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THE MORPHOLOGY AND LIFE HISTORY OF ACROCHAETIUM DASYAE COLLINS (RHODOPHYTA, NEMALIALES)

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SUMMARY

The morphology of *Acrochaetium dasyae* Collins is described in detail from material collected along the Dutch coast. This material consists of predominantly unisexual gametophytes with a prominent persistent basal spore and a multicellular filamentous prostrate system, which may be more or less endophytic in *Dasya pedicellata* (C. Ag.) C. Ag.. Some additional remarks are made on field-collected specimens of *A. dasyae* from Swedish and Eastern-Canadian coasts. The life-history was completed in culture and turned out to be a diplobiontic cycle consisting of slightly heteromorphic generations. Gametophyte and tetrasporophyte differ in persistence or non-persistence of the basal spore, and to a lesser degree in morphology of the basal system and arrangement of the monosporangia.

Material presumably representing the tetrasporophyte was found in two Dutch and several Canadian samples and provisionally identified as *Audouinella saviana* (Menegh.) Woelkerling; it occurs as an epiphyte on several macroalgae and on *Zostera* sp..

No decision could yet be made concerning the possible conspecificity of *A. dasyae* with several other species, described either as gametophytes or tetrasporophytes.

1. INTRODUCTION

Acrochaetium dasyae Collins is one of the taller species of the genus and, according to various authors, found exclusively on *Dasya pedicellata* (C. Ag.) C. Ag., either epiphytic or partly endophytic. When it was first described by COLLINS (1906) it was found in an asexual state only. Sexual reproductive organs were first reported by AZIZ (1965), who concluded to a haplobiontic life-history (AZIZ 1965, 1967). Judging from literature (AZIZ 1965, EDELSTEIN et al. 1967, WOELKERLING 1973) the distribution is limited to the North-American Atlantic coast. The nameless species described by NIENHUIS (1968) from one Dutch locality is apparently the same as delt with in this paper.

The host of *A. dasyae*, *Dasya pedicellata*, is mainly North-Atlantic and Mediterranean in its distribution; it occurs very rarely on the western European coast and is recorded only from a few Dutch and Swedish localities. It seems to prefer brackish eutrophic water with reduced tidal influence; in the Netherlands it is a late summer annual. Ecology and algal vegetations of the Dutch localities have been described in more detail by DEN HARTOG (1964) and NIENHUIS (1968).

In the present study the culture method was used to elucidate the life-history and to obtain more information about morphological variability in different environmental conditions.

Previous studies of this type have revealed a diplobiontic life-history in some other *Acrochaetium* species, consisting of more or less heteromorphic gametophytes and tetrasporophytes (BOILLOT & MAGNE 1973, BORSJE 1973, WEST 1968).

Finally some remarks will be presented concerning the systematic position of *A. dasyae* and its possible relationships to other species of the genus.

2. MATERIALS AND METHODS

Morphological investigations on field-collected material of *A. dasyae* in this study are mainly based on samples taken from the two known Dutch populations, occurring in the "Gat van Ouwerkerk" and "Kanaal door Zuid Beveland". These localities will furtheron be referred to as "GvO" and "KdZB" respectively.

Collections were made on 3-X-1969, 15-XII-1969 and 21-X-1970 at both localities. Samples were partly preserved in formalin 4% to study morphology afterwards; observations on cell contents invariably were made on live material only.

In addition some observations were made on material from the Swedish west coast, while one of us had the opportunity to study part of the collections of the Atlantic Regional Laboratory of the National Research Council, Halifax, N.S., Canada. Relevant sample numbers of the latter collections are listed below.

A number of cultures was started from material collected on 3-X-1969 and grown either unialgal or in combination with the host *Dasya*. As a culture medium the ES-enrichment (PROVASOLI 1968) was used, both of full salinity and reduced salinity (50% seawater). Cultures were kept in petridishes or 80×50 mm storage dishes. Plants were grown at various temperatures (8, 12 and 16°C) and daylengths (8/16, 12/12 and 16/8 h). Lightintensity in all experiments was about 1750 lux, illumination cool white fluorescent light (Philips TL 33).

Morphologic development of the gametophytes was studied in a 10 weeks experiment at 8, 12 and 16°C and photoperiod 12/12 h. During this period the culture medium was not changed. Fertilization and post-fertilization development were studied in aerated cultures.

Samples examined at the Atl. Reg. Lab., Halifax:

Barachois Pond, Nova Scotia: 27-VII-1971, nrs 5238, 5244, 5245, 5249; 17-VIII-1972, nrs 5641, 5642, 5643, 5645, 5646, 5647, 5654, 5656, 5657, 5658, 5659, 5663, 5665; 2-X-1972: nrs 5743, 5746, 5748, 5749;

Point Town, Antigonish, N.S.: 22-IX-1965, nr 1962;

Pomquet Harbour, N.S.: 12-II-1966, nr 2267; 13-II-1966, nr 2273; 22-VI-1966, nr 2829; 19-VII-1966, nrs 2871, 2876, 2888, 2889; 24-VI-1971, nr 5430; 15-VIII-1972, nr 5700;

Pomquet Pond, N.S.: 23-IX-1965, nr 1907;

Bras d'Or Lake, Cape Breton Island: 6-VIII-1970, nrs 4526, 4530, 4542; 7-VIII-1970, nr 4585; 11-VIII-1970, nr 4688;

Malpeque Bay, Prince Edward Island: 5-VIII-1966, nrs 2560, 2561, 2562, 2563, 2569;

Stanley Bridge, P.E.I.: 12-VIII-1965, nrs 1808, 1811.

3. MORPHOLOGY OF THE GAMETOPHYTE FROM THE DUTCH LOCALITIES

Vegetative structure *(fig. 1)*

The basal system. This consists of a persistent spore and a number of creeping filaments. Basal spore (14)16–18(20) μm in diameter, on germination first forming a downward cuneate process which gives rise to the first creeping filament.

On the opposite side of the spore the first erect filament arises. More creeping filaments may develop from the spore and from the lowermost cells of the erect filaments, the latter mainly in KdZB-plants. Cells of the basal system are irregular in shape, 5–10 μm in diameter, their length up to 100 μm; the cells are nearly colourless, a small chromatophore is situated parietally.

If growing on a pinnule of *Dasya*, the cells of the prostrate system are generally long and rhizoidal; a basal system consisting of many short-celled branched filaments as shown in *fig. 1d* is rather exceptional. If growing on a main branch of *Dasya*, the filaments frequently become endophytic; in this case the cells are shorter (± 25 μm) and the prostrate system remains less extensive. Very extensive endophytic systems (up to 1500 μm long) consisting of branched filaments running lengthwhise along the medulla cells of *Dasya*, possibly represent potentially erect filaments developed within the host; the cells of these filaments contain a large brightcoloured chromatophore.

The erect system Generally one, rarely two erect filaments are given off by the basal spore; more erect filaments may arise from the prostrate system, giving the plant a bushy appearance. Maximum height of the erect system is about 3.5 mm. Filaments are 6–10 μm (GvO) and 8–11.5 μm (KdZB) in diameter. Cells are cylindric, average cell length in mature plants 35 μm (GvO) and 45 μm (KdZB), varying between (10)15–50(60) μm. The chromatophore is a parietal band, at first rather narrow and situated in the distal part of the cell, later on extending downward; pyrenoid rather prominent and parietal in position. Branching of the main filaments is multilateral or in short secund series; branching rather frequent: one lateral is found per 2–5 main filament cells; branches inserted at an angle of (12)20–50(75)° to the main axis.

Reproductive structures

Monosporangia *(fig. 1b)* are generally present on erect parts of plants larger than 600 μm (GvO) or 1200 μm (KdZB). They occur mainly in short uniseriate rows on the adaxial face of the branches and are sessile or pedicellate; sometimes two sporangia occur on one pedicel. In KdZB-plants repeatedly branched corymbose structures were observed, bearing many monosporangia. Monosporangia are oblong ovoid, (10)11–15 × 16–25 μm (GvO) and (10)12–18(21) × (15)21–28(31) μm (KdZB); the chromatophore is an irregularly shaped parietal structure, the pyrenoid often rather inconspicuous.

Monospores are released by apical rupture of the sporangium wall. Frequently within the old sporangium wall a new sporangium develops from the

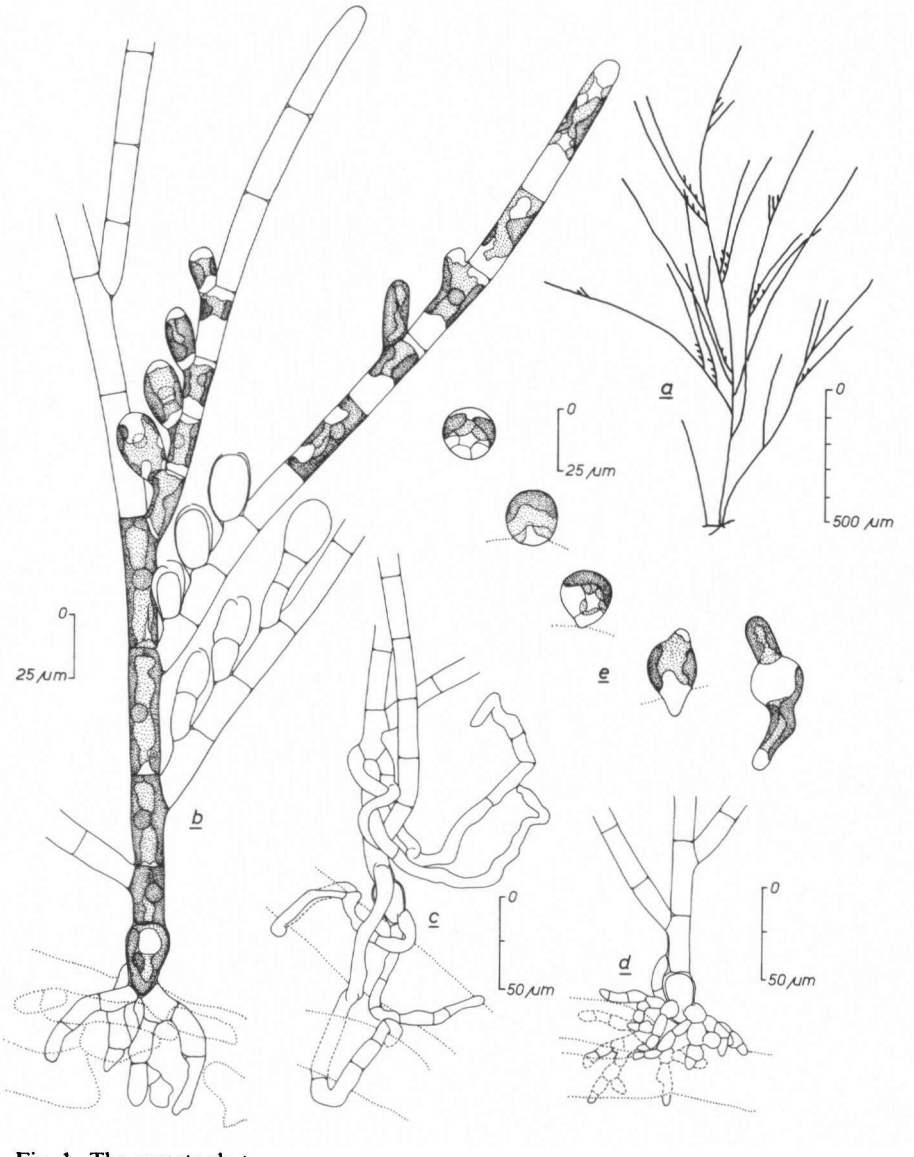

Fig. 1. The gametophyte.
a. Habit of plant on *Dasya pedicellata*. *b*. Detail of thallus showing endophytic base and monosporangial arrangement; note shape of chromatophore in vegetative cells and monosporangia. *c*, *d*. Variation of basal morphology in epiphytic specimens. *e*. Stages in germination of monospores.

underlying cell. Monospores at first lack a rigid wall and are amoeboid. Their development after settling is shown in *fig. 1e*.

Carpogonia were observed only in GvO plants. Arrangement is like that of monosporangia, although carpogonia occur in lower numbers. Except for a small chromatophore their cell content is hyaline and shows some large vacuoles; the trichogyn may contain many small vacuoles. Carpogonial length, exclusive the trichogyn is 16–26(35) μm, with a diameter of 6–7 μm; trichogyn length up to 50 μm, diameter about 2 μm.

Spermatangia were observed in small numbers only on KdZB plants collected 21-X-1970. They occur on the apical cells of corymbose structures. Spermatangial clusters mostly occur in short secund series on the branches. Mature spermatangia are nearly globose and measure about 6 μm; their cell content is entirely hyaline.

4. MORPHOLOGY AND LIFE HISTORY IN CULTURE

In agreement with the findings of NYGREN (1970) *Dasya pedicellata* was found to grow best in a medium of reduced salinity. *Acrochaetium dasyae* is easily grown in unialgal culture both in full and reduced salinity. However, isolated monospores will germinate only in presence of *Dasya.* unless spore density is high.

Vegetative morphology

Vegetative morphology and development is essentially the same as in field collected plants.

The diameter of the basal spore is 18–19 μm. The basal system is rhizoidal and rarely develops endophytically; in the latter case it is less extensive. Under suitable conditions the erect part continues its growth; consequently plants may become a few cm's tall in several months. In the tested conditions maximal growth occurred at 16 °C.

Diameter of the filaments up to 9(10) μm, apically 6.5–7.5(8.5) μm (GvO) and 10(11) μm, apically 7.5–9 μm (KdZB). Cell length varies from 15–75 μm, averaging 40–60 μm in the main axes. Average cell length was shown to be related to temperature, while moreover there is an evident difference between some clones grown at the same temperature *(fig. 2)*.

Reproductive structures

Under favourable conditions reproductive structures, sexual as well as asexual, are produced in large quantities. Monosporangia occur in long uniseriate rows; dimensions 11–17 × (17)19–26(30) μm; liberated monospores are 17–20 μm in diameter. Subsequent formation of monosporangia within an old sporangium wall occurs more often than in nature.

The gametophytes are essentially unisexual, while a few clones never developed sex organs.

Carpogonia *(fig. 3c)* developed in large quantities on GvO plants, but only

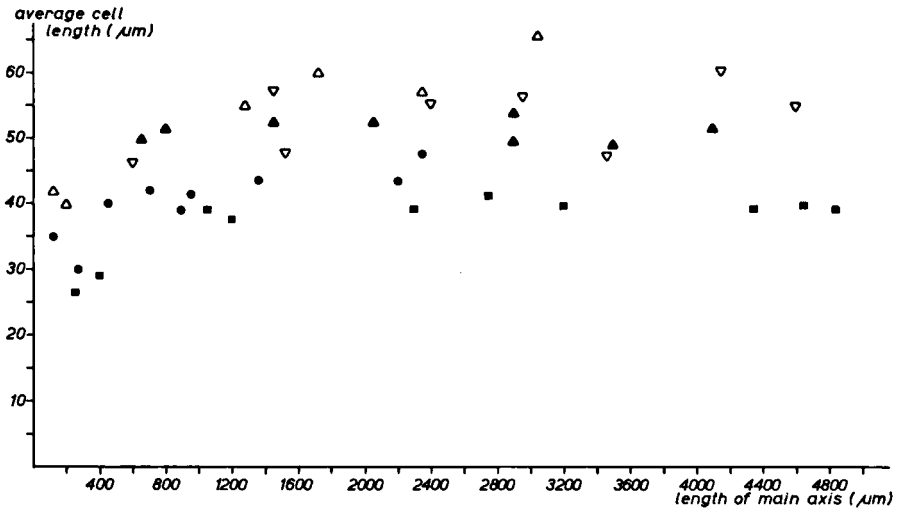

Fig. 2. Relation of plant height and average cell length of main axis in gametophytes in culture (△ = clone 161, at 12 °C; ▽ = clone 164, 12 °C; ▲ = clone 165, 12 °C; ● = clone 165, 8 °C; ■ = clone 165, 16 °C).

occasionally and in very small numbers on KdZB plants. Mature carpogonia measure 6.5–7.5 × 24–28 μm, the trichogyn length is up to 100 μm.

Spermatangia *(fig. 3a, b)* were observed only on KdZB plants and are situated terminally on the branchlets of short-celled corymbose structures. Often also monosporangia occur on these clusters. Spermatangial clusters may be rather abundant, in secund series on the distal part of the branches. Mature spermatangia measure 6–7 μm in diameter. Spermatia are released by apical rupture of the spermatangial wall.

Post-fertilization development *(fig. 3c–i)*

Carposporophytes developed within a few weeks in aerated cultures of a ♂ and ♀ clone combined. Fertilization of the carpogonium takes place by a spermatium which adheres to the trichogyn. After fertilization the carpogonium increases in length and the desintegrating trichogyn is pushed aside. The first division of the carpogonium is transverse. From the thus formed two-celled structure a number of gonimoblast filaments arises; these branch frequently and consist of short colourless cells; the terminal cells finally enlarge to form the carposporangia. The carposporangia measure about 16 × 24 μm; the chromatophore of the carposporangia is rather prominent again. After carpospore release, within the old sporangium wall a new carposporangium may develop from the underlying cell. Mature carposporophytes are nearly globular with diameters up to 100 μm.

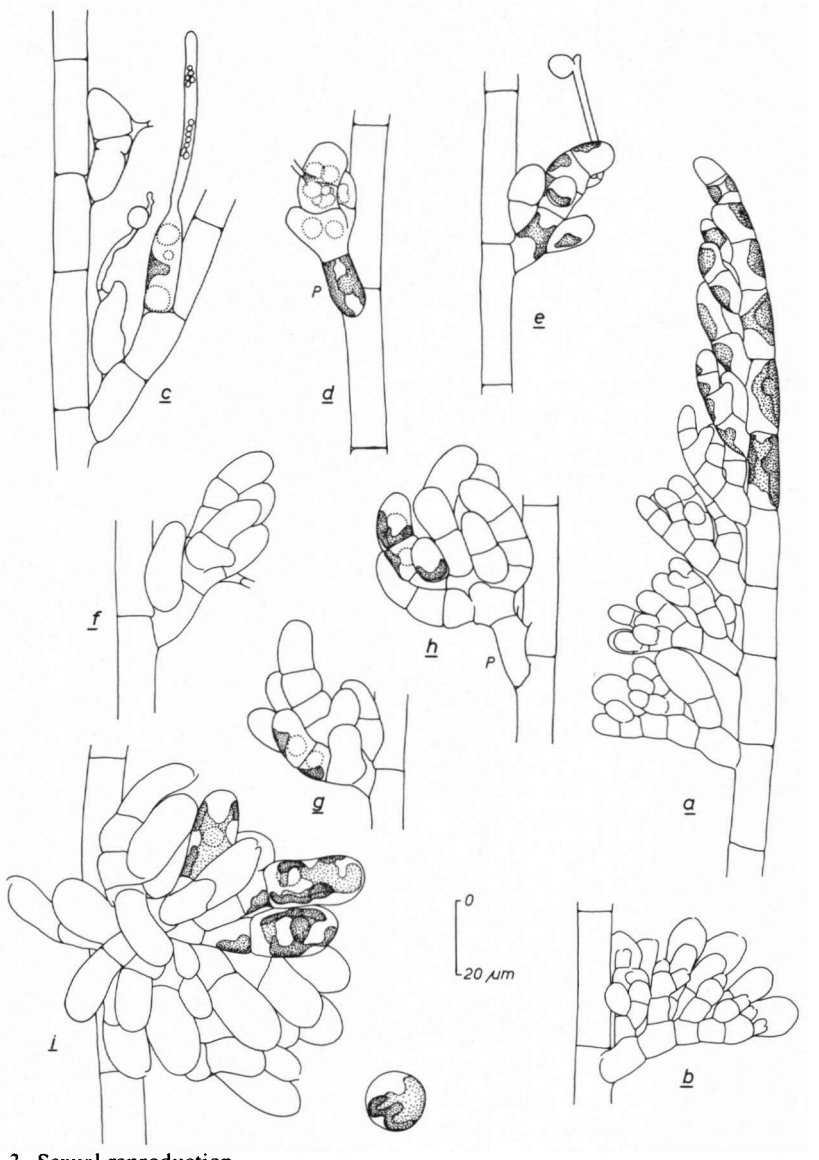

Fig. 3. Sexual reproduction.
a, *b*. Branch with spermatangial clusters, in *b*. postmature and bearing monosporangia. *c*. Carpogonium, fertilization and first division of fertilized carpogonium. *d–h*. Developmental stages of carposporophyte (p = stalkcell of pedicellate carposporophytes). *i*. Mature carposporophyte with carposporangia and released carpospore.

The tetrasporophyte *(fig. 4)*

Mature carposporophytes were isolated and subcultured to enable observation of released carpospores. Carpospores germinate in a typical fashion: from the spore a creeping filament is given off, consisting of somewhat irregularly shaped cells and developing into a branched prostrate system. Usually the spore desintegrated after germination; only in a few cases it persists and subsequently may give rise to more filaments, either creeping or erect. From the first cell of the basal system an erect filament is given off and several more erect filaments may arise from the other cells of the prostrate system. On a firm substrate like glass or the green alga *Chaetomorpha* the base develops into a pseudoparenchymatic disc; when free-floating or grown on *Dasya* it consists of long rhizoidal filaments, scarcely branched. Diameter of the creeping filaments 6.5–11.5 μm, tapering toward the apex to 4 μm; cell length 25–35 μm, cells with a well developed parietal chromatophore, containing a pyrenoid.

The erect filaments strongly resemble those of the gametophytes; mode of branching is essentially the same; creeping filaments may arise from the lowermost cells of the erect filaments. Diameter of erect filaments 8–10 μm, cell length 25–50 μm, apical cells up to 70 μm. The chromatophore is a parietal plate with a prominent pyrenoid. Rarely, laterals may taper into multicellular pseudohairs with feebly developed chromatophores.

In tetrasporophytes over 2 mm tall, monosporangia are produced, mostly in uniseriate rows on the adaxial face of the branches. Monosporangia are sessile or pedicellate and sometimes occur in small clusters. Dimensions of sporangia 12–13 $\times$ 22–30 μm; shape of the chromatophore is similar to that of gametophytic monosporangia. Tetrasporophytic monospores germinate in the same way as carpospores.

Tetrasporangia were observed on plants over 3 mm tall, grown at 16°C; no daylength induction was observed as tetrasporangia developed under all three daylength regimes. They always occur in small numbers, solitary on 1–4 celled branchlets or on branched structures, together with monosporangia.

Division of the tetrasporangium is cruciate, the first division being a transverse one; as the second division is not necessarily in the same plane in the upper and lower half of the tetrasporangium, the result is often suggestive of a trisporangium. Tetrasporangia are oval in shape, their dimensions being 19–24 $\times$ 28–38 μm. On maturation, the tetraspores all have a parietal chromatophore, often located in the center of the sporangium. Released tetraspores measure about 20 μm in diameter.

Tetraspore germination is hard to obtain in culture. It appeared possible only when large tetrasporangium-bearing fragments were transferred to well-established cultures of *Dasya*. These fragments were kept continually under a water-immersed objective in order to check the nature of the offspring. Germlings obtained from tetraspores had a gametophytic morphology.

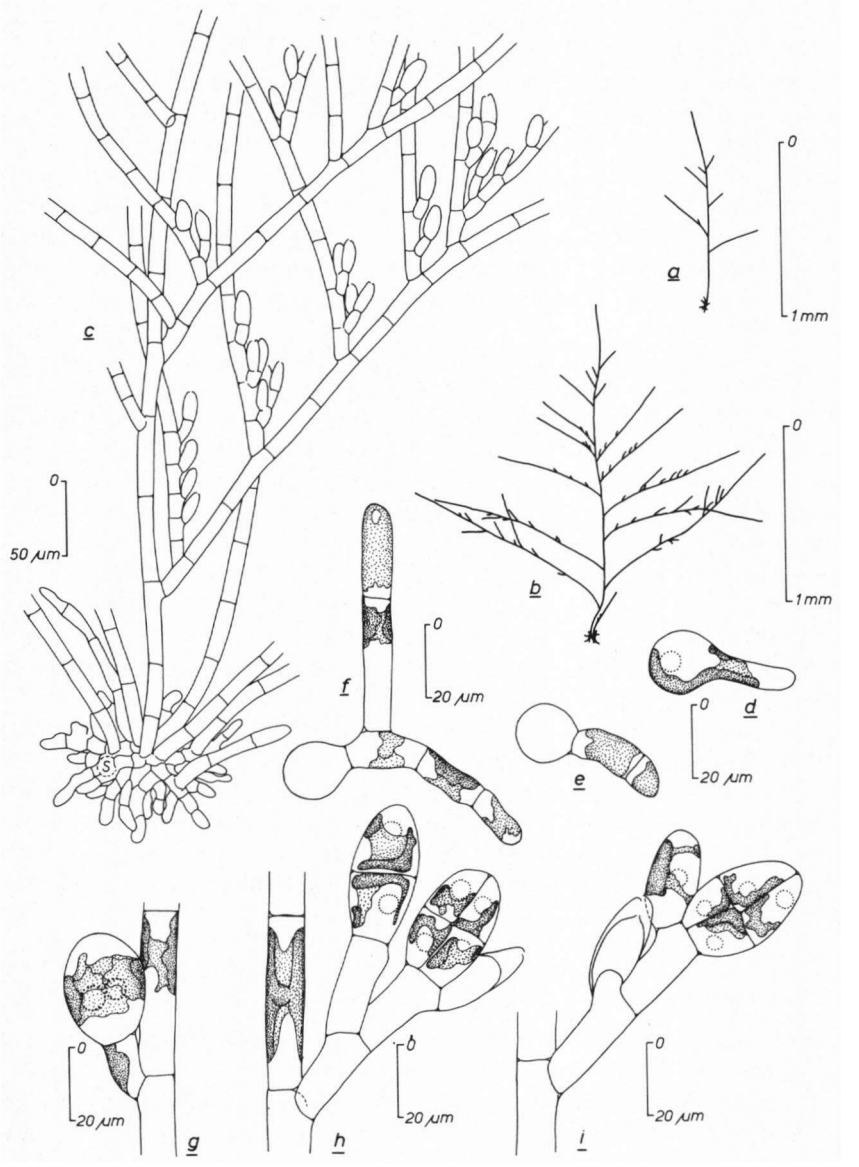

Fig. 4. The tetrasporophyte.
a, *b*. Habit of young plants in culture. *c*. Detail of older plant, showing basal morphology and monosporangial arrangement (s = remains of spore). *d*, *e*, *f*. Germination of carpospores or tetrasporophytic monospores. *g*, *h*, *i*. Development of tetrasporangium.

OBSERVATIONS ON A. DASYAE FROM OTHER LOCALITIES

The gametophytes of *A. dasyae* from the Swedish west coast and some Canadian localities appeared nearly identical to the Dutch material. Dimensions of cells and reproductive structures fall within the range of the described plants.

In addition to unisexual plants a small number of bisexual plants was found on both sites. Morphological differences between ♂ and ♀ plants, as suggested by the diversity in Dutch material, could not be found in the Swedish population. Carposporophytes in various stages of development were observed in Swedish as well as Canadian material. On *Dasya* no tetrasporophytes were ever found.

In samples from several Canadian localities (Prince Edward Island, Cape Breton Island, Nova Scotia) the tetrasporophyte was easily recognized. It occurred as an epiphyte on *Gracilaria foliifera*, *Ceramium fastigiatum*, *Lomentaria baileyana*, *Callithamnion* sp. and *Zostera marina*, even in some places where no *Dasya pedicellata* has been recorded. Plants were up to 6 mm tall. Ontogeny and general structure is similar to plants obtained in culture. The basal system remains rather restricted and forms a small disc, consisting of short branched filaments and giving rise to several erect filaments. Erect filaments are 8–9 μm in diameter, cells of the main axes about 50 μm long, varying between 20 and 70 μm. Monosporangia 12–14 × 20–26 μm, sessile or pedicellate. Tetrasporangia, often rather scarce, sessile or pedicellate, measure 18–20 × 25–28 μm.

Only recently (3-X-1974, 2-XII-1974) tetrasporophytes were isolated from the Dutch coast, on the last sampling date bearing tetrasporangia. They were collected near Yerseke (Eastern Scheldt) growing on *Chondria dasyphylla*. In culture they easily formed tetrasporangia, strange enough only at low temperature (8 °C), while again no daylength induction could be shown. Unfortunately, up to this time we have not been able to obtain any offspring from the tetraspores.

6. DISCUSSION

In the present study *Acrochaetium dasyae* Collins has been shown to possess a diplobiontic life history, consisting of slightly heteromorphic generations. The usually unisexual gametophytes bear spermatangia and carpogonia, fertilized carpogonia develop into carposporophytes which remain seated on the female gametophyte, carpospores on germination give rise to a tetrasporophytic generation, tetraspores in turn render the gametophyte. Both gametophytes and tetrasporophytes reproduce asexually by means of monospores.

As we have no cytological data to be compared with the morphological cycle, we cannot exactly define the type of life history (cf. CHAPMAN & CHAPMAN 1961, DIXON 1973). Our results contradict the thus far assumed haplobiontic life history of *A. dasyae* (AZIZ 1967). On the other hand it most closely resembles the life history of *Acrochaetium pectinatum* (Kylin) Hamel (WEST

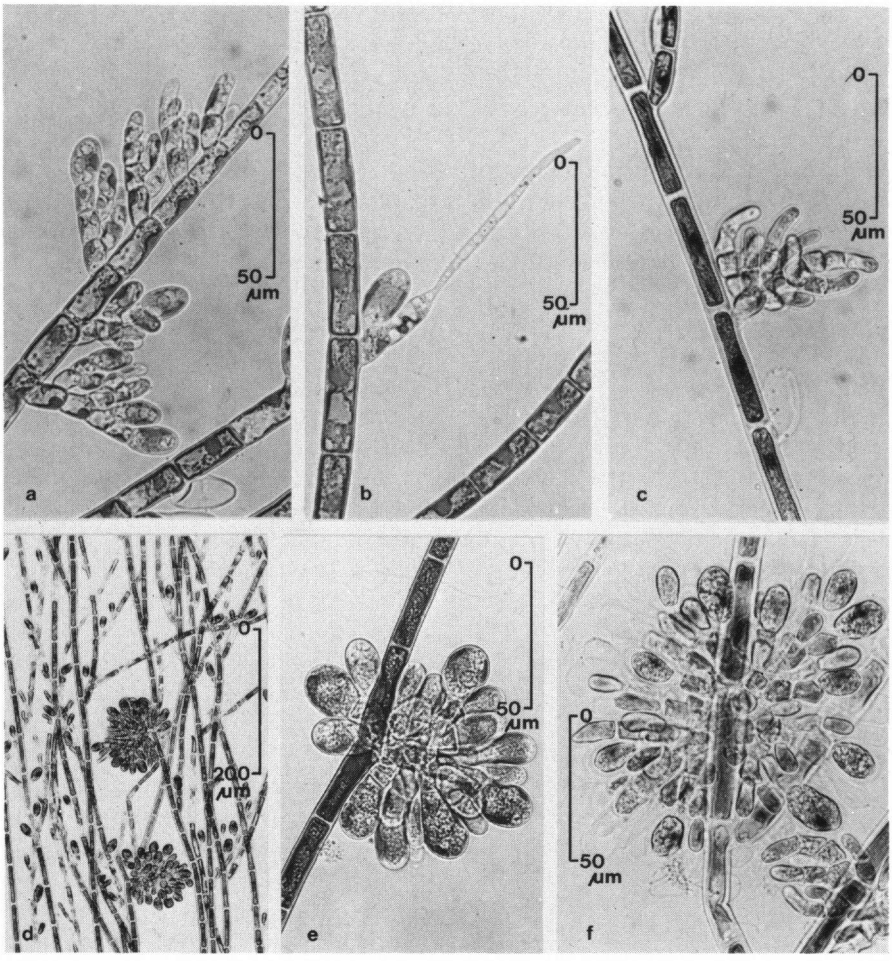

Fig. 5. *a*. Spermatangial clusters. *b*. Carpogonium, pedicel bearing monosporangium as well. *c*. Young carposporophyte. *d*. Gametophyte with carposporophytes. *e, f*. Mature carposporophytes, in *f*. with many empty carposporangia and internal proliferation.

1968) and *Acrochaetium virgatulum* (Harv.) J. Ag. (BORSJE 1973).

Acrochaetium dasyae was originally described by COLLINS (1906) from Woods Hole, Mass., where it was found only with monosporangia, growing on *Dasya pedicellata*. Later on JAO (1936) described *A. intermedium* as an epiphyte of *Dasya* from the same locality. In more recent papers (AZIZ 1965, WOELKERLING 1973) these two species are considered conspecific. Together with *A. opetigenum* Børgesen (BØRGESEN 1915), another species found exclusively on *Dasya*, they might represent only forms of one and the same species, collected at different ages and reflecting growth under different environmental conditions.

WOELKERLING (1973) moreover concludes conspecificity with *A. zosterae* Papenfuss (= *A. subseriatum* Jao), while he suggests possible synonymy of *A. robustum* Børgesen and *A. unipes* Børgesen with *A. dasyae*. All these species would have been distinguished on taxonomically unreliable criteria (see WOELKERLING 1971).

We hold the opinion that the tetrasporic plants of *A. zosterae* as recorded by EDELSTEIN et al. (1967) in fact represent the tetrasporophyte of *A. dasyae*; reexamination of relevant collections has revealed only tetrasporic plants without the persistent basal spore that should be present in *A. zosterae* (cf. JAO 1936).

Also *A. dasyae* should be checked against possible synonymy with *A. bornetii* Papenfuss (= *A. corymbiferum* (Thur.) Batt.) and the sexual phase of *A. thuretii* (Born.) Collins et Herv., These two species are known to possess a persistent spore and resemble *A. dasyae* in many other aspects; they have been recorded from many European and North-American localities and from a variety of substrates (PAPENFUSS 1945, 1947; ROSENVINGE 1909) From our observations it is clear that characters like the morphology of the basal system, the filaments being more or less endophytic, and the degree of branching may vary considerably, both in the field and in culture. Hence these characters do not warrant distinction at the species level. Likewise, mono- or dioecism turned out to be an unreliable character.

So far, the most stable characters of *A. dasyae* appeared to be the presence of the persistent spore in the gametophyte, the structure of the chromatophore, the diameter of the filaments, and to a certain extent monosporangial dimensions and general structure of the plant.

At present the reliability of host specificity as a species character in acrochaetioid algae is not known, and awaits a more detailed experimental approach as exemplified by WHITE & BONEY (1969). Our experiments suggest that the gametophyte of *A. dasyae* has a fairly strong preference for *Dasya* as a substrate.

Judging from literature concerning the European region, the tetrasporic phase must be identified as *A. thuretii*, forma *agama* Rosenv. or as *A. savianum* (Menegh.) Näg. The material also fits the description of *A. nemalionis* (De Not.) Born., if the assumption is right that endophytism in our species is a feature which may arise by chance, mainly depending on the type of substrate. *A. thuretii* is often recorded as a gametophyte; in that case it has a persistent spore, though not as prominent as in *A. dasyae*. *A. savianum* has only rarely been recorded.

On the North-American Atlantic coast identification would lead to *A. sagreanum* (Mont.) Born. (e.g. TAYLOR 1957). Reexamination of the type of *A. sagreanum* has revealed, however, that this probably belongs to the genus *Cladophora* and thus is excluded from the Rhodophyta (WOELKERLING 1973). Woelkerling considers many of the specimens hitherto referred to *A. sagreanum*, as belonging to *A. savianum* (as *Audouinella saviana* (Menegh.) Woelk.), in which species he includes *A. thuretii*. Possible relationship to some other species (*A. avrainvillea* Børg., *A. hypneae* Børg. and *A. pallens* (Zanard.)

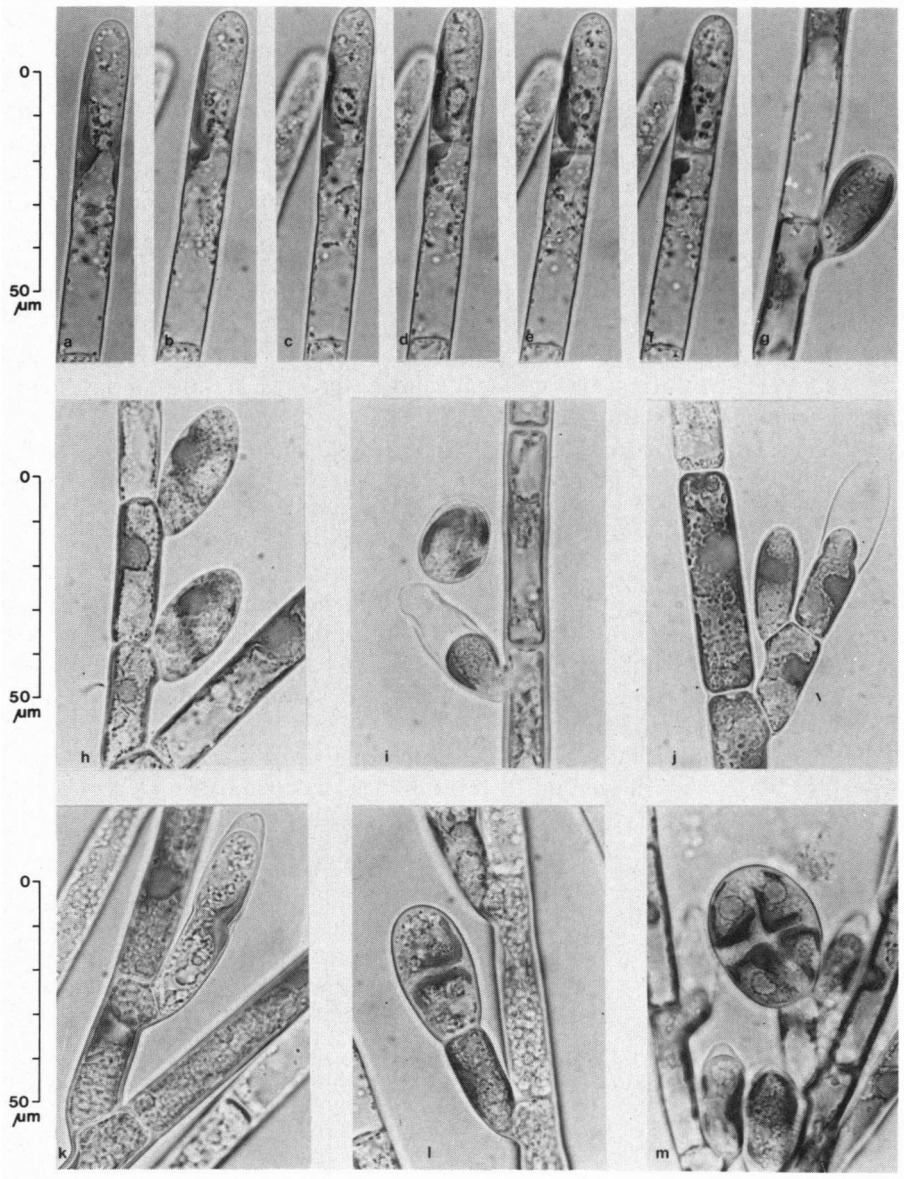

Fig. 6. *a–f.* Division of apical cell. *g, h.* Monosporangia. *i.* Release of monospore. *j, k.* Internal proliferation. *l.* Tetrasporangium after first division. *m.* Mature tetrasporangium.

Näg.) is also stressed by Woelkerling. At this moment we feel it would be premature to try to answer the nomenclatural questions that have arisen. It seems better to await the examination of all possibly related species, both by comparing type material and by an experimental approach as presented in this paper. This type of research is the more important as our study has shown that there possibly exists a great deal of genetical variation in *A. dasyae*. Some differences between GvO and KdZB populations disappeared in culture, like size of monosporangia, but others persisted, like average cell dimensions and the number of creeping filaments arising from the erect axes.

The curious difference of the two Dutch populations, even in sexuality, probably reflects the small genetical variation within each of the populations; the Swedish population apparently is more variable, as male, female and bisexual plants occurred and no significant differences in morphology were found between the sexes.

Neither plants obtained in culture, nor field isolated specimens of the tetrasporophyte have shown influence of daylength on the formation of tetrasporangia. In this respect *A. dasyae* differs from some other *Acrochaetium* species (e.g. BORSJE 1973, WEST 1968) where daylength effects were evident.

The relation of tetrasporangium formation to temperature was obvious; however, plants obtained in culture preferred higher temperatures (16 °C) as compared to field-isolated specimens (8 °C). A similar variation was suggested by data from fixed samples: In Canadian material tetrasporangia were found on plants collected from June till September, the Dutch tetrasporophyte was found fructificating in December.

At this moment it is impossible to indicate whether in *A. dasyae* the generations are seasonally alternating or more or less independent and persisting year-round, either vegetatively or by means of asexual reproduction.

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