter; it remains recognizable for a considerable time in older plants. Growth of the prostrate filaments is indeterminate.

Erect axes much resemble those of the gametophyte, and at first are just as



Figs. 12–20. *Chromastrum moniliforme*, sexual reproduction and tetrasporophyte. Fig. 12. Carpogonia, once and twice divided after fertilization. Fig. 13. Mature carposporophytes with carposporangia (arrows indicate base of carposporophyte). Figs. 14–16. Germlings of tetrasporophyte. Fig. 17. Monosporangial tetrasporophyte. Figs 18–20. Developmental stages of tetrasporangia.



Figs. 21–30. *Chromastrum collopodum*, gametophyte. Figs. 21–26. Field-collected specimens, Stora Testholmen, 5 August 1976 (assimilatory filaments of *Chordaria* hatched). Figs 27–30. Cultured material. Fig. 27. Monosporangial plant. Fig. 28. Spermatangia. Figs. 29, 30. Carpogonia.

determinate in growth because of terminal formation of monosporangia; however, growth was found to continue after monosporangium production had ceased (*fig. 39*; 22 and 26°, high light intensity). Cell diameter in the middle part of the erect filaments is (5)6–10 μm; lowest cell diameters were measured on immature plants (2°C and lowest light intensities) and should not be taken as effects of either temperature or light. In mature filaments cell diameter is somewhat influenced by temperature, highest diameters occurring at 8 and 15°C. Cell length varied between 5 and 12 μm, and increased with light intensity (*fig. 40*). Monosporangia measure (9.5)10–12(13.5) × (6).5–8 μm; on an average, monosporangia were 2 μm longer under high light intensity than under low light intensity. Tetrasporangia were formed in low quantities, at 8°C, neutral and long day; on maturity they measured *c.* 20 × 10 μm, their division is cruciate.

Interclonal variation of both generations of the few clones isolated as *C. moniliforme* was insignificant, as illustrated by *table 1*.

3.2.2 *C. collopodum (figs. 27–36; tables 2, 3)*

The gametophyte (*fig. 27*). The basal cell (without mucilaginous thickening) is 5–9.5 μm in diameter; typically, the thick layer of cementing substance is also formed in culture, but usually in a semi-globose shape. Spores germinated in low quantity, and development often seemed aberrant. Best results were obtained immediately after isolation, when plants could be grown for a while in combination with the substrate *Chordaria flagelliformis*.

2–3 erect filaments arise from the basal cell. Cell diameter is 5–8 μm, cell length

Table 2. *Chromastrum collopodum:* Morphological characteristics of the gametophyte (392, ♀) under various experimental conditions. Values are averages of measurements on 5 plants; measurements at 4 and 8°C after 4 weeks, otherwise after 2 weeks; cell dimensions in μm; – means absence of relevant structure. N.B.: Deviation of culture scheme at 12°, 12/12 because of breakdown of 12°, 8/16 facilities.

temperature (°C)	daylength	basal cell diameter	number of erect axes	vegetative cells (length × diameter)	monosporangia (length × width)	carpogonia (length × diameter)	max. trichogyne length	max. hair length
4	8/16	7.7	2.7	11.0 × 5.6	11.4 × 5.8	13.3 × 5.4	42.2	336
	16/8	8.0	2.6	12.0 × 6.0	12.4 × 6.6	–	–	420
8	8/16	7.6	2.0	10.9 × 7.5	11.5 × 6.2	13.3 × 6.4	45.0	285
	16/8	7.9	3.0	13.6 × 5.8	11.7 × 5.8	–	–	547
12	12/12	7.1	2.4	10.8 × 5.6	11.0 × 5.8	12.1 × 5.6	32.6	365
	16/8	7.0	2.8	11.3 × 6.6	11.3 × 6.2	–	–	570
16	8/16	10.3	3.4	10.1 × 7.5	11.8 × 6.9	13.7 × 6.4	40.0	245
	16/8	7.7	3.6	12.4 × 6.5	12.3 × 6.5	–	–	422
20	8/16	7.5	2.4	10.9 × 6.1	10.2 × 5.9	15.3 × 6.2	26.9	269
	16/8	7.3	3.4	11.9 × 7.1	12.0 × 6.9	14.8 × 6.3	22.5	425

Table 3. *Chromastrum collopodum:* Morphological characteristics of the tetrasporophyte (392) under various experimental conditions. Measurements after 2 and 4 weeks; () means occurence in los numbers. For other remarks see table 2.

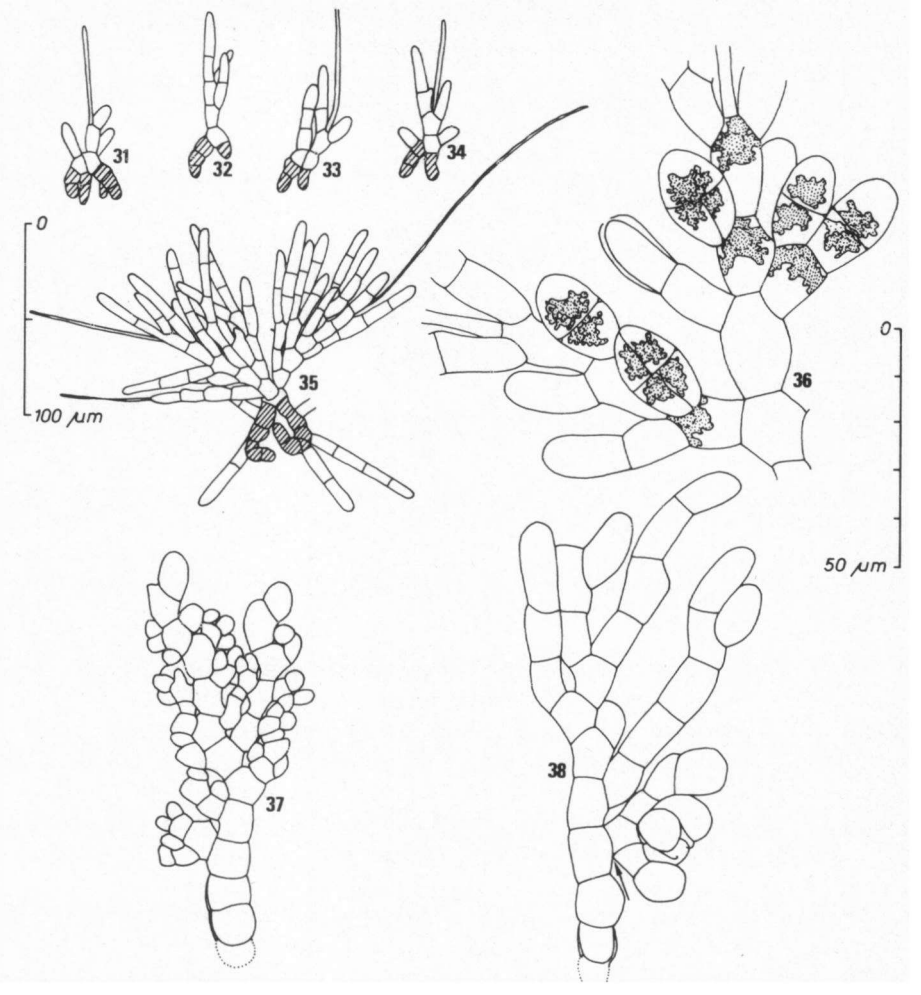
temperature (°C)	daylength	vegetative cells (length × diameter)	monosporangia (length × width)	tetrasporangia (length × width)	Max. hair length
4	8/16	17.3×6.5	17.6×8.1	(19.2×7.7)	–
	16/8	15.7×6.5	18.7×9.0	(22.5×7.5)	155
8	8/16	14.9×7.4	16.5×7.5	–	(105)
	16/8	13.7×7.7	16.6×7.1	–	282
12	12/12	16.6×7.1	16.8×8.0	–	336
	16/8	16.9×8.0	15.5×7.7	–	408
16	8/16	14.1×8.1	16.8×8.6	–	–
	16/8	16.8×7.3	17.8×8.3	–	547
20	8/16	14.6×6.3	16.3×8.7	–	(123)
	16/8	15.2×7.3	16.3×7.6	–	385

(7)10–15 μm. Indeterminate laterals are scarce, but reproductive organs are often numerous, be it monosporangia or gametangia, the ♀ and ♂ sexual reproductive structures being formed on separate plants. Monosporangia are borne in opposite positions on the main axes and measure 9.5–13 × 5.5–8 μm. Plants were found to survive in a temperature range of 4–20°C, and they developed monosporangia in all these conditions. The variation of cell dimensions in connection with variation in experimental conditions was insignificant *(table 2)*.

Sexual reproduction *(figs. 28–30)*. Spermatangia, terminal on main axes and branchlets, measure 5–7 × 3.5–4 μm. Carpogonia develop principally on the main filaments; they measure 12–16 × 5.5–8 μm; trichogynes are up to 45 μm long and 3–4 μm in diameter. Carpogonia were formed in the temperature range 4–20°C, usually only at short day *(table 2)*.

Although we did not observe fertilization and development of carposporophytes in this species, we rather soon found germlings with aberrant germination type in gametophyte cultures; these germlings turned out to represent tetrasporophytes.

The tetrasporophyte *(figs. 31–36)*. A spore germinates septately to form a two-celled structure, or an aseptate spore directly gives rise to creeping filaments. In either case the prostrate system remains very small. Erect filaments arise from the prostrate system, including the original spore. Filament diameter is (4)6–10 μm, the narrowest cells occurring near the apex; cell length is (10)13.5–17.5(23) μm. The number of indeterminate laterals is in general higher than in the



Figs. 31–36. *Chromastrum collopodum*, tetrasporophyte. Figs. 31–35. Young plants in culture, showing development from divided or undivided spore (prostrate filaments hatched). Fig. 36. Tetrasporangia.
Figs. 37, 38. *Chromastrum microscopicum*, type material. Fig. 37. ♂ reproductive plant. Fig. 38. Possible carposporophyte (arrow indicates base).

gametophyte. Hairs are formed under most conditions, and attain lengths over 500 µm, about the same as in gametophytes. Monosporangia measure (13.5)15–19(23) × 7.5–9.5 µm. Tetrasporangia, formed at 4 and 8°C, both short and long day, measured (16)20–23 × 7.5–14 µm.

The influence of temperature and daylength on cell dimensions is comparatively small *(table 3)*. Germination of spores was best at low temperatures (4–12°C), but plants survived at temperatures up to 20°C.

4. DISCUSSION

The *Chromastrum microscopicum* complex is a group of apparently closely related forms in the genus *Chromastrum*. On critical examination of the literature one must conclude that WOELKERLING's (1972) study is not exhaustive, if all potential synonyms are to be considered. Many species have a unicellular base from which rather short-celled filaments arise, the only criterion which appears to be used; WOELKERLING (1972) found a number of taxonomic characters unreliable for specific distinction; cell dimensions showed a very wide range (diameter 3–16 μm) and overlap between the constituent species. A parallel is found in AZIZ's (1965) treatment of *Acrochaetium trifilum*, a complex including several of the same species, though not *A. microscopicum*.

Also the tetrasporophyte which we found to belong to the same life history, seems to have many potential synonyms; at least 15 species of *Chromastrum* (see survey below) have been described to possess a septate spore consisting of 2 semiglobose cells.

The present study has shown that forms belonging to this complex may differ a great deal from each other, even when collected from the same locality; from the Swedish west coast we also collected *Chromastrum densum* (Drew) Stegenga & Mulder, comb. nov., the gametophyte of which was earlier identified as *Chromastrum catenulatum* (Howe) Stegenga & Mulder, comb. nov. (STEGENGA & VROMAN 1976 – as *Acrochaetium catenulatum*); the latter species has been assigned to the *Audouinella microscopica* complex (WOELKERLING 1972).

Differences between these forms were not obliterated in culture, but remained well expressed when entire life histories were compared. Thus, a large proportion of the variation in the field appears to have a genetic basis. We think the magnitude of differences between *C. moniliforme*, *C. collopodum* and *C. catenulatum* is sufficient to distinguish these taxa at the species level.

Although our purpose has not been to revise the *Audouinella microscopica* complex, but rather to determine the nature of the variation between some of its members, we have consulted the type material of *C. microscopicum*. Characters of the *C. microscopicum* type *(figs. 37, 38)* can be summarized as follows: Plants with a unicellular base, often provided with a thick mucilaginous foot, and generally giving rise to only one erect filament consisting of up to 15 or 20 cells; filaments 7–10 μm in diameter, hardly tapering from base to apex; cells isodiametric to twice as long as broad; branching irregular and scarce; monosporangia not observed during this study, but according to WOELKERLING (1972) measuring 7–10 × 5–7 μm; spermatangia on a minority of the plants, in small clusters alternate or opposite on main axes; carpogonia not observed; possible carposporophytes with a three-celled axis and a number of carposporangia; inferred carposporangia measuring *c.* 13 × 9 μm.

Consultation of this type material has only partially facilitated identification of the cultured specimens. Especially the thick mucilaginous foot, the cell length being up to twice the diameter, and the scarce and irregular branching make *C. collopodum* a likely synonym of *C. microscopicum*. On the other hand, the

number of erect filaments hardly shows overlap, and of course, the substrate is different: the type of *C. microscopicum* is found on *Enteromorpha* sp. Probably in connection with the substrate, the distribution of *C. collopodum* is reported to be exclusively northern (PAPENFUSS 1945), whereas *C. microscopicum* is more widely distributed. The temperature range that allowed growth in *C. collopodum* also suggests a potential distribution only in high latitudes. In culture work on *C. collopodum* we found a strong indication of substrate specificity; spore germination often took place at a low rate, and plants developed aberrantly in the absence of *Chordaria flagelliformis*. Substrate is nowadays not generally taken as a reliable taxonomic criterion in the Acrochaetiaceae (WOELKERLING 1971), but specialization of a form on one or a few substrates must certainly be considered as a possible direction in speciation. Perhaps the best approach to the taxonomic position of *C. collopodum* is to return to ROSENVINGE's (1898) original concept, namely to accept it as a variety or subspecies of *C. microscopicum*.

C. moniliforme shows less similarities with the type of *C. microscopicum*, and for the moment we tend to consider it as a separate species. Discriminating characters of *C. moniliforme* are the less prominent mucilaginous foot, the smaller cell length/diameter ratio and the luxurious branching.

Relationships of the other members of the *Audouinella microscopica* complex remain uncertain. STEGENGA & VAN WISSEN (1979) have pointed out the similarities, especially with respect to the minor dimensions, between *Chromastrum microfilum* (Jao) Stegenga & Mulder, comb. nov. and *C. kylinoides* (Feldm.) Stegenga & Van Wissen. *C. crassipes* (Børgesen) Papenfuss has often been recorded from tropical areas. EDWARDS (1969) performed several culture experiments with *C. crassipes* from the Texas coast; the maximum growth at high temperature (24.5–29.5°C), and deleterious effects of low temperature (9.5°C) show this species to be highly adapted to tropical conditions, and at least in this character genetically different from all our material. Unfortunately EDWARDS (1969) found no other reproductive structures than monosporangia; a comparison of life histories is not possible. *C. compactum* (Jao) Papenfuss, according to the original description (JAO 1936), appears to take an intermediate position between *C. microfilum* and *C. moniliforme*.

Identification of the tetrasporophyte of *C. moniliforme* presented us with the usual problems. *C. humile* (Rosenvinge) Papenfuss or *C. polyblastum* (Rosenvinge) Papenfuss might be the best solution, but the type descriptions of neither make mention of the typical habit of the erect filaments; one should be aware, however, that material in the field is often less luxuriously developed than in culture, and especially not comparable on general habit. For the sake of convenience, the name *C. polyblastum* having been used in connection with *C. hallandicum* (Kylin) Papenfuss (STEGENGA & BORSJE 1977), we have applied the name *C. humile* in the present study. On the European Atlantic coast, *C. densum* and *C. reductum* seem to be the other closely related species of the *C. moniliforme* tetrasporophyte, but not conspecific; the first species differs by its seriate sporangia, the second by its much more reduced erect filaments and smaller cell dimensions.

Since the tetrasporophyte of *C. collopodum* has not been found in the field, we cannot say much about its identity. Its development in culture was often aberrant and spores germinated in low numbers; this may suggest a strong substrate dependency and may indicate a semi-endophytic nature. Some species have indeed been described to possess little developed endophytic bases, namely *C. dumontiae* (Rosenvinge) Papenfuss and *C. cytophagum* (Rosenvinge) Papenfuss; they are found on/in *Dumontia* and *Porphyra* respectively, and may represent the tetrasporophyte of *C. collopodum*; morphological characteristics are not much different.

Our conclusions emphasize the difference in approach and outcome between the culture method and the herbarium method in this group of algae; the herbarium method does not usually allow comparison of entire life histories, the culture method yields some results which are not immediately comparable to field data. We want to stress here the need for comparative studies of populations of several regions, while taking into account such factors as temperature, light, exposition and substrate. Live material is preferrable in such studies, and the collecting would best be followed by comparative culturing of a number of clones.

5. SURVEY OF THE GENUS CHROMASTRUM

5.1 Delimitation of the genus

The genus *Chromastrum* was proposed by PAPENFUSS (1945) who later (PAPENFUSS 1947) replaced the name *Chromastrum* by *Kylinia*, be it on erroneous grounds (FELDMANN 1958; STEGENGA & VAN WISSEN 1979). The genus was defined to comprise all species with stellate chromatophores; both species with unicellular and multicellular bases were included. *C. virgatulum* (Harvey) Papenfuss was designated as the type species.

As a result of several life history studies (BORSJE 1973; STEGENGA & VROMAN 1976; STEGENGA & BORSJE 1977; STEGENGA & VAN WISSEN 1979; the present communication) we have concluded that *Chromastrum* indeed can be distinguished as a separate genus within the Acrochaetiaceae. It is defined now not only by its stellate chromatophores, but also by a characteristic alternation of morphological phases in the life history, differing from other members in the family. Typically, the gametophyte has a unicellular base, the tetrasporophyte has a multicellular base, arising from a septately germinating spore; also, the carposporophyte is comparatively small.

Accepting the above mentioned characters as systematic criteria, we scanned the literature for species that could belong to this genus. The compiled list is necessarily of a tentative nature and will contain a number of inaccuracies, and does not claim completeness. The genus *Chromastrum* is now thought to comprise at least 60 species described in the literature. The type localities of 60 species are shown in *fig. 41*. Of these, 25 species are gametophytes and 35 species are tetrasporophytes. It should be noted that gametophytic or tetrasporophytic nature of plants in this case has in general not been concluded from presence of

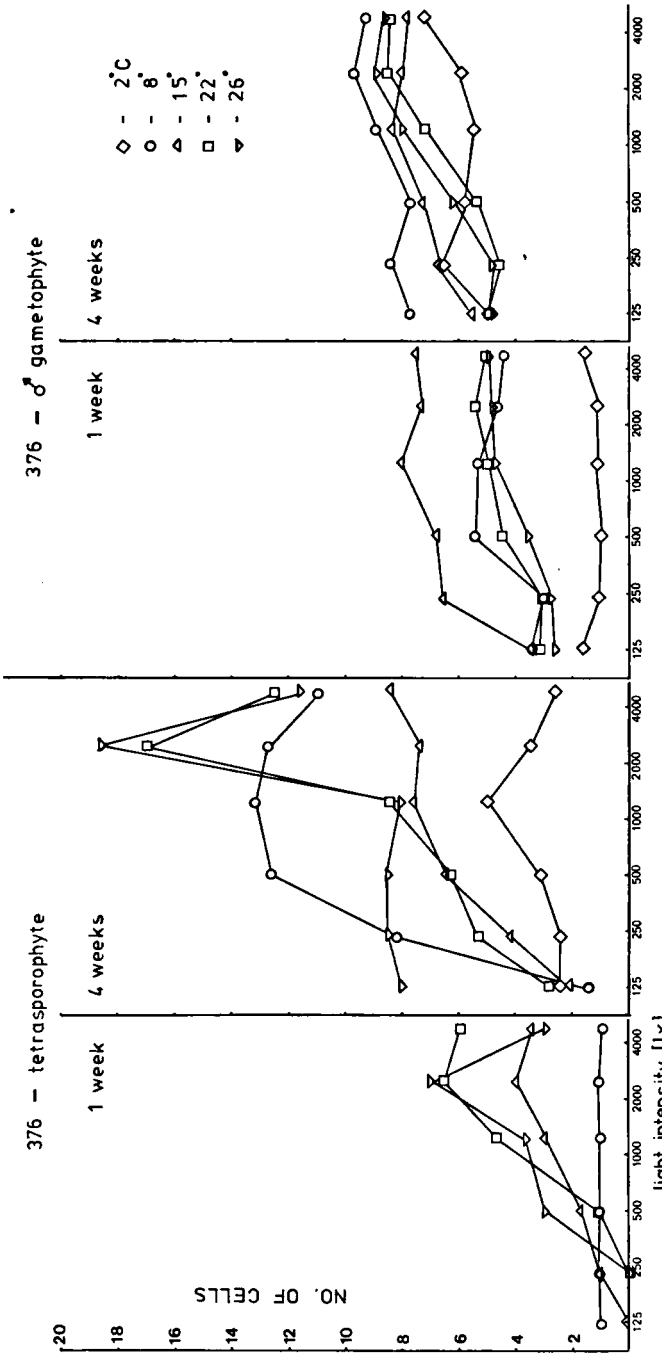


Fig. 39. Growth of *Chromastrum moniliforme* under various conditions of light intensity and temperature: number of cells in the main axis, 1 and 4 weeks after culture initiation.

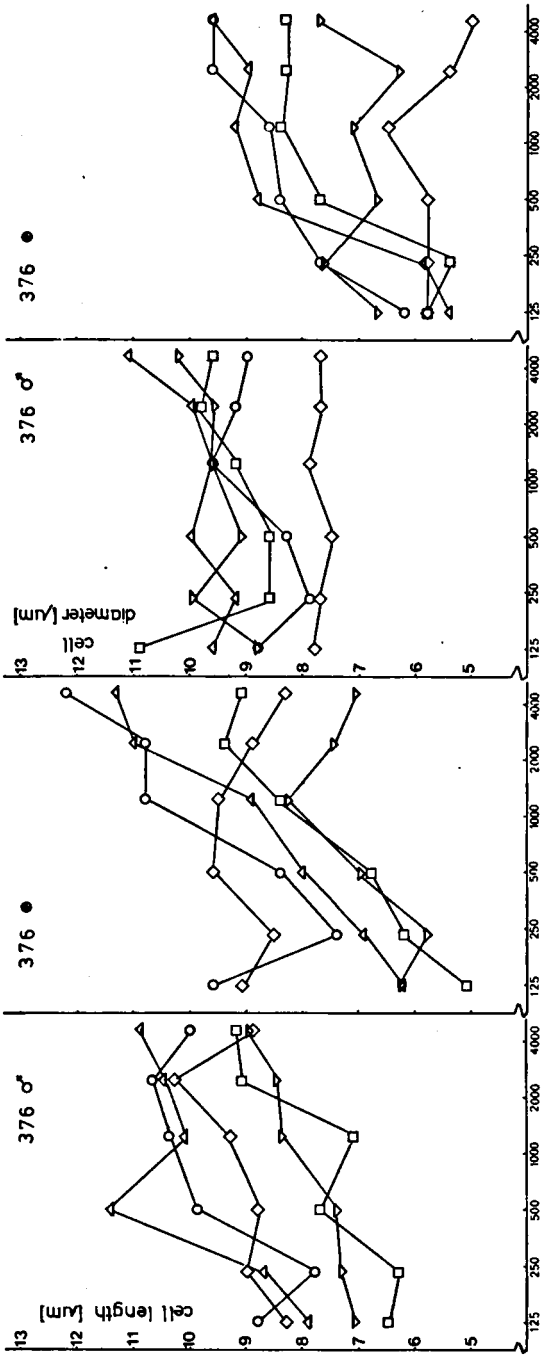


Fig. 40. *Chromastrum moniliforme*, average cell dimensions under various conditions of light intensity and temperature; symbols for different temperatures as in fig. 39.

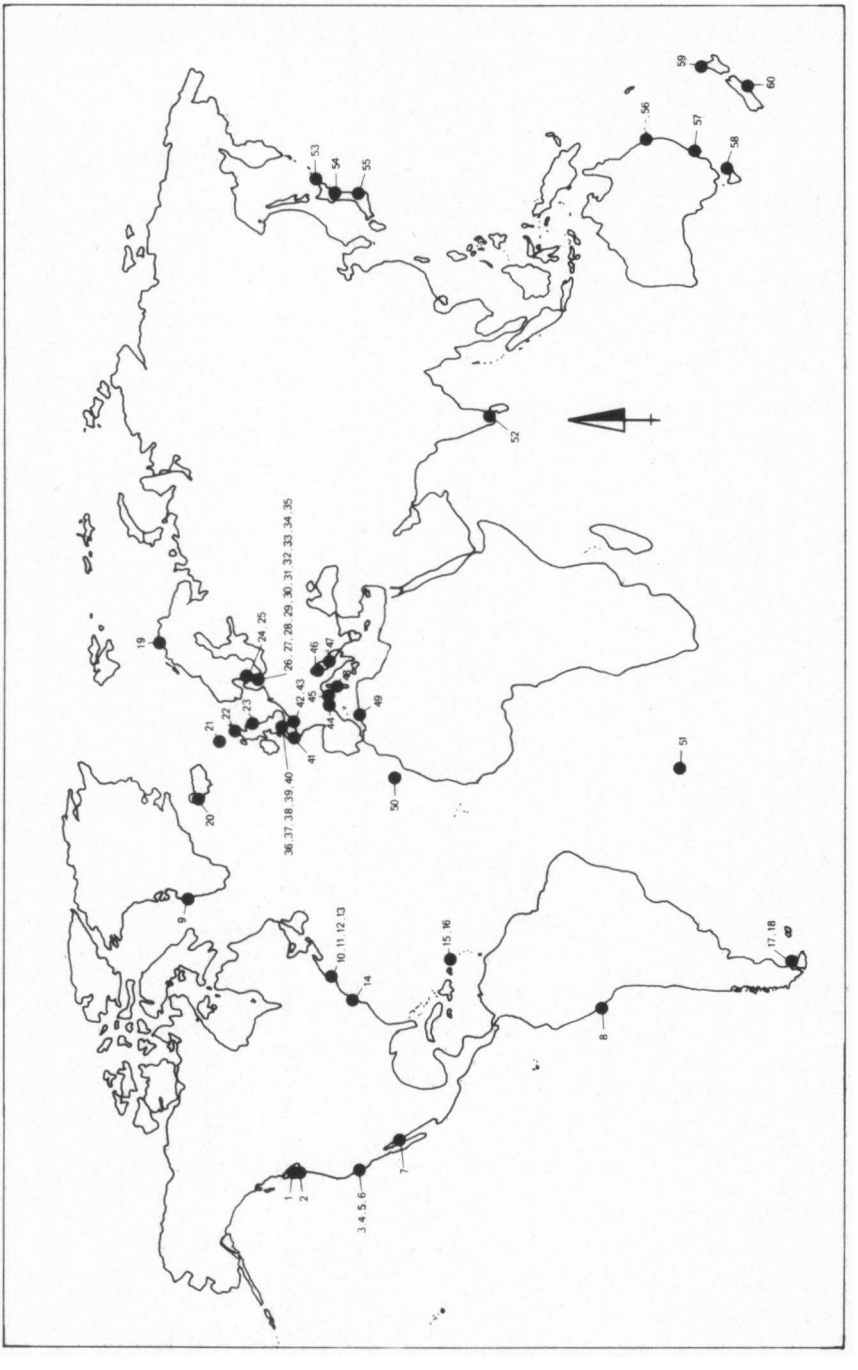

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Fig. 41. Type localities of species presently believed to belong to *Chromastrum*. Species marked ⊕ presumably represent tetrasporophytic generations, other species are gametophytes.

1. C. hirsutum (DREW 1928)
2. C. vagum – ⊕ (DREW 1928)
3. C. densum – ⊕(DREW 1928)
4. C. arcuatum (DREW 1928)
5. C. porphyrae – ⊕ (DREW 1928)
6. C. implicatum – ⊕ (DREW 1928)
7. C. seriasporum – ⊕ (DAWSON 1952)
8. C. catenulatum (HOWE 1914)
9. C. collopodum (ROSENVINGE 1898)
10. C. microfilum (JAO 1936)
11. C. compactum (JAO 1936)
12. C. unifilum (JAO 1936)
13. C. radiatum – ⊕ (JAO 1936)
14. C. hummii – ⊕ (AZIZ 1965)
15. C. crassipes (BØRGESEN 1909)
16. C. pulchellum – ⊕ (BØRGESEN 1915)
17. C. macropus (KYLIN & SKOTTSBERG 1919)
18. C. fuegiense – ⊕ (KYLIN & SKOTTSBERG 1919)
19. C. sertulariae – ⊕ (JAASUND 1965)
20. C. alariae (JONSSON 1901)
21. C. secundatum – ⊕ (LYNGBYE 1819)
22. C. scapae (LYLE 1929) (KYLIN 1906)
23. C. battersianum (HAMEL 1928b)
24. C. parvulum
25. C. hallandicum (KYLIN 1906)
26. C. moniliforme (ROSENVINGE 1909)
27. C. rhipidandrum (ROSENVINGE 1909)
28. C. balticum (ROSENVINGE 1909)
29. C. reductum – ⊕ (ROSENVINGE 1909)
30. C. humile – ⊕ (ROSENVINGE 1909)
31. C. maculae – ⊕ (ROSENVINGE 1909)
32. C. dumontiae – ⊕ (ROSENVINGE 1909)
33. C. cytophagum – ⊕ (ROSENVINGE 1909)
34. C. polyblastum – ⊕ (ROSENVINGE 1909)
35. C. leptonema – ⊕ (ROSENVINGE 1909)
36. C. microscopicum (NÄGELI in KÜTZING 1849)
37. C. trifilum (BUFFHAM 1892)
38. C. virgatulum – ⊕ (HARVEY in HOOKER 1833)
39. C. griffithsianum – ⊕ (NÄGELI 1861)
40. C. pulvereum – ⊕ (NÄGELI 1861)
41. C. kylinoides (FELDMANN 1958)
42. C. maluinum (HAMEL 1928a)
43. C. lenormandii – ⊕ (SUHR in KÜTZING 1849)
44. C. duboscqii – ⊕ (FELDMANN 1935)
45. C. molinieri – ⊕ (COPPEJANS & BOUDOURESQUE 1976)
46. C. subpinnatum (BORNET ex HAMEL 1928a)
47. C. børgesenii – ⊕ (SCHIFFNER 1931)
48. C. mediterranea (LEVRING 1942)
49. C. mahumetanum – ⊕ (HAMEL 1928a)
50. C. canariense – ⊕ (BØRGESEN 1927)
51. C. curtum (BAARDSETH 1941)
52. C. tuticorinense – ⊕ (BØRGESEN 1937)
53. C. kurilense – ⊕ (NAGAI 1941)
54. C. sessile – ⊕ (NAKAMURA 1941)
55. C. terminale – ⊕ (NAKAMURA 1944)
56. C. pulvinatum – ⊕ (LEVRING 1953)
57. C. subreductum – ⊕ (LEVRING 1953)
58. C. subsimplex – ⊕ (LEVRING 1953)
59. C. neozeelandicum (LEVRING 1955)
60. C. leptonemoides – ⊕ (LEVRING 1955)

relevant reproductive structures, but rather from a characteristic morphology. Also, we will remark here that distribution of type localities may only demonstrate the intensity of phycological research in the past, although we hold the opinion that indeed the North Atlantic Ocean is the site of highest diversity of the genus *Chromastrum* (see below).

Not all the species considered here were originally included in *Chromastrum* by PAPENFUSS (1945), as some had been reported to possess parietal chromatophores. Relevant species are included in *Chromastrum* now because of other morphological evidence: especially where tetrasporophytes are concerned, we have used the character of the septate division of the spore. On the other hand, it should be noted that there are definitely species that combine a unicellular base with parietal chromatophores, e.g. *Kylinia rosulata;* in that case a quite different tetrasporophyte is involved in the life history (STEGENGA & VAN WISSEN 1979).

Rhodochorton floridulum, a species included in *Chromastrum* by PAPENFUSS (1945) is now excluded because of the parietal position of the (stellate) chromatophores, and the entirely different life history pattern (STEGENGA 1978). Moreover, a number of extremely endophytic and endozoic species have been left out of this survey; interpretation of their morphology is difficult, their life histories are very incompletely known and germination patterns often unknown.

5.2 Criteria in species delimitation

It is generally accepted now (WOELKERLING 1971, 1973; DIXON & IRVINE 1977) that a number of the described species of the Acrochaetiaceae are to be considered conspecific, but the number of remaining true species depends on the species concept. In *table 4*, concerning 6 species which were investigated for their life histories and morphological variability in culture, an outline is given of characters which were found rather stable, and hence applicable in species delimitation. We think that these species cover a fair amount of the variation in the whole genus, and we estimate that recognition of 10–12 true species in the genus *Chromastrum* would adequately deal with this group of acrochaetioid algae.

Table 4. *Chromastrum*, discriminating characters in 6 cultured species. Height and cell diameter in µm. Spore germination: septation pattern, immediately prior to formation of either erect or prostrate filaments. Carposporophyte: mature stage, with terminal carpospores present. Maximum height in *C. collopodum* given for the gametophyte because of uncertain systematic affinities of the tetrasporophyte.

	maximum height (tetrasporophyte)	cell diameter (tetrasporophyte)	spore germination (tetrasporophyte)	carposporophyte
C. virgatulum/rhipidandrum	3000	10-15		
C. densum/catenulatum	1000	7-10		
C. polyblastum/hallandicum	500	7-10		
C. humile/moniliforme	100	6-11		
C. reductum/kylinoides	20	5.5-7		
C. collopodum	(100 - gametophyte)	6-10		?

We will now briefly review the characters used in species delimitation:
– Height of plants is of course only of value as far as mature specimens are concerned. The character can be used for gametophytes as well as for tetrasporophytes; although the latter generation is often the largest, both phases are generally proportionate in size. A limited height of plants is usually connected with terminal formation of monosporangia in a certain ontogenetic stage.
– Cell diameter (and monosporangial dimensions) are often a few μm more in the tetrasporophyte than in the gametophyte, but may also be practically alike (*C. moniliforme*, the present study). Monosporangial dimensions are often proportionate to dimensions of the vegetative cells.
– Spore germination in the tetrasporophyte is nearly always septate; the primary pattern may take different forms, from a two-celled spore (most species) to a 4–6-celled disc *(C. secundatum)*. In *C. collopodum* septation of the spore is sometimes left out, but the filamentous base is formed as well, be it often reduced to a few cells.
– The carposporophyte structure is always rather simple in comparison to species with parietal chromatophores. A form range exists, from an undivided carpogonium bearing *c.* 3 carposporangia *(C. kylinoides)* to a twice divided carpogonium bearing up to 10 carposporangia and occasionally provided with a few unicellular branchlets *(C. moniliforme)*. A slight variability in size of the carposporophyte is found in most species. Since carposporophytes are seldom found in nature, this character has a limited value for identification purposes.
– Additional characters may be valuable to distinguish single species, e.g. seriate sporangia in *C. densum* and a thick mucilaginous foot in *C. collopodum*.

Branching frequency and pattern, although sometimes useful for identification purposes, are too variable to be used in species delimitation. Uniseriate branching predominates in most species. Cell length is also considerably influenced by external factors, but probably average cell lengths in the main axes would be more informative in descriptions than the often used extremes. Presence or absence of hairs is clearly linked to external conditions, the formation of them being stimulated by high light intensity or long day; in culture, no *Chromastrum* species has been found to be completely devoid of hairs. The number of erect axes in the gametophytes is limited, and subject to modification by external factors; it may be used in identification of such forms as *C. kylinoides*, where the maximum is rather high. Extension and shape of the basal part of the tetrasporophyte is varied, but beyond the initial germination stage always filamentous; it is often not practical to use it in identification.

The investigated species all showed that an alternation of external conditions is necessary to have their sexual cycles completed. Of these conditions especially light and temperature have been studied in various experiments *(table 5)*. No general rule can be given for the genus as a whole. Some species prefer high or low light intensity for formation of both gametangia and tetrasporangia, while temperature seems to be the main factor in determining which type of reproductive organ will be formed. Other species require an alternation of light conditions, often combined with temperature fluctuations. Also, the reaction to

Table 5. *Chromastrum;* required or preferred temperature and light conditions for development of different reproductive structures in 6 species in culture.

	tetrasporangia		gametangia	
	temp.(°C)	light conditions	temp.(°C)	light conditions
C. vigatulum/rhipidandrum	8–16	short day	8–16	long day
C. densum/catenulatum	14–20	low light int.	8	low light int.
C. polyblastum/hallandicum	4–8(12)	high light int.	14–20	neutral – long day
C. humile/moniliforme	8	neutral – long day	16	short day
C. reductum/kylinoides	8(16)	long day	16	short day
C. collopodum	8–16	short – long day	16	neutral day

controlling factors is not always uniform within a single species, but may vary between various clones (*C. kylinoides*, STEGENGA & VAN WISSEN 1979). It is a common experience in culture work on these algae, to find some clones that exhibit no sexual reproduction under any of the tested conditions, but reproduce only asexually. Although our research has not been centred on the exact regulation of reproduction, we have the impression that long day and short day can in general be replaced by high and low light intensity respectively, to obtain the same results regarding the formation of reproductive structures.

5.3 Geographical distribution

The genus *Chromastrum* is cosmopolitan. In *fig. 41* the distribution of type localities of the species presumed to belong to this genus, is shown. The first striking feature is the high abundance of species on the European Atlantic coast; this of course reflects the activity of phycologists in this area, especially during the first years of this century (KYLIN 1906; ROSENVINGE 1909), but also the variety of forms that apparently could be distinguished. Subsequent authors, working in other parts of the world, did not often recognize these European species and gave descriptions of additional taxa (e.g. DREW 1928; JAO 1936; LEVRING 1953, 1955). However, the North Atlantic remains the area with the highest diversity in recorded species. As for tropical regions, not many new species have been recorded from there (e.g. BØRGESEN 1909, 1915), and most of the other species were never found in those areas. An estimate of the relative importance of the genus *Chromastrum* in the total acrochaetioid flora is compared for different regions in *table 6;* only records have been listed of well known areas, having a total acrochaetioid flora of 20 species or more; conservative estimates have been used to avoid obliteration by later accepted larger numbers of conspecificities. Even after considering a number of species as probable synonyms, we could distinguish at least 6 true species (= 12 generations) from the European west coast (see *table 4*), as compared to usually 1 or 2 species from tropical areas. The species most commonly reported from the tropics is *C. crassipes*, a member of the *Audouinella microscopica* complex. In *table 6* it is interesting to observe the sharp break along the North American Atlantic coast, which contrasts with the more gradual transition in species composition on the

Table 6. Proportion of *Chromastrum* species, in relation to total acrochaetioid flora. Under proportion of *Chromastrum*, the first number is the number of species belonging to the genus in that area, the second number the total amount of species of Acrochaetiaceae.

Area covered and reference	Proportion of Chromastrum
Sweden (KYLIN 1944)	12 out of 26 = 46%
Denmark (ROSENVINGE 1909)	12 out of 28 = 43%
Great Britain (DIXON & IRVINE 1977)	9 out of 33 = 27%
Atlantic France (HAMEL 1928a)	7 out of 24 = 29%
Eastern Canada (SOUTH & CARDINAL 1970)	10 out of 28 = 36%
North Eastern North America (TAYLOR 1957)	9 out of 26 = 35%
South Eastern North America (TAYLOR 1960)	2 out of 38 = 5%
Virgin Islands (BØRGESEN 1915–1920)	2 out of 25 = 8%
Pacific North America (DREW 1928)	7 out of 34 = 21%
Pacific Mexico (DAWSON 1952)	5 out of 22 = 23%
Japan (NAKAMURA 1941, 1944)	4 out of 20 = 20%
Australia (LEVRING 1953)	5 out of 21 = 24%

European side of the Atlantic, such in agreement with general patterns in algal distribution in the North Atlantic (VAN DEN HOEK 1975).

The total numbers of tetrasporophytes and gametophytes do not differ too much, and both groups of generations have about the same range of geographical distribution; this does not imply that pairs of species (= generations) can easily be detected in the literature for any given region. A curious example is found in the flora of the British Isles (DIXON & IRVINE 1977), where 7 gametophytes were recorded, compared to only 2 tetrasporophytes. The same applies to the French west coast, where according to HAMEL (1928a) 5 gametophytes were recorded, compared to 2 tetrasporophytes, with the latter 2 probably conspecific; the study of FELDMANN (1958) added one more gametophyte, while no corresponding tetrasporophyte was found. On the Norwegian coast, the numbers of gametophytes and tetrasporophytes are more in balance: RUENESS (1977) mentioned 4 species of each generation, accepting a number of conspecificities; original records from this area would add up to 9 gametophytes and 8 tetrasporophytes. It is a matter of further research, whether these curious distribution patterns are a result of incomplete investigations, or of peculiarities in the life histories.

ACKNOWLEDGEMENTS

The authors are indebted to Dr. M. Vroman for critically reading the manuscript and to Mrs. M. J. van Wissen for carrying out part of the experiments. Mr G. W. H. van den Berg prepared most of the drawings. Thanks are also due to Dr. J. O. Strömberg (Kristineberg) for provided room and facilities, and to the director of the Rijksherbarium (L) for loan of the type of *C. microscopicum*.

REFERENCES

AZIZ, K. M. S. (1965): *Acrochaetium and Kylinia in the southwestern North Atlantic Ocean.* PhD Thesis Duke University, Univ. Microfilms, Ann Arbor, 245 pp.

BAARDSETH, E. (1941): The marine algae of Tristan da Cunha. *Results Norw. Sci. Exp. Tristan da Cunha* 1937–1938, **9**: 1–174.

BØRGESEN, F. (1909): Some new or little known West Indian Florideae I. *Bot. Tidsskr.* **30**: 1–19.

— (1915–1920): The marine algae of the Danish West Indies. Part 3. Rhodophyceae. *Dansk Bot. Arkiv*, 498 pp.

— (1927): Marine algae from the Canary Islands III. Rhodophyceae. Part I. Bangiales and Nemalionales. *Kgl. Danske Vidensk. Selsk. Biol. Medd.* **6**(6): 1–97.

— (1937): Contributions to a South Indian marine algal flora 1. *Jour. Indian Bot. Soc.* **16**: 1–56.

BORSJE, W. J. (1973): The life history of Acrochaetium virgatulum (Harv.) J. Ag. in culture. *Br. Phycol. J.* **8**: 205.

BUFFHAM, T. H. (1892): Chantransia trifila, a new marine alga. *J. Quekett microsc. Club, ser.* 2, **5**: 24–26.

COPPEJANS, E. & C. F. BOUDOURESQUE (1976): Végétation marine de l'Ile de Port-Cros (Parc National) XII: Sur Acrochaetium molinierii sp. nov. et Lophosiphonia cristata Falkenberg. *Giorn. Bot. Ital.* **110**(3): 219–229.

DAWSON, E. Y. (1952): Marine red algae of Pacific Mexico. Part I. *Allan Hancock Pacific Expeditions* **17**(1): 1–239.

DIXON, P. S. & L. M. IRVINE (1977): *Seaweeds of the British Isles.* Vol. **1** Rhodophyta. Part 1 Introduction, Nemaliales, Gigartinales. British Museum (Natural History), 252 pp.

DREW, K. M. (1928): A revision of the genera Chantransia, Rhodochorton and Acrochaetium. *Univ. Cal. Publ. Bot.* **14**: 139–224.

EDWARDS, P. (1969): Field and cultural studies on the seasonal periodicity of growth and reproduction of selected Texas benthic marine algae. *Contr. mar. Sci. Univ. Tex.* **14**: 59–114.

FELDMANN, J. (1935): Algae marinae mediterranae novae. *Bull. Soc. Hist. Nat. Afr. Nord* **26**: 362–369.

— (1958): Le genre Kylinia Rosenvinge (Acrochaetiales) et sa reproduction. *Bull. Soc. Bot. France* **105**: 493–500.

HAMEL, G. (1928a): Floridées de France 5. *Rev. Alg.* **3**: 99–158.

— (1928b): Sur les genres Acrochaetium Näg. et Rhodochorton Näg. *Rev. Alg.* **3**: 159–210.

HOEK, C. VAN DEN (1975): Phytogeographic provinces along the coasts of the northern Atlantic Ocean. *Phycologia* **14**(4): 317–330.

HOOKER, W. J. (1833): *The English flora* 5. London.

HOWE, M. A. (1914): The marine algae of Peru. *Torrey Bot. Club, Mem.* **15**: 1–185.

JAASUND, E. (1965): Aspects of the marine algal vegetation of North Norway. *Bot. Gothoburg.* **4**: 1–174.

JAO, C. C. (1936): New Rhodophyceae from Woods Hole. *Bull. Torrey Bot. Club* **63**: 237–257.

JONSSON, H. (1901): The marine algae of Iceland 1. Rhodophyceae. *Bot. Tidsskr.* **24**(2): 127–155.

KÜTZING, F. T. (1849): *Species Algarum.* Leipzig.

KYLIN, H. (1906): Zur Kenntnis einiger Schwedischen Chantransia-Arten. *Bot. Studiertillägn. F. R. Kjellman*, 113–126.

— (1944): Die Rhodophyceen der schwedischen Westküste. *Lunds Univ. Årsskr. N.F.* Avd. 2. **40**(2): 1–104.

— & C. SKOTTSBERG (1919): Zur Kenntnis der subantarktischen und antarktischen Meeresalgen. 2. Rhodophyceen. *Wissenschaftl. Ergebn. Schwed. Südpolar-Exped.* 1901–1903, **4**(15).

LEVRING, T. (1942): Meeresalgen aus dem Adriatischen Meer, Sizilien und dem Golf von Neapel. *Kgl. Fysiogr. Sällskap Lund Förhandl.* **12**(3): 25–41.

— (1953): The marine algae of Australia I. Rhodophyta: Goniotrichales, Bangiales and Nemalionales. *Arkiv för Botanik* **2**(6): 457–530.

— (1955): Contributions to the marine algae of New Zealand I. Rhodophyta: Goniotrichales, Bangiales, Nemalionales and Bonnemaisoniales. *Arkiv för Botanik* **3**(11): 407–432.

LYLE, L. (1929): Marine algae of some German warships in Scapa Flow and of the neighbouring shores. *J. Linn. Soc., Bot.* **48**: 231–257.

LYNGBYE, H. C. (1819): *Tentamen Hydrophytologiae Danicae*. Copenhagen.

NÄGELI, C. (1861): Beiträge zur Morphologie und Systematik der Ceramiaceae. *Sitzungsber. k. b. Akad. Wiss. München* **2**: 279–415.

NAGAI, M. (1941): Marine Algae of the Kurile Islands II. *Journ. Facul. Agr., Hokkaido Imp. Univ.* **46**(2): 139–310, pl. IV-VI.

NAKAMURA, Y. (1941): The species of Rhodochorton from Japan I. *Sci. Papers Inst. Alg. Research Hokkaido Imp. Univ.* **2**(2): 273–291.

— (1944): The species of Rhodochorton from Japan II. *Sci. Papers Inst. Alg. Research Hokkaido Imp. Univ.* **3**: 89–119.

PAPENFUSS, G. F. (1945): Review of the Acrochaetium-Rhodochorton complex of the red algae. *Univ. Cal. Publ. Bot.* **18**(14): 299–334.

— (1947): Further contributions toward an understanding of the Acrochaetium-Rhodochorton complex of the red algae. *Univ. Cal. Publ. Bot.* **18**(19): 433–447.

PROVASOLI, L. (1968): Media and prospects for the cultivation of marine algae. In: WATANABE, A. & A. HATORI (eds.): *Cultures and Collection of Algae*. Proc. US – Japan Conf. Hakone, Sept. 1966. Jap. Soc. Plant Physiol. pp. 63–75.

ROSENVINGE, L. K. (1898): Deuxième mémoire sur les algues du Groenland. *Medd. om Grønland* **20**: 1–125.

— (1909): The marine algae of Denmark I. Rhodophyceae I. *Kgl. Danske Vidensk. Selsk. Skr., Naturv. og Mathem. Afd.*, 7. Raekke **7**(1): 1–151.

RUENESS, J. (1977): *Norsk Algeflora*. Universitetsforlaget, Oslo, 266 pp.

SCHIFFNER, V. (1931): Neue und bemerkenswerte Meeresalgen. *Hedwigia* **71**: 139–205.

SOUTH, G. R. & A. CARDINAL (1970): A checklist of marine algae of eastern Canada. *Can J. Bot.* **48**: 2077–2095.

STEGENGA, H. (1978): The life histories of Rhodochorton purpureum and Rhodochorton floridulum (Rhodophyta, Nemaliales) in culture. *Br. phycol. J.* **13**: 279–289.

— & W. J. Borsje (1977): The morphology and life history of Acrochaetium polyblastum (Rosenv.) Børg. and Acrochaetium hallandicum (Kylin) Hamel (Rhodophyta, Nemaliales). *Acta Bot. Neerl.* **26**(6): 451–470.

— & M. VROMAN (1976): The morphology and life history of Acrochaetium densum (Drew) Papenfuss (Rhodophyta, Nemaliales). *Acta Bot. Neerl.* **25**(4): 257–280.

— & — (1977): The significance of life history characters for the systematics of the Acrochaetiaceae (abstract). *J. Phycol.* **13** (suppl.): 64.

— & M. J. VAN WISSEN (1979): Remarks on the life histories of three acrochaetioid algae (Rhodophyta, Nemaliales). *Acta Bot. Neerl.* **28**(2): 97–115.

TAYLOR, W. R. (1957): *Marine algae of the Northeastern coast of North America*. 2nd ed. Ann Arbor, 509 pp.

— (1960): *Marine algae of the eastern tropical and subtropical coasts of the Americas*. Ann Arbor, 870 pp.

WOELKERLING, W. J. (1971): Morphology and taxonomy of the Audouinella complex (Rhodophyta) in Southern Australia. *Aust. J. Bot., Suppl. Ser.* **1**, 91 pp.

— (1972): Studies on the Audouinella microscopica (Näg.) Woelk. complex (Rhodophyta). *Rhodora* **74**: 85–96.

— (1973): The morphology and systematics of the Audouinella complex (Acrochaetiaceae, Rhodophyta) in northeastern United States. *Rhodora* **75**: 517–621.