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THE MORPHOLOGY AND LIFE HISTORY OF ACROCHAETIUM POLYBLASTUM (ROSENV.) BØRG. AND ACROCHAETIUM HALLANDICUM (KYLIN) HAMEL (RHODOPHYTA, NEMALIALES)

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SUMMARY

The morphology of two species of *Acrochaetium*, provisionally identified as *A. polyblastum* (Rosenv.) Børg. and *A. hallandicum* (Kylin) Hamel, is described in some detail. They are shown to be tetrasporophyte and gametophyte respectively in the same life history. Both phases are characterized by the possession of a stellate chromatophore with a central pyrenoid; the tetrasporophyte has a spore which germinates septately and subsequently develops a multicellular filamentous base, the gametophyte has a unicellular base.

The sexual cycle is mainly temperature-controlled, the gametangia being formed under higher temperature than the tetrasporangia. Both generations reproduce asexually by means of monospores, in a wide temperature range.

The morphological variability, as affected by different environmental conditions, appears to be very large; moreover there is an ample variation between different clones grown under uniform conditions. General structure of the plant, the type of spore germination in each phase, and cell diameter are the most reliable characters in delimiting the species from other acrochaetioid taxa.

The life histories of *Acrochaetium* species possessing stellate chromatophores, as exemplified by a number of different species now, show a remarkably uniform pattern, as far as alternation of morphological phases is concerned. It is suggested that characters of the total life history provide a reasonable basis for the systematics of the acrochaetioid algae.

1. INTRODUCTION

Culture studies on acrochaetioid algae have yielded a good deal of information on the life histories of some species (KNAGGS & CONWAY 1964; KNAGGS 1968; WEST 1968, 1969; BORSJE 1973; STEGENGA & BORSJE 1976; STEGENGA & VROMAN 1976). Until this time, however, these studies have not led to a new view on the systematics of the whole group. On the contrary, WOELKERLING (1971) and DIXON (in PARKE & DIXON 1976) have expressed the opinion that morphotaxonomic characters in the acrochaetioid algae are of too little value to warrant separation into more than one genus. WOELKERLING still retains a form genus, *Colaconema*, for "imperfect Acrochaetiaceae", DIXON only recognizes the genus *Audouinella*. Similar views have earlier been expressed by DREW (1928) and followed by others (e.g. NAKAMURA 1941, 1944).

Although some "key-characters" like basal structure, shape and number of chromatophores and reproductive features may have proved unsatisfactory when used separately, a combination of several characters may lead to a more natural classification of the group. Hence, what is needed first, is a detailed

study of the life histories of more species, and the present paper may be regarded as such a contribution.

Acrochaetium polyblastum (Rosenv.) Børg. and *Acrochaetium hallandicum* (Kylin) Hamel are species, both characterized by the possession of a stellate chromatophore with a central pyrenoid. In overall morphology they differ a great deal, *A. polyblastum* having a multicellular filamentous base, whereas *A. hallandicum* possesses a single basal cell. In the course of this study we have found ample evidence that the two species actually are phases of one and the same life history, *A. polyblastum* representing the tetrasporophyte and *A. hallandicum* the gametophyte. For ease of survey we will first give an outline of the morphology of field-collected material of both phases, and afterwards pay attention to the life history as reconstructed in culture.

Both *A. polyblastum* and *A. hallandicum* were found in the southwestern part of the Netherlands, *i.c.* the Eastern Scheldt; *A. polyblastum* was collected once near Huisduinen (province of North-Holland). They were always collected near low tide level. Their usual substrate is *Polysiphonia nigrescens*, and to a lesser degree *Ceramium rubrum*. Moreover *A. hallandicum* may sometimes be found abundantly on *Porphyra umbilicalis* and *Sphacelaria plumigera*, and occasionally on other *Polysiphonia* spp., *A. polyblastum* was collected from January to April; *A. hallandicum* is possibly present throughout the year but owing to the absence of the usual substrate, *Polysiphonia nigrescens*, it was only occasionally met with in the summer (July to October).

In addition to the elucidation of the life history we have paid attention to the morphological variability of both phases. Inter- as well as intraclonal variation were established, with the purpose of evaluating the morphological characters as taxonomic criteria. Identification of the material has been carried out using data from the literature only, and must be considered provisional.

2. MATERIALS AND METHODS

Material of *A. polyblastum* was collected at the following localities: Huisduinen: 16-IV-1969 (139); Wemeldinge: 4-III-1976; Westkapelle: 2-IV-1976; Zierikzee: 15-III-1968, from *Polysiphonia nigrescens* and *Ceramium rubrum* (85); 21-IV-1969 (137); 5-I-1971, from *Polysiphonia nigrescens* and *Ceramium rubrum* (154); 31-I-1975.

Material of *A. hallandicum* was collected at the following localities: Kattendijke: 4-IX-1967, from *Polysiphonia violacea*; Sas van Goes: 21-IV-1969 (131); 5-I-1971 (146); 17-II-1971, from *Polysiphonia nigrescens* and *Ceramium rubrum;* 16-V-1972; 2-XII-1974 (213, 215, 216); 31-I-1975; 1-IV-1975; 24-V-1975; 12-VI-1975; 28-VI-1976, from *Porphyra umbilicalis;* Wemeldinge: 7-XII-1967 (32); 4-III-1976, from *Polysiphonia nigrescens*, *Ceramium rubrum* and *Sphacelaria plumigera;* Zierikzee: 15-III-1968, from *Polysiphonia* spp. and *Ceramium rubrum* (63); 21-IV-1969; 5-I-1971.

If not stated otherwise, the only substrate was *Polysiphonia nigrescens*. Numbers in brackets indicate serial numbers of clones isolated and taken into

culture; cultures are stored at the Botanical Laboratory of our University.

Standard culture techniques were applied (see STEGENGA & VROMAN 1976), and as a culture medium an enriched seawater (PROVASOLI 1968) was used.

One gametophytic and one tetrasporophytic clone were tested for their morphological variability under different conditions of temperature, light intensity and daylength. Interclonal variation of the tetrasporophyte was studied by growing different isolates under uniform conditions.

3. MORPHOLOGY OF FIELD-COLLECTED MATERIAL

3.1. The tetrasporophyte *(figs. 1, 3a-c)*

The basal part of the plants consists of a septate spore and a number of branched prostrate filaments. Typically, the germinated spore is a (3)4-celled structure, measuring *c.* 10–12 × 15–18 μm. Each of these cells may give rise to one or two creeping filaments, consisting of irregularly shaped cells. The basal part may be very extensive (up to 250 μm) and form a dense mat of filaments on the substrate *(fig. 1f)*.

The erect filaments may arise from the original spore and other cells of the prostrate part. Often they look poorly developed in comparison to the base; in such cases they are scarcely branched. On a few occasions plants had a larger erect part, the filaments up to 400 μm in length; these filaments were frequently branched, usually secundly. Erect filaments measure 7–10 μm in diameter, cell length averages 9–15(20) μm, the larger cells occurring on plants with a well developed erect part.

Monosporangia are numerous only on plants with a well developed erect part; they occur mostly in secund series on the adaxial face of the laterals, and are usually sessile, sometimes pedicellate. In small plants they measure 9–15.5 × 7.5–11.5 μm, in bigger plants 15–18 × 9.5–11.5 μm.

Tetrasporangia were observed only once (15-III-1968) and in small numbers; they measured *c.* 18 × 10.5 μm.

3.2. The gametophyte *(figs. 2, 3d)*

The base is unicellular and in shape and size quite well distinguishable from the cells of the erect filaments; it measures 10–12 μm in diameter. 1–3(4) erect filaments are given off; they are up to 400 μm (= *c.* 40 cells) high. In older plants they are more or less secundly branched and sometimes arcuate. The diameter of the filaments is (5)6–7.5(8) μm, the average cell length in the main axis is 8.5–14(16) μm. Unicellular hairs may occur in small numbers, terminal or lateral on main axes and laterals.

Monosporangia are found on the main axes and laterals, in the latter case usually in adaxial position. They are mostly sessile, occasionally pedicellate. Monosporangia measure (7.5)10–14(16) × (5)6.5–10 μm. Indeterminate laterals and monosporangia both may occur in opposite positions.

On one occasion (21-IV-1969) carpogonia were found, measuring 7.5–10 × 5–5.5 μm, trichogyn length up to 20 μm.

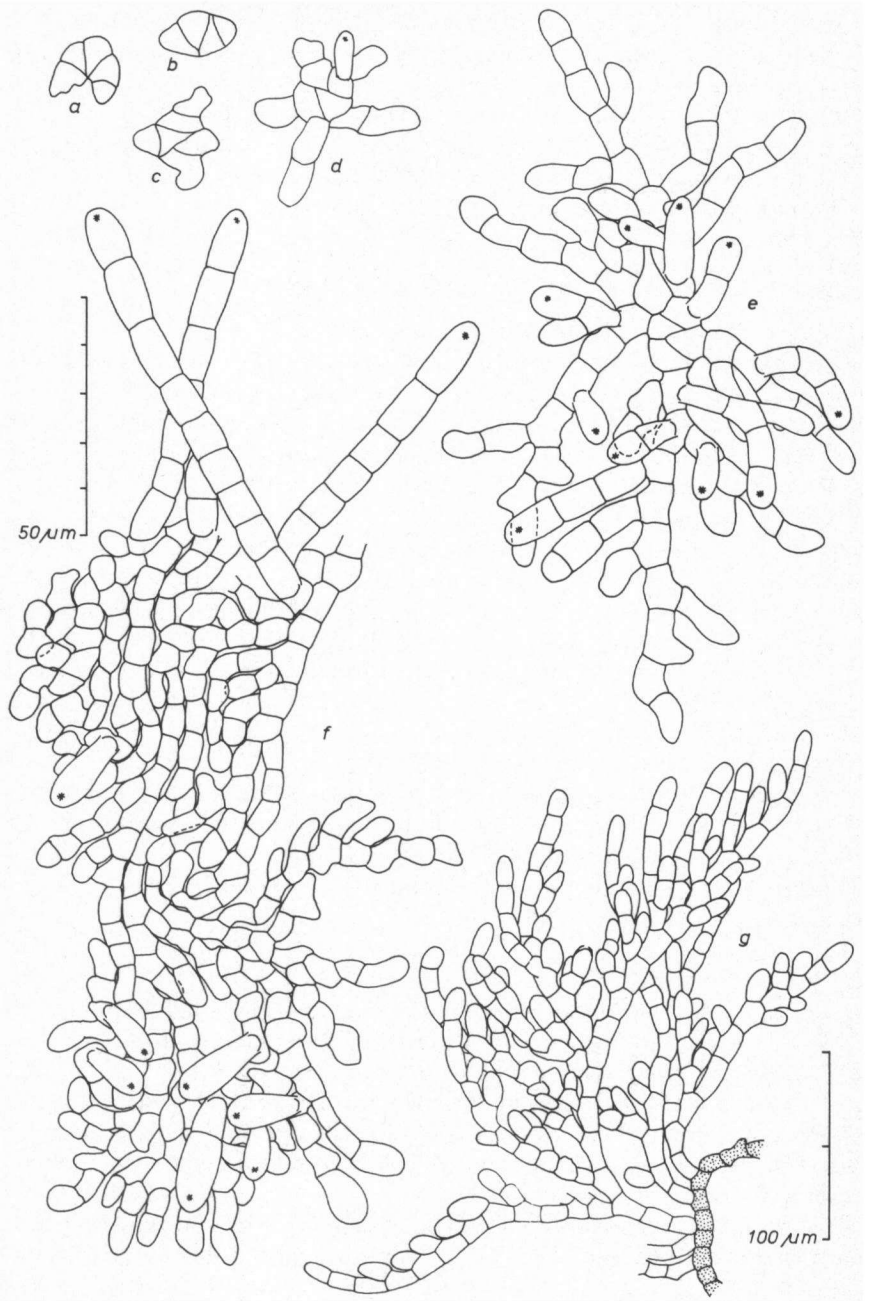

Fig. 1. Tetrasporophyte; field-collected material. *a-d.* germinating spores; *e-f.* plants with extensive prostrate part and short erect axes (marked *); *g.* larger erect part with monosporangia.

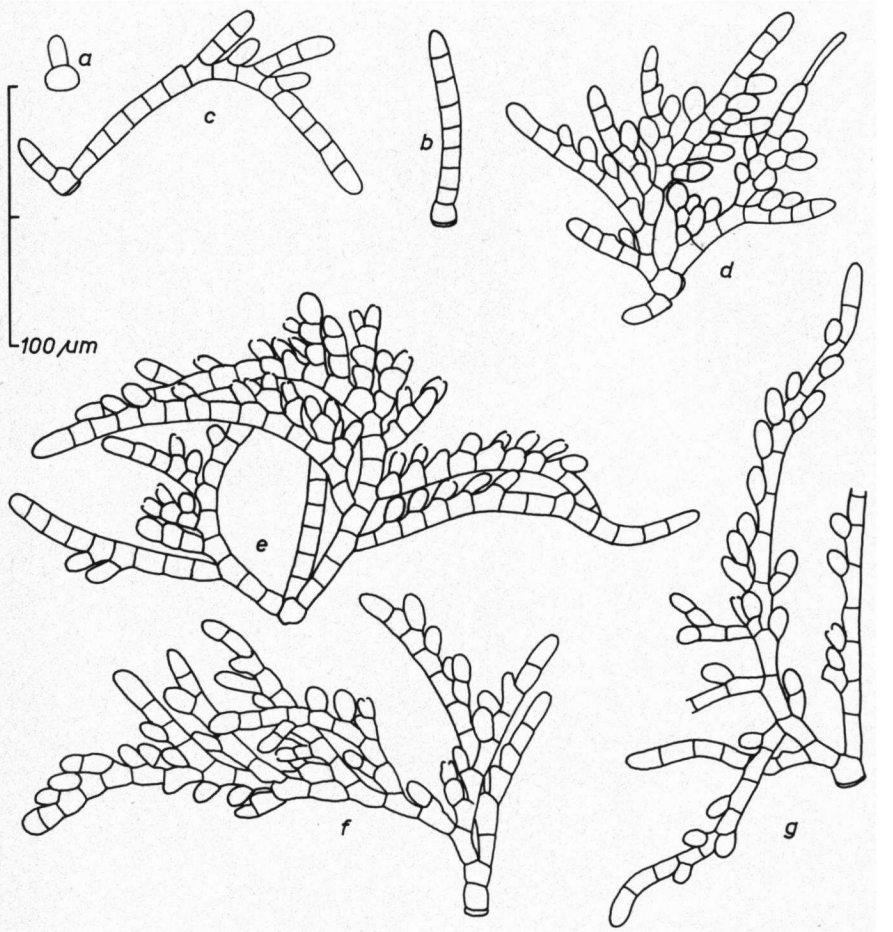

Fig. 2. Gametophyte; field-collected material. *a-c.* juvenile stages; *d-g.* monosporangial plants.

4. LIFE HISTORY IN CULTURE

The life history of the present species was established by initiating cultures both from the tetrasporophyte and from the gametophyte.

The tetrasporophyte forms tetrasporangia under conditions of relatively low temperature (4–8(12)°C) while both long day conditions and high light intensity seem to promote tetrasporangium formation somewhat. Tetrasporangia in these clones, however, never become abundant *(fig. 4a)*; on maturity they measure 17.5–25 × 11.5–14.5 µm. Division of the tetrasporangium is cruciate, the first division in transverse. Released tetraspores are *c.* 10 µm in diameter.

Tetraspores germinate to form gametophytes with a single basal cell. These

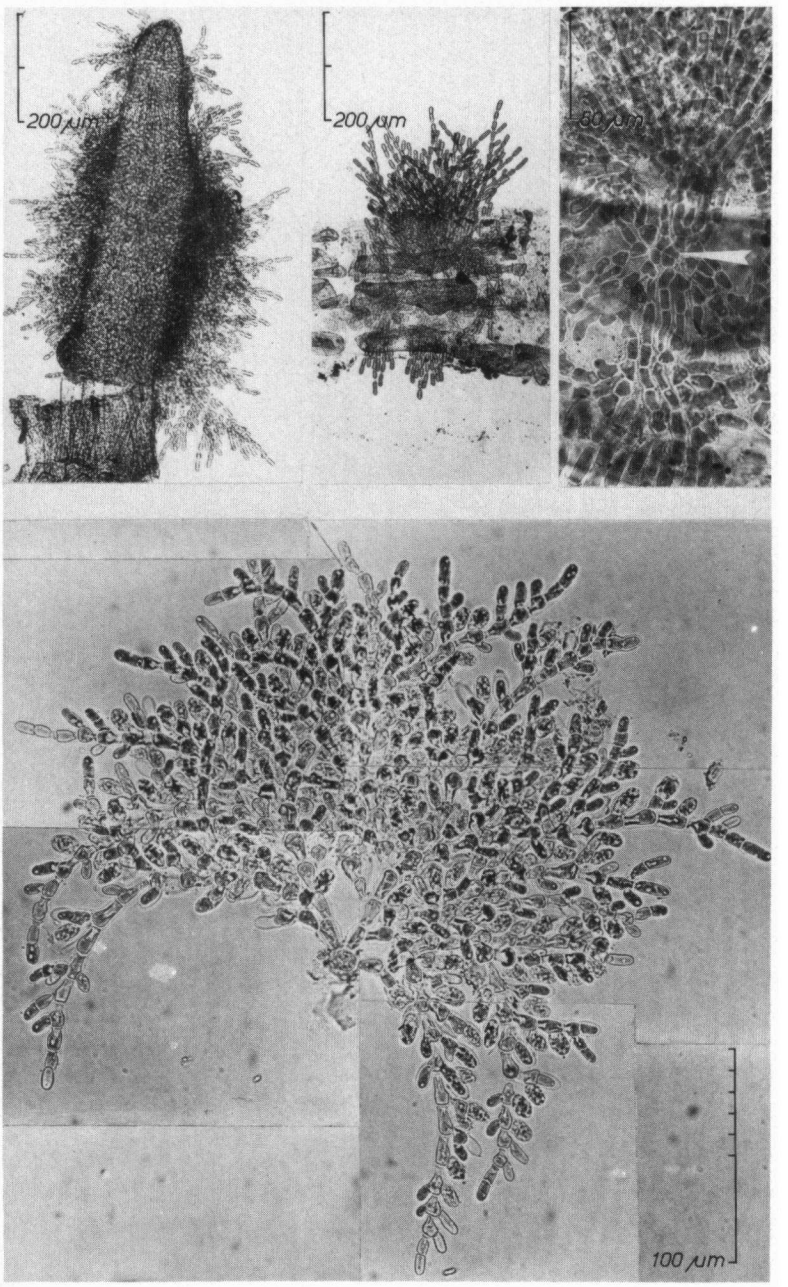

Fig. 3. *a, b.* tetrasporophytes on *Polysiphonia nigrescens*, Wemeldinge, 4-III-1976; *c.* detail of extensive prostrate part (arrow indicates original spore); *d.* well developed gametophyte, bearing numerous monosporangia; from *Polysiphonia nigrescens*, Sas van Goes, 21-IV-1969.

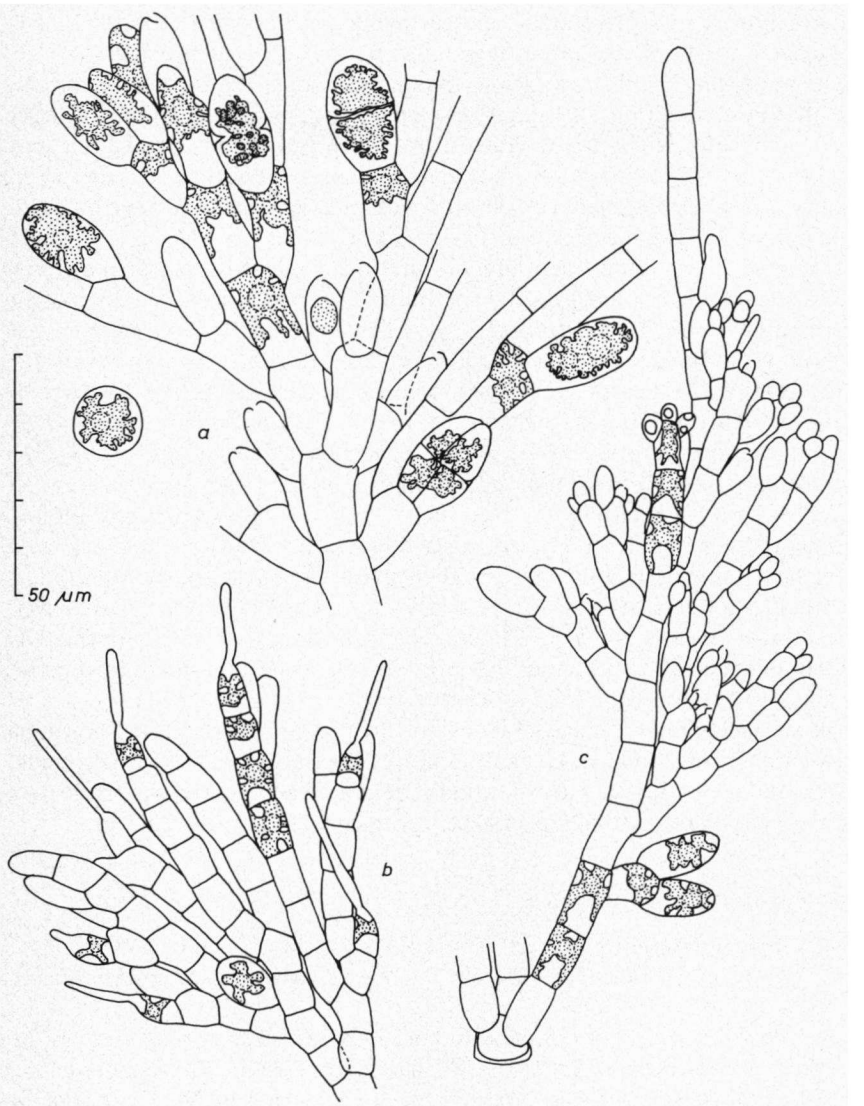

Fig. 4. Reproductive structures in culture.
a. detail of tetrasporophyte (clone 137) with monosporangia and tetrasporangia in various stages of development; 8°C, 16/8; *b*. detail of ♀ gametophyte (clone 216) with carpogonia; 16°C, 12/12; *c*. detail of ♂ gametophyte (clone 63) with monosporangia and spermatangia; 12°C, 12/12.

gametophytes form gametangia under higher temperature (12–20°C). Reproductive gametophytes often have a strongly arcuate appearance and are typically bisexual. Both carpogonia and spermatangia are formed terminally and laterally on the branches, singly or in groups of 2 to 3. Carpogonia measure 12–16 × 5–7 μm, trichogyn length up to 35 μm. Aberrant carpogonia may possess a forked trichogyn or sometimes bear a spermatangium (*fig. 5l,m;* actually a subspermatangial cell develops into a carpogonium). Spermatangia are slightly oval and measure 5–6 × 4–5 μm.

A bisexual clone under high temperature forms numerous carposporophytes, as carpogonia are fertilized by spermatia *(fig. 5h)*. After fertilization the carpogonium either divides transversally, or remains undivided. In either case the resulting structure gives rise to a number of sessile carposporangia *(fig. 5n-s)*; usually 3 or 4 carposporangia are borne by each cell of the divided carpogonium. Carposporangia measure 14–16 × 8–11 μm. After carpospore release internal proliferation of the empty carposporangia may take place. Carpospores germinate in a septate fashion and render the tetrasporophyte.

Field-isolated gametophytes, like those obtained from tetrasporophytes, form gametangia under relatively high temperature. However, all isolated clones were unisexual *(fig. 4b,c)* and in culture their shape is usually less arcuate. Carpogonia measure 10–12 × 5–6 μm, trichogyn length up to 25 μm; spermatangia measure 4–5 × 3–4 μm. Fertilization could be established by combining a ♂ and ♀ clone in aerated cultures. The resulting carposporophytes are much the same as the ones described above.

The tetrasporophytes, derived from these carpospores form tetrasporangia at low temperature, and in greater abundance than the field-isolated specimens; under suitable conditions tetrasporangia are practically the only reproductive structures to be formed. Tetrasporangia measure 15–23 × 10–12.5 μm.

5. MORPHOLOGICAL VARIABILITY

Morphological variability of a tetrasporophyte (clone 137) and a gametophyte (clone 215) were tested under different regimes of temperature, light intensity and daylength.

The combined effects of temperature and light intensity were studied in the same way as described by STEGENGA & VROMAN (1976) on *Acrochaetium densum*. The main results of this experiment are illustrated in *fig. 6* and will be briefly discussed now:

– Growth, measured as increase in cell number of the main axis, for both clones is maximal at 20°C and amounts up to 9 or 10 cells per week. Only the lowest light intensities affect growth negatively and mostly so under high temperature *(fig. 7)*. Both clones showed low survival and aberrant spore germination at 25°C.

– Average cell length is quite variable in the tetrasporophyte (10–24 μm) and increases with high light intensity and low temperature. In the gametophyte it is much less variable (10–15 μm).

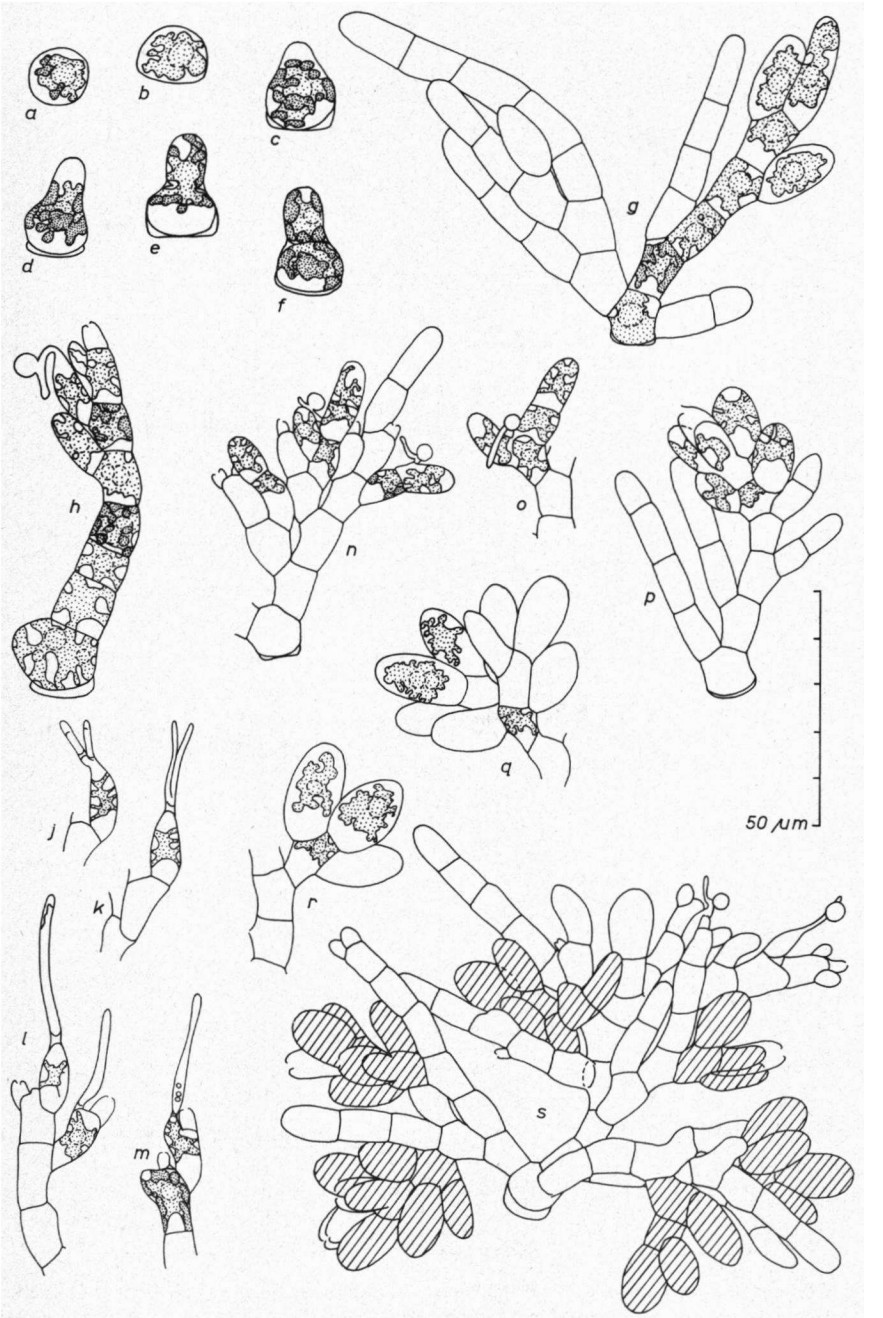

Fig. 5. Sexual reproduction in culture of a bisexual plant (offspring from clone 154). *a-f.* germination of gametophytic monospores; *g.* monosporangial gametophyte; *h.* gametophyte with spermatangia and fertilized carpogonium; *j-m.* aberrant carpogonia; *n-q.* development stages of carposporophyte; *r.* carposporophyte from undivided carpogonium; *s.* gametophyte with several carposporophytes.

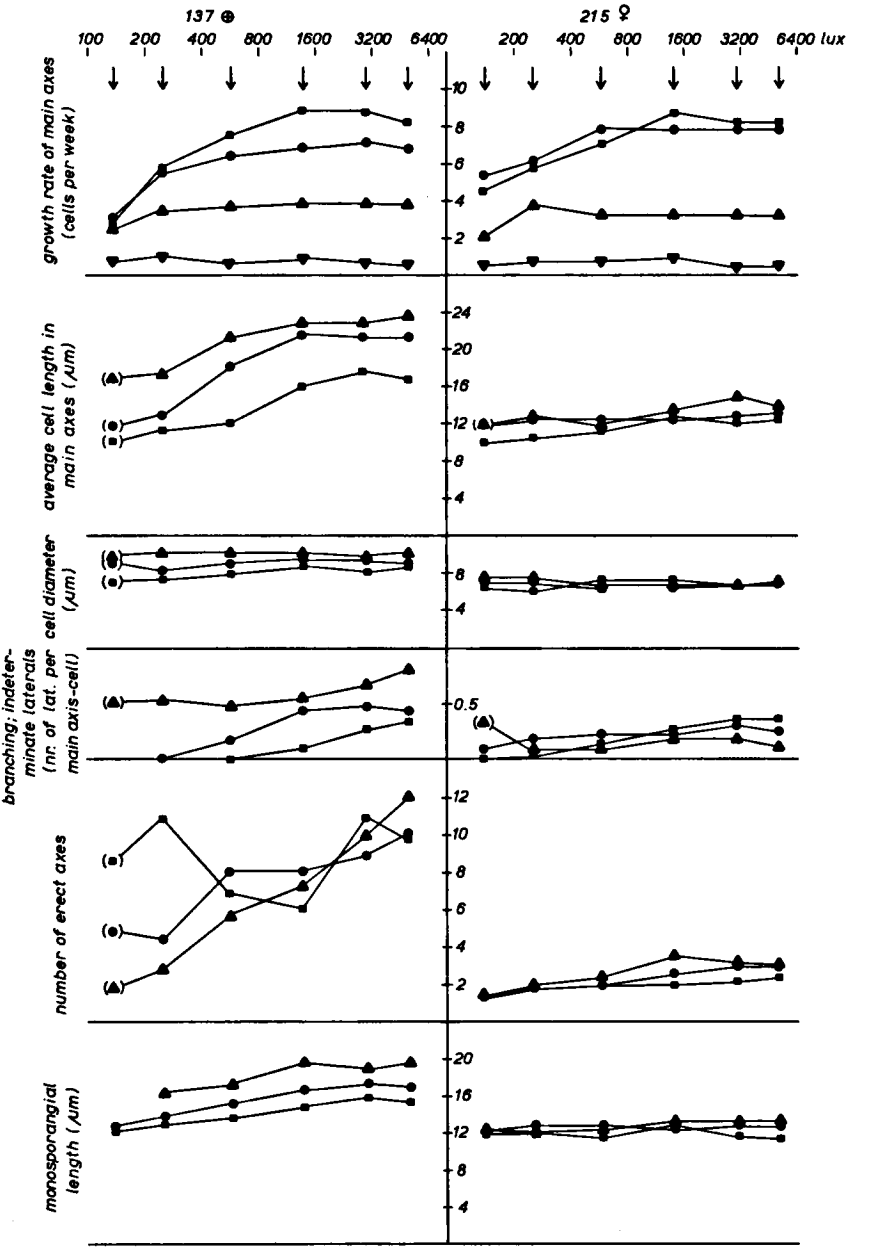

Fig. 6. Effect of light intensity and temperature on a number of morphological characters. All values, except for monosporangial length, as calculated for plants with 15-celled erect axes. Tested light intensities: 140, 250, 580, 1400, 3100 and 5000 lux; temperatures: ▼ = 1°C, ▲ = 7°C, ● = 14°C, ■ = 20°C.

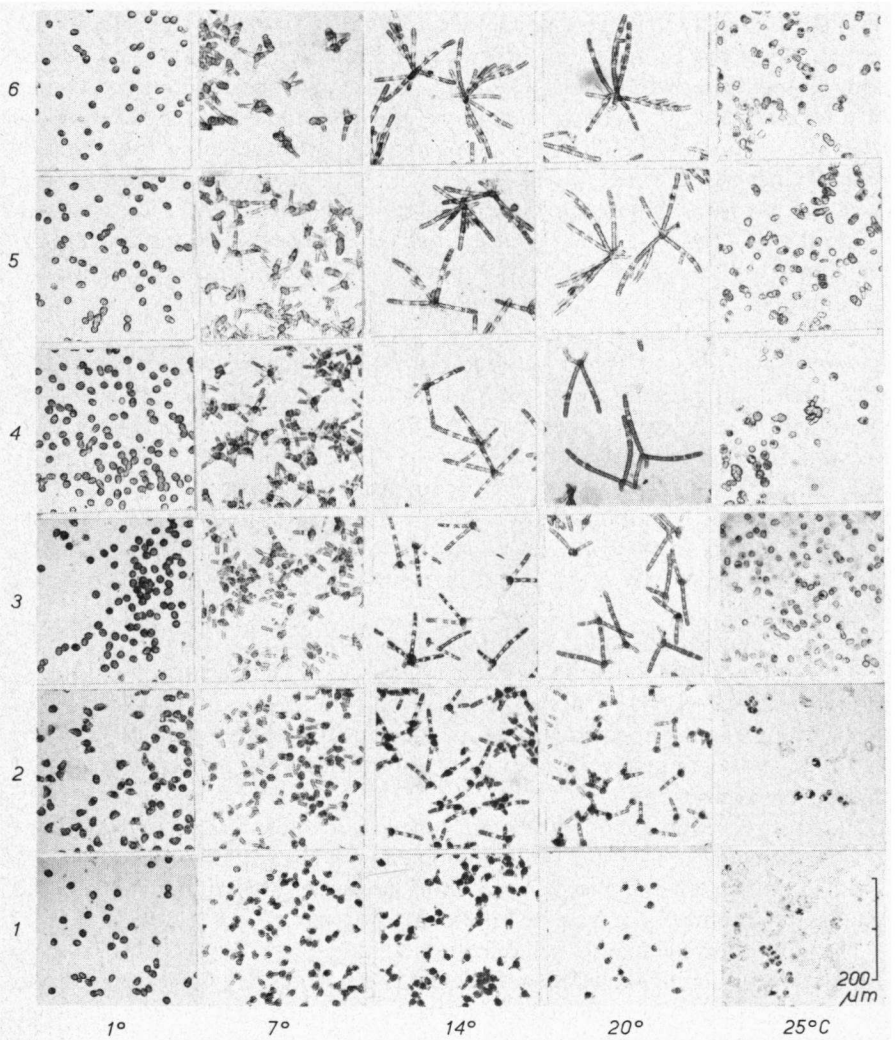

Fig. 7. Development of the tetrasporophyte (clone 137) in crossed gradients of light intensity and temperature, one week after culture initiation. Light intensities 1–6 as in fig. 6.

– Cell diameter is only slightly variable, but in the tetrasporophyte decreases somewhat when low light intensity and high temperature are combined. On the whole, cells are wider in the tetrasporophyte ((7)8–10 µm) than in the gametophyte (6–7.5 µm). Cells are mostly cylindrical, but in short-celled forms somewhat barrel-shaped; they contain one stellate chromatophore with a central pyrenoid; the occurrence of two pyrenoids per cell is, however, not infrequent.
– Under most circumstances the number of indeterminate laterals is higher in the tetrasporophyte than it is in the gametophyte (a maximum of 0.80 laterals

per main axis cell in the tetrasporophyte as opposed to 0.40 in the gametophyte). In the tetrasporophyte this degree of branching is negatively correlated with temperature, while under low light intensity indeterminate laterals may be altogether absent; in the gametophyte effects of light and temperature are much less pronounced. The total number of laterals, including sporangia, is much higher in the gametophyte.

– In the tetrasporophyte, the number of erect axes in general increases with light intensity, but at high temperature light effects seem to be more complex. Of course, in the gametophyte the number of erect filaments is limited; a maximum of 5 erect axes was observed.

– Monosporangial dimensions, like cell length, are rather variable in the tetrasporophyte; length varies between (10.5)12–19.5(21.5) μm, and increases with high light intensity and low temperature. In the gametophyte monosporangial length varies between (9.5)11.5–13.5(15.5) μm, while neither temperature nor light effects can be discerned.

There are no marked effects of light intensity or temperature on the basal structure of the tetrasporophyte. The prostrate part of clone 137 remains rather restricted anyway; it may be more extensive in other clones *(fig. 9e)*, but as compared to the erect part it is mostly smaller than in field-collected material.

On both generations, hairs were formed under high light intensity.

Formation of reproductive structures was noted in the following conditions: monosporangia on both generations, 8–20°C, while high light intensity somewhat promotes this process; carpogonia were formed at temperatures between 14–20°C, while light effects were not obvious; tetrasporangia were not formed during this experiment.

In a second experiment, the same clones were subjected to two different daylength regimes (8/16 and 16/8), combined with four different temperatures (4, 8, 12 and 16°C) and two different light intensities (300 and 2000 lux). The results are graphically represented in *fig. 8*.

The values for cell length, cell diameter, etc., in general agree with those of the first experiment. The effects of short day and long day conditions on the recorded characters have the same tendency as the effects of lower and higher light intensity respectively.

Monosporangia were formed under all tested conditions; tetrasporangium formation took place at low temperature (4–8(12)°C) – it was not exclusively related to any light condition, but occurred only very occasionally when short day and low light intensity were combined; carpogonia were formed at higher temperatures ((8)12–16°C) – under long day conditions they were absent.

In a third experiment four different clones of the tetrasporophyte were compared under uniform conditions (8 and 16°C, 12/12, 1500 lux). Three clones were field-isolated tetrasporophytes (85, 137, 139), the fourth (348) was obtained as offspring from two field-isolated gametophytes (63♂ and 215♀). The four clones are compared in *table 1*.

Besides the expected difference in development between plants grown at 8

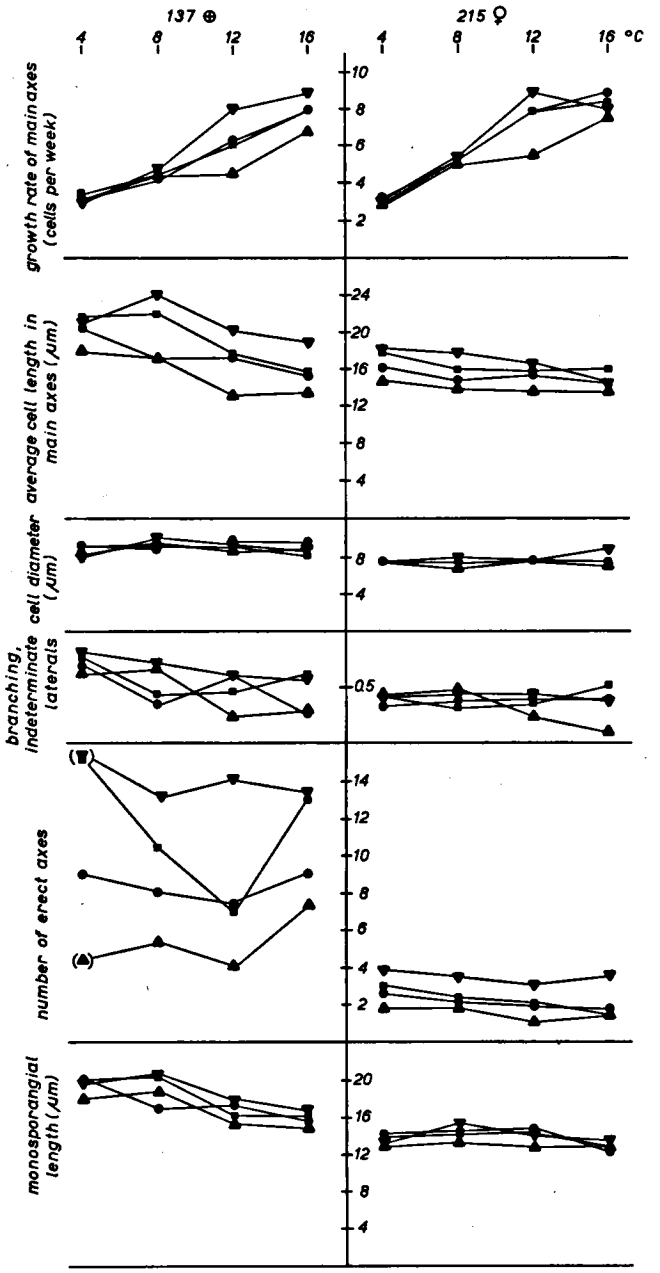

Fig. 8. Effect of daylength and temperature on a number of morphological characters. ▲ = 8/16, 300 lux; ● = 8/16, 2000 lux; ■ = 16/8, 300 lux; ▼ = 16/8, 2000 lux.

Table 1. Comparison of four different tetrasporophyte clones under two different temperatures. Whenever possible, averages are given of plants with 15-celled erect axes.

	8°C				16°C			
Clone	85	137	139	348	85	137	139	348
Growth rate (cells per week)	3.6	4.4	2.5	3.9	7.0	8.5	4.7	8.0
Cell length (μm)	20.4	22.4	(11.0)*	12.0	14.4	15.5	7.6	13.6
Cell diameter (μm)	9.7	9.5	(7.5)*	7.6	9.6	9.5	9.4	7.1
Degree of branching (indeterminate laterals per main axis cell)	0.43	0.46	(0.33)*	0.35	0.40	0.33	0.15	0.17
Monosporangial length (μm)	17.7	20.6	17.1	(16.5)**	14.7	16.4	13.1	16.2

* 15-celled stage not reached during experiment.
** only tetrasporangia present.

and 16°C, there appears to be a great deal of variation between the different clones. For example, cell length varied about 100% (8°C: 11–22 μm; 16°C: 8–16 μm), causing quite different habits of the plants *(fig. 9e-h)*. Interestingly the intraclonal variability of this character is much larger in the field-isolated tetrasporophytes than in clone 348; probably the reverse holds true for the gametophytes: compare the slight variability of clone 215 with the offspring of clone 137 *(fig. 10g,h;* cell length in clone 137 varies from 7.5 to 13.5 μm, as opposed to 15–17 μm in clone 215 under a comparable range of conditions).

The rather small diameter of the filaments in clone 348 is probably not characteristic for culture-obtained tetrasporophytes, as other clones resulting from crosses possessed cell diameters of *c.* 10 μm.

6. DISCUSSION

Two species, provisionally identified as *Acrochaetium polyblastum* (Rosenv.) Børg. and *Acrochaetium hallandicum* (Kylin) Hamel, have been shown to represent phases of one and the same life history. This then is one more case of a diplobiontic life history in the acrochaetioid algae. The types of morphological phases that alternate in this life history show much resemblance to those in other species with a stellate chromatophore, e.g. *A. virgatulum* (BORSJE 1973) and *A. densum* (STEGENGA & VROMAN 1976).

Although in both generations there have remained differences between field-isolated and culture-obtained clones, we prefer to consider the whole complex as a single species, since morphological variability within and between different clones is very large. Also mono- or dioeciousness is not considered sufficient for distinction at the species level (see also STEGENGA & BORSJE 1976).

The effects of light and temperature on morphological characters are partly comparable to those in *A. densum* (STEGENGA & VROMAN 1976), but the present species is clearly less tolerant for high temperature and survival at 1°C is much

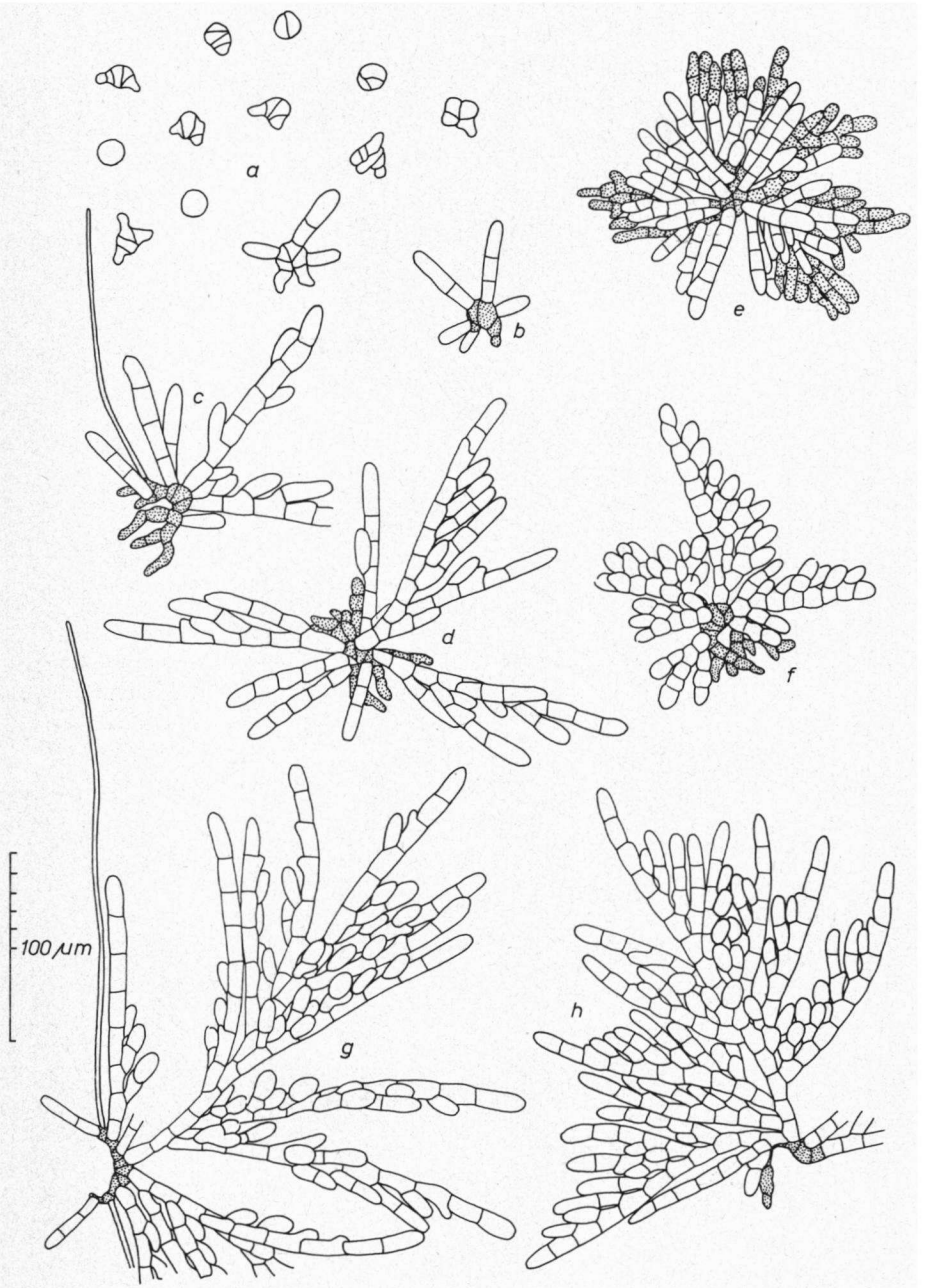

Fig. 9. Variation of the tetrasporophyte in culture.
a-d. germination and young developmental stages (clone 137); *e-h.* mature plants; *e.* clone 154, 16°C, 12/12; *f.* clone 139, 16°C, 12/12; *g.* clone 137, 8°C, 12/12; *h.* clone 137, 16°C, 12/12.

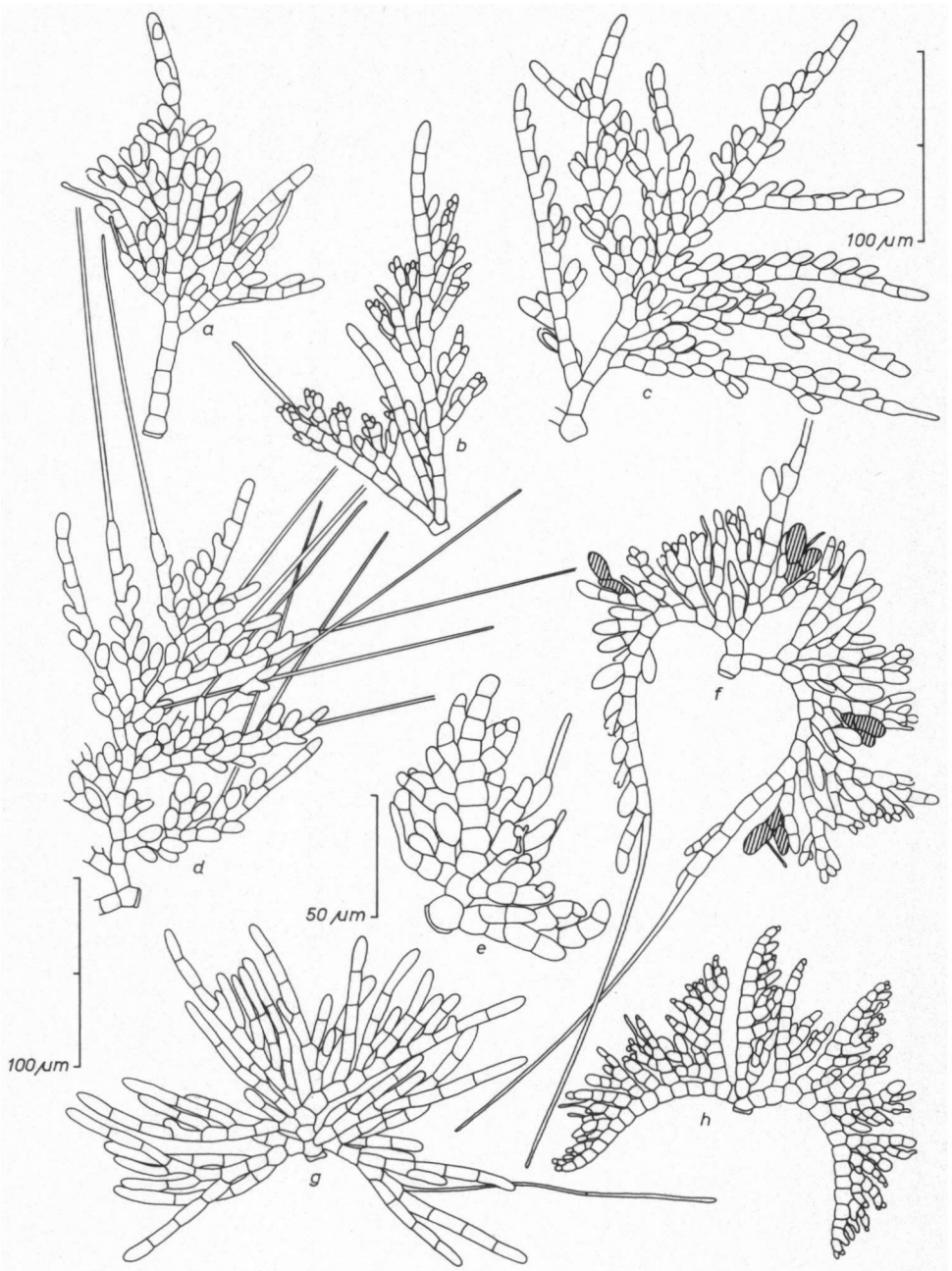

Fig. 10. Variation of the gametophyte in culture.
a-d. field-isolated clones; *e-h.* obtained in culture from tetrasporophytes; *a.* clone 216, 16°C, 12/12; *b.* clone 63, 12°C, 12/12; *c.* clone 215, 16°C, 12/12; *d.* clone 213, 16°C, 20/4; *e.* clone 139, 16°C, 12/12; *f.* clone 154, 16°C, 12/12; *g.* clone 137, 8°C, 16/8; *h.* clone 137, 16°C, 12/12.

better. This may well fit in with the geographical distribution, which seems to be limited to the temperate part of the Northern Atlantic (see below).

Both generations were found in the field to be most abundant during winter. Their near-absence during summer is possibly due, however, to the disappearance of *Polysiphonia nigrescens* in that period. From the position of the sample stations of both generations it appears that the tetrasporophyte prefers more exposed sites than the gametophyte. It is therefore unclear, whether on the Dutch coast this species completes its sexual cycle; undoubtedly the asexual reproduction by means of monospores is far more important. Production of monospores may take place in a wide range of temperatures and light conditions, and is apparently not limited to a special season. In the field-collected material tetrasporangia and gametangia are of too rare occurrence to allow any conclusions about possible seasonal periodicity in reproduction; the culture studies suggest that tetrasporangia are likely to be found during spring (low seawater temperature, high light intensity), and gametangia in autumn (high seawater temperature, short day/low light intensity), but a strict limitation to these periods is not necessary.

Identification of the material, as in several other *Acrochaetium* species, presents considerable difficulties. In case of the tetrasporophyte, besides the cell diameter and the chromatophore shape, the spore germination and the filamentous structure of the base are the most reliable characters. From the European Atlantic coast a number of different species have been described to possess a septately germinating spore, that gives rise to a filamentous base, i.e.: *A. polyblastum* (Rosenv.) Børg., *A. humilis* (Rosenv.) Børg., *A. dumontiae* (Rosenv.) Hamel, *A. cytophagum* (Rosenv.) Hamel and *A. reductum* (Rosenv.) Hamel. In most of these species there is not the typical 3 or 4-celled spore however, but a 2-celled spore instead, if stated explicitly in the literature. Since the original description of ROSENVINGE (1909), very few figures of *A. polyblastum* and related species have been published and no new information is available about the type of spore germination (cf. LEVRING 1935, 1937; EDELSTEIN & MCLACHLAN 1966; PANKOW 1971). *A. cytophagum* and *A. dumontiae* have only occasionally been reported and the validity of distinguishing these superficially semi-endophytic forms as separate species is questionable; their general habit and cell dimensions are not much different from *A. polyblastum*. *A. cytophagum* is reported to possess no pyrenoids (ROSENVINGE 1909) although this is questioned by KYLIN (1944) and contradicted by PANKOW (1971). *A. reductum* at present is thought to represent the tetrasporophyte of *A. kylinoides* and is definitely a different species (Stegenga, unpublished observation).

We have chosen the name *A. polyblastum* to accommodate the material with large erect filaments, but plants with short unbranched erect filaments do rather well agree with *A. humilis*. Moreover there is a chance that plants with a well developed erect part have formerly been identified as a narrow-celled form of *A. secundatum*.

Many species have been described, possessing a single basal cell. In trying to identify the gametophyte then, there are hardly any characters left than the

chromatophore shape and the cell diameter. We have arbitrarily chosen an upper limit of the diameter of 8(9) μm. This results in rejection of the names *A. alariae* (Jonss.) Born. and *A. rhipidandrum* (Rosenv.) Hamel. Actually we think that the latter species represent gametophytes of *A. virgatulum/secundatum*.

Remaining species on the European Atlantic coast are *A. hallandicum* (Kylin) Hamel, *A. parvulum* (Kylin) Hoyt, *A. balticum* (Rosenv.) Aziz and *A. maluinum* Hamel. Extremely short-celled plants may strongly resemble species of the *A. microscopicum* complex; STEGENGA & VROMAN (1976) have pointed out that the gametophyte of *A. densum* is possibly related to the *A. microscopicum* complex, and most material referred to this complex has probably little to do with *A. hallandicum*. Compared to the other species, our material agrees best with *A. parvulum* and *A. maluinum*, as far as cell length/diameter ratio is concerned. *A. parvulum* was considered a form of *A. hallandicum* by ROSENVINGE (1909) and HAMEL (1928). KYLIN (1944), who retains *A. parvulum* as a separate species, notes that *A. rhipidandrum* is wrongly described as a species different from *A. parvulum;* moreover KYLIN *(l.c.)* sees no difference between *A. parvulum* and *A. maluinum*, and notes that *Kylinia rosulata* (sensu KYLIN = *Acrochaetium kylinoides* Feldm.) has sometimes been identified as *A. parvulum*. Indeed we have found that at least *A. kylinoides* is a distinct species (Stegenga, unpublished observation). WOELKERLING (1973) merges *A. dufourii* (Collins) Børg. and *A. sargassi* Børg. with *A. hallandicum* and notes that the relation of *A. hallandicum* to a large number of species remains to be clarified.

From the above it will be clear that a satisfactory identification of the material is hardly possible and nomenclatural problems must remain unsolved as yet.

Some remarks must be made concerning the use of the generic name *Acrochaetium*. DIXON (in PARKE & DIXON 1976) has preferred to give the whole group the status of a single genus: *Audouinella*, more or less in agreement with the systematic views of WOELKERLING (1971). At present we feel we have not enough information either to support or to oppose this view, as details about the life histories of most acrochaetioid algae are still lacking. Hence we prefer at this moment to retain the frequently used name *Acrochaetium* for the species we are dealing with in this paper.

On the other hand we are convinced that within the Acrochaetiaceae certain clusters of closely related species may be distinguished. One such group consists of the species possessing stellate chromatophores with a central pyrenoid. Their relationship is not only expressed in the possession of a stellate chromatophore, but their entire life histories are much alike; the following species,

A. virgatulum and *A. rhipidandrum* (Borsje 1973)

A. densum and *A. catenulatum* (Stegenga & Vroman 1976)

A. polyblastum and *A. hallandicum* (the present paper)

A. reductum and *A. kylinoides* (Stegenga, unpublished observations),

all have an alternation of a tetrasporophyte with septately germinating spore and multicellular base, and a gametophyte with a single basal cell. Moreover

the mature carposporophyte is characteristically of a simple structure and consists of the transversally divided or undivided carpogonium, each cell of which bears a few carposporangia. By the combination of these characters the group is well distinguished from forms with other types of chromatophores.

Many more studies on life histories should be done however, to attain a more natural classification of the Acrochaetiaceae.

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REFERENCES

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

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

EDELSTEIN, T. & J. MCLACHLAN (1966): Species of Acrochaetium and Kylinia new to North America. *Br. Phycol. Bull.* **3**: 37–42.

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

KNAGGS, F. W. (1968): Rhodochorton purpureum (Lightf.) Rosenvinge. The morphology of the gametophytes and of the young carposporophyte. *Nova Hedw.* XVI: 449–457 + tab. 170–174.

KNAGGS, F. W. & E. CONWAY (1964): The life-history of Rhodochorton floridulum (Dillwyn) Näg. 1. Spore germination and the form of the sporelings. *Brit. phycol. Bull.* **2(5)**: 339–341.

KYLIN, H. (1944): Die Rhodophyceen der schwedischen Westküste. *Lunds Univ. Arsskr., N.F., Avd.* **2**, Bd. **40**.

LEVRING, T. (1935): Zur Kenntnis der Algenflora von Kullen an der schwedischen Westküste. *Lunds Univ. Arsskr., N.F., Avd.* **2**, Bd. **31**.

— (1937): Zur Kenntnis der Algenflora der norwegischen Westküste. *Lunds Univ. Arsskr., N.F., Avd.* **2**, Bd. **33**.

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

— (1944): The species of Rhodochorton from Japan, II. *Scient. Papers Inst. Algol. Res., Fac. of Sci., Hokkaido Imp. Univ.* **3**: 89–119.

PANKOW, H. (1971): *Algenflora der Ostsee.* Gustav Fischer Verlag Jena, 419 pp.

PARKE, M. & P. S. DIXON (1976): Check-list of British marine Algae – Third revision. *J. mar. biol. Ass. U.K.* **56**: 527–594.

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

ROSENVINGE, L. K. (1909): The marine algae of Denmark, I. Rhodophyceae 1. *K. Danske Vidensk. Selsk. Skr., 7 Raekke, Naturvidensk. og Mathem. Afd.*, **7**(1): 1–151.

STEGENGA, H. & W. J. BORSJE (1976): The morphology and life history of Acrochaetium dasyae Collins (Rhodophyta, Nemaliales). *Acta Bot. Neerl.* **25**(1): 15–29.

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

WEST, J. A. (1968): Morphology and reproduction of the red alga Acrochaetium pectinatum in culture. *J. Phycol.* **4**: 89–99.

— (1969): The life histories of Rhodochorton purpureum and Rhodochorton tenue in culture. *J. Phycol.* **5**: 12–21.

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

— (1973): The Audouinella complex (Rhodophyta) in the Western Sargasso Sea. *Rhodora* **75**: 78–101.