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REMARKS ON THE LIFE HISTORIES OF THREE ACROCHAETIOID ALGAE (RHODOPHYTA, NEMALIALES)

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SUMMARY

Observations are presented on the morphology and life histories of *Chromastrum kylinoides* (Feldm.) comb. nov., *Kylinia rosulata* Rosenv., and *Audouinella pectinata* (Kylin) Papenfuss. Each species shows an alternation of dissimilar generations.

Although in earlier publications *C. kylinoides* and *K. rosulata* have been confused, and *A. pectinata* has been considered conspecific with *K. rosulata*, it is concluded in the present study that the species are quite different and should be assigned to separate genera.

The tetrasporophyte of *C. kylinoides* is *Chromastrum reductum* (Rosenv.) comb. nov.. The tetrasporophyte of *K. rosulata* was indentified as *Acrochaetium strictum* (Rosenv.) Hamel. The gametophyte of *A. pectinata* appears not to have been described as a separate entity from the European coast.

A critical evaluation of life histories in the Acrochaetiaceae is supposed to alter the current classifications of the species in this family of red algae.

1. INTRODUCTION

Acrochaetium kylinoides Feldm. and *Kylinia rosulata* Rosenv. are among the smallest species of acrochaetioid algae; both species possess a unicellular base. FELDMANN (1958) solved the confusion which had arisen when KYLIN (1944) altered ROSENVINGE's (1909) description of *K. rosulata* and of the genus *Kylinia* as such. ROSENVINGE (1909) defined *Kylinia* as a genus, characterized by possession of special androphore cells; the only species *K. rosulata* was observed to have parietal chromatophores, while the presence of pyrenoids was left uncertain. KYLIN (1944) included in *Kylinia* all forms with unicellular bases, and stated that *K. rosulata* possessed stellate chromatophores with central pyrenoids.

The result of FELDMANN's (1958) study was that *K. rosulata* once again included the form with parietal chromatophores and special androphore cells, whereas *Acrochaetium kylinoides* was recognized as a new species, possessing stellate chromatophores and no known reproductive structures other than monosporangia; the latter species was suggested to be identical to the material which KYLIN had assigned to *K. rosulata.*

BOILLOT & MAGNE (1973) linked *K. rosulata* to *Acrochaetium pectinatum* (Kylin) Hamel, the latter said to represent the tetrasporophyte in the life history. However, earlier WEST (1968) had described gametophytes of Pacific material of *A. pectinatum*, which had a morphology quite different from *K. rosulata:* the spermatangia were not born on special narrow androphore cells, and also the chromatophore seemed to have a more complex morphology than in *K. rosulata.*

The gametophyte of *A. pectinatum* is not often recognized in the field. If so, it attains larger dimensions than *K. rosulata* (see WOELKERLING 1971).

The taxonomic problems connected with the three above-mentioned species prompted us to study the complex anew, by comparative culturing of material of each species; all three species originally having been described from the European Atlantic coast, the collecting of this material from the Swedish west coast proved relatively easy.

In addition to comparative morphology life histories were also studied, as far as possible; based on these life history studies, some comment will be given on the systematics of the Acrochaetiaceae. Throughout the descriptive part of this paper the name *Acrochaetium* will be used for all species considered, except for *Kylinia rosulata*, since these generic names have gained most renown in the literature; as will become evident from the discussion, this does not express the systematic view of the authors.

2. MATERIALS AND METHODS

During a visit to Kristinebergs Marine Biological Station (Bohuslän, Sweden), August 1976, the following samples were collected:

Acrochaetium kylinoides: 5-VIII-1976, St. Testholmen, from *Polysiphonia* sp., epiphyte on *Leathesia difformis* (382), and from *Cladophora* sp. (388).

Kylinia rosulata: 3-VIII-1976, near Kristineberg, from *Ectocarpus* sp., epiphyte on *Chordaria flagelliformis* (378, 379); 5-VIII-1976, St. Testholmen, from *Cladophora* sp. (426).

Acrochaetium reductum (tetrasporophyte of *A. kylinoides*): 3-VIII-1976, near Kristineberg, from *Polysiphonia* sp.; 5-VIII-1976, St. Testholmen, from *Polysiphonia* sp. (384) and *Cladophora* sp. (390).

Acrochaetium strictum (tetrasporophyte of *K. rosulata*): 3-VIII-1976, near Kristineberg, from *Sphacelaria bipinnata* (377); *A. strictum* was also collected 19-VI-1976, at Varberg (Halland), from *Ceramium* sp. and *Polysiphonia* sp. (409, 410, 411, 412), material washed ashore.

Acrochaetium pectinatum: 3-VIII-1976, near Kristineberg, from *Phycodrys sinuosa* (361, dredge sample 10–20 m depth); 9-VIII-1976, Smedja, from *Odonthalia dentata* (401, 402) and from a bryozoan (406, 408, dredge sample 10–20 m depth).

No material was found that could represent the gametophyte of *A. pectinatum*.

Samples were hand-collected from various depths between the water mark and −4 m, if not stated otherwise; tides in this area are of small amplitude, and all samples can be regarded as of sublittoral origin.

Part of the material was preserved in 4% formalin for morphological study, and part was taken into culture; numbers in brackets refer to serial numbers of strains which are in store at the Botanical Laboratory, Free University, Amsterdam.

A number of these clones was investigated for their morphological variability under some different combinations of daylength (8/16 h and 16/8 h) and tem-

perature (8 and 16 °C), while this treatment in most strains also allowed induction of reproductive structures of various kinds, and subsequent completion of the life history. Culture methods did not deviate from those used in earlier work on *Acrochaetium* species (e.g. STEGENGA & VROMAN 1976).

3. OBSERVATIONS

3.1. *Acrochaetium kylinoides – Acrochaetium reductum*

3.1.1. Field observations (*figs. 1–6, 20–25*)

Acrochaetium kylinoides has a single basal cell, 6–8 μm in diameter. Up to 6 filaments arise from this basal cell; their length is limited and hardly ever exceeds 4 cells. The filaments are usually adpressed against the substrate. Cell dimensions are 5–7 × 5–7 μm. Monosporangia measure *c.* 8 × 6 μm, occurring terminally or laterally on the filaments. Spermatangia were found on plants from *Cladophora* sp. (5-VIII-1976); they measured 3–4 × 3 μm. Carpogonia were not observed, but some possible carposporophytes were present, the supposed carposporangia measuring *c.* 8.5 × 7 μm. Plants occasionally bear unicellular hairs.

Acrochaetium reductum has a multicellular filamentous base arising from a septate 2-celled spore, in mature plants *c.* 8–12 μm in largest diameter. Creeping filaments are sparingly branched and give off a number of erect filaments. Cells of the prostrate filaments measure 7–10 × 4–5 μm. Erect "filaments" usually do not exceed 1 cell, which often turns into a monosporangium. Mature monosporangia measure *c.* 10 × 7 μm. Other reproductive structures, as well as hairs, were not noticed on this generation.

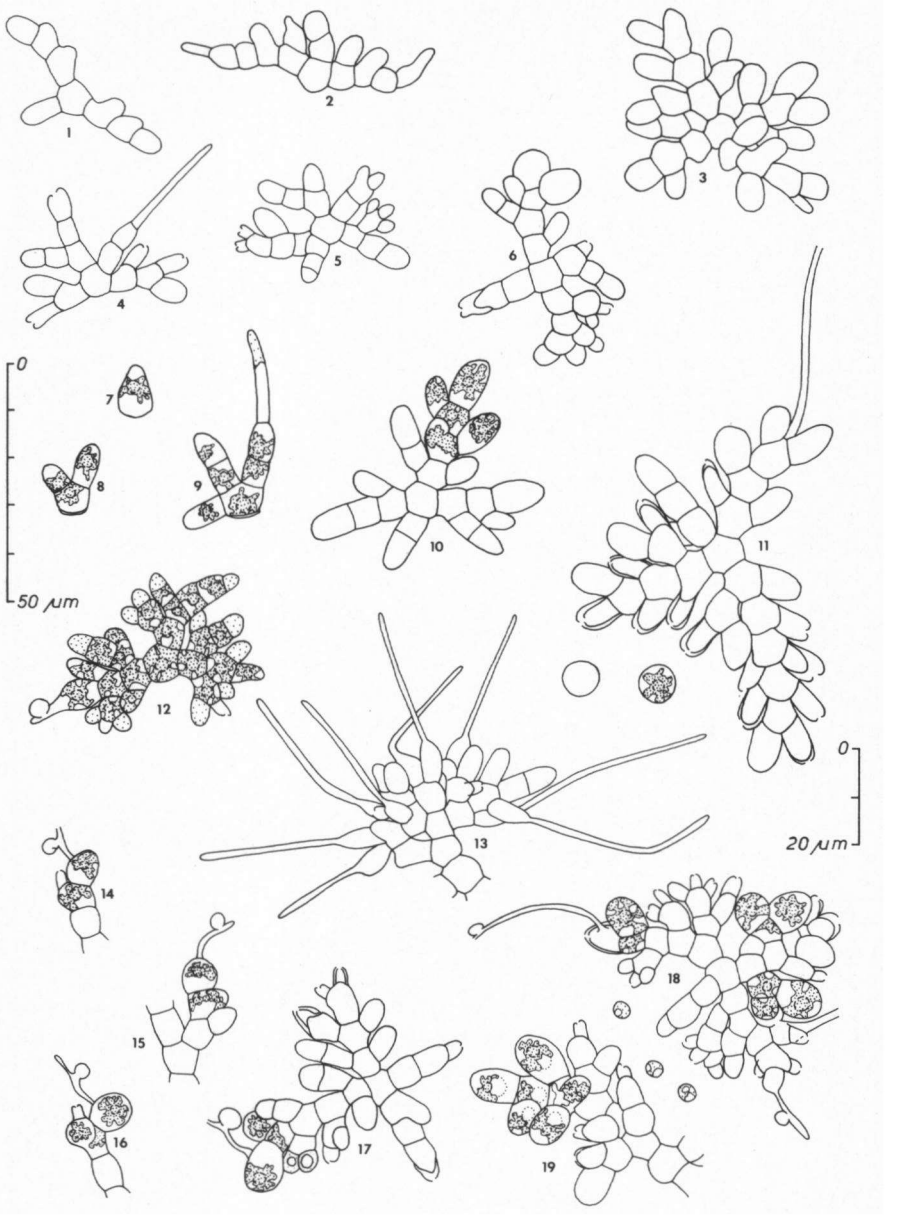
3.1.2. Culture observations (*figs. 7–19, 26–32*)

The life history of this species was followed both by starting from the gametophyte (clones 382 and 388) and from the tetrasporophyte (clones 384 and 390). As no consistent differences between these two groups emerged, morphological data will be presented here for the whole complex (*tables 1 and 2*).

The gametophyte has a basal cell 6–8 μm in diameter, giving off up to 6 erect filaments. Vegetative cells measure 6–7.5 × 5.5–6 μm; they are provided with a single stellate chromatophore and a central pyrenoid. Monosporangia are formed under a large range of external conditions. They occur terminally and laterally on the erect axes, in the latter case often opposite; they measure 7.5–9 × 5.5–6 μm. Unicellular hairs are abundant under various conditions, their length measures up to 150 μm.

Plants were bisexual in some clones (388, 390) but unisexual in another (382). Tetraspores from clone 384 failed to germinate. Plants formed abundant gametangia at 16 °C, short day, but clone 382 became fertile under all tested conditions. Spermatangia measure *c.* 3.5 × 3 μm; carpogonia measure 7–9 × 4–5 μm, with the trichogynes up to 40 μm. Fertilized carpogonia usually remain undivided and give off 3 carposporangia; infrequently the carpogonium divides transversally first. Mature carposporangia measure 8.5–10 × 6.5–7.5 μm.

Carpospores or tetrasporophytic monospores germinate septately; each of the



Figs. 1–19. *Acrochaetium kylinoides/reductum* – gametophyte. Figs. 1–6. Field-collected material. Figs. 1–4. Plants bearing monosporangia. Fig. 5. Male reproductive plant. Fig. 6. Spermatangia and possible carposporophyte. Figs. 7–19. Cultured material. Figs. 7–9. Germlings. Figs. 10, 11. Monosporangia. Fig. 12. Bisexual plant. Fig. 13. Carpogonia. Figs. 14–18. Developmental stages of carposporophytes. Fig. 19. Carposporophyte resulting from transversally divided carpogonium.

Table 1. Cell dimensions in gametophytes under various experimental conditions. Given data are averages of measurements on 10 plants, half of which were examined after 2 weeks, the other half after 4 weeks of culturing. All measures in μm (– means absence of relevant structure).

species and strain number	temperature (°C)	daylength (l/d)	basal spore ϕ	vegetative cells	monosporangia	spermatangia	carpogonia	trichogynes (maximal length)	carposporangia	hairs (maximal length)
A. kylinoides	8	8/16	6.3	5.5×5.5	7.6×5.3	3.7×3.6	8.0×4.5	28.8	–	94
382 (♂&♀)		16/8	6.0	5.9×5.7	6.9×5.5	3.8×3.5	9.4×4.8	28.8	–	117
	16	8/16	6.1	5.0×5.7	6.6×4.5	3.3×3.1	8.2×4.6	40.3	–	106
		16/8	6.1	5.2×5.4	6.3×5.0	3.8×3.4	7.9×4.7	38.4	–	108
A. kylinoides	8	8/16	7.3	6.5×5.9	8.8×5.6	–	–	–	–	144
388 (♀)		16/8	8.0	7.2×5.4	8.4×5.8	–	–	–	–	157
	16	8/16	7.7	5.9×5.8	7.5×5.7	3.6×2.9	8.3×4.1	42.0	9.2×7.1	134
		16/8	7.5	6.1×5.8	8.3×5.9	–	–	–	–	154
A. reductum	8	8/16	7.1	5.8×5.8	8.4×5.5	–	–	–	–	115
390 (♀)		16/8	7.1	6.4×5.6	8.0×5.4	–	–	–	–	131
	16	8/16	7.1	5.2×5.4	7.8×5.4	3.5×3.2	8.6×4.2	40.3	10.0×8.1	131
		16/8	7.3	6.2×5.8	7.9×5.4	–	–	–	–	123
K. rosulata	8	8/16	8.6	9.2×5.8	9.4×6.3	–	–	–	–	205
379 (♀)		16/8	9.4	9.0×5.9	10.3×6.4	–	–	–	–	288
	16	8/16	8.3	10.1×5.0	9.2×5.8	3.8×3.4	9.0×4.2	50.0	–	88
		16/8	9.1	9.4×5.6	9.8×5.9	–	–	–	–	403
A. strictum	8	8/16	7.7	11.4×6.1	9.6×6.5	4.3×2.9	–	–	–	384
410 (♂)		16/8	8.2	13.1×5.3	9.1×6.5	–	–	–	–	250
	16	8/16	8.5	10.6×6.4	9.5×5.4	3.5×2.9	–	–	–	288
		16/8	7.7	11.3×5.9	10.1×6.0	3.7×2.9	–	–	–	480

two resulting cells usually gives off one or two prostrate filaments. Cells of the original spore and the creeping filaments may bear one or two erect filaments, these often not exceeding 2 or 3 cells in height. The extension of the prostrate part is highly variable between different clones. Vegetative cells of the erect filaments measure 6–8.5 × 5.5–7 μm. Hairs are abundant in most clones, and up to 230 μm in length. Monosporangia measure 8.5–11 × 6–7.5 μm; they are formed in terminal and lateral positions on the erect axes and also sessile on the prostrate filaments.

Tetrasporangia were formed at 8 °C, long day, in some clones also at 16 °C, long day. Tetrasporangial dimensions are 11–13.5 × 9–11 μm, division is cruciate. Tetraspores render the gametophyte.

Gametophytes in culture much resemble field collected specimens, except that hairs and sexual reproductive organs are more abundant under the appropriate conditions. Cell and sporangial dimensions hardly differ from wild material and are not markedly influenced by external conditions (*table 1*).

Tetrasporophytes compare less easily to field collected material, as in the latter specimens more-celled erect axes are lacking. Like in the gametophyte, cell dimensions in the tetrasporophyte are not clearly affected by different conditions of temperature and daylength (*table 2*).

Table 2. Cell dimensions in tetrasporophytes under various experimental conditions. See remarks under table 1.

species and strain number	temperature (°C)	daylength (l/d)	vegetative cells	monosporangia	tetrasporangia	hairs (maximal length)
A. kylinoides	8	8/16	6.7 × 6.3	9.6 × 7.0	–	163
382		16/8	8.2 × 6.0	9.6 × 6.3	11.8 × 9.1	210
	16	8/16	5.9 × 5.6	9.0 × 6.1	–	119
		16/8	6.7 × 6.0	9.7 × 6.0	–	173
A. kylinoides	8	8/16	7.7 × 6.9	10.8 × 7.5	–	221
388		16/8	7.7 × 6.3	10.2 × 7.3	13.5 × 9.9	184
	16	8/16	6.4 × 5.8	9.8 × 6.9	–	192
		16/8	7.3 × 5.8	10.5 × 7.0	13.0 × 10.7	230
A. reductum	8	8/16	7.8 × 6.5	10.1 × 6.7	–	131
384		16/8	7.5 × 6.6	8.8 × 6.8	11.3 × 9.4	182
	16	8/16	7.3 × 6.0	8.7 × 6.8	–	127
		16/8	6.3 × 6.0	8.8 × 7.0	–	159
A. reductum	8	8/16	6.8 × 6.8	11.0 × 7.3	–	27
390		16/8	8.3 × 6.4	10.4 × 6.3	12.9 × 9.8	126
	16	8/16	6.2 × 6.0	9.6 × 6.4	–	63
		16/8	7.8 × 5.8	10.4 × 6.9	11.4 × 9.9	175
K. rosulata	8	8/16	15.9 × 5.0	13.7 × 8.1	–	460
379		16/8	18.2 × 5.4	–	14.8 × 11.7	451
	16	8/16	14.8 × 5.1	13.4 × 7.1	–	470
		16/8	16.7 × 5.6	–	13.9 × 12.5	518
A. strictum	8	8/16	21.1 × 5.7	13.4 × 6.5	–	605
410		16/8	22.7 × 5.8	13.4 × 7.5	15.0 × 11.5	614
	16	8/16	16.5 × 5.3	12.4 × 6.8	–	518
		16/8	23.5 × 5.8	13.4 × 7.0	15.8 × 10.7	692
A. strictum	8	8/16	16.8 × 5.8	13.3 × 7.4	–	633
411		16/8	22.1 × 6.1	13.5 × 8.3	–	768
	16	8/16	15.4 × 5.8	13.2 × 7.4	–	499
		16/8	25.7 × 6.2	13.6 × 8.2	16.0 × 10.7	614
A. pectinatum	8	8/16	20.0 × 7.4	9.1 × 7.8	16.0 × 13.6	–
361		16/8	18.0 × 7.5	8.7 × 7.5	–	–
	16	8/16	16.5 × 7.1	8.7 × 7.1	–	–
		16/8	22.8 × 6.7	9.8 × 7.8	–	–
A. pectinatum	8	8/16	17.0 × 5.4	10.4 × 6.1	11.7 × 9.6	173
408		16/8	18.9 × 5.2	10.6 × 6.0	–	193
	16	8/16	15.9 × 5.0	9.8 × 6.1	–	142
		16/8	24.1 × 5.9	11.2 × 6.1	–	334

3.2. *Kylinia rosulata – Acrochaetium strictum*

3.2.1. Field observations (*figs. 33–40*)

Kylinia rosulata has a single basal cell, 8–9 μm in diameter, considerably flattened on the side attached to the substrate. A number of up to 6 erect filaments are given off in lateral directions. Sometimes a hair is formed first. Generally erect filaments do not exceed 4 cells in height. Vegetative cells measure 6–9 × 5–7 μm. Hairs may be present, attaining lengths up to 100 μm. Monosporangia occur sessile on the basal cell or on erect filaments; they measure 7–8 × 5–6 μm. Spermatangia are born terminally on a filament of 2–4 narrow, elongate cells, forming an "androphore". Androphore cells are up to 15(25) μm long and, at the narrowest point, 2.5 μm in diameter. The terminal androphore cell has a swollen tip, bearing 2–5 spermatangia. Spermatangia measure *c.* 4 × 3 μm. Despite intensive search we have not yet found carpogonia or carposporophytes in the field material.

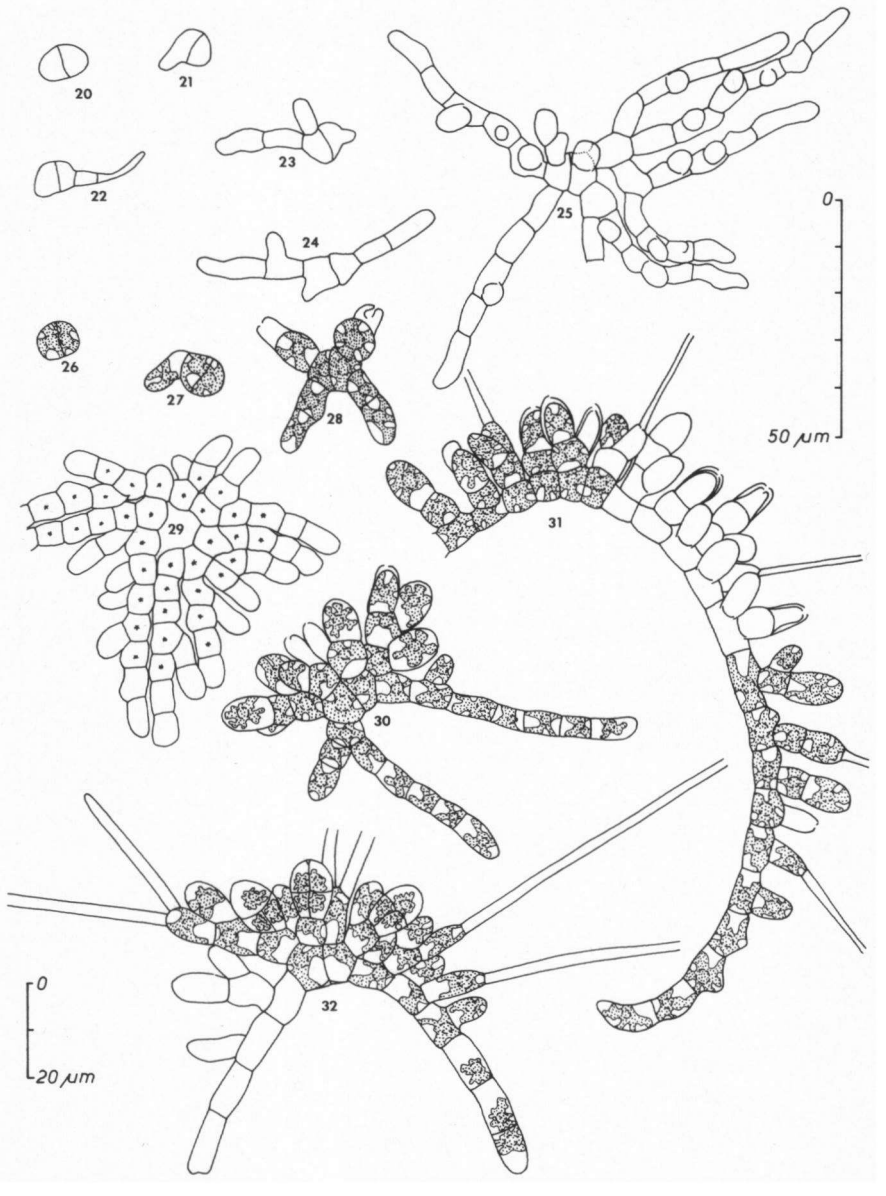
Observations on wild material of *Acrochaetium strictum* could not be made, owing to the ill-preserved state. Identification of *Acrochaetium strictum* has taken place from the cultured plants.

3.2.2. Culture observations (*figs. 41–67, 79–81*)

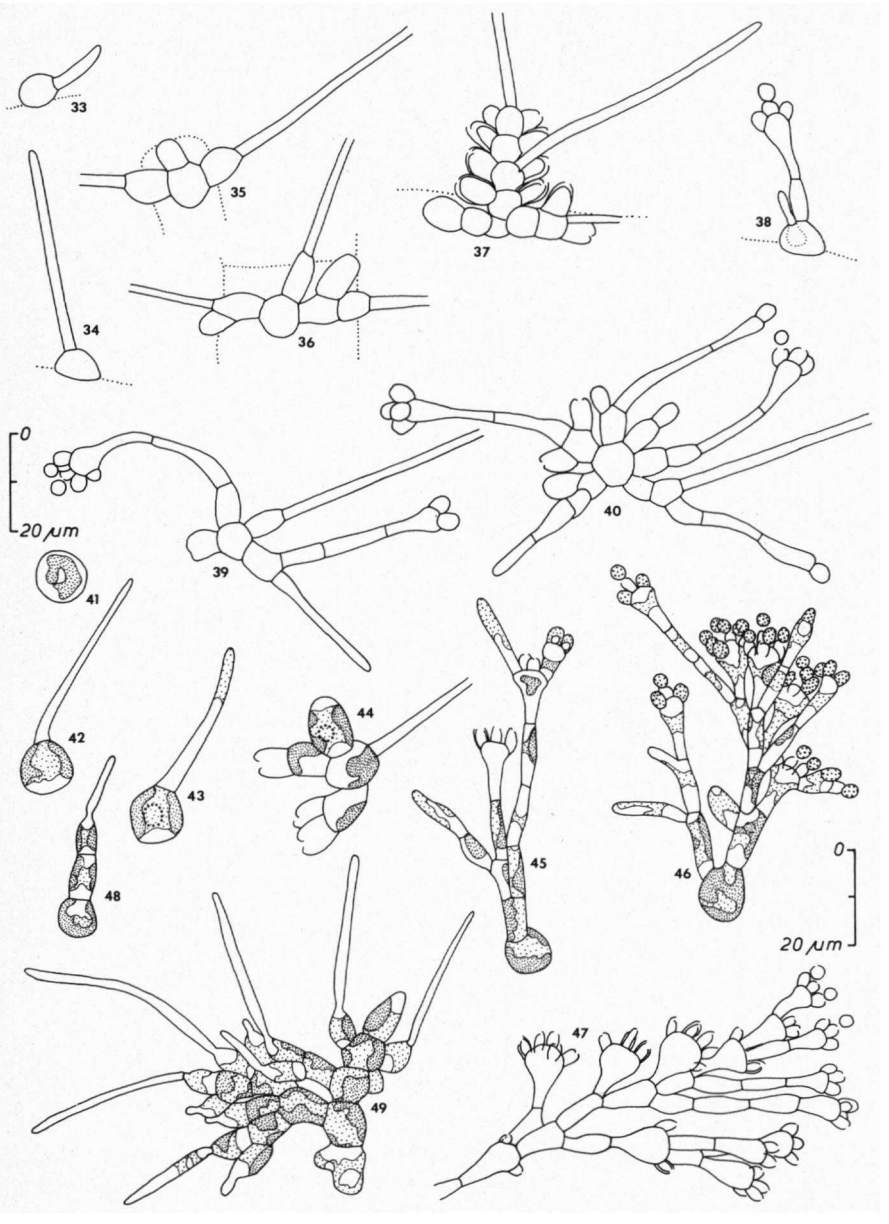
The life history of this species also was completed by starting from different clones (379 – gametophyte, and 410, 411 – tetrasporophytes). For comparative characteristics see *tables 1* and *2*.

The basal cell of the gametophyte is 7.5–9.5 μm in diameter, and emits up to 6 erect filaments, which remain adpressed against the substrate. Often, on germination, the first structures emerging from the spore are hairs and/or monosporangia or sometimes carpogonia or androphores. In a later stage more-celled erect filaments are formed, in the appropriate conditions also provided with hairs, monosporangia or gametangia. Plants certainly grow beyond dimensions attained in the field, but are reproductive at a very early stage. Vegetative cells measure 7.5–13 × 5–6 μm; they contain one parietal chromatophore in which sometimes a small pyrenoid is discernable. Monosporangia measure 9–11 × 5–7 μm. Hairs are unicellular and up to 500 μm long; they are scarce at 16 °C/short day, otherwise abundant.

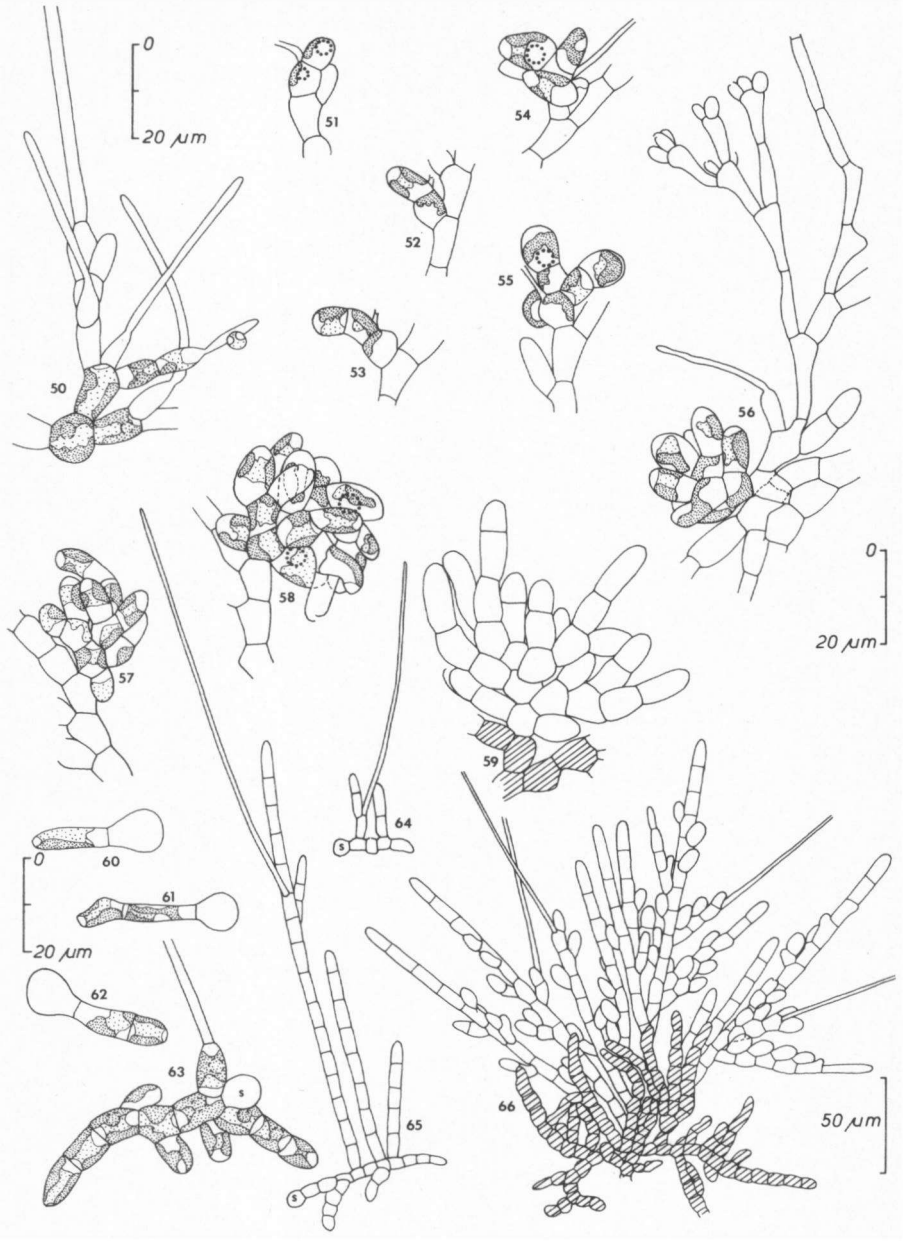
Gametangia in clone 379 were formed at 16 °C/short day, in clone 410 also under other conditions, but in lower abundance. Gametophytic offspring of clone 411 were not followed in this experiment. Plants may be unisexual, but especially female plants have been observed to form additional spermatangia in a later stage. Spermatangia are born on "androphores"; first these have much the same shape and dimensions as in field-collected material, but in a later stage they may frequently branch and bear spermatangia on several levels. Androphore cells are up to 20 μm long, at the narrowest point 2–3 μm in diameter, toward the apex widening to a maximum of 10 μm. The tip bears up to 7 spermatangia. Androphore cells contain a small chromatophore, spermatangia are colourless; they measure 3.5–4.5 × 3–4 μm. Carpogonia are born on the erect axes; they measure 7–11 × 4–5 μm, with trichogynes up to 50 μm long.



Figs. 20–32. *Acrochaetium kylinoides/reductum* – tetrasporophyte. Figs. 20–25. Field-collected material. Figs. 20–24. Germinating spores. Fig. 25. Monosporangia bearing plant. Figs. 26–32. Cultured material. Figs. 26–28. Germlings. Fig. 29. Basal part seen from below (cells marked* emit erect filaments or monosporangia). Figs. 30, 31. Monosporangia. Fig. 32. Tetrasporangia.



Figs. 33–49. *Kylinia rosulata*/*Acrochaetium strictum* – gametophyte. Figs. 33–40. Field-collected material. Figs. 33–35. Germlings. Figs. 36, 37. Monosporangia. Figs. 38–40. Androphores with spermatangia. Figs. 41–49. Cultured material. Figs. 41–43. Germinating spores. Fig. 44. Monosporangia. Figs. 45–47. Male reproductive plants. Figs. 48, 49. Female reproductive plants.



Figs. 50–66. *Kylinia rosulata*/*Acrochaetium strictum* – carposporophyte and tetrasporophyte in culture. Figs. 50–59. Fertilization and developmental stages of carposporophytes. Figs. 60–63. Germlings of tetrasporophytes. Figs. 64, 65. Juvenile tetrasporophytes. Fig. 66. Tetrasporophyte with monosporangia; prostrate part (hatched) seen from below. s = original spore.

The fertilized carpogonium divides transversally a few times to form a short axis; meanwhile cells give off laterals, on which finally terminal carposporangia develop. During this process the initially insignificant chloroplast becomes more prominent again. Mature carposporangia measure *c.* 11–13 × 8 μm. We sometimes had the impression that gonimoblast filaments could continue growth to form the tetrasporophyte without intermediate free carpospores, but this has not been established with certainty.

Carpospores or tetrasporophytic monospores germinate in a unipolar way, usually under loss of cell contents. First a creeping filament is formed. From the branching prostrate filament a number of erect axes emerges, with, in principle, unlimited growth. Cell dimensions in erect axes average 12–28 × 5–7 μm. Cells contain a parietal chromatophore with one pyrenoid. Cell length is affected by daylength as well as by temperature, the shortest cells occurring under a combination of high temperature and short day. Cell diameter and monosporangial dimensions do not show an evident response to variation in these factors. Monosporangia measure 12–15 × 6–9 μm. Hairs are always abundant, and up to 750 μm long.

Tetrasporangia are formed under long day conditions; division is cruciate, but not seldom irregularities occur in the process of division. Tetrasporangial dimensions are 14–17 × 10–12.5 μm. Tetraspores, although germinating in low numbers, render the gametophyte; occasionally in situ germination of tetraspores has been observed in this species.

In the gametophyte dimensions of cells and sporangia are not seriously affected by daylength and temperature. Vegetative cells compare reasonably well with wild material, monosporangia are slightly longer in culture. The culture data of the tetrasporophyte cannot be compared with field collected material due to the poor state of preservation of the latter.

3.3. *Acrochaetium pectinatum*

3.3.1. Field observations (*fig. 68*)

Plants have a prostrate part of intertwined filaments. Germination type of the

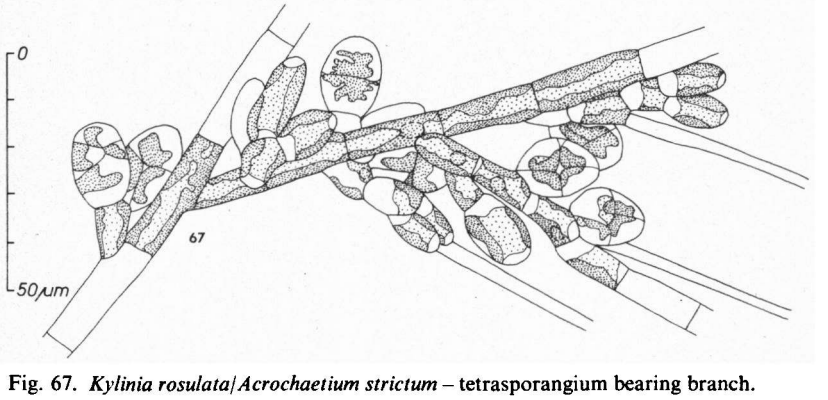
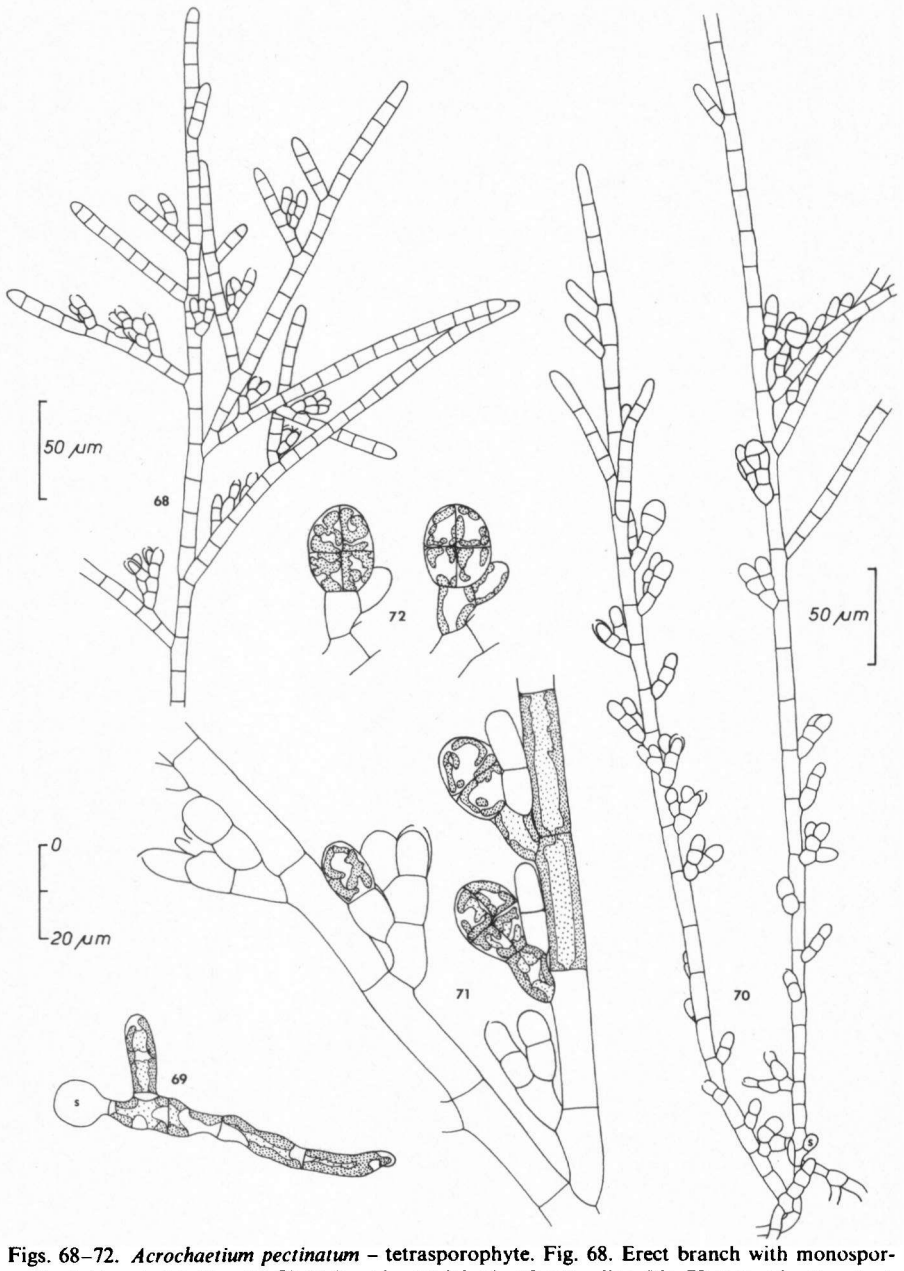
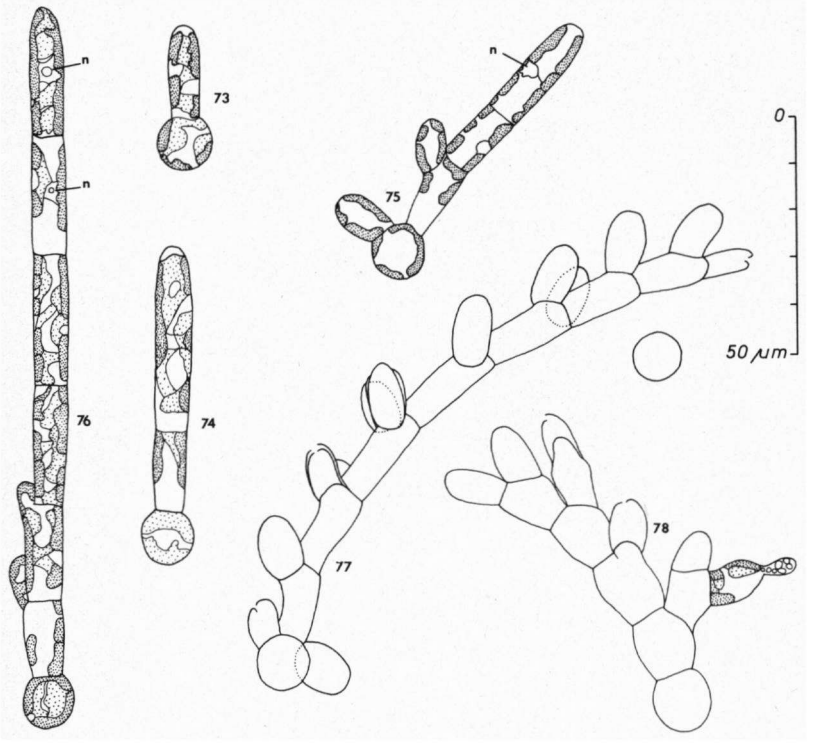


Fig. 67. *Kylinia rosulata*/*Acrochaetium strictum* – tetrasporangium bearing branch.



Figs. 68–72. *Acrochaetium pectinatum* – tetrasporophyte. Fig. 68. Erect branch with monosporangia, field material. Figs. 69–72. Cultured material. Fig. 69. Germling. Fig. 70. Reproductive plant. Figs. 71, 72. Tetrasporangia. s = original spore.

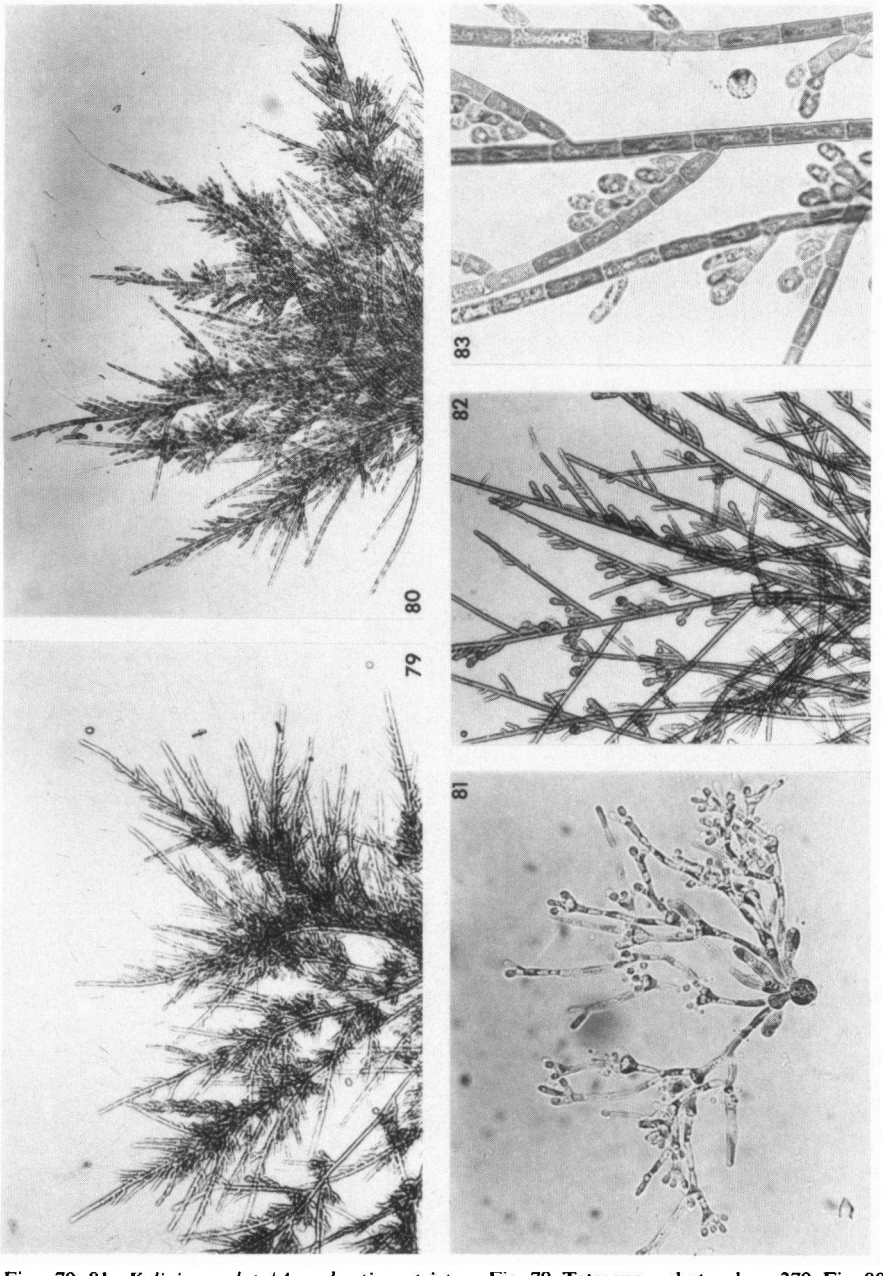


Figs. 73–78. *Acrochaetium pectinatum* – gametophyte in culture. Figs. 73–76. Germlings. Fig. 77. Plant with monosporangia. Fig. 78. Possible carpogonium. n = nucleus.

spores could not be detected in the wild material. Erect filaments are numerous and several hundred µm long. Cells are cylindric, in main axes on an average measuring 10–13 × 6–7 µm. Monosporangia occur in small clusters on the main axes or on the adaxial face of laterals; monosporangia measure 7–10 × 6–7 µm. Other reproductive structures have not been observed. Hairs are virtually absent from field-collected material.

3.3.2. Culture observations (*figs. 69–78, 82, 83*)

Monospores germinate in a unipolar fashion, usually under loss of cell contents. From the first formed prostrate filaments a large number of erect filaments arises. Cells of the erect filaments are cylindric and measure 13–28 × 5–7.5 µm, the shortest cells occurring under high temperature and short day (*table 2*). Cells have one or two chloroplasts, in young cells spiral or irregularly shaped, in older cells forming a continuous parietal belt; apparently there are no pyrenoids. There is a slight but constant difference in cell diameter and in sporangial dimensions between the two tested clones (*table 2*). Hairs were abundant on clone 408, measuring up to 300 µm, but completely absent from clone 361.



Figs. 79–81. *Kylinia rosulata*/*Acrochaetium strictum*. Fig. 79. Tetrasporophyte, clone 379. Fig. 80. Tetrasporophyte, clone 410. Fig. 81. Gametophyte, clone 410.
Figs. 82, 83. *Acrochaetium pectinatum*. Fig. 82. Tetrasporophyte, erect thallus, clone 361. Fig. 83. Tetrasporophyte, monosporangia, clone 408.

Monosporangia measure 8–12 × 5.5–8 μm; they are arranged in small clusters on main axes and laterals.

Tetrasporangia occupy identical positions as monosporangia, but are never as abundant. They were formed at 8 °C/short day, and measure 12–17 × 9–14 μm, their division is cruciate.

Tetraspores germinate in a unipolar fashion; the spore is persistent and forms the unicellular base of the resulting gametophyte; it is then 10–12 μm in diameter. One or more erect filaments are formed. Vegetative cells measure 15–30 × 6–8 μm (clone 361). Chromatophore shape is the same as in the tetrasporophyte. Monospores are produced in an early ontogenetic stage; monosporangial dimensions are 13–15 × 8–9 μm.

Possible carpogonia were observed on plants grown at high temperature (14–20 °C) and low light intensity (150–500 lux). Spermatangia and fertilized carpogonia were not found, and the life history must remain incomplete as yet.

Due to the large proportion of aberrant growth, morphological variability of the gametophytes was not tested. Anyway we had the impression that optimal growth of the gametophyte took place outside the usual range of experimental conditions, and rather at low light intensity.

4. DISCUSSION

This study again demonstrates the common occurrence of diplobiontic life histories in the Acrochaetiaceae (see also STEGENGA & BORSJE 1977). Also it clearly demonstrates that the three species under investigation have relatively little in common regarding their morphology, and their differences are actually thought to warrant distinction at the genus level.

The life history of *Acrochaetium kylinoides/reductum* fits in well with the scheme that was assumed for species with stellate chromatophores (STEGENGA & BORSJE 1977). It has been argued (STEGENGA & VROMAN 1977) that such species constitute the genus *Chromastrum* Papenfuss. The genus *Chromastrum* thus has about the same extent as when it was erected by PAPENFUSS (1945). Papenfuss (l.c.) created *Chromastrum* for species with stellate chromatophores, irrespective of their further morphology. Apparently this has been the reason why *Acrochaetium reductum* had not been included, as this species was described by ROSENVINGE (1909) to possess parietal chromatophores. Still, we have not hesitated to attach the name *Chromastrum reductum* to our material; the minor cell dimensions of *C. reductum* make observations on the exact chloroplast structure difficult. The overall morphological likeness on the other hand, is very considerable, and there is no reasonable alternative described from the European coast; other species exhibiting the typical germination have more extensive erect thalli. On the New England coast, *Acrochaetium radiatum* is rather similar (JAO 1936), the virtual absence of multi-celled erect filaments being characteristic.

The identity of *Chromastrum kylinoides*, as a species apart from *Kylinia rosulata*, has sufficiently been discussed by FELDMANN (1958) and need not be repeated here. The group of acrochaetioid algae with unicellular bases comprises

at least some 35 species, most of them with stellate chromatophores, and hence to be assigned to the genus *Chromastrum*. The remainder of *Chromastrum* is made up of tetrasporophytes with septately germinating spores.

A few other species, e.g. *Acrochaetium microfilum* Jao (JAO 1936) and *A. curtum* Baardseth (BAARDSETH 1941) have typical adpressed filaments like *Chromastrum kylinoides*. The above-mentioned *A. radiatum* and *A. microfilum* might well represent phases of one life history, since they are reported from the same locality and substrate at the same time (JAO 1936); this condition was also found in *C. kylinoides* and *C. reductum* a few times. On the whole, *A. radiatum* and *A. microfilum* are of somewhat smaller dimensions than *C. reductum* and *C. kylinoides*.

Within the genus *Chromastrum*, *C. kylinoides/reductum* obviously represents one of the most primitive forms, as expressed in the very limited development of the vegetative thallus and the simple postfertilization structure. However, we have not observed direct development of one carposporangium from the fertilized carpogonium, a fact claimed for *Acrochaetium hummii* (AZIZ 1965).

It should be noted that although *Chromastrum kylinoides* and *Chromastrum reductum* are both presented here as new nomenclatural combinations, in view of their conspecificity the name *C. reductum* has priority and *C. kylinoides* is a superfluous combination. Since some other species may prove conspecific, and since examination of type specimens has not taken place, these nomenclatural changes must be considered provisional. The gametophyte, for example, also agrees rather well with the original description of *Chantransia parvula* Kylin (KYLIN 1906); subsequent authors have denied the specific status of *C. parvula* (e.g. ROSENVINGE 1909) and sometimes attributed it larger cell dimensions (HAMEL 1928). A decision concerning these nomenclatural questions should be based upon examination of a large number of described species, gametophytes as well as tetrasporophytes.

The life history of *Kylinia rosulata/Acrochaetium strictum* is related to that of other acrochaetioid species with parietal chromatophores, e.g. *A. dasyae* (STEGENGA & BORSJE 1976) and *A. thuretii* (Stegenga, unpublished observation). Spore germination and structure of prostrate and erect parts in the tetrasporophyte, as well as carposporophyte morphology are similar. The difference between *Kylinia* and *Acrochaetium* concerns the gametophyte, which has a unicellular base and special androphore cells in *K. rosulata*. The combination of parietal chromatophore and unicellular base may indeed occur in only a few species; other species with a unicellular base in general have stellate chloroplasts and hence belong to *Chromastrum*. The recognition of androphores, originally the key character of the genus *Kylinia* (ROSENVINGE 1909), is probably a matter of taste: in many Acrochaetiaceae spermatangia are born on corymbose structures of diminutive cells (see also WOELKERLING's (1971) comment on *Kylinia australis*). It cannot be denied, however, that *K. rosulata*, *K. australis* Levring (LEVRING 1952) and also *K. blomquistii* Aziz (AZIZ 1965) have a great deal in common. *K. scapae* Lyle (LYLE 1929), the fourth species assigned to this genus on the ground of possession of androphores, is of a doubtful status (see DIXON & IRVINE 1977).

For the moment we prefer to keep *Kylinia* as a separate genus, defined by a combination of unicellular base with a single parietal chromatophore in the gametophyte and a multicellular filamentous base in the tetrasporophyte. We must admit that recognition of the tetrasporophyte as a species apart from the genus *Acrochaetium* is impossible without elaborate culture studies. This also makes speculating about the identity of tetrasporophytes of the related species of *K. rosulata* difficult.

The difference of our results and the interpretation of BOILLOT & MAGNE (1973), concerning the life history of *K. rosulata* will be discussed under *Acrochaetium pectinatum*. Suffice it to say that in identification of the gametophyte, on the European coast *Acrochaetium gynandrum* (Rosenv.) Hamel would be the only alternative to *K. rosulata*; this species, although like our material found on *Ectocarpus*, has a different overall morphology and no known androphores in connection with its spermatangia.

The tetrasporophyte agrees with *Acrochaetium strictum* with respect to cell and sporangial dimensions, but at least in culture, our species may branch frequently. A possible alternative is *A. attenuatum* (Rosenv.) Hamel, which has smaller sporangia, however. Both *A. strictum* and *A. attenuatum* have unicellular hairs, which otherwise seem to be rare in species with parietal chloroplasts.

The life history of *Acrochaetium pectinatum*, as far as reconstructed, most closely agrees with the results of WEST (1968). On the other hand, there is a considerable discrepancy between our interpretation and the results of BOILLOT & MAGNE (1973): they cultured a tetrasporophyte, identified as *A. pectinatum*, from a small gametophyte, presumably *Kylinia rosulata*. We have, however, little reason to doubt the identity of the species we call *A. pectinatum*, and rather think that the gametophyte of *A. pectinatum* is not *K. rosulata*. The gametophyte of *A. pectinatum* has larger cells and a distinctly more complex chromatophore. Moreover, androphores appear to be absent from male reproductive plants: in WEST's (1968) material the cells bearing spermatangia are *c.* 3–4 μm in diameter, and thus less developed than vegetative cells, but not as narrow as androphore cells are.

European material of *A. pectinatum* differs from Pacific American specimens in the smaller dimensions of the sporangia: monosporangia measure 8–12 × 5.5–8 μm as opposed to 15–21 × 7–10 μm, tetrasporangia measure 12–17 × 9–14 μm as opposed to 20–33 × 9–15 μm. Monosporangia of the gametophytes, on the other hand, show nearly complete overlap in dimensions.

The gametophyte of *A. pectinatum* is, apart from BOILLOT & MAGNE's (1973) interpretation, not described from the European coast. Not from the American coast either, unless ABBOTT & HOLLENBERG's (1976) inclusion of *Rhodochorton simplex* Drew in this species is to be interpreted as such a record. Abbott & Hollenberg (l.c.) retained *K. rosulata* as a separate species, also present on the Pacific coast of N. America. From the Australian coast only the gametophyte of *A. pectinatum* is known (WOELKERLING 1971). WEST's (1968) cultured gametophytes and WOELKERLING's (1971) field collected specimens attained a larger size than our material ever did, but the unicellular base persisted as such.

We prefer to assign the species under consideration to the genus *Audouinella* Bory. *Audouinella* is distinguished then mainly by its spiral chromatophores without pyrenoids (cf. PAPENFUSS 1945). Life histories in this group are not uniform: *A. pectinata* has dissimilar generations, whereas in *A. efflorescens* (J. Agardh) Papenfuss and the type species *A. hermanni* (Roth) Duby these phases seem to be less heteromorphic. The composition of the genus *Audouinella* as accepted here, is therefore to be considered provisional. A re-evaluation of relevant species is necessary; especially knowledge of postfertilization developments is needed to find out the relationships with other Acrochaetiaceae.

In this context it is clear, however, that we do not support Dixon's (in DIXON & IRVINE 1977) concept of the genus *Audouinella*. We hold the opinion that the acrochaetioid algae should be split up into at least 5 genera (STEGENGA & VROMAN 1977). Future research on life histories and other features must reveal the value of this hypothesis.

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REFERENCES

ABBOTT, I. A. & G. J. HOLLENBERG (1976): *Marine algae of California*. Stanford University Press, Stanford, Calif., 827 pp.

AZIZ, K. M. S. (1965): *Acrochaetium and Kylinia in the southwestern North Atlantic Ocean*. PhD Thesis Duke Univ., Ann Arbor, Mich., Univ. Microfilms, 66–79, 245 pp.

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

BOILLOT, A. & F. MAGNE (1973): Le cycle biologique de Kylinia rosulata Rosenvinge (Rhodophycées, Acrochaetiales). *Bull. Soc. Phycol. de France* **18**: 47–53.

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.

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

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

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

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

— (1944): die Rhodophyceen der schwedischen Westküste. *Lunds Univ. Årsskr., N.F., Avd.* 2, Bd. **31**.

LEVRING, T. (1952): The marine algae of Australia I. Rhodophyta: Goniotrichales, Bangiales and Nemalionales. *Arkiv för Botanik* **2**(6): 457–530.

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

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

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.

—& — (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.

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

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