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THE MORPHOLOGY AND LIFE HISTORY OF ACROCHAETIUM DENSUM (DREW) PAPENFUSS (RHODOPHYTA, NEMALIALES)

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SUMMARY

The morphology of field-collected plants of *Acrochaetium densum* (Drew) Papenfuss from the Dutch coast is described in some detail. This species is characterized by a persistent septate spore, a multicellular filamentous prostrate part and numerous rather short erect axes, which are secundly branched in mature plants. Reproduction takes place by monospores which are typically formed in rows of two or three successive monosporangia, ripening simultaneously.

In culture the plants also formed tetrasporangia and subsequently the life-history could be completed. It appeared to be a diplobiontic cycle consisting of morphologically dissimilar generations: the unisexual gametophytes have a unicellular base from which 1–5 erect filaments arise. The life cycle seems to be mainly temperature-controlled.

From experiments in crossed light and temperature gradients it could be concluded that spore germination and dimensions of cells and sporangia are the least modifiable and hence the most useful characters in delimiting the species from other acrochaetioid taxa.

The name *Acrochaetium densum* was chosen rather arbitrarily. Identification of both the tetrasporophyte and the gametophyte presents considerable difficulties: a large number of described species shows resemblance to one or the other generation.

1. INTRODUCTION

Acrochaetium densum (Drew) Papenfuss is a minute species which has not been recorded from the European coast before, although, as will be shown, several others of the described species are closely related and even may be conspecific. It was found on several localities in the "Delta-area" (province of Zeeland) in the southwestern part of the Netherlands, occurring as an epiphyte on several macroalgae, preferably *Chaetomorpha* spp., but also on *Enteromorpha* sp., *Dictyota dichotoma*, *Dumontia incrassata*, *Polysiphonia elongata* and *Polysiphonia nigrescens*. It is found in areas with tidal influence (Eastern Scheldt) as well as in stagnant salt or brackish waters (Grevelingen, Gat van Ouwerkerk). *A. densum* may be collected throughout the year in these localities.

The aim of the present study was to describe the morphology and to elucidate the life history by applying standard culture techniques. Moreover morphological variability was studied in order to estimate the value of some morphotaxonomic criteria which are in use to distinguish *Acrochaetium* species. Identification of the material has taken place by literature study only and must be considered provisional; no type collections have been compared yet.

2. MATERIALS AND METHODS

Material underlying the morphological description was collected at the following dates and localities:
7-XII-1967, Gat van Ouwerkerk, from *Chaetomorpha linum:*
V-1970, Oysterponds near Yerseke, from *Chaetomorpha linum;*
5-I-1971, Oysterponds near Yerseke, from *Polysiphonia nigrescens;*
4-X-1974, Sas van Goes, from *Chaetomorpha linum;*
2-XII-1974, Gat van Ouwerkerk, from *Chaetomorpha linum;*
31-I-1975, Sas van Goes, from *Dumontia incrassata;*
31-I-1975, Gat van Ouwerkerk, from *Chaetomorpha linum;*
14-VII-1975, Oysterponds near Yerseke, from *Dictyota dichotoma;*
6-VIII-1975, Grevelingen, from *Chaetomorpha linum* and *Polysiphonia elongata,*
19-VIII-1975, Sas van Goes, from *Enteromorpha* sp.

All samples collected for morphological study were preserved in formalin 4%.

On several occasions also plants were isolated and taken into culture. Plants were grown in an enriched seawater medium (PROVASOLI 1968) and kept under various combinations of temperature and daylength. For illumination cool white fluorescent light (Philips TL 33) was used. Sometimes aeration of the cultures was applied.

Morphological variability was studied in a modified version of Edwards and van Baalen's light-temperature gradient plate (EDWARDS & VAN BAALEN 1970).

In all experiments the culture medium was changed every two weeks.

3. MORPHOLOGY OF FIELD-COLLECTED PLANTS

Vegetative structure *(figs. 1, 7a, b, c).*
The basal part consists of a persistent septate spore and a number of creeping filaments. The spore measures 7–10 μm in diameter and usualy remains visible as a two-celled structure for a considerable time after germination. One to four prostrate filaments arise from this spore. They consist of irregularly shaped cells and may be more or less branched. Often these filaments are embedded in the wall material of the substrate, i.c. *Chaetomorpha.* In older plants there is some variation in cell shape in the creeping filaments, connected with the exact site of these plants on the *Chaetomorpha* filaments: if a plant is located on the wall between two host cells the base consists of rather short cells; if it is situated in the middle of a host cell the base consists of relatively long cylindric cells, the filaments running lengthwise along the *Chaetomorpha* cells. This variation is probably caused by the rapid growth of *Chaetomorpha* filaments.

The erect filaments arise from the original spore and from the creeping filaments. In older plants they may be very numerous and attain a maximal height of 25 cells or 200 μm, usually less. Diameter of the filaments is 6–8(9) μm, cell

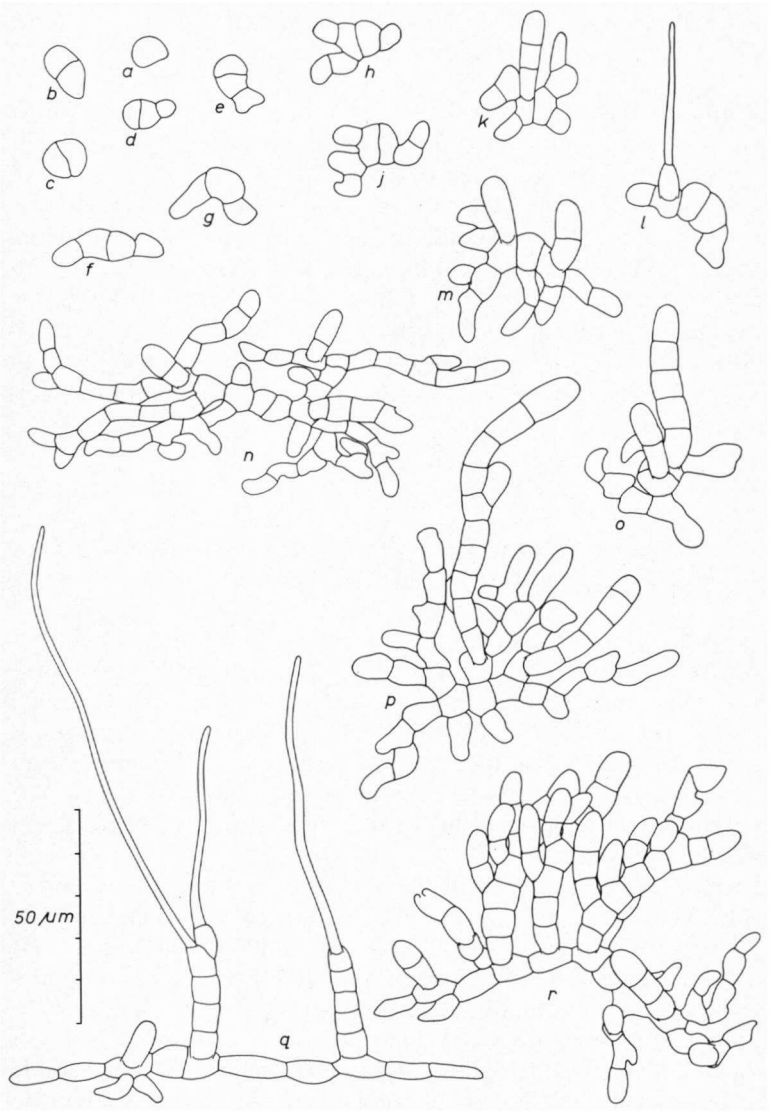

Fig. 1. Tetrasporophyte; field-collected material.
a-g. stages in germination of monospores. *h-r.* various developmental stages (note variation in prostrate and erect system).

length about equal to twice the diameter. Cells are cylindric or slightly barrel-shaped, provided with a stellate chromatophore and a central pyrenoid. Branching of the erect filaments is nearly always secund, rarely opposite or alternate. Strongly branched filaments are more or less arcuate. Primary laterals hardly ever exceed 4 cells in length and mostly are terminated by monospor-

angia. Occasionally terminal or subterminal unicellular hairs occur on the erect axes; they were found especially on plants from the Grevelingen locality.

Reproduction *(fig. 2)*.
The only observed reproductive structures are monosporangia. They occur terminally on the main axes and laterals, usually in 2–3(4) – celled rows of successive sporangia, which shed their spores about simultanuously. Release of the monospores takes place by rupture of the sporangial wall; in terminal sporangia the pore is situated apically, in subterminal sporangia laterally.

Terminal sporangia measure 9–10 × 7 μm, intercalary sporangia 6–9 × 7–9 μm. After the first monospores have been released, internal proliferation of new monosporangia may occur; if so, the new cell row emerges through the pore of the lowermost sporangium, while the rest of the empty sporangia is pushed aside.

4. MORPHOLOGY AND LIFE HISTORY IN CULTURE

A number of clones was isolated from various localities and substrates. They could be grown without difficulties in an enriched seawater medium.

The tetrasporophyte *(figs. 3, 4, 7d, e, f, 8)*.
In culture the morphology is largely the same as that of fieldcollected plants. Monospore germination is generally septate, although occasionally aseptate spores directly give rise to creeping filaments. On germination, monospores measure 9–10 μm. The prostrate part consists either of frequently branched filaments, forming a disc-like structure, or of less branched filaments. The environmental conditions underlying this and other variations will be discussed in a separate section of this paper.

Numerous erect filaments arise from the basal system, especially when the latter is disc-like. The erect part becomes much larger in culture than in the field; under optimal conditions filaments attain a length of 800 μm or 70 cells in 4 weeks. Filament diameter is 6–7.5(8) μm, cell length 8–15 μm. The chromatophore of vegetative cells is essentially stellate, with a conspicuous central pyrenoid; sometimes two pyrenoids per cell occur.

The radial parts of the chromatophore may in older cells form considerable extensions against the cell wall, thus giving the suggestion of a parietal structure of the chromatophore *(fig. 3n)*. Branching of the erect axes is extremely variable: varying from completely no branches to 1 lateral per cell, in the latter case usually secund. As a result the filaments are straight or arcuate. Unicellular hairs are formed only sporadically.
Monosporangia are formed in large quantities and usually in series of three. Dimensions of terminal sporangia are (7.5) 9.5–11.5 (13.5) × 6–7 (8.5) μm, of intercalary sporangia (6) 6.5–8.5 (11.5) × (6) 6.5–8.5 μm.

Under conditions of low light intensity and moderate temperatures (14–20°C) in addition to monosporangia tetrasporangia are formed. They occur

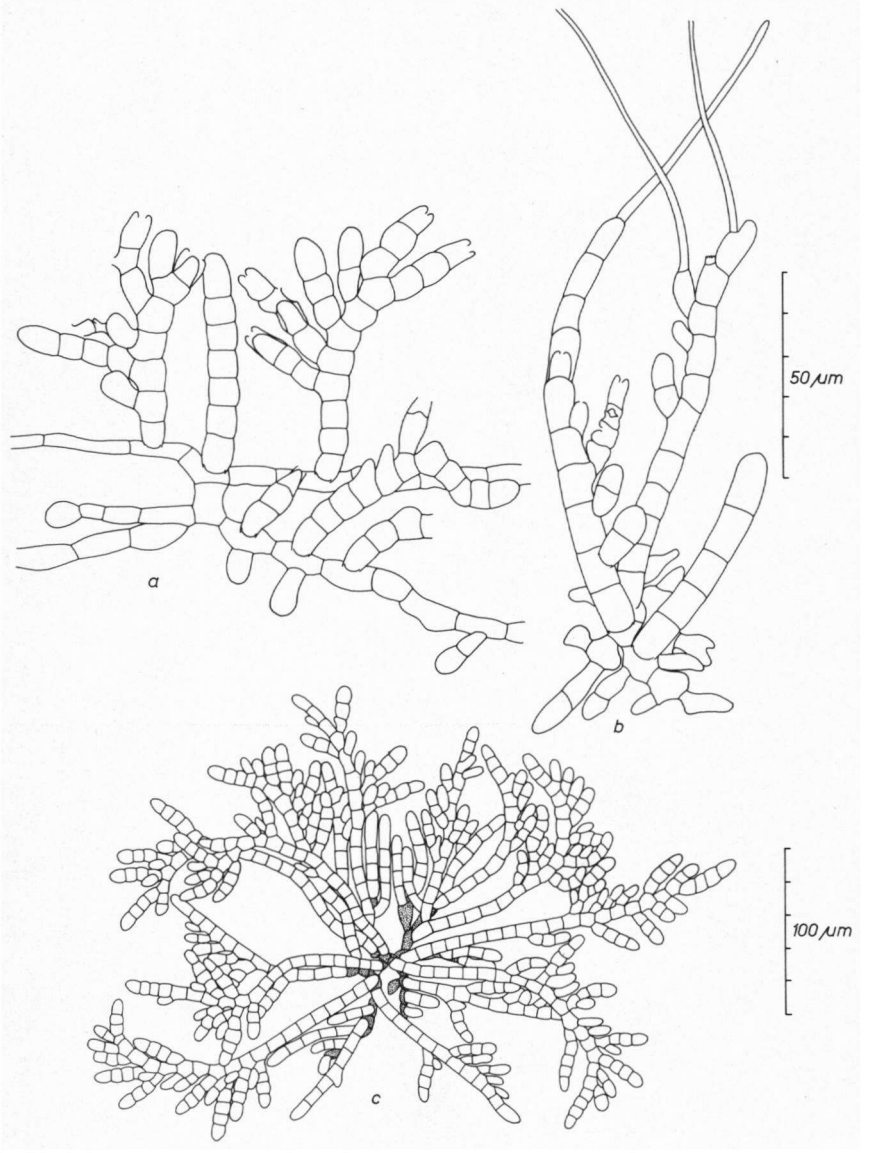

Fig. 2. Tetrasporophyte; field-collected material – reproductive plants, bearing monosporangia.
a. from *Chaetomorpha linum*, Gat van Ouwerkerk, 7-XII-1967.
b. from *Chaetomorpha linum*, Grevelingen, 6-VIII-1975.
c. from *Enteromorpha* sp., Sas van Goes, 18-VIII-1975.

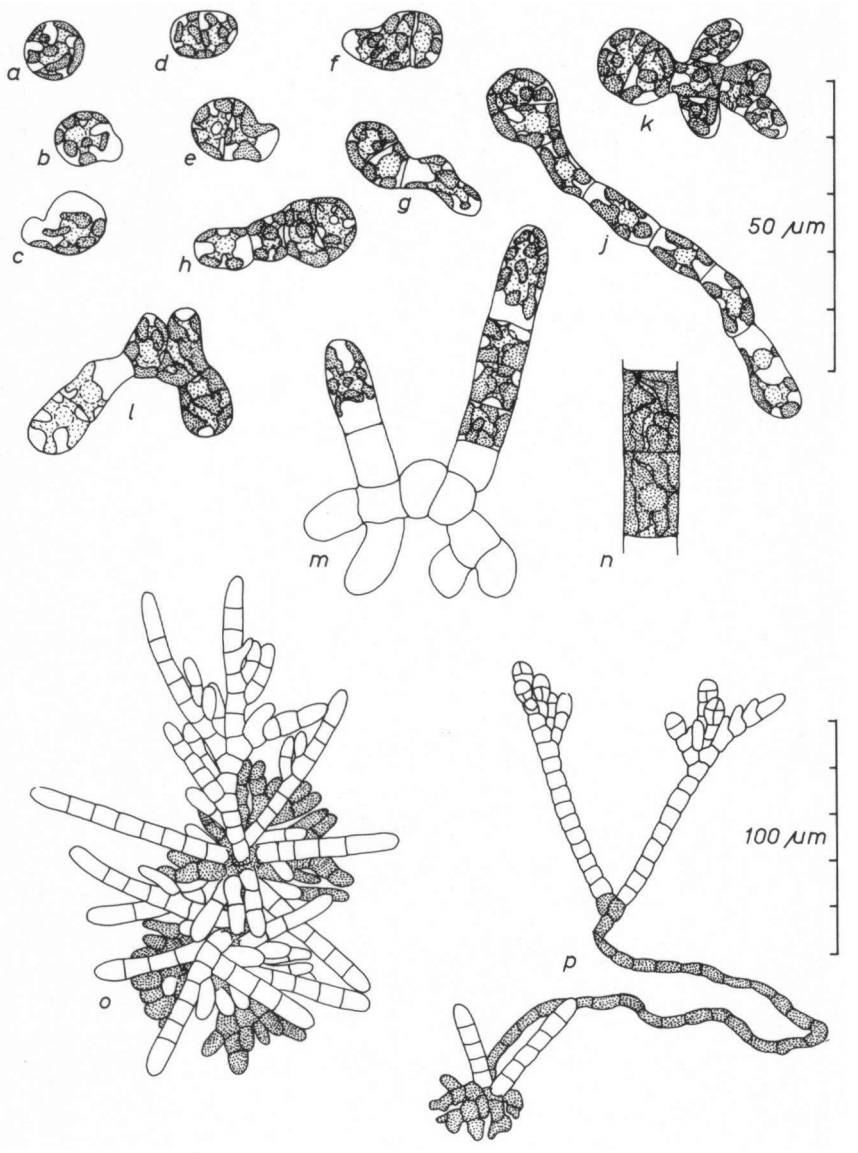

Fig. 3. Tetrasporophyte; culture material.
a-m. germination of monospores and first developmental stages. *n.* chromatophore in older cells of erect filaments. *o, p.* variation in morphology in basal and erect parts; *o:* grown at 16°C., 2000 lux, *p.* grown at 20°C., 150 lux.

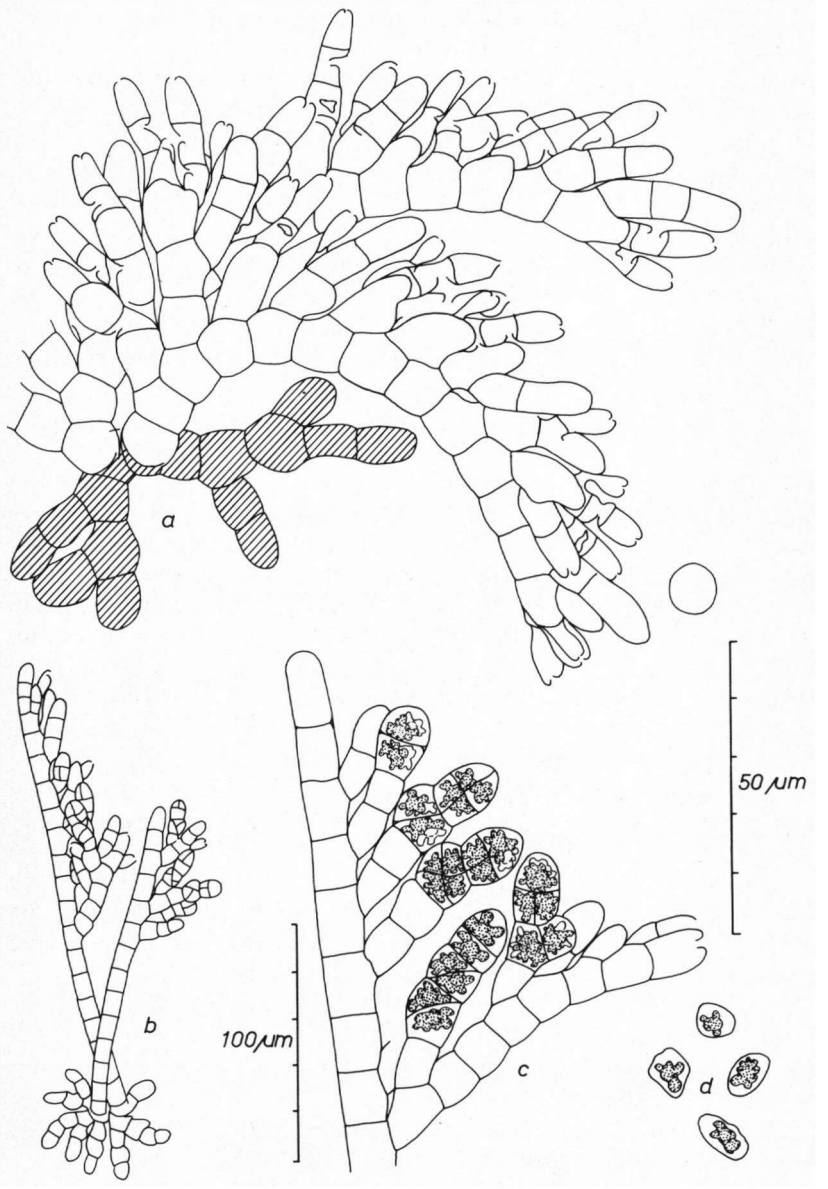

Fig. 4. Tetrasporophyte; culture material – reproductive structures. *a*. monosporangia. *b*, *c*. tetrasporangia. *d*. tetraspores.

singly or in series of 2, rarely 3. Division of these tetrasporangia is cruciate, the first division being transverse.

Intercalary tetrasporangia have the first division oblique to the length axis of the filament, the plane of the second division is perpendicular to the first. This development is apparently caused by the special shape of such tetrasporangia, which have a lateral protrusion. Mature tetrasporangia measure (8.5) 10.5–12.5 (15.5) × 6–8.5 (9.5) μm when situated terminally and (8.5) 9.5–11.5 × 7.5–8.5 μm when formed intercalary.

Liberated tetraspores measure 5–6 μm in diameter and like the monospores they have a centrally located stellate chromatophore, as a rule of a paler red colour. Both types of spores initially show amoeboid movement.

Not all isolated clones could be induced to form tetrasporangia; some reproduced by means of monospores only.

The gametophyte *(figs. 5, 9a, b).*

Tetraspores germinate in a unipolar fashion, usually under some increase in diameter. From this one-celled base 1 to 5 erect filaments arise. In mature plants the basal cell is usually not morphologically distinct from the other vegetative cells. The filaments consist of barrel-shaped cells. The diameter of the filaments is 8–10 μm, toward the apex tapering to (3.5)4–6 μm. Cell length is (3)4–8(10) μm. The cells contain a stellate chromatophore and a central pyrenoid.

Branching of the filaments in the gametophyte is as variable as it is in the tetrasporophyte and generally secund, but under low temperatures also multilateral. Strongly branched plants are often arcuate.

On the gametophytes monosporangia may be formed in large quantities. They nearly always occur in series of 3 to 4, rarely up to 7. Terminal monosporangia measure (5)6–7.5(9.5) × (4)5–6(6.5) μm, intercalary ones (4)5–6 (6.5) × (4)5–6(6.5) μm. The gametophytic monospores germinate in the same fashion as tetraspores, however, division of the spore may take place before the first erect filament has been formed. The result is then suggestive of a septate spore resembling that of the tetrasporophyte.

Sexual reproduction *(figs. 6, 9c–h).*

Under conditions of low temperature (8 °C) gametangia are formed, in largest quantity when light intensity is low.

Spermatangia and carpogonia occur on separate plants and usually only on ontogenetically young stages.

The spermatangia are found apically or laterally on main axes and laterals, usually 1 or 2 per vegetative cell. They are colourless, vacuolate and measure 3–4 μm in diameter. After release of the spermatium internal proliferation may occur. The occurrence of seriate spermatangia is infrequent.

The position of the carpogonia is identical to that of spermatangia, but they are rarely formed in quantities of more than three per plant. Carpogonial length, exclusive the trichogyn, is 8–12 μm, the diameter 4–6 μm and trichogyn

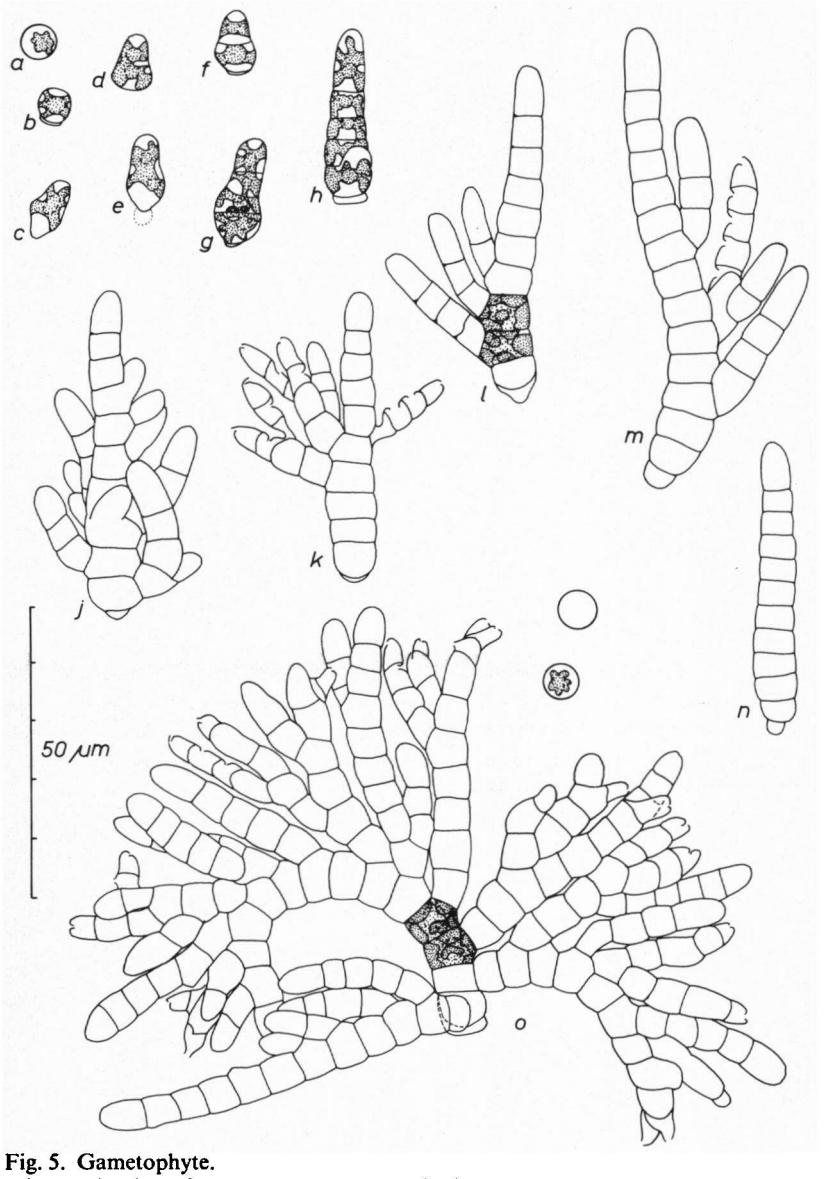

Fig. 5. Gametophyte.
a-h. germination of tetraspores or gametophytic monospores.
j-o. variation in morphology of older plants; *k*, *m*, *o;* reproductive plants, bearing monosporangia.

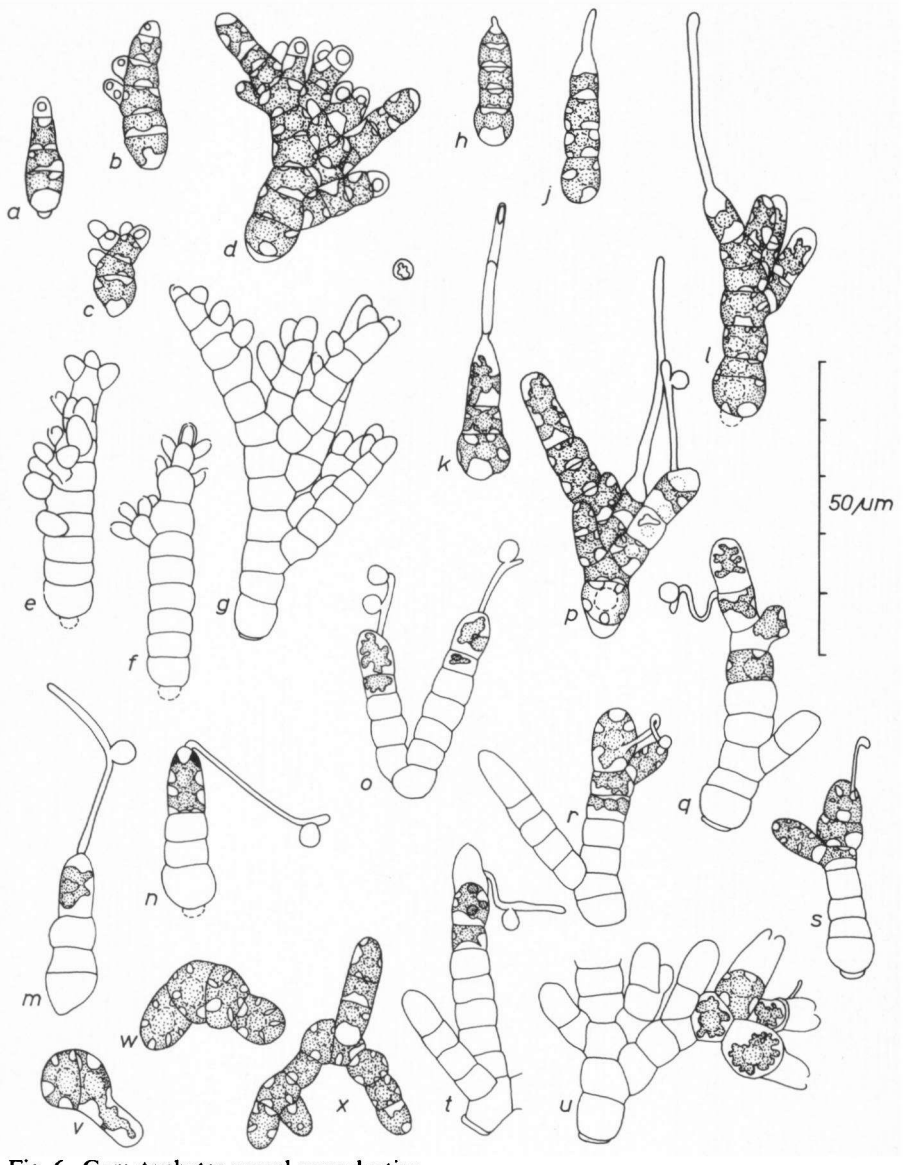

Fig. 6. Gametophyte; sexual reproduction.
a-g. ♂ gametophytes, bearing spermatangia. *h-l.* ♀ gametophytes, bearing carpogonia. *m.* fertilization. *n-q.* post-fertilization development. *r-u.* mature carposporophytes, in *t* and *u* with empty carposporangia. *v-x.* germinating carpospores.

length up to 40 μm. Carpogonia contain a small chromatophore, the trichogyn is colourless and vacuolate.

Fertilization was established in aerated cultures of a ♂ and ♀ clone combined. The fertilized carpogonium increases in length and divides transversally; the trichogyn is then pushed aside.

Mature carposporophytes are rather simple in structure; in their most primitive form they consist of a three-celled filament of which the terminal cell transforms into a carposporangium. Larger carposporophytes consist of a two-celled axis, each cell of which bears a few carposporangia. The carposporangia are sessile or pedicellate, and measure about 10–12 × 7–9 μm. The possible occurrence of seriate carposporangia could not be established with certainty. The carpospores germinate in a septate fashion and render the tetrasporophyte.

Variability of morphological and reproductive features

Both a tetrasporophyte and a male gametophyte were tested for their morphological variability in crossed gradients of light intensity and temperature. The applied conditions were all possible combinations of the temperatures 2, 8, 14, 20, 25 and 29 °C (in *figs. 11–13*: *A–F*) and light intensities 150, 270, 650, 1550, 3400 and 5700 lux (in *figs. 11–13*: *1–6*). During the experiments the temperature varied not more than 1 °C and light intensity decreased about 5%; the day-length regime was 12/12 h. In these experiments plants were observed at 7-days intervals during 4 weeks. The cultures were initiated from monospores which had been allowed to settle on coverslides during 2 days under suitable conditions (16 °C, 1500 lux) before being transferred to experimental conditions. As a rule, five plants from each culture were measured each time of observation.

A general characteristic of the developments in 4 weeks is shown in *figs. 11* and *12*. *Fig. 13a, b* illustrate the variation of two characters (average cell length and degree of branching) in relation to the separate factors light intensity and temperature; in these graphs plants are compared which have the same age (i.c. 3 weeks) and plants which have about the same height (i.c. 15-celled erect axes). The latter comparison has been made in order to eliminate the effects that possibly are connected with the ontogenetical stage of the plants; moreover plants of this size are more reliable in comparison with field-collected specimens.

A. The tetrasporophyte

The results of these experiments will be summarized now:

1. Apparently 2 °C is too low a temperature for the tetrasporophyte to allow growth of some significance. Anyway very few spores survived.
2. Growth, measured as increase in cell number in the erect axes is maximal at 25 °C and in the tested range of conditions much less influenced by light intensity than by temperature.
3. Degree of branching is temperature dependent and highest (up to an average of 0.80 laterals per cell) at 8 °C. At low temperature the degree of branching is positively correlated with light intensity. The nature of branching is independent of either factor and always secund.

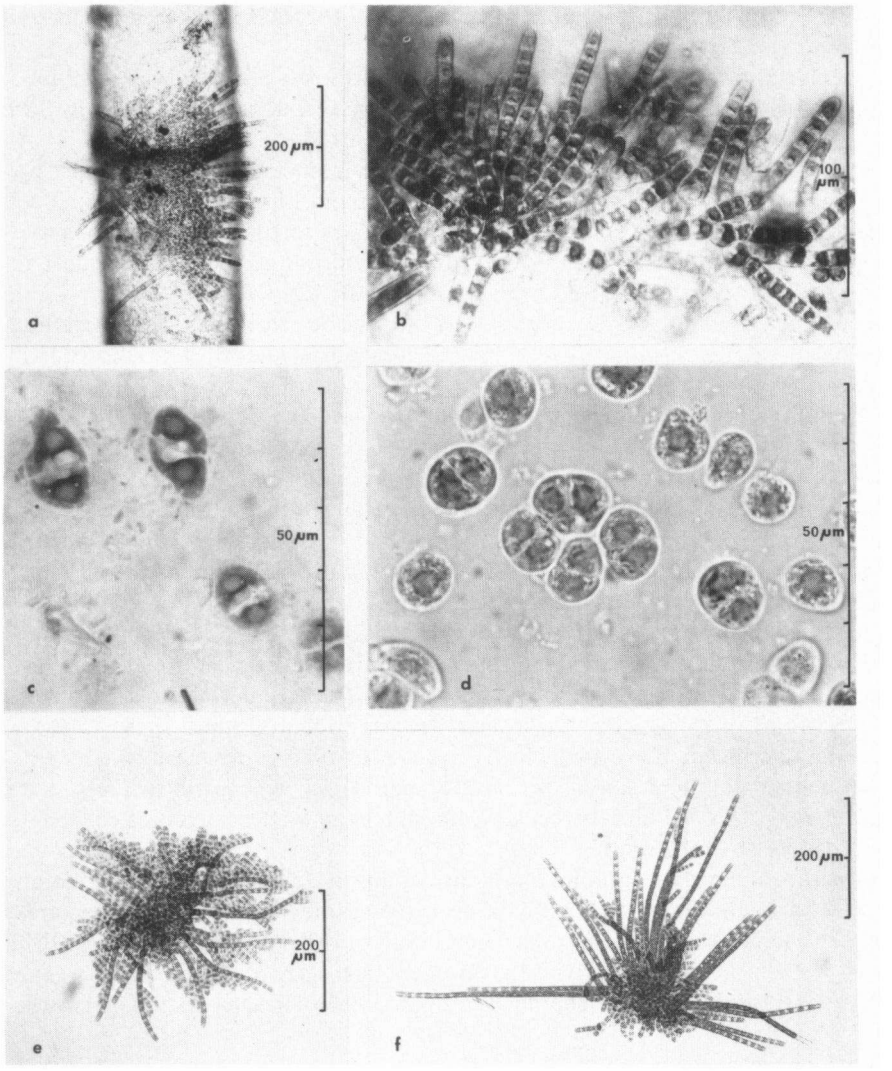

Fig. 7. *a, b.* Tetrasporophyte on *Chaetomorpha linum*, Gat van Ouwerkerk. *c, d.* germination of tetrasporophytic monospores, *c* field-collected material, on *Chaetomorpha*, *d* in culture, on glass slide. *e,f.* tetrasporophytes in culture.

4. Average cell length increases with increasing height of the plants, and the only response to any of the tested factors is a slight increase under conditions of both high temperature and light intensity (Note the difference between 3-weeks old and 15-celled plants!).
5. Monosporangia are formed over a fairly large temperature range (8–20 °C) and in largest quantity under high light intensity. Whole plants or fragments initially form monosporangia also when transferred to 25 °C.

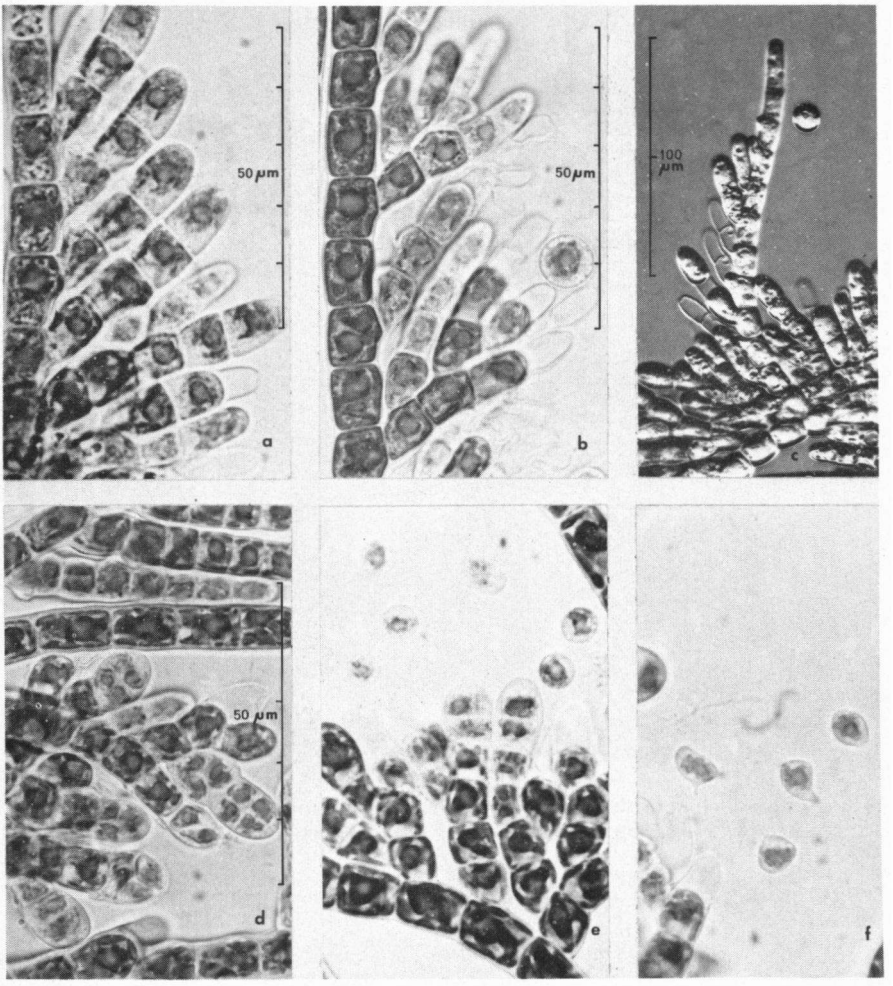

Fig. 8. *a*, *b*, *c*. monosporangia on the tetrasporophyte (in *c* note lateral pores in subterminal sporangia). *d*, *e*. tetrasporangia. *f*. released tetraspores, showing amoeboid deformation.

6. Tetrasporangia are formed in a more limited temperature range (14–20°C) and in quantity only under lower light intensities; here they nearly completely replace the monosporangia.
7. Morphology of the prostrate system is dependent on light intensity: under high light intensity the prostrate system forms a disclike structure of branched filaments, under low light intensity it often forms long unbranched filaments that do not give off erect filaments either (compare figs. 3 o and p). Consequently the number of erect filaments in a plant increases with light intensity.

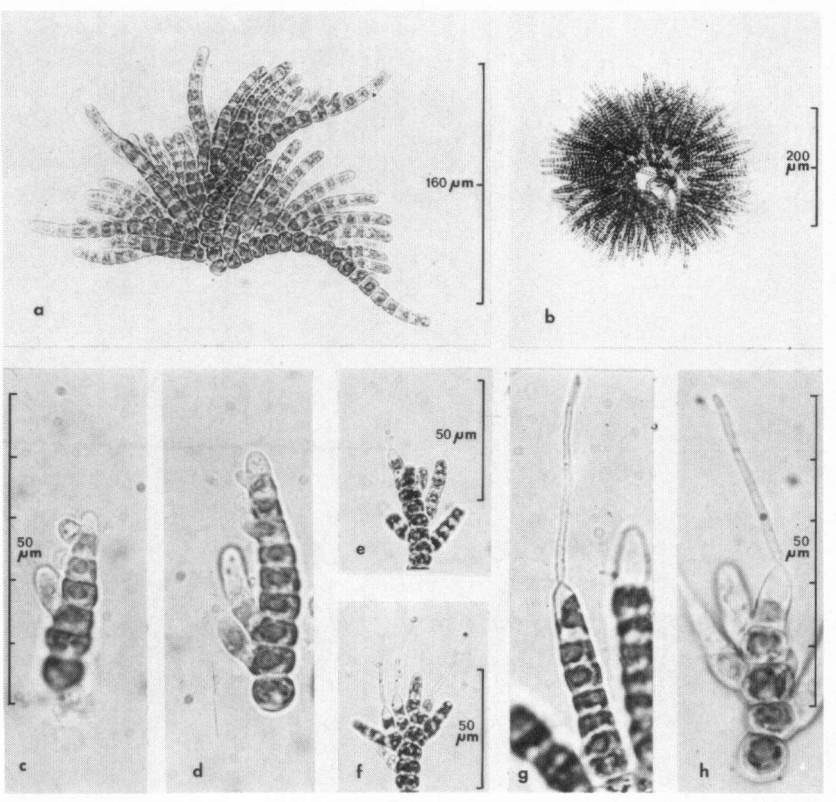

Fig. 9. *a,b.* non-reproductive gametophytes, *c,d.* ♂ gametophytes bearing spermatangia. *e-h.* ♀ gametophytes bearing carpogonia.

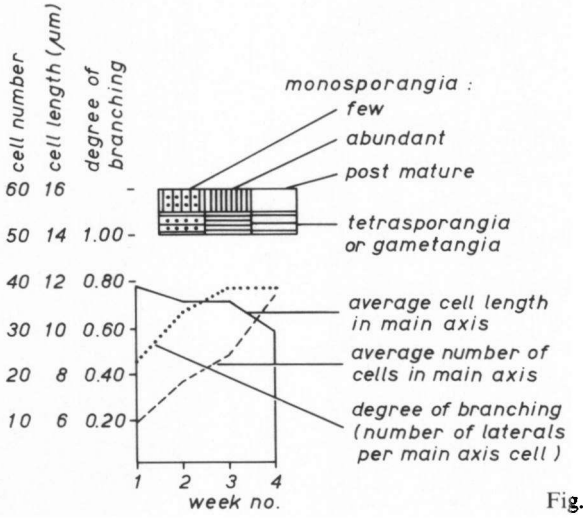

Fig. 10. Legend to *figs. 11.* and *12.*

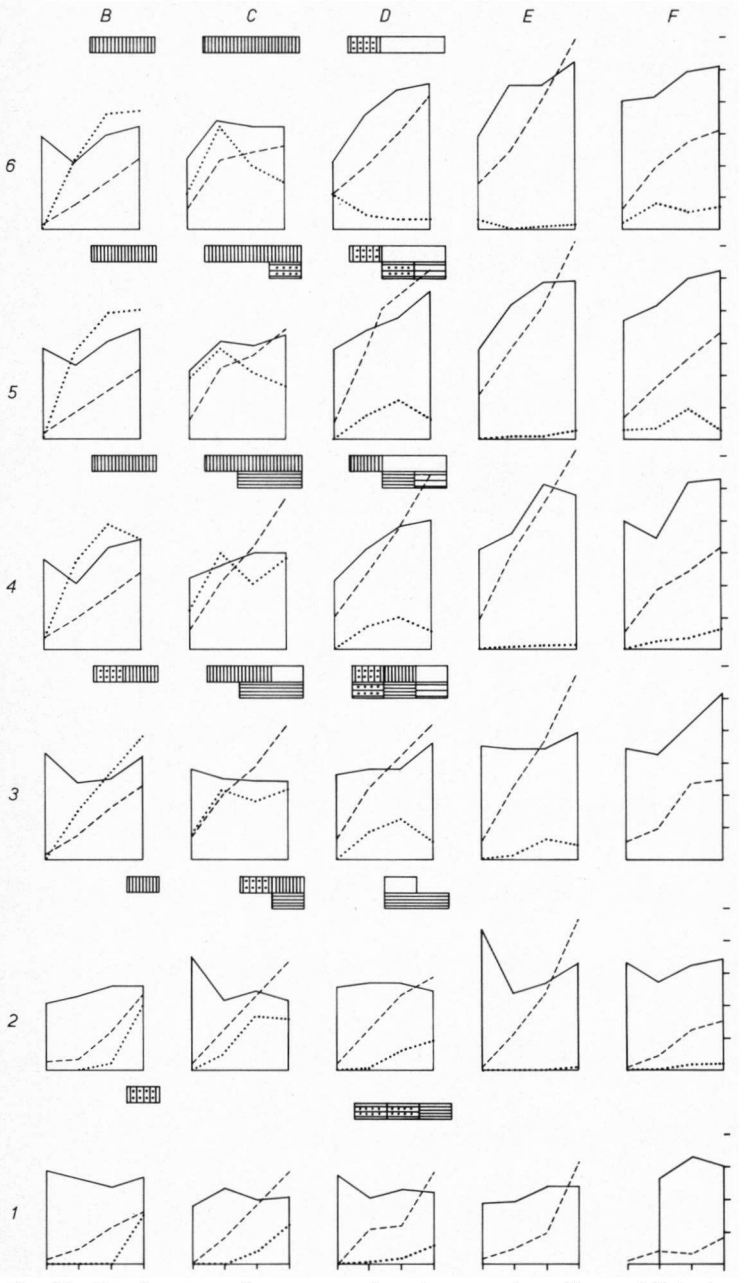

Fig. 11. Development of tetrasporophyte in crossed gradients of light intensity and temperature; light intensities 1–6: 150, 270, 650, 1550, 3400 and 5700 lux; temperatures A-F: 2, 8, 14, 20, 25 and 29°C. Further legend in *fig. 10*.

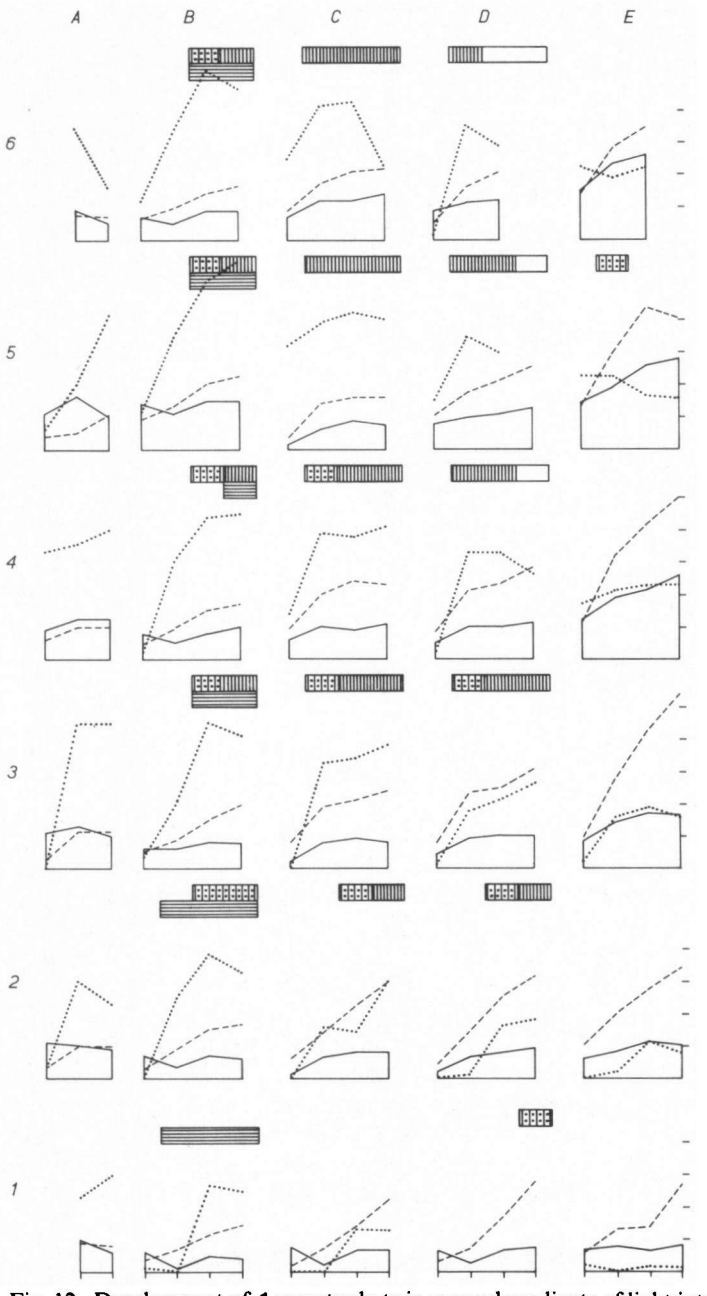

Fig. 12. Development of ♂ gametophyte in crossed gradients of light intensity and temperature; light intensities and temperatures as in *fig. 11.*, further legend in *fig. 10.*

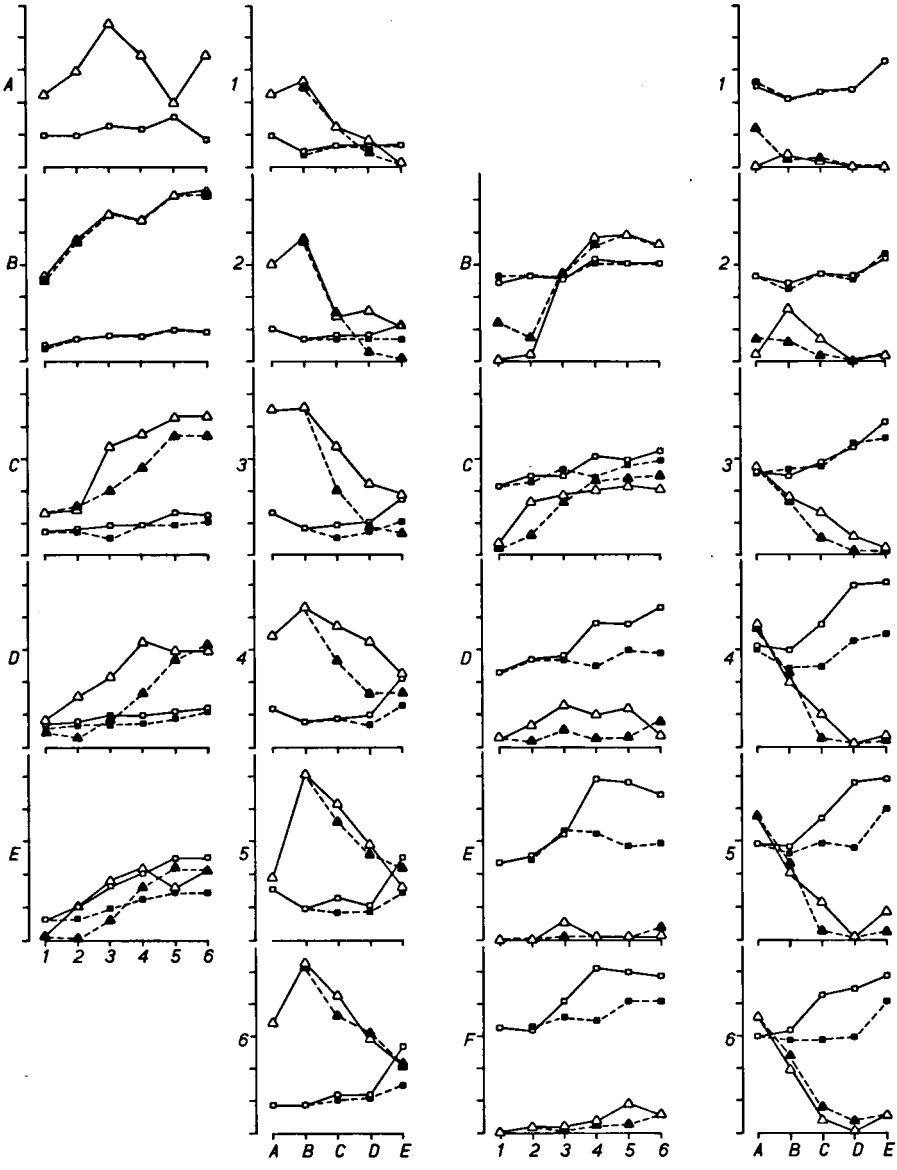

Fig. 13. *a*. Column 1 and 2: Relation of cell length and degree of branching in the gametophyte to light intensity and temperature.
b. Column 3 and 4: Relation of cell length and degree of branching in the tetrasporophyte to light intensity and temperature.
(□ = cell length in 3 weeks plants, ■ = cell length in 15-celled plants; △ = degree of branching in 3 weeks plants, ▲ = degree of branching in 15-celled plants; units as in *fig. 10*.).

8. High light intensity promotes the formation of hairs, although hairs never become abundant.
9. Two pyrenoids per chromatophore may be found in plants grown under high light intensity.
10. Diameter of the filaments and dimensions of monosporangia and tetrasporangia are rather uniform throughout the range of experimental conditions.

B. **The gametophyte:**

1. Growth of the gametophyte occurred over a temperature range of 2–25 °C, although the survival rate of the spores at 2 °C was very low. At 29 °C neither spores nor whole plants survived.
2. Growth is maximal at 25 °C and, like in the tetrasporophyte, more affected by temperature than by light intensity.
3. Degree of branching is related to temperature and highest at 8 °C (up to 1.20 laterals per cell) while again a positive correlation with light intensity exists. Under a combination of low temperature and high light intensity branching tends to be multilateral, under all other conditions it is secund. On the average, gametophytes are stronger branched than tetrasporophytes,
4. Average cell length is fairly constant over a large range of tested conditions, but it increases somewhat when high temperature and high light intensity are combined.
5. Monosporangia are regularly formed in a temperature range of 8–20 °C and only occasionally at 25 °C. They occur in largest quantity under high light intensity. Transformed whole plants may form monosporangia at 2 °C as well.
6. Gametangia (i.c. spermatangia) are formed at 8 °C only and in largest quantity under low light intensity.
7. The number of filaments arising from the basal cell increases with increasing light intensity and shows no relation to temperature. It hardly ever exceeds 1 under the lowest light intensity and reaches an average of 2.5 under the highest light intensity.
8. Hairs have never been observed on the gametophytic generation.
9. The number of pyrenoids is nearly always one per chromatophore.
10. Filament diameter and dimensions of monosporangia are rather constant and are not related to one of the tested factors.

5. DISCUSSION

Acrochaetium densum (Drew) Papenfuss has been 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 *Acrochaetium* species: e.g. WEST (1968), BORSJE (1973) and STEGENGA & BORSJE (1976) have found diplobiontic life histories in *A. pectinatum*, *A. virga-*

tulum and *A. dasyae* respectively.

The nature of the dissimilarity of the generations in *A. densum* closely resembles that in *A. virgatulum:* both species have a tetrasporophyte with a multicellular base and a gametophyte with a unicellular base. It is different, however, from *A. dasyae*, in which species the dissimilarity is mainly expressed in the manner of spore germination.

From the present study and above mentioned previous records it can be concluded that certain described *Acrochaetium* species in fact may represent phases in the life histories of other species. This confirms the suggestion made by DIXON (1963) that two forms found with either tetrasporangia or gametangia only, may form part of a single life history. On the other hand, the heteromorphy of the generations implies that species which have been recorded in nature to possess both kinds of reproductive organs must be regarded with utmost care as long as the life history has not been verified experimentally. In the field such species only can be recognized as a single entity if the generations are more or less isomorphic.

WOELKERLING (1971) has devided the acrochaetioid algae into the genus *Audouinella* and the form genus *Colaconema*, the latter composed of species of which sexual reproductive structures are unknown. From our observations it follows that at least some of the species thus far referred to *Colaconema* possibly can be transferred to the genus *Audouinella.*

The form genus *Colaconema* appears to be partly composed of tetrasporophytic phases, but possibly also some gametophytes, of which only asexual reproduction has been recorded, are included. However, the species we are dealing with in this paper, has not directly been mentioned in one of WOELKERLING'S recent revisions (WOELKERLING 1971, 1972, 1973 a, b).

The life history we have found seems to be temperature controlled only, as far as alternation of phases is concerned. Low light intensity promotes both tetrasporangium and gametangium formation. The influence of temperature in culture suggests a seasonal alternation of the generations at least as far as their reproduction is concerned; a weaker response but with the same tendency was found in their vegetative development: gametophytes can stand low temperature better while tetrasporophytes more easily survive at high temperature.

Considering the conditions along the Dutch coast, the tetrasporophyte then would be expected to form tetrasporangia in summer, while the gametophyte would be found with sexual reproductive organs during winter. Unfortunately we never found the gametophyte on the Dutch coast. The only *Acrochaetium* species with a unicellular base occurring in this area, is very different in morphology and probably identical to *A. hallandicum* or *A. rhipidandrum.*

Moreover the tetrasporophyte has never been found with any other reproductive structures than monosporangia in the field. Therefore it is more likely that the tetrasporophyte, which occurs all the year round, only renders itself by means of monospores. NORRIS & WEST (1967) report the occurrence of *A. densum* and *Kylinia arcuata* from Washington at the same time and from the same substrate. As will be shown later in this section, *K. arcuata* is possibly one

of the species, identical to the gametophyte of *A. densum*.

The effect of light on tetrasporangium and gametangium formation is primarily one of light intensity: experiments with different daylengths yielded formation of the relevant reproductive organs under all conditions if the light intensity was sufficiently low. We have not exactly established, however, the combined effect of daylength and light intensity.

The apparent lack of daylength control on the sexual cycle contrasts with the findings in *Acrochaetium pectinatum* and *A. virgatulum* (WEST 1968, BORSJE 1973) where such effects were rather pronounced. In *A. pectinatum* WEST (1968) found no influence of light intensity on formation of tetrasporangia.

From the experiments in the light and temperature gradients it may be concluded that a number of morphological characters may vary extremely and hence cannot be used in distinguishing the species from other acrochaetioid taxa. The most stable characters in both generations are cell and monosporangial dimensions; we also found that the type of spore germination and the structure of the chromatophore are reasonably constant.

On the other hand, the morphology of the prostrate system (in the tetrasporophyte), degree of branching, number of erect axes, possession of hairs and number of pyrenoids per chromatophore, turned out to be too variable for use as morphotaxonomic criteria. Also the presence or absence of reproductive organs of any kind is too much related to certain environmental conditions to be used in typification.

In general, these results agree with the views of WOELKERLING (1971) on this matter, but he attaches more value to the number of pyrenoids per chromatophore.

The name *Acrochaetium densum* was chosen rather arbitrarily for the species we are dealing with in the present paper and is based on literature study only. Several species of acrochaetioid algae have been described which show resemblance to our material. In identification of the tetrasporophyte we have considered the following characters to be of crucial importance: the septate spore and multicellular base, erect filaments with relatively short cells and a diameter within certain limits, and possession of monosporangia or tetrasporangia in series. To our knowledge four species have been recorded which more or less fit this description: *Rhodochorton densum* Drew (1928); *Rhodochorton kurilense* Nagai (1941); *Kylinia seriaspora* Dawson (1952) and *Acrochaetium hummii* Aziz (1965). For identification of the gametophyte we used the following characters: unicellular base, shortcelled erect filaments and monosporangia in series. Two series fit this description: *Acrochaetium catenulatum* Howe (1914) and *Rhodochorton arcuatum* Drew (1928). In *tables 1* and *2* these species are compared with our material. It may be noted that there appears a great deal of similarity in these species. A few points of difference will be discussed now:

– The shape of the chromatophore is recorded differently in the various species, but as we have seen, in our material the chromatophore may be interpreted as parietal as well as stellate, especially in older cells (note that in *Rhodochorton*

Table 1. Comparison of the tetrasporophyte with four described species (according to original descriptions).

	Rh. densum Drew	*Rh. kurilense* Nagai	*K. seriaspora* Daws	*A. hummii* Aziz	tetrasporophyte (incl. culture obs.)
spore germination	septate	septate	?	septate	septate
base	creeping filamentous	creeping filamentous	monostromatic basal stratum	creeping filamentous	creeping filamentous
maximal height	C. 100 µm (in figure)	165–450 µm	600–800 µm	500 µm	200–? µm
branching (incl. branchlets)	secund, rather frequent	secund	secund, partly alternate; frequent	sparse to frequent secund, alternate or opposite;	none to frequent; usually secund
chromatophore structure	parietal, lobed; central pyrenoid; stellate in monosporangia	parietal or fenestrate; with pyrenoid	stellate; central pyrenoid	parietal or stellate; with pyrenoid	essentially stellate with central pyrenoid
cell diameter	apic.: 7 µm basal: 10 µm	apic.: 4.5–6 µm basal: 7.5–9 µm	5–7 µm	6–8 (13) µm	6–8 (9) µm
ratio length/ diameter cell	1.5–2	1.6–2.8	2–4	1.5–3	(0.75) 1–2
monosporangia	11.0 × 8.5 µm	10.5–12 × 7–7.5 µm; "bisp.": 13.5–22.5 × 7.5–9 µm	6 µm dam.; ovoid	10–13 × 7–10 µm; "bisp": 18–22 × 7–10 µm; "trisp.": 23–27 × 7–10 µm	term.: (7.5) 9–11 (13.5) × 6–7.5 (8.5) µm int.: (6) 6.5–9 (11.5) × (6) 6.5–9 µm
tetrasporangia	–	–	7–8 µm diam.	–	term.: (8.5) 10–12 (15.5 × 6–8.5 (9.5) µm int.: (8.5) 9.5–11.5 × 7.5–8.5 µm
spermatangia	–	–	–	5–7 × 3–4 µm	–
carpogonia	–	–	–	21 × 4–5 µm, trich. 13 µm	–

Table 2. Comparison of the gametophyte with two described species (according to original descriptions).

	A. catenulatum Howe	*Rh. arcuatum* Drew	gametophyte (culture)
spore germination	unipolar	unipolar	unipolar
base	unicellular	unicellular	unicellular
number of erect axes	1	1–4	1–5
maximal height	50–150 µm	C. 70 µm (in figure)	irrelevant in culture
branching (incl. "branchlets")	secund or alternate, rarely opposite; frequent	secund or alternate	very sparse to very frequent; usually secund
chromatophore structure	occupying nearly whole cell	stellate; central pyrenoid	essentially stellate with central pyrenoid
cell diameter	apic.: 7–8 µm basal: 9–11 µm	(6) 8 (10) µm	apic.: (3.5) 4–6 µm basal: 8–10 µm
ratio length/ diameter cell	(0.75) 1 (2)	1–2	(0.5) 1 (2)
monosporangia	9–11 × 5.5–7 µm	10–14 × 7–10 µm	term.: (5) 6–7.5 (9.5) × (4) 5–6 (6.5) µm int.: (4) 5–6 (6.5) × (4) 5–6 (6.5) µm
spermatangia	–	4 µm diam.	3–4 µm diam.
carpogonia	–	–	8–12 × 4–6 µm, trichogyn to 40 µm

densum, the chromatophore is termed parietal but containing a central pyrenoid).

– The interpretation of the seriate monosporangia has varied a great deal; sometimes they are considered as immature tetrasporangia (NAGAI 1941) or termed di- or trisporangia (AZIZ 1965). DREW (1928) has suggested maturation of the subterminal sporangia only after release of the spore from the terminal sporangium; we have found that this is not necessarily the case: the subterminal sporangia may be the first ones to shed their spores.

– True tetrasporangia have only been reported in *Kylinia seriaspora;* they are identical to the ones we found in culture. *K. seriaspora* seems to lack seriate monosporangia; the nature of spore germination is unknown in *K. seriaspora.* (DAWSON 1952).

– Gametangia are known from *Rhodochorton arcuatum* (only spermatangia) and, strange enough, from *Acrochaetium hummii.* Since the latter species is morphologically identical to our tetrasporophyte, it would seem that *A. hummii* either contains two different morphological forms or occasionally forms generation-uncharacteristic reproductive organs. AZIZ (1965) remarks that sexual plants are rare; the fertilized carpogonium is reported to give rise to one carposporangium directly, without an intermediate carposporophytic phase. Although, in our material, the morphology of the carposporophyte is very simple, we have never found such an extreme reduction.

– *Acrochaetium catenulatum* is the most frequently recorded of the hitherto

mentioned species. Since its original description (HOWE 1914) it is not always reported, however, to possess seriate monosporangia (e.g. LEVRING 1952).

– The only serious deviation in cell dimensions occurs in *Rhodochorton arcuatum:* its monosporangia are considerably larger than in the gametophyte of our species.

The thus far mentioned species have been recorded from a variety of substrates, mostly macroalgae, among which *Chaetomorpha* spp. takes a prominent place. Except for *A. hummii*, all species were recorded from Pacific coasts or adjacent areas (*fig. 14*). However, some *Acrochaetium* clones we have isolated from the Roscoff area (France) undoubtedly belong to this complex and it may prove to be more widely distributed.

If the possession of seriate monosporangia is considered to be of no importance for distinction at the species level, several other acrochaetioid taxa come into scope, e.g. in the European Atlantic region (cf. ROSENVINGE 1909, HAMEL 1928, BØRGESEN 1927).

For the tetrasporophyte: *Acrochaetium humile* (Rosenv.) Børg.; *A. reductum* (Rosenv.) Hamel; *A. canariense* Børg.; *A. mahumetanum* Hamel.

For the gametophyte: *Acrochaetium microscopicum* (Näg.) Näg.; *A. trifilum* (Buff.) Batters; *A. moniliforme* (Rosenv.) Børg.; *A. crassipes* (Børg.) Børg. Part of the species of the latter group have been merged with other species (among which *A. catenulatum!*) into the *Audouinella microscopicum* complex (WOELKERLING 1972).

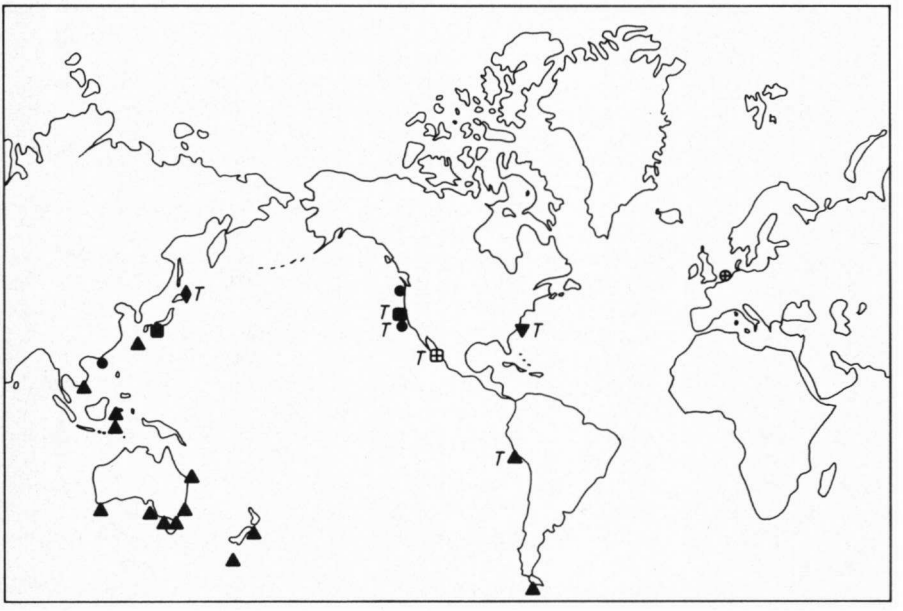

Fig. 14. World distribution of *Acrochaetium densum* and morphologically closely related species (▲ = *A. catenulatum*, ● = *A. arcuatum*, ■ = *A. densum*, ♦ = *A. kurilense*, ▼ = *A. hummii*, ⊞ = *A. seriaspora*, ⊕ = *A.* sp. (own material); T = type locality).

A final settling of the nomenclatural problems will have to await further research on other members of this group of species, preferably by a combination of experimental approach and study of the type-specimens.

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