THE TAXONOMY, LIFE HISTORY AND ECOLOGY OF SOME SPECIES OF THE CERAMIACEAE (RHODOPHYTA) IN THE NORTH-WEST ATLANTIC

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THE TAXONOMY, LIFE HISTORY AND ECOLOGY OF SOME SPECIES OF THE CERAMIACEAE (RHODOPHYTA) IN THE NORTH-WEST ATLANTIC

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ABSTRACT

Three genera of the Ceramiaceae, *Antithamnion* Näg., *Callithamnion* C. Ag. and *Plumaria* Schmitz from the north west Atlantic were examined. Populations from insular Newfoundland were studied in the field, cultured, and cytologically examined to determine life histories and the factors inducing fertility. In addition a taxonomic re-assessment of the genus *Antithamnion* in the region is presented.

A. boreale (Gobi) Kjellm., *A. pylaisaei* (Mont.) Kjellm. and *A. americanum* (Harv.) Farl. in Kjellm. are morphologically indistinct and were studied in field and in culture to determine the degree of phenotypic variation. They are combined and transferred to *Scagelia* Wollaston as *S. pylaisaei* (Mont.) nov. comb. Two genotypically distinct varieties are recognised; var. *pylaisaei* (Mont.) nov. comb. and var. *boreale* (Gobi) nov. comb., both have a *Polysiphonia*-type of life history with the addition of apomeiotic tetrasporangia on the gametophyte phase. Induction of fertility is independent of temperature or daylength.

A. floccosa (O. F. Müll.) Kleen is re-described and transferred to *Antithamnionella* Lyle. Plants remained sterile in culture, but field and cytological observations revealed no deviations from the *Polysiphonia*-type of life history. A fungal parasite of *A. floccosa* is described as a new species *Olpidiopsis antithamnionis* Whittick and South.

Voucher specimens for the occurrence in eastern Canada of

A. cruciatum (C. Ag.) Näg., *A. plumula* (Ellis) Thur. in Le Jol. and *A. pacificum* (Harv.) Kylin, were examined. Only a single genuine specimen of *A. cruciatum* was located, most records being mis-identifications of *S. pylaisaei*. The records of *A. pacificum* are due to mis-identification of *A. floccosa*. No material of *A. plumula* could be located.

The life histories of three species of *Callithamnion; C. corymbosum* (Sm.) Lyngb., *C. tetragonum* (With.) S. F. Gray and *C. roseum sensu* Harvey were investigated. *C. roseum* has a *Polysiphonia*-type of life history with no deviations, *C. tetragonum* is similar, but has monoecious gametophytes, and procarps and spermatangia were also observed on tetrasporophytes in culture. Only tetrasporangial plants of *C. corymbosum* were found, and in Newfoundland it reproduces by fragmentation. In all the species of *Callithamnion* the induction of fertility is temperature dependent, and *C. roseum* also requires long daylengths.

Plumaria elegans (Bonnem.) Schmitz only occurs in Newfoundland as the triploid parasporangial generation, and fertility is controlled by water temperature.

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GENERAL INTRODUCTION

During the last decade there has been a considerable increase in the number of studies of the benthic marine algae of eastern Canada. This work has been mainly basic exploration and surveys of the previously poorly known flora. South and Cardinal (1970) have compiled much of this floristic information as a check list, and have indicated the urgent need for more detailed examination of many of the representatives of the eastern Canadian flora.

This study is an attempt to elucidate the biology of several species of the Ceramiaceae occurring on the north east coast of North America. The study area is, from New Jersey northwards, but with special emphasis placed on the eastern Canadian region (South and Cardinal, 1970) in view of the forthcoming Flora of the marine algae of this area. Logistics have, however, limited culture and phenological studies to material obtained from insular Newfoundland.

The Ceramiaceae are the most primitive members of the Ceramiales (Kylin, 1928; Hommersand, 1963) a well defined order of the Rhodophyta erected by Oltmanns (1904) and characterised by procarps in which the auxiliary cell is formed after fertilization. The Ceramiaceae lack pericentral cells and their procarps either lack or possess only a single group of sterile cells. The carposporophyte is usually naked, but if enclosed in the thallus of

the female gametophyte it is not in a pericarp with an ostiole.

In addition to the information contained in general works (Fritsch, 1945; Kylin, 1956) there are a number of extensive studies and reviews of anatomy, classification and phylogeny of the Ceramiaceae (Nägeli, 1861; Cramer, 1864; Schmitz and Hauptfleisch, 1897; Kylin, 1923, 1928, 1930a; Feldmann-Mazoyer, 1940; Hommersand, 1963; Wollaston, 1968; Gordon, 1972), but most data are in publications on single genera or species.

Information on the floristics and ecology of the Ceramiaceae in the study area is limited mainly to general Floras and phytogeographic studies (Harvey, 1853; Farlow, 1881; Taylor, 1957; Wilce, 1959). The majority of the species from this area are, however, widespread throughout the colder coastal waters of the North Atlantic and Arctic Oceans, a number of other regional works are thus relevant (Kleen, 1874; Gobi, 1878; Kjellman, 1883; Foslie, 1890; Rosenvinge, 1893, 1899, 1923-1924; Jønsson, 1901; Børgesen, 1902; Kylin, 1907; Printz, 1926; Levring, 1937; Zinova, 1955; Lund, 1959a, 1959b; Svendsen, 1959; Jaasund, 1965). More detailed phenological and distributional studies on members of the Ceramiaceae in eastern North America (e.g. Lamb and Zimmermann, 1964; Edelstein and McLachlan, 1966; Edelstein *et al.*, 1969, 1970; Hehre and Mathieson, 1970) are found in qualitative accounts of reproductive periodicity and depth of occurrence of marine algae in this region.

The Ceramiaceae are a cosmopolitan family, but the majority of genera and the greatest number of species are found in Australasia (Kylin, 1956). The phytogeographic importance of this region has

been furthur emphasised by the recent work of Wollaston (1968) and Gordon (1972). The family is not well represented in the western North Atlantic and the majority of species, in common with other members of the Rhodophyta, are found in warmer seas. Taylor (1960) lists 19 genera and 88 species for the eastern tropical and sub-tropical Americas while South and Cardinal (1970) record only 7 genera and 27 species from eastern Canada; for many species of the Ceramiaceae Newfoundland is the most northerly locality in North America.

There is evidence, based on field observations, that at the northern limits of their distribution in Europe some species of the Rhodophyta exhibit different life histories from those recorded at their centre of distribution (Dixon, 1965). It is generally assumed that members of the Ceramiaceae possess a *Polysiphonia*-type of life history (Dixon,1963a) as first revealed by Yamanouchi (1906a, 1906b) for *Polysiphonia flexicaulis* (Harv.) Coll. (as *P. violacea*). This consists of a sequence of diploid carposporophytes, diploid tetrasporophytes and dioecious haploid gametophytes, with meiosis occurring during tetrasporogenesis. The gametophytes and the tetrasporophytes are isomorphic. Field observations (Lewis,1912) and cytological studies (Lewis,1909;Kylin, 1916; Westbrook, 1930; Drew,1934,1937,1939,1943) have supported this assumption. Proof was eventually obtained in culture by Hassinger-Huizinga (1952) who produced several successive generations of *Callithamnion corymbosum* (Sm.) Lyngbye and correlated these with cytological data. Furthur culture studies of members of

the Ceramiaceae (Drew, 1955; Sundene, 1959, 1964a, 1964b; Edwards, 1969a; Rueness, 1971) have confirmed these findings. The *Polysiphonia*-type of life history thus appears widespread in the Ceramiaceae, there is, however, considerable evidence that it may not represent the full potential life history of a number of species.

Various combinations of tetrasporangia, spermatangia, procarps and carposporophytes have been recorded on single plants and these are listed by Knaggs (1969). A number of gametophytes of the Ceramiaceae are reportedly monoecious *Callithamnion baileyi* Harv., *C. tetragonum* (With.) S. F. Gray (Farlow, 1881), *C. bipinnatum* Crouan frat. (Levring, 1937), *Spermothamnion repens* (Dillw.) Rosenvinge (as *S. turneri*) (Drew, 1934). Field observations have frequently revealed a preponderance of a single phase of the life cycle, usually the tetrasporophytes, while in extreme instances one or more phases may be absent. The potential for vegetative reproduction (Dixon, 1965) is also frequently overlooked.

Culture studies on members of the Ceramiaceae have revealed a number of anomalies (Hassinger-Huizinga, 1952; Drew, 1955; West and Norris, 1966) principally involving the formation of tetrasporangia on plants bearing either spermatangia or procarps. Sundene (1962) and Rueness (1968) have cultured, respectively, *Antithamnion boreale* (Gobi) Kjellm. and *Plumaria elegans* (Bonnem.) Schmitz and shown them to bear only apomeiotic sporangia, which reproduce the parent plant. In *A. boreale* they are morphologically normal cruciate tetrasporangia, but are parasporangia forming an

irregular number of spores in *P. elegans*. Drew (1939) has shown cytologically that parasporangial plants of *P. elegans* are triploid, found in addition to, and genetically isolated from, the normal haploid and diploid *Polysiphonia*-type of generations. In addition, Drew (1934, 1943) has shown cytologically, the existence of triploid and tetraploid phases in the life history of *Spermothamnion repens*.

The development of artificial media, or enrichments for natural seawater (Provasoli, 1964, 1968; Provasoli *et al.*, 1957) has allowed the maintenance of many marine algae in culture for extended periods. In the last decade many species of the Rhodophyta have had their life histories elucidated in culture and much of this work has been reviewed by Knaggs (1969) and Dixon (1970a). The majority of these studies have been on members of the Nemaliales Cryptonemiales and Gigartinales which in nature apparently lack one or more of the generations characterising the *Polysiphonia*-type of life history. Though important the value of many of these studies is often limited by three major omissions:

i. they lack corroborative cytological data.

ii. cultures are frequently incubated under a single condition, giving little or no information on the factors controlling growth and reproduction.

iii. parallel phenological information for natural populations is frequently lacking.

The lack of cytological data is principally due to technical problems, and members of the Rhodophyta have acquired a justifiable

reputation as 'difficult' material. Nuclei and chromosomes are small, and the latter are closely aggregated and individually indistinguishable in metaphase. Counts must therefore be obtained from nuclei in late prophase and errors may arise from incompletely condensed chromosomes. The problems are compounded in that one of the most valuable cytological techniques, the Feulgen nucleal stain, produces inconsistent results with the Rhodophyta (Dixon, 1966a) and the majority of studies have utilized less specific stains, usually either acetocarmine or haematoxylin and its analogs. In spite of these problems much cytological data has been accumulated and this is reviewed by Magne (1964) and Dixon (1966a). In the majority of instances no photographic evidence is produced and a number of studies appear of doubtful validity.

Although the majority of previous life history studies have been carried out under single culture conditions, several recent studies have investigated the effects of physical and chemical factors on the induction of reproductive organs. The most obvious factor is light and for the Rhodophyta the known effects of light intensity and photoperiod are summarised by Dixon (1970a) and Dixon and Richardson (1970). It is apparent that true photoperiodism (Terborgh and Thimann, 1964) circadian rhythms (Bünning, 1967) and total irradiance, the so called photosynthetic effect (Dixon, 1970a) are interacting and frequently confused factors. Reports of true photoperiodic responses are rare (Dring, 1967; Rentschler, 1967; Richardson and Dixon, 1968) and confined to members of the Bangiales. Daylength effects, while not satisfying all the criteria of true

photoperiodism have, however, been implicated in reproductive induction in several Florideophycidae (West, 1966, 1968, 1969) including a member of the Ceramiaceae, *Callithamnion byssiodes* Arnott *ex* Harv. *in* Hook. (Edwards, 1969b, 1971). In cultures of *Rhodochorton purpureum* (Light.) Rosenvinge (Knaggs, 1966a) and *Pikea californica* Harv. (Scott and Dixon, 1971) tetrasporogenesis was induced by the transfer to higher light intensities, than those to which the plants had been acclimatized. Tetrasporogenesis has also been induced by lowering nutrient levels, nitrate and phosphate in *Rhodochorton floridulum* (Dillw.) Näg. (Knaggs, 1967) and nitrate in *Pseudogloiophloea confusa* (Setchell) Levring in Svedelius (Ramus, 1969).

Few studies have attempted to relate data obtained on growth and reproduction in culture to phenological observations in the field. A notable exception among studies on the Ceramiaceae is the work of Edwards (1969b, 1971) on *Callithamnion byssoides*.

The Ceramiaceae selected for study were members of the genera *Antithamnion* Nägeli, *Callithamnion* Lyngbye and *Plumaria* Schmitz. The principal aim of the study was to obtain their life histories in culture and to elucidate the effects of physical environmental factors on the control of growth and reproduction. Such data would then be used to interpret phenological observations on natural populations. Difficulties were, however, encountered in the identification of several species of *Antithamnion*. The taxonomic criteria of cell dimensions and branching patterns were found to be unreliable as intergradations occurred between a number of described

taxa. Marked seasonal changes in morphology were also observed in some species.

Static studies on growth and form in the Ceramiaceae have been made by L'Hardy-Halos (1970) and Dixon (1970a, 1971). Detailed analysis of morphogenesis of members of the family in culture were recently reported (Konrad-Hawkins, 1964a, 1964b, 1968, 1972; Duffield *et al.*, 1972; Waaland and Cleland, 1972). Temperature, light intensity and photoperiod have been shown to affect the rate of apical cell division and the enlargement of the derived cells, factors which control thallus morphology in the Florideophycidae (Dixon, 1970a). While the taxonomic implications of such studies were realised (Waaland and Cleland, 1972) there appears to have been no previous attempt to apply them to the solution of specific problems.

Cultures incubated under defined conditions have been used in this study, to delimit ecotypic and genotypic variation and to establish the factors controlling thallus morphology. The studies have resulted in the clarification of a number of taxonomic problems involving specific delimitations.

In addition to the specific delimitations the generic status of the species of *Antithamnion* listed by South and Cardinal (1970) is also reviewed. This review is necessary in light of the recent monographic treatment of several tribes of the Ceramiaceae in south Australia (Wollaston, 1968) and of *Antithamnion* and related genera on the Pacific coast of North America (Wollaston, 1971).

The form of the Rhodophyta, especially of the reproductive

structures, differs markedly from that found in other algal divisions, and this has led to the creation of a specialized descriptive terminology. Confusion, however, exists due to the inconsistent application of such terms and the use of single terms for structures of dubious homology. For the most part terms used in this work are either self-evident, or widely used, even though some e.g. carpogonial branch (Dixon, 1964), may defy rigid anatomical definition.

Chadefaud (1954, 1960) has proposed a terminology in which he suggests that the algal thallus is constructed of a series of fundamental structural units. This concept has been strongly criticized (Wollaston, 1968; Dixon, 1971) and its analogy with the older and now largely discredited histogen theory of angiosperm morphogenesis has been pointed out. The terminology has, however, gained widespread acceptance among French phycologists and has been applied in detail to the Ceramiaceae (L'Hardy-Halos, 1970), together with a further proliferation of terms to describe what are merely stages of a dynamic process. These terms are neither utilized nor accepted in this work, as to do so could imply an acceptance of Chadefaud's interpretation of algal morphogenesis. In addition to this objection it seems unnecessarily pedantic to create new names for structures or processes which can adequately be described using a few simple terms.

Four basic terms are used in this study to describe vegetative morphology; *main axis* and *lateral indeterminate branch* are self explanatory, *whorl branchlet* is used as defined by

Wollaston (1968) and *pinnule* is a vegetative branch borne on a whorl branchlet cell. Secondary pinnules may be borne on pinnule cells.

MATERIALS AND METHODS

HERBARIUM MATERIAL

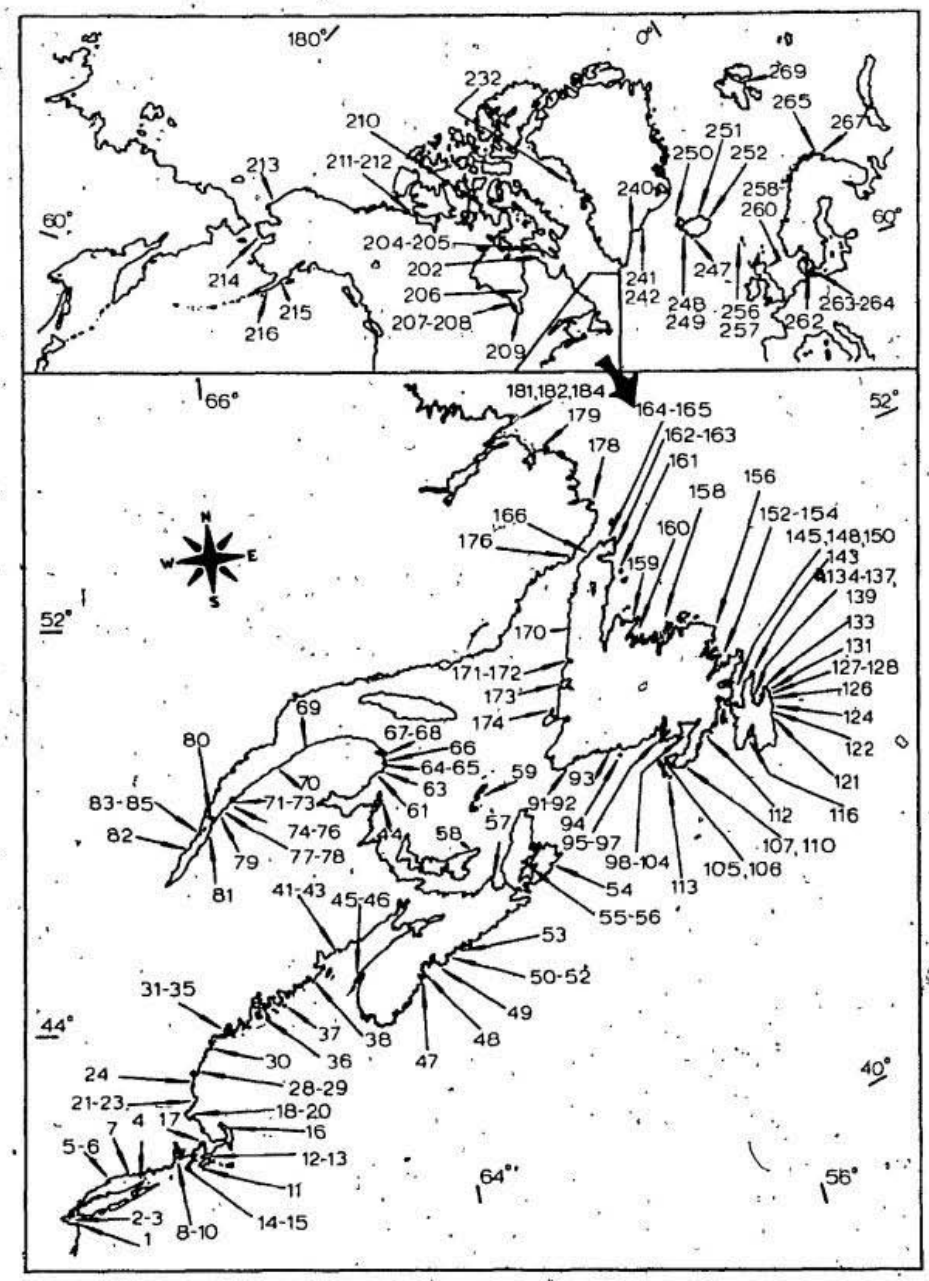
Specimens have been examined from 178 sites (Figure 1.) in the North Atlantic, North Pacific and Arctic Oceans. These include material obtained by personal collection and specimens held in the following hebaria: Memorial University of Newfoundland,(NFLD),St. Johns; National Research Council of Canada, Atlantic Regional Laboratory, (ARL), Halifax; New York Botanical Garden,(NY),New York; British Museum(Natural History), (BM), London; Trinity College,(TCD), Dublin; Botanical Museum, (C), Copenhagen; National Herbarium of Canada,(CANA), Ottawa; University of New Hampshire,(NHA), Durham,N.H.; and the personal collections of Dr. A. Cardinal of Université Laval, Quebec City (QAC); my own collections have been deposited in NFLD. All the specimens examined have been given a station/date number (Appendix II) and this will be used throughout to indicate the source of the described material.

Dried herbarium specimens were reconstituted by wetting with distilled water, transferred to a microscope slide and mounted in 1% lactophenol-cotton blue. The slides were made semi-permanent by ringing the cover slips with nail varnish. A comparison of fresh and reconstituted material showed that there was no alteration in cell dimensions or external morphology.

FIGURE 1

LOCATION OF STATION NUMBERS

Localities from which specimens of the species examined in this work have been obtained. The numbers are the station numbers and their detailed location is given in Appendix II.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FIELD MATERIAL

All collections were made by divers. Two sites, Boone Pt., Bay Bulls (St. 124) and St. Bernard, Fortune Bay (St. 104) were chosen for intensive observation and were visited at approximately monthly intervals, between September 1970 and May 1972. Other sites were also repeatedly visited, but at irregular intervals.

All data on seasonal morphological variation and on reproductive periodicity are based on material collected at these two sites, from the same location within each site. Algae for culture studies were separated from the main body of the collection, placed in seawater in a Twistlock polythene bag, and transported back to the laboratory in a bucket of seawater. If transportation was delayed beyond a few hours, the polythene bags were packed in ice in an insulated container; specimens stored in this manner were still viable after four days. Material was preserved either as an herbarium specimen or in 5% formalin seawater buffered with Tris. (pH 7.6, 0.1 M).

Material collected for phenological study was sorted into fertile male gametophytes, female gametophytes bearing carposporophytes, fertile tetrasporophytes and sterile plants; the ratio of these was calculated.

CYTOLOGICAL STUDIES

Fixation

Specimens for cytological examination were fixed immediately on removal from the ocean, in a 2:1 mixture of ethanol and acetic acid

diluted to 50% with seawater. This proved a rapid fixative and caused a minimum of morphological distortion. It was used either directly or in combination with a mordant. Adequate fixation occurred after 20 min. at room temperature (ca. 18°C), but better results were obtained after 24 h. Storage in daylight hastened chloroplast bleaching, and whenever possible material was stained immediately after fixation. Rapid esterification of the acid alcohol mixture occurred at room temperature along with disintegration of the algal material, though adequate cytological preparations could still be obtained even after periods of a year in storage. Material transferred to 70% ethanol did not disintegrate but became hardened and the subsequent squash treatment was difficult. When prolonged storage was needed material was kept in the original fixative at -10°C in a deep-freeze, which reduced the amount of thallus fragmentation. Fixation was neither carried out at specific times of day or states of tide, nor were cultures fixed at any given period in the 24 h light-dark cycle.

Mordanting and Staining

A variety of stains have been used in the observation of red algal chromosomes and these have been reviewed by Dixon (1966a). Throughout this study acetocarmine staining was used exclusively; the method was essentially that of Austin (1959) with a number of minor modifications. It has been shown to give consistently good results for chromosome counting (Magne, 1964) but to obscure other details of nuclear structure. Experience indicated that the routine application of any one procedure gave inconsistent results and modification of

detail had to be made for different algal material as well as for different batches and ages of stain. The method requires the application of a mordant, either separately as a 1% ferric alum aqueous solution, or in combination with the fixative. In this instance a 2% solution of ferric alum in glacial acetic acid was used in the preparation of the acid alcohol mixture. This combined fixation and mordanting produced good results with *Antithamnion* and *Plumaria*, but the subsequent staining of the *Callithamnion* species was weak, and these were separately mordanted.

Various sources of carmine were examined and carmine alum lake obtained from Matheson, Coleman and Bell Co., Cincinnati was found to produce good results. The acetocarmine was prepared by refluxing an excess of the carmine in 45% aqueous acetic acid for 1 hour. This was then cooled and filtered, and a 1% aqueous solution of ferric alum was added dropwise until the stain acquired a smoky grey appearance, but no precipitation occurred.

Material removed from the fixative was briefly (ca. 2 sec.) rinsed in distilled water and if necessary transferred to the mordant solution for between 30 sec. and 5 min. It was again briefly rinsed in distilled water, placed on a microscope slide and flooded with acetocarmine solution. The slide was allowed to stand at room temperature for one minute to ensure even penetration of the stain. It was then heated from 30 sec. to 2 min. on an electric heating block set at a temperature just below the boiling point of the acetocarmine. Heating was carried out until the solution became dark grey, but no precipitate was formed: it was sometimes necessary to

add more mordant to achieve this colour and this was done by stirring with the blade of a rusty knife. The material was covered with a coverslip, the slide sandwiched between two layers of bibulous paper and the specimen squashed by brisk tapping with the eraser end of a pencil.

After squashing, the material was examined using the high-dry objective of a microscope; if further differentiation of the staining was necessary the slide was reheated for periods of up to 5 min. During this reheating the edges of the coverslip were flooded with stain to prevent the drying of the preparation. When the correct degree of differentiation had been achieved the slide was examined with an oil-immersion objective, using a green filter to provide contrast. The edges of the coverslip were ringed with melted paraffin wax. The slides thus prepared remained in good condition for periods of from three to six months; however, during this time the cytoplasm gradually darkened and eventually obscured the nuclear details.

CULTURE STUDIES

Culture Media

Seawater, obtained from the seawater system of the Marine Sciences Research Laboratory at Logy Bay, formed the basis of the media used in this study. The water was allowed to stand for between fourteen and thirty days at room temperature, and decanted from the settled material as required. It was heat treated either by tyndallization, the seawater being heated to 70°C for 1 h on three consecutive days, or by autoclaving at 80°C for 1½ h on a single

occasion. Both these treatments avoid precipitation and produce a seawater free from algal contaminants. The autoclave treatment was less tedious than tyndallization and as no attempt was made to isolate bacteria free cultures it appeared adequate. Treated seawater was stored at 5°C until required.

Two culture media were used:

(i) Erd-Screiber (Føyn, 1934) with an added enrichment based on Provasoli *et al.*, (1957) ASP_2 medium as modified by Burrows (1958). On occasion a precipitate occurred in the final culture medium and this was traced to inconsistencies in the soil extract.

(ii) Provasoli (1968) ES medium which avoids the use of soil extract.

Cultures utilizing Erd-Screiber medium are designated ER and Provasoli medium ES. Details of the preparation of these media are given in Appendix I.

A 1% solution of germanium dioxide (as sodium germanate, Appendix I) was added to achieve a final concentration of 3 mg per litre of culture medium, and this (Lewin, 1966) inhibited growth of contaminating diatoms. Reduced salinity medium was obtained from steamed seawater, the salinity of which had been adjusted to 30‰, measured by a portable salinometer (RS 5-1, Beckman Instruments, New Jersey). This adjusted seawater was proportionally diluted with distilled water to achieve the desired salinity, the ES concentrate was added to produce the culture medium.

Culture Vessels

Deep petri dishes of Pyrex glass, containing approximately 250 ml of medium, were used for general cultures and straight-sided (100 ml) storage jars of sodium glass containing 50 ml of medium and covered with a plastic petri-dish lid were used for the isolated culture of single spores and plants. The glassware was washed in detergent and rinsed in tap water before being washed in distilled water and autoclaved at 15 lb/sq in for 15 min. Immediately before use the vessels were rinsed in culture medium.

Culture Facilities

Cultures were maintained in three walk-in and three reach-in incubators (Sherer Gillett Co., Marshall, Michigan) equipped with air circulating fans and maintaining a set temperature $\pm$ 0.5°C, or in a domestic refrigerator modified by the addition of lights and adjusted to maintain a temperature of 2° $\pm$ 1° C. Lighting was provided throughout by General Electric cool white tubes on time circuits permitting various combinations of light-dark sequences in a 24 h cycle. Light intensities were measured with a selenium photometer (Photovolt Corp. New York, Model 200), and are expressed in lx. The desired light intensity was usually achieved by varying the distance between the cultures and the light source, but this was often inconvenient and dishes were masked with Whatman #1 filter paper to reduce the incident illumination.

Culture conditions are expressed throughout this work as a three part set of figures: the first refers to the temperature, the second to the photoperiod with the light period preceding the dark, and the

third to light intensity. Hence 10:16-8:500 refers to a culture condition of 10°C under a sixteen hour light, eight hour dark photoregime at a light intensity of 500 lx.

Isolation Procedures

Cultures were obtained from carpospores, tetraspores and from vegetative fragments of the algae. No attempt was made to clean the field material beyond a brisk rinsing in culture medium, and the initial cultures were usually not unialgal. Major contaminants included members of the Cyanophyta, unicellular Chlorophyta and small ectocarpalean Phaeophyta.

Vegetative Culture

Cultures were derived by excising apical portions of plants, placing these in culture medium. The apical regions are usually actively growing and relatively free from other epiphytic algal growth. If the initial vegetative cultures were contaminated the apical fragments were allowed to grow and the process was repeated; the subsequent subcultures were usually unialgal.

Culture from Spores

Plants which bore mature carposporophytes or tetrasporangia were placed in culture vessels the bottom of which were strewn with 24 x 24 mm coverslips. These cultures were incubated, usually at 10°C, under low light intensities (ca. 150 lx). The parent plant was kept in the culture until spore discharge occurred, after which it was removed and the spores allowed to germinate. Coverslips with attached,

germinated spores were then removed, rinsed in sterile medium and placed in new cultures which were incubated under the desired conditions. The cultures were frequently examined in their early stages and contaminating algae were removed from the coverslips with a fine brush. This simple treatment was usually adequate to produce unialgal cultures, but occasionally a persistent contamination occurred. Such contaminated cultures were either discarded, or if the sporelings were of sufficient size they were individually transferred, by means of fine forceps to new culture medium.

Hybridization Techniques

For the most part no special techniques were employed beyond bringing together the appropriate male and female plants in one culture dish. An exception was the use of a mechanical shaker as utilized by Sundene (1959) to optimize the transfer of spermatia. The shaker (Precision Scientific, Chicago Model 16-X-10) was set at its lowest rate of agitation.

Examination of Cultures

Cultures were routinely examined with a stereo dissecting microscope. Samples for more detailed study were removed and mounted on a microscope slide in lactophenol cotton blue.

COLLECTION SITES

SITE LOCATIONS

All the sites from which material has been examined are listed in Appendix II together with their latitudes and longitudes, the date of collection, the species collected and, where possible, the surface water temperature at the time of collection. Each collection is identified by a station/date number; numbers have been given to all sites from which specimens have been examined and as these include species not reported here the numbers do not run consecutively. The location of the sites is given in Figure 1.

SITES OF SPECIAL STUDY

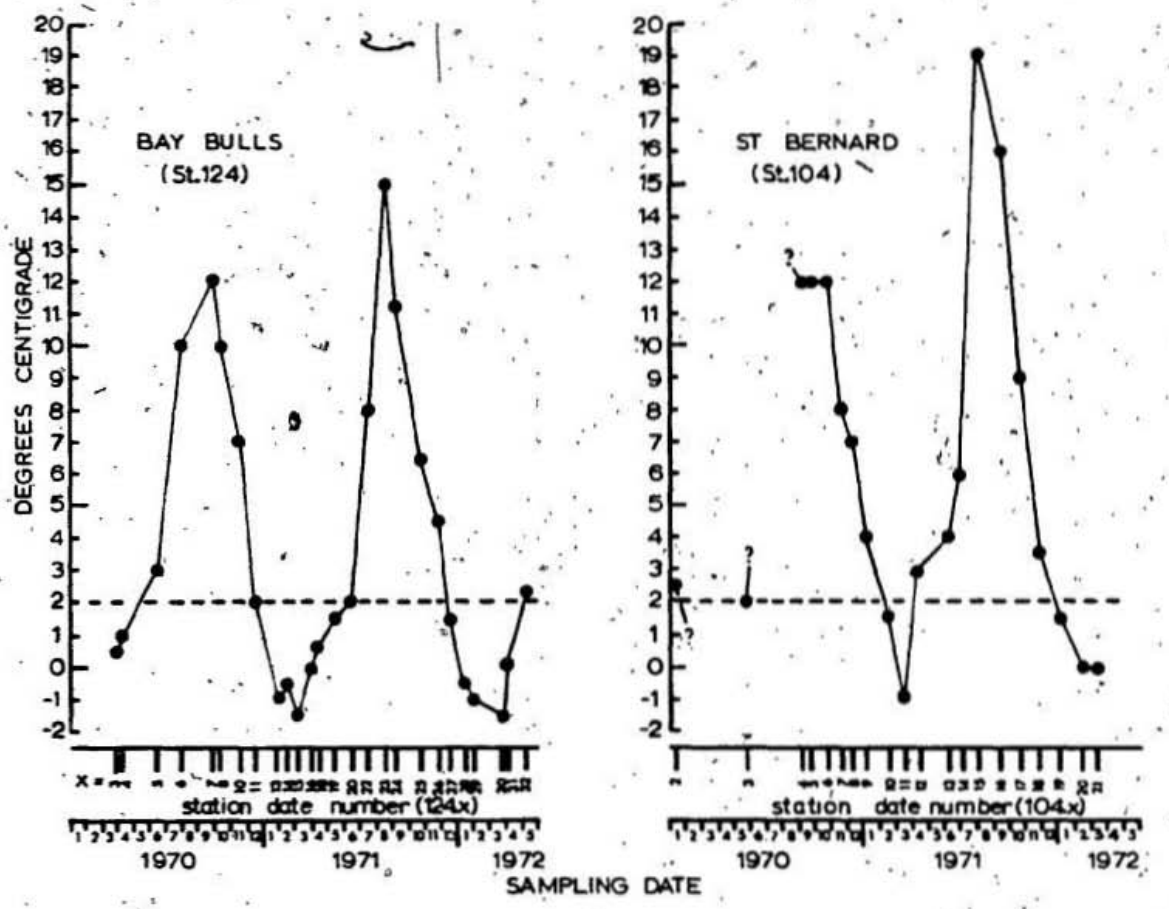
Bay Bulls (St. 124) and St. Bernard (St. 104) were studied in detail; seasonal variations in temperature at the two sites are given in Figure 2. It is realised that short term fluctuations in temperatures occur in coastal waters and individual single surface temperature measurements have little significance. The two localities, however, show considerable seasonal temperature variations, both showing the same general trends. The highest temperature recorded from the Bay Bulls site was 15°C in August 1971 and the lowest of -1.5°C in March; for approximately half the year the surface temperature is below 2°C. The lowest temperature recorded for St. Bernard was -1°C in March 1971 and the highest 19°C in August 1971; the temperature was below 2°C for only three months of 1971. No

FIGURE 2

SEASONAL VARIATION IN WATER TEMPERATURE

AT MAIN SAMPLING SITES

Spot measurements of surface water temperature at the two main sampling sites, Bay Bulls (St. 124) and St. Bernard (St. 104) in 1970, 1971 and 1972. Broken line indicates 2°C for comparison of winter temperatures at the two sites.


BAY BULLS
(St.124)
ST BERNARD
(St.104)
DEGREES CENTIGRADE
station date number (124x)
station date number (104x)
1970
1971
1972
SAMPLING DATE

complete data are available for other years. Both localities are moderately exposed and have negligible fresh water influence. The sites are free from all but minor domestic pollution, but the collection areas within the sites are remote from these sources; the water has low turbidity.

THE GENUS *ANTITHAMNION*

The genus *Antithamnion* was erected by Nägeli (1847) and based on *Callithamnion cruciatum* C. Agardh (1827). The justification for the new genus was that each cell of the main axis bore two equal, opposite, branches of determinate growth (whorl branchlets) in contrast to the single, alternately arranged indeterminate branches of the parent genus. Nägeli (1847) illustrated gland cells and these, along with the cruciate division of the tetrasporangia he subsequently incorporated in his re-description of the genus (Nägeli, 1861). *Antithamnion*, by the description of new species and by the transfer of species previously assigned to other genera, principally *Callithamnion*, has been expanded to include species bearing determinate branchlets of equal or unequal length arranged in whorls of from two to five on each axial cell (De Toni, 1903). Gland cells are absent in some species, but present in others and may be of several types (Schiffner and Biebl, 1944; Tokida, 1954).

The genus *Antithamnionella* was first described by Lyle (1922) to accommodate species having the vegetative appearance of *Antithamnion* but possessing tetrahedrally divided tetrasporangia. Feldmann-Mazoyer (1940) showed that *Antithamnion elegans* Berthold could possess both tetrahedrally and cruciately divided spores and hence regarded this character as unreliable for generic separation. This has been confirmed by Sundene (1964a) who showed that *Antithamnionella sarniense* Lyle (*Antithamnion spirographidis* Schiffner), the type species of the genus, also may appear to have both types of sporangia. The concept of

the genus *Antithamnion* has consequently been further expanded to include the species with tetrahedrally divided sporangia.

Wollaston (1968, 1971) has advocated a return to the more limited concepts of the genus set out in the early descriptions (Nägeli, 1847, 1861), but also based on modern analysis of the development of the carposporophyte (L'Hardy-Halos, 1968) and the post fertilization changes occurring in the female gametophyte of *Antithamnion cruciatum*.

Seven species of *Antithamnion: Antithamnion americanum* (Harv.) Farl. in Kjellm., *A. boreale* (Gobi) Kjellm., *A. cruciatum* (C. Ag.) Näg., *A. floccosum* (O. F. Müll.) Kleen, *A. pacificum* (Harv.) Kylin, *A. plumula* (Ellis) Thur. in Le Jol. and *A. pylaisaei* (Mont.) Kjellm. are recorded from the study area. Examination of herbarium material of these species has revealed many errors of identification as well as divergences of opinion on the exact delimitations of the taxa. The literature is equally confused, and numerous interrelationships and possible synonymies between these taxa have been postulated. Perhaps the most extreme opinion was that of Rosenvinge (1893) who treated *A. boreale*, *A. pylaisaei* and *A. floccosum* as varieties of *A. plumula*.

As will be shown the taxa dealt with in this study fall into four groups:

I. The *pylaisaei-americanum-boreale* group which will be combined in a single species *Scagelia pylaisaei* (Mont.) nov. comb.

II. The *floccosum-pacificum* group which will be transferred to the genus *Antithamnionella* Lyle.

III. *Antithamnion cruciatum.*

IV. *Antithamnion plumula.*

SCAGELIA PYLAISAEI (MONT.) NOV. COMB.

Introduction

Taxonomic Introduction

Antithamnion pylaisaei, *A. americanum* and *A. boreale* do not fall within the circumscription of the genus *Antithamnion* Nägeli as outlined by Wollaston (1968); moreover their delimitation as separate species is artificial and their combination as a single species *Scagelia pylaisaei* (Mont.) nov. comb. is proposed. This will include in synonymy the following:

Callithamnion pylaisaei Mont. (1837).

Pterothamnion pylaisaei Nägeli (1861).

Antithamnion pylaisaei (Mont.) Kjellm. (1883).

Antithamnion pylaisaei f. *norvegica* Kjellm. (1883).

Callithamnion americanum Harv. (1853).

Pterothamnion americanum Nägeli (1861).

Antithamnion americanum (Harv.) Farl. in Kjellm. (1883).

Callithamnion lapponicum Rupr. (1851).

Callithamnion corallina Rupr. (1851),

Pterothamnion lapponicum Nägeli (1861).

Pterothamnion corallina Nägeli (1861),

Antithamnion plumula var. *boreale* Gobi (1878).

Antithamnion plumula var. *boreale* f. *corallina* (Rupr.) Børgesen (1902).

Antithamnion boreale (Gobi) Kjellm. (1883).

Antithamnion boreale f. *corallina* (Rupr.) Kjellm. (1883).

Antithamnion boreale f. *lapponicum* (Rupr.) Kjellm. (1883).

Antithamnion boreale f. *baltica* Reinke (1889).

Antithamnion boreale var. *corallina* (Rupr.) Sundene (1962).

Antithamnion boreale var. *droebachense* Sundene (1962).

S. pylaisaei, as it occurs in the study area, is composed of two genetically isolated but morphologically indistinct entities, these have been referred to throughout this work as Form A and Form B. The use of the word Form is merely for convenience and does not imply a rank within the International Code of Botanical Nomenclature (Stafleu, 1972). It is tentatively proposed to give Form A and Form B varietal status as *Scagelia pylaisaei* var. *pylaisaei* (Mont.) nov. comb. and *Scagelia pylaisaei* var. *boreale* (Gobi) nov. comb. respectively.

An alga collected by de la Pylaie in Newfoundland was named in his honour *Callithamnion pylaisaei* by Montagne (1837), who gave a good description (summarized in Table 1.) but provided no illustration.

Harvey (1853) described *Callithamnion americanum* principally from material collected on the Massachusetts coast (Table 1.), noted its similarity to *C. pylaisaei*, but distinguished it by its more delicate appearance, the less regular arrangement of the pinnules on the whorl branchlets and the more slender nature of the whorl branchlet cells. He also illustrated and expanded the description of *Callithamnion pylaisaei*, differing from Montagne (1837) only by recording cruciate rather than tripartite tetrasporangia. No descriptions of favellae (an archaic term for groups of carpospores or gonimolobes) are given by either author, nor were they seen by Agardh (1863) who transferred *C. pylaisaei* to the genus *Wrangelia*

TABLE 1

DIAGNOSTIC CHARACTERS OF *CALLITHAMNION PYLAISAEI* MONTAGNE (1837), *CALLITHAMNION AMERICANUM* HARVEY (1853) AND *ANTITHAMNION PLUMULA* VAR. *BOREALE* GOBI (1878) GIVEN IN THE TYPE DESCRIPTIONS

	Callithamnion pylaisaei Montagne 1837	*Callithamnion americanum* Harvey 1853	*Antithamnion plumula* var *boreale* Gobi 1878
Overall size	7.5 cm	10 cm	1.5 cm
Axial cell length to breadth ratio a. basal region b. apical region	a. 8x b. 1-1.5x	a. 5-6x b. many times as long as broad	a. 6x b. not reported
Distribution of the whorl branchlets	tetrastichous opposite, paired	opposite and paired	paired opposite distichous, rarely tetrastichous
Form of branching of the whorl branchlets	opposite secund or alternate	secund or opposite pinnate or bipinnate	secund, rarely pinnate in basal region of branch
Whorl branchlet cells length to breadth ratio	not reported	(4-5)-6-8x	not reported
Tetrasporangia	sessile tripartite	sessile, elliptical cruciate	sessile, cruciate rarely tetrahedral
Gland cells	small tubercules on the whorl branches	not reported	not reported

purely on vegetative grounds. This transfer was not accepted by Harvey (1853).[1]

Kützing (1861) described and illustrated *C. pylaisaei* from material collected in Newfoundland by de la Pylaie, and sent to him by Montagne; this may be taken as an authentic specimen. His illustration differs from that of Harvey's (1853) in that the branchlets are borne in whorls of three. Nägeli (1861) transferred *C. pylaisaei* and *C. americanum* to his genus *Pterothamnion* Nägeli (1855), which was based on *Callithamnion plumula* Lyngbye. Favellae were described by Farlow (1881), who on the basis of their form and distribution showed that *C. pylaisaei* was incorrectly placed in *Wrangelia*. He placed both *C. pylaisaei* and *C. americanum* in the subgenus *Antithamnion* but retained this within the genus *Callithamnion*.

Gobi (1878) described an alga (Table 1.) from the White Sea as *Antithamnion plumula* var. *boreale* and noted its resemblance to *Callithamnion americanum*, but discussed it principally in relation to

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[1]There is no reason to suspect that the date of publication of Harvey's work (1853) is incorrect; in it he cites *Wrangelia pylaisaei* J. Ag. Sp. Alg. 2, p. 705 which is the correct pagination, however, the title page of this work is dated 1863. Agardh's Species, genera et ordines Algarum appeared in four volumes and numerous dated parts over the period 1848-1901. Volume 2 appeared in three parts the title page dates being 1851, 1852, and 1863 for parts I-III respectively. According to Dixon (Irvine, pers. comm.) there is some evidence that part III was printed in sections as there are differences in the type of paper used in different parts of this work. He believes the first section may have appeared as early as 1856. Further evidence to support this contention is that there is an appendix added to part II which overlaps with the pagination of part III. It seems unlikely that a decade would pass between the printing of these two parts without this error being rectified. Harvey and Agardh were at this time in close communication, thus it would appear that an early section of part III was at least in the page proof stage prior to 1853.

A. plumula. He separated his variety from *A. plumula* because it possessed sessile tetrasporangia and basal portions of its whorl branchlets occasionally bore pinnately arranged pinnules.

The previous work was synthesized by Kjellman (1883) who pointed out the similarities between the taxa and formally transferred *C. pylaisaei* and *C. americanum* to the genus *Antithamnion*, crediting the transfer of the latter to Farlow. They are hence named *Antithamnion pylaisaei* (Mont.) Kjellm. and *A. americanum* (Harv.) Farl. in Kjellm., the currently accepted names. Kjellman (1883) raised *A. plumula* var. *boreale* to specific status as *Antithamnion boreale* and stressed the sessile nature of the tetrasporangia and the form of the whorl branchlets in distinguishing it from *Antithamnion plumula*. He included in his *A. boreale* two forms, f. *lapponicum* and f. *corallina*, based on Ruprecht's (1851) *Callithamnion lapponicum* and *Callithamnion corallina* respectively, which were described from material collected in the Okhotsk Sea. *A. boreale* f. *lapponicum* closely resembled *A. plumula* in having pinnules borne secundly on the adaxial face of the whorl branchlets, but differed in that these were more lax and more irregular in arrangement; it also possessed sessile tetrasporangia. The similarity of these taxa had previously been noted by Gobi (1878). *A. boreale* f. *corallina* had three whorl branchlets arising from each axial cell, and these formed dense tufts in the apical regions.

A. boreale was not immediately accepted as a species distinct from *A. plumula* (Rosenvinge, 1893, 1899; Jønsson, 1901; Børgesen, 1902; De Toni, 1903) and was maintained with varietal status. It was, however, later regarded as a distinct specific entity (Kylin, 1907;

Rosenvinge, 1923-1924) although recently it had been suggested that it should be returned to varietal status of *A. plumula* (Knaggs, 1969).

Subsequent to its original description f. *lapponicum* has been little reported (Zinova, 1955), but f. *corallina* has become increasingly distinguished and is maintained as a separate species by Japanese workers (Tokida, 1932a, 1932b, 1954). Kylin (in Tokida, 1932a) states that this is justifiable as *A. corallina* possesses a gametophyte stage in its life history, while female gametophytes and carposporophytes are apparently lacking in *A. boreale*. Sundene (1962) also described a new variety, var. *droebachense*, differing vegetatively only slightly from the typical form, but possessing abortive tetrasporangia and reproducing solely by fragmentation.

Reinke (1889) described *A. boreale* f. *baltica* from the Baltic which differs from the typical form principally in its lack of gland cells. Kjellman (1883) also described a diminutive form of *A. pylaisaei* as f. *norvegica* which was separated from the typical species on the basis of its small size, but this form has been considered merely a stunted specimen (Foslie, 1890).

A. americanum (Harvey, 1862), *A. boreale*, *A. pylaisaei* (Setchell and Gardner, 1903) have been reported from the Pacific coast of North America, and these, as they occur in this region, have been synonymized (Kylin, 1925) as *A. occidentale* which, according to Kylin (1925), is distinct from *A. americanum* in that it possesses branches in whorls of three and bears gland cells, features which he believed were absent in *A. americanum*. These vegetative characters together with an analysis of the development of the carposporophyte, have led Wollaston (1971) to

transfer the species to a new genus, *Scagelia* Wollaston. Kylin (1925) pointed out the similarities between *A. occidentale* and his concept of *A. subulatum* Harv., but stated that these could be separated on the width of the basal cell of the whorl branchlets. Recently Wollaston (1971) has shown that *A. subulatum* Harv., differs considerably from Kylin's (1925) concept of the species and that this appears merely to be a robust form of *Scagelia occidentale*.

Taxonomic Criteria

It would appear therefore from the earlier literature (Montagne, 1837; Harvey, 1853; Farlow, 1881; Kjellman, 1883) that the species and the forms of this group can be distinguished on the basis of:

I. Overall size.

II. The size and the ratio of the dimensions of the whorl branchlet cells.

III. The arrangement of the whorl branchlets on the axial cells; whether these are opposite in pairs or verticillate in whorls of three.

IV. The arrangement of the pinnules on the whorl branchlets; whether these are predominantly secund on the adaxial surfaces or borne pinnately, two on each cell.

These characters are those essentially used in more modern treatments (Zinova, 1955; Taylor, 1957), but in addition the presence or absence of gland cells may also be used as a character. When present in species of this group they are borne on a single cell of a whorl branchlet or pinnule as in *Antithamnion plumula* (L'Hardy-Halos, 1968).

They are reported in *A. boreale* (Rosenvinge, 1923-1924; Schiffner and Biebl, 1944; Sundene, 1962), but apparently are absent in this species as it occurs in the Baltic (Reinke, 1889; Pankow, 1971) and in other localities they have been reported as present in some plants but absent in others (Jønsson, 1901; Rosenvinge, 1923-1924; Lund, 1959a).

Gland cells are present in *A. pylaisaei* (Montagne, 1837; Foslie, 1890; Schiffner and Biebl, 1944; Zinova, 1955). In *A. americanum* they have been reported both absent (Kylin, 1925) and present (Rosenvinge, 1923-1924; Schiffner and Biebl, 1944), but these authors did not examine the type material.

Gland cells in the Ceramiaceae are enigmatic structures, and have been the subject of much speculation, leading to bizarre conclusions, often on the basis of little evidence. The literature of these has been reviewed by Feldmann-Mazoyer (1940) and Wollaston (1971). According to these workers gland cells were first recognised by Nägeli (1861) who considered them as abortive spores, however, Montagne (1837) had mentioned spore-like bodies on the branches of *A. pylaisaei:*

> Adsunt et pinnularum articuli incrassati materiam grumosam gongyloideam continentes quae an ad fructificationem pertineat; me latet.

This appears to be a reasonable description of what we now identify as gland cells, but this work does not appear to have been previously recognised.

Gland cells have been considered as fungal parasites (Cohn, 1865), accumulations of reserve material (Berthold, 1882), lenses for focusing light (Bruns, 1894), to have a nutritive function (Nestler,

1899), to be flotation organs (Schussnig, 1914) and excretory organs (Schussnig, 1927). They have been shown to contain protein bodies (Nestler, 1899; Kylin, 1915, 1927) and it has been claimed that they contain free bromine (Sauvageau, 1926), although this has been questioned (Kylin, 1930b). Schiffner and Biebl (1944) have described the occurrence of gland cells throughout the genus *Antithamnion*, and Biebl (1959) has reported on their osmotic relationships in *A. plumula* and *A. sarniense*.

Typification

Antithamnion americanum.

In Harvey's herbarium, held in Trinity College Dublin, there are eight specimens of *Callithamnion americanum* originating from the Atlantic coast of North America; though separately mounted they have been attached to a single herbarium sheet. This sheet has been annotated by Dr. A. R. A. Taylor "type material for *Callithamnion americanum*." The annotation is attached to the sheet in proximity to a specimen labelled "*Callithamnion americanum* H. New Bedford, Dr. Roche" in Harvey's handwriting, and is mentioned by him in his description of the species (Harvey, 1853). This would appear to be a reasonable choice for the lectotype. The plant was sterile, had whorl branchlets in opposite pairs and the main axial cells were eight to ten times as long as broad in the lower regions of the plant, and were 1000-1200 µm in length. The arrangement of the pinnules on the whorl branchlets is as figured by Harvey (1853), no gland cells were observed, and the cells of the pinnules and whorl branchlets ranged from four to fifteen times

as long as broad. The other specimens on this sheet were essentially similar in morphology.

A specimen from Prince Edward Island bore carposporophytes with mature carpospores and was initially labelled *C. hoseii* but this was crossed through and replaced with *C. americanum*. Harvey (1853) also cited in his description of *C. americanum* a specimen collected by Dr. Durkee at Portsmouth N.H., and this specimen bore branchlets in whorls of three, though these were rare and the whorl branchlets were predominantly opposite and paired; this specimen did not appear to have gland cells. One plant was labelled "Lyn Massachusetts Miss Estes," though the specimen mentioned by Harvey (1853) from this locality is credited to a Mrs. Mudge, this specimen bore gland cells adventitiously on a single cell of both the pinnules and the whorl branchlets.

Antithamnion pylaisaei.

A single sheet in Harvey's herbarium (TCD) bears four specimens. One of these was collected by Dr. Durkee, in South Boston, and was used by Harvey (1853) to prepare his illustration. The cells in the lower part of the axis are eight to ten times as long as broad and it bears numerous sessile, cruciately divided tetrasporangia on the adaxial side of the whorl branchlets. The cells of the whorl branchlets are two to three times as long as broad and the pinnules are borne pinnately as in Harvey's (1853) illustration. There are numerous gland cells on single cells of the whorl branchlets and pinnules.

Another specimen on this sheet is labelled in Harvey's handwriting "*Wrangelia pylaisaei* J. Ag." and immediately below this

"*Callithamnion pylaisaei* Mont.". The base of the sheet bears the inscription "De la Pylaie Newfoundland." A slip accompanying the material is labelled "Ex herb Montag.". This specimen is probably isotype material of *Callithamnion pylaisaei* Mont. The specimen has the same general appearance as the Durkee material illustrated by Harvey, but a considerable number of the branchlets are borne in whorls of three and these bear sessile, cruciately divided tetrasporangia on their adaxial face as well as numerous, prominent gland cells. Both these specimens are cited by Harvey (1853) in his redescription of the species (Harvey, 1853). The other two specimens on the sheet have a general appearance intermediate between the type material of *C. americanum* and *C. pylaisaei;* both specimens possess gland cells and one bears carposporophytes with mature carpospores. This latter specimen is labelled by Harvey "Murray Bay, St. Lawrence, Miss Casey, No. 11, *C. pylaisaei*, favellae" the other simply "No. 8, *Callithamnion* Murray Bay." This material is presumably from Murray Bay, Prince Edward Island and communicated to Harvey after the publication of the Nereis (Harvey, 1853), as neither specimen is cited and moreover he states that he has not observed favellae in this species.

Antithamnion boreale.

I have seen no material cited by Gobi originating from the White Sea, or any material of *Callithamnion lapponicum*, or *C. corallina* examined by Ruprecht from the Okhotsk Sea. In his description of *A. plumula* var. *boreale* Gobi (1878) cited material collected by Kjellman from Musselbay, Spitzbergen (St. 269). I have examined specimens from

this source held in the Botanical Museum, Copenhagen (A.W. 817a & 817b). These specimens are labelled by Kjellman *A. boreale* f. *corallina* and appear quite typical of his illustrations of the material (Kjellman, 1883). They bear branchlets in whorls of two and three, their longest axial cells are 1000 µm long and six to eleven times as long as broad, the cells of the whorl branchlets are four to five times as long as broad and they possess gland cells. In the upper portions of the plants the whorl branchlets bear predominantly secund pinnules on their adaxial surface, but in the more mature regions the branching pattern is more irregular and the pinnules are borne oppositely and alternately on the whorl branchlets.

Geographical Distribution

A study of the reported distribution of three species *A. americanum*, *A. boreale* and *A. pylaisaei* has been made by reference to the pertinent literature with particular emphasis on the extremes of the ranges. Figure 3 shows the distribution of these species. The maps are not intended to be inclusive of all records but to show the overall distribution of the species and especially the limits of their distribution along the major coastlines. The reported occurrence of these species in eastern Canada, prior to 1968, has been tabulated by Cardinal (1968).

Vertical Distribution

A. americanum, *A. boreale* and *A. pylaisaei* are sublittoral algae, though they have on occasion been found on the lower littoral. They have been reported both as epiphytes on larger algae and growing

FIGURE 3 (Continued)

Nor. (70°50'N 29°09'E) (Foslie, 1890); 7. Arctic coast of Russia (Zinova, 1955); 8. Japan Sea (Zinova, 1940b).

[a]The record of *A. pylaisaei* from Whidbey Island is now regarded as *Scagelia occidentale* (Wollaston, 1971).

Antithamnion americanum 1. Esquimalt, Vancouver Is., B.C. (48°25'N 123°29'W) (Harvey, 1862)[a]; 2. Fifty miles southwest of Pt. Barrow, Alaska (70°51'N 158°08'W) (Mohr *et al.*, 1957); 3. Disko Is., Grnld. (ca. 70°N 54°W) (Kjellman, 1883); 4. Cumberland Sound, Baffin Is., (ca. 65°N 65°W) (Dickie, 1865-66); 5. Ungava Bay (58°-60°N 65°-70°W) (Farlow, 1886); 6. New Jersey, U.S.A. (Taylor, 1957); 7. Arctic coast of Russia (Zinova, 1955).

[a]The record of *A. americanum* from Esquimalt is now regarded as *Scagelia occidentale* (Wollaston, 1971).

FIGURE 3

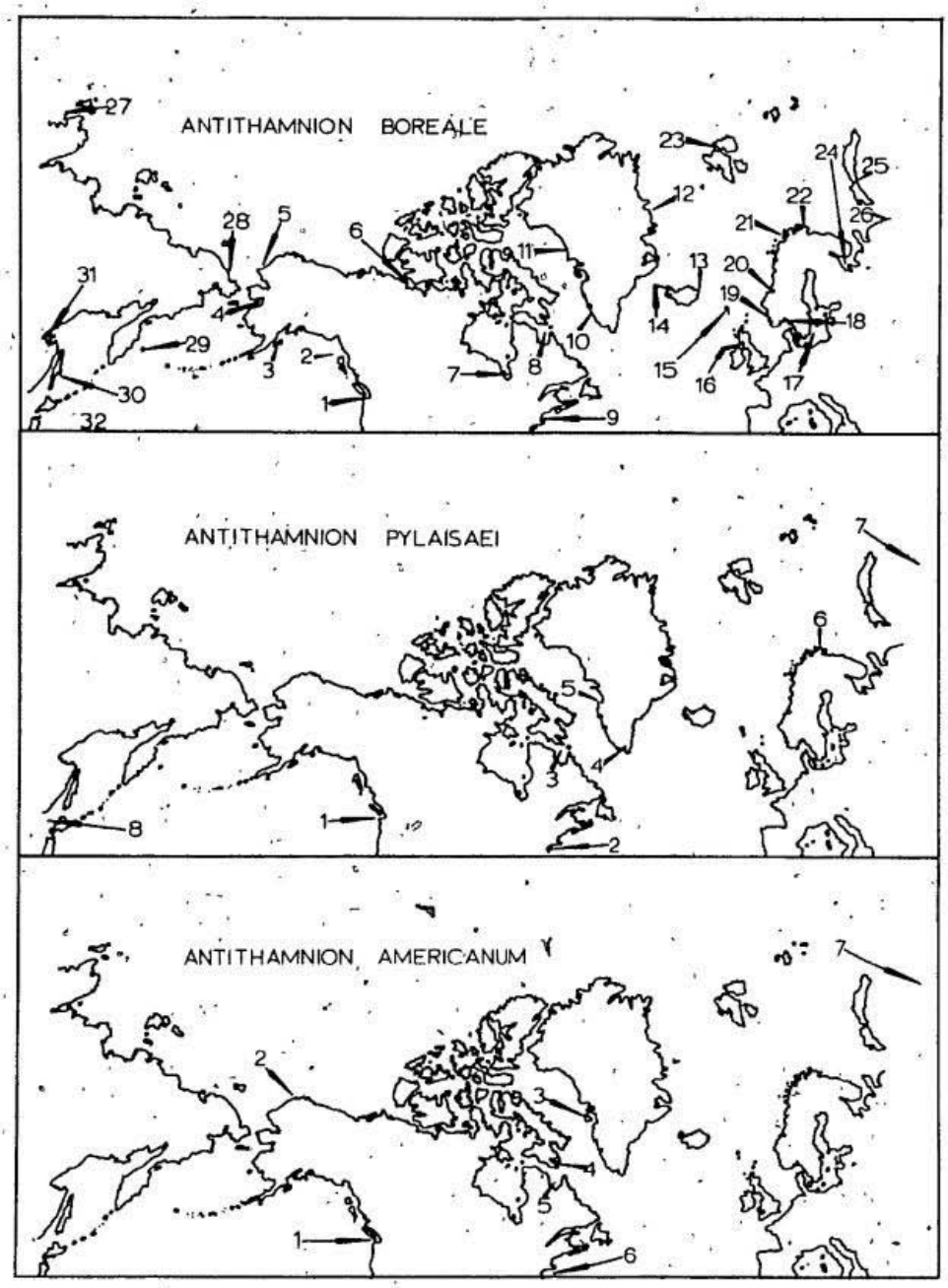
DISTRIBUTION OF *ANTITHAMNION BOREALE*, *A. PYLAISAEI* AND *A. AMERICANUM* FROM LITERATURE RECORDS

Antithamnion boreale 1. Friday Harbor, Washington (48°33'N 123°04'W) (Setchell and Gardner, 1903)[a]; 2. Sitka, Alaska (57°03'N 135°18'W) (Saunders, 1901); 3. Kodiak Is., Alaska (57°48'N 152°21'W) (Setchell and Gardner, 1903); 4. Besboro, Alaska (64°10'N 161°20'W) (Setchell and Gardner, 1903); 5. Alaska (69°39'N 166°27'W) (Collins, 1927); 6. Dolphin and Union Strait (68-70°N 113-118°W) (Collins, 1927); 7. Grey Goose Is., Hudson Bay (55°55'N 79°54'W) (Howe, 1927); 8. Ungava Bay (58°-60°N 65°-70°W) (Wilce, 1959); 9. Northern Massachusetts (Taylor, 1957); 10. Godthaab, Grnld (64°10'N 51°40'W) (Rosenvinge, 1893); 11. Upernivik, Grnld (72°50'N 56°00'W) (Rosenvinge, 1893); 12. N.E. Coast of Grnld (76°30'N) (Rosenvinge, 1910); 13. Seydisfjordur, Ice. (56°16'N 14°02'W) (Jønsson, 1901); 14. Dyrafjordur, Ice. (65°55'N 23°35'W) (Jønsson, 1901); 15. Torshavn, Faer. (62°02'N 6°47'W) (Børgesen, 1902); 16. Cumbrae, Scot. (55°46'N 4°55'W) (Batters, 1902)[b]; 17. Bornholm, Den. (55°02'N 15°00'E) (Rosenvinge, 1935); 18. Oslofjord, Nor. (59°00'N 10°30'E) (Sundene, 1953); 19. Herdla, Nor. (60°34'N 4°56'E) (Hygen and Jorde, 1934); 20. Trondheimfjord, Nor. (63°36'N 10°23'E) (Printz, 1926); 21. Trømso, Nor. (69°42'N 19°00'E) (Sundene, 1962); 22. Beerlvaag, Nor. (70°50'N 29°09'E) (Foslie, 1890); 23. Mussel Bay. Spitz. (79° 50'N 15°30'E) (Kjellman, 1883); 24. Solovetskiye Is., White Sea (ca. 65°N 36°E) (Gobi, 1878); 25. Matochkin Strait, Novaya Zemlya (76°16'N 56°27'E) (Kjellman, 1883); 26. Yugor Strait, U.S.S.R. (70° 30'N 60°00'E) (Kjellman, 1883); 27. Actinia Bay, U.S.S.R. (ca. 76°N 95°E) (Kjellman, 1883); 28. Kolyuchin Is., U.S.S.R. (67°28'N 174°25'W) (Kjellman, 1883); 29. Komandorskie Is., U.S.S.R. (ca. 55°N 166°E) (Zinova, 1940a); 30. Robblen Is., Saghalien (48°30'N 144°50'E) (Tokida, 1932a); 31. Dzhudshandran, Okhotsk Sea (ca. 55°N 136°E) (Ruprecht, 1851); 32. Muroran Harbour, Hokkaido (42°21'N 140°59'E) (Tokida, 1932b).

[a]The records of *A. boreale* from Friday Harbor are now considered as *Scagelia occidentale* (Wollaston, 1971).

[b]A voucher specimen of this record is held in BM and has been annotated *A. plumula* by Dr. O. Sundene (pers. comm. Mrs. L. Irvine). The record of *A. boreale* must therefore be rejected.

Antithamnion pylaisaei 1. Whidbey Is., Washington (48°20'N 122°40'W) (Setchell and Gardner, 1903)[a]; 2. Long Is., N.Y. (ca. 41°N 73°W) (Taylor, 1957); 3. Ungava Bay (58°-60°N 65°-70°W) (Farlow, 1886); 4. Julianhaab, Grnld (60°45'N 46°00'W) (Rosenvinge, 1893); 5. Godhavn, Grnld (69°20'N 57°30'W) (Kjellman, 1883); 6. Beerlvaag,


ANTITHAMNION BOREALE
ANTITHAMNION PYLAISAEI
ANTITHAMNION AMERICANUM

epilithically, as well as on wharves and other man-made objects. The lower depth limits of *A. americanum* and *A. pylaisaei* are poorly defined. Taylor (1957) lists them simply as below low water mark and the only detailed description is by Edelstein *et al.*, (1969) with a lower depth limit of 29 m for *A. pylaisaei*, and 16 m for *A. americanum* on the Atlantic coast of Nova Scotia. There are better data for *A. boreale;* Lamb and Zimmermann (1964) record it as present to depths of 15 m in Massachusetts and it reaches a maximum depth of 50 m in Greenland (Lund, 1959b) and in the Faeroes (Børgesen, 1902). Svendsen (1959) records it from 40 m in Spitzbergen, the same depth to which it occurs on its southern limit in the Baltic Sea (Rosenvinge, 1923-1924).

Reproductive Periodicity

There are little data on the seasonal behaviour of these algae. On the Atlantic coast of North America both *A. americanum* and *A. pylaisaei* are abundant in spring (Farlow, 1881; Taylor, 1957), but there is no information on whether they are annual or perennial. *A. americanum* may be annual in New Hampshire (Hehre and Mathieson, 1970); both are reported as fertile in spring. In Northern Norway *A. pylaisaei* bears tetrasporangia in June and July (Foslie, 1890).

A. boreale is considered a perennial in Greenland (Lund, 1959a) and in Spitzbergen (Kjellman, 1883), but in Norway it has been reported as an annual, first found in the spring and disappearing in the late summer (Printz, 1926; Sundene, 1953). *A. boreale* is reported from the Atlantic coast of North America as fruiting in the summer (Taylor, 1957) and in Greenland tetraspores occur, between June and October

(Rosenvinge, 1899; Jønsson, 1904; Lund, 1959a), but it is sterile in winter in Spitzbergen (Kjellman, 1883). In the Faeroes (Børgesen, 1902) and Norway (Printz, 1926) tetraspores first occur in May, while in Denmark they have been reported in April (Rosenvinge, 1923-1924). Edelstein and McLachlan (1968) report the occurrence of monospores on specimens from Nova Scotia.

Previous Culture Studies

No culture studies have been reported on *A. americanum*, or on *A. pylaisaei*. Sundene (1962) has cultured four strains of *A. boreale* from Norway, Sweden and Spitzbergen, of which three showed a direct life history with tetraspores germinating to produce tetraspore-bearing plants. The other strain (var. *droebachense* Sundene) produced only abortive sporangia both in culture and in the field. A single culture of the Spitzbergen strain (var. *corallina*) produced spermatangia on tetraspore-bearing plants, and these were also found in nature. Three of the strains showed only minor morphological differences in culture but var. *corallina* was distinct, with shorter broader cells and with the branchlets borne predominantly in whorls of three.

West and Norris (1966) have cultured the closely related *Scagelia occidentale* (as *Antithamnion occidentale*), and found tetraspore-bearing plants with functional spermatangia. The tetraspores from these plants produced offspring which bore only spermatangia. They also found a functional female gametophyte bearing abortive tetrasporangia.

Previous Cytological Studies

There have been no chromosome studies on *A. boreale*, *A. americanum* or on *A. pylaisaei*. The only work in this genus is on *A. plumula* (Magne, 1964, n = 23, 2n = 46) and on *A. spirographidis* (Rao, 1960, n = 32-34).

Aims of the Study of *Scagelia pylaisaei*

1. To examine the type material and to establish the original authors concept of the species occurring on the N.E. coast of North America included in the proposed combination.
2. To examine material from as wide a geographic and ecological range as possible with particular reference to the characters which have been used for taxonomic delimitation; to establish if any distinct groups of plants occur within this material.
3. To establish the number of genetically distinct forms occurring in nature by culturing material under constant, defined environmental conditions; with particular emphasis on specimens showing similarity with type material and descriptions.
4. To assess the seasonal variation in morphology and the reproductive periodicity in nature of the distinct forms established in culture.
5. To provide an accurate detailed description of all stages of the growth and development of the algae.
6. To grow these forms in culture under a variety of defined conditions to establish the factors controlling morphology and reproductive periodicity.

7. To establish the life history in culture from various sources of material and by varying the culture conditions to establish the effects of these on reproduction.
8. To undertake cytological studies to establish the chromosome number of the field material and to confirm the life history of the species as determined in culture.

Observations and Results

Morphological Variation in Herbarium Material

It became apparent after a cursory examination of the collected material and the herbarium specimens (Appendix III) that the criteria used by previous workers to separate the taxa, now combined as *S. pylaisaei*, were unworkable. Characters involving cell dimensions showed large variations, branchlets were found in whorls of two, three and four, and gland cells were an abundant and prominent feature of some specimens, but either rare or absent in others.

All the available material was therefore examined to assess the distribution of these characters. The examination was restricted to herbarium material, which is usually a single specimen from any one locality at any one time.

The characters chosen for study were:

i. The dimensions of the largest axial cell on the slide made from the herbarium material.
ii. The dimensions of the longest cell and the basal cell of the largest whorl branchlet occurring on the largest axial cell.
iii. The number of whorl branchlets; two, three or four, borne on

each axial cell was recorded and these are expressed as a percentage of the total number of axial cells examined.

iv. A quantitative measure of gland cells was made by counting the number present on one hundred whorl branchlet and pinnule cells from the region of the plant where the cell dimensions were obtained. Gland cells are thus expressed as a percentage of the whorl branchlet and pinnule cells.

The data were obtained from the examination of 245 specimens from 126 localities. The localities are shown in Figure 4 , and the data are given in Appendix III.

The dimensions of the axial cells (Figure 5a) show a range from two to twenty times as long as broad with the majority in the five to ten times range. The sizes of the whorl branchlet cells, both longest (Figure 5c) and basal (Figure 5b), show a similar spread, the former from one to twenty, the latter from one to ten times as long as broad. The majority of the longest cells are from two to ten times, the basal one to four times as long as broad. There is no evidence in these measurements of any segregation into separate groups of specimens; instead there is a complete spread of data.

There is a variety of whorl branchlet patterns, which are not completely random. Whorls of two and four branchlets were never observed on the same plant, though all proportions of whorls of two and three branchlets and various proportions of three and four branchlets were found. These data are summarized in Figure 5e ; for convenience they have been grouped in ten percent intervals. The spread of data is from plants which bear all their whorl branchlets in pairs (2:100%) to

FIGURE 4

COLLECTION SITES OF EXAMINED SPECIMENS OF
SCAGELIA PYLAISAEI

Localities from which specimens of *S. pylaisaei* examined in this study were obtained. The localities indicated by the station numbers are given in Appendix II and the specimen data in Appendix III.

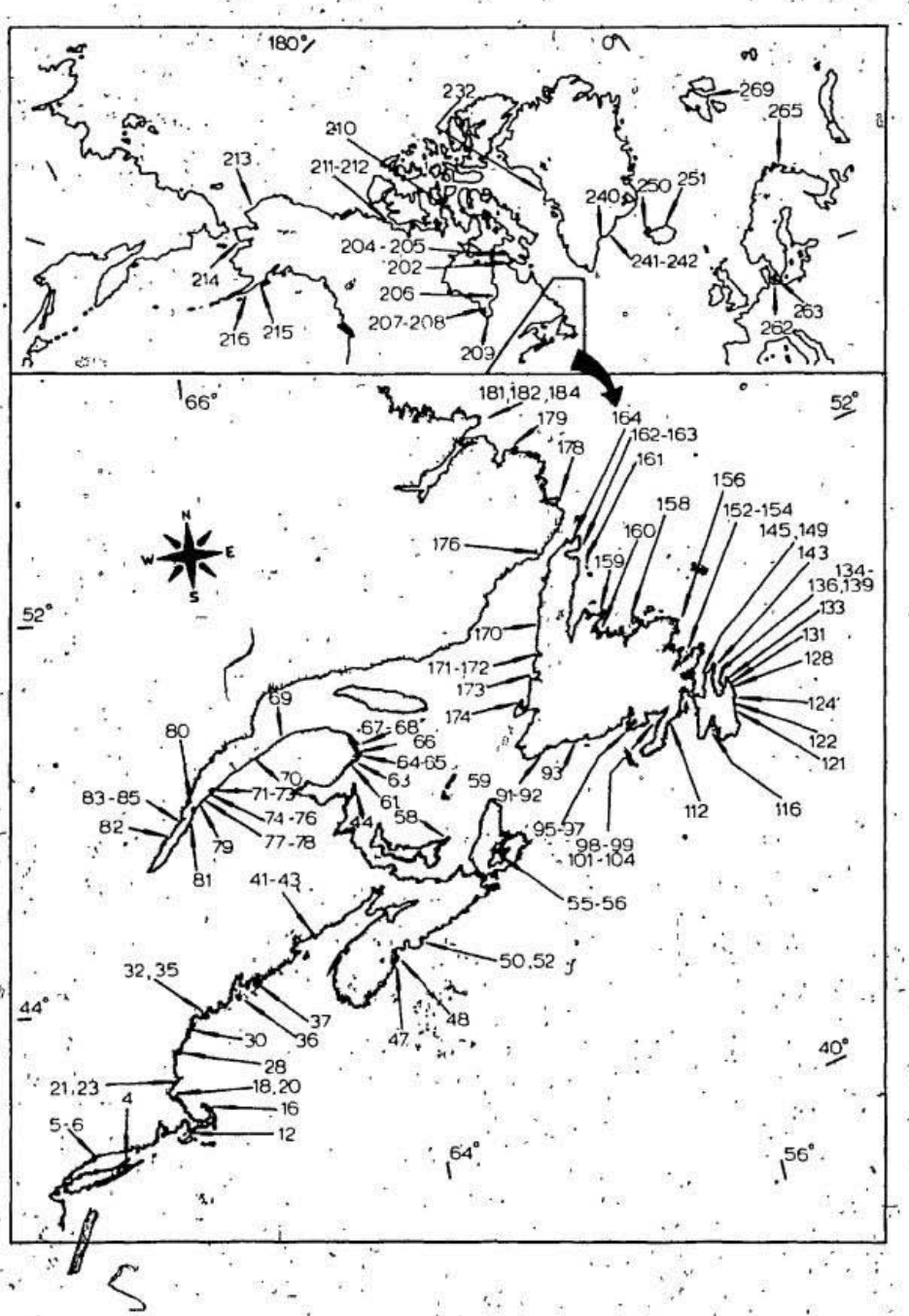

180°
232
269
265
210
213
211-212
240
250
251
241-242
204-205
202
214
206
207-208
216
215
209
263
262
66°
52°
181,182,184
179
164
178
162-163
161
156
158
152-154
160
145,149
176
159
143
134-
136,139
133
52°
170
131
171-172
128
173
69
124
174
67-68
80
66
64-65
122
70
63
59
93
121
83-85
71-73
61
91-92
112
116
82
74-76
44
58
95-97
79
77-78
98-99
101-104
81
41-43
55-56
50,52
32,35
44°
37
48
30
36
47
40°
28
21,23
4
18,20
16
5-6
12
64°
56°

FIGURE 5

VARIATION IN HERBARIUM MATERIAL OF *SCAGELIA PYLAISAEI*

Summary of the data presented in Appendix III for the herbarium material examined of the three species, *Antithamnion boreale*, *A. pylaisaei* and *A. americanum* together with their varieties and forms, combined as *S. pylaisaei* in this work.

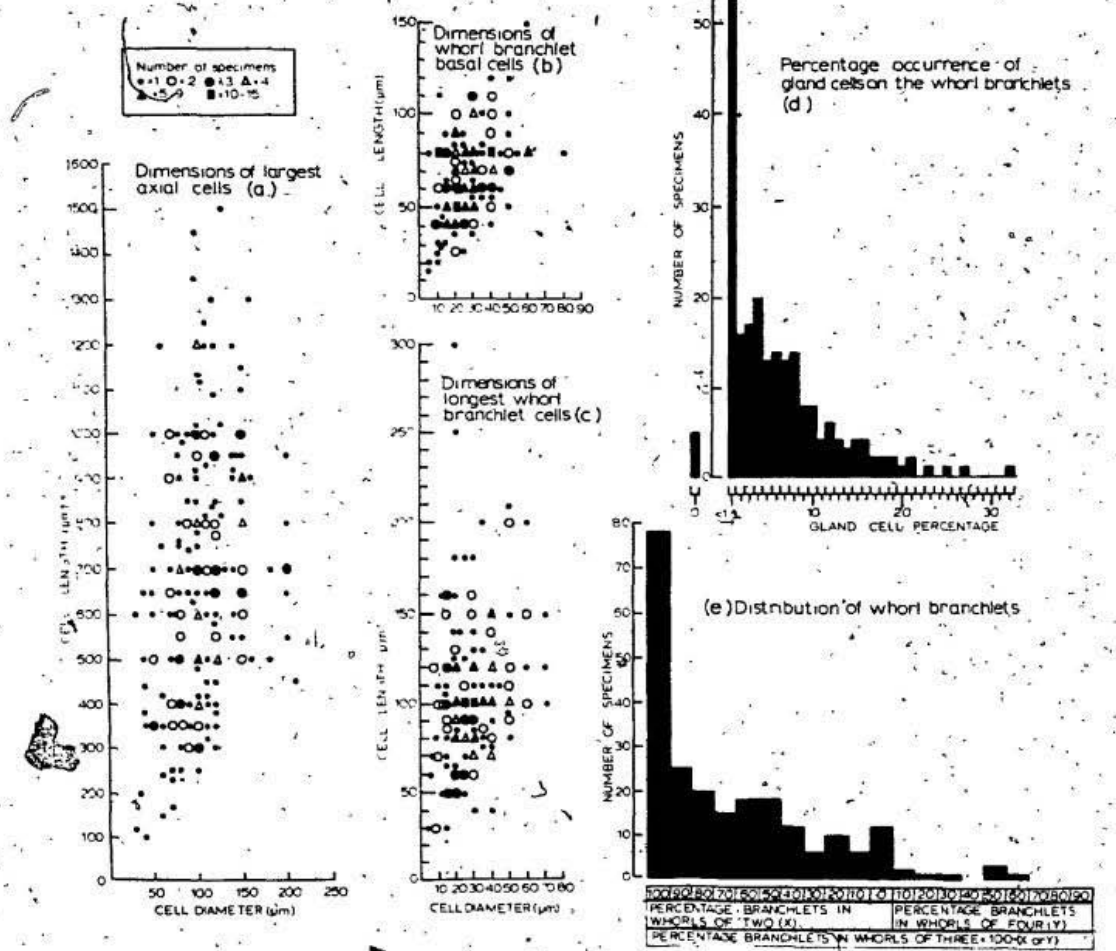
(a) Dimensions of the largest axial cells: Scatter diagram of length to diameter of the largest axial cells of the specimens examined.

(b) Dimensions of the whorl branchlet basal cells: Scatter diagram of the length to diameter of the basal cells of the largest whorl branchlet borne of the largest axial cell (a) above.

(c) Dimensions of longest whorl branchlet cells: as for (b) above, but for the longest cell in the whorl branchlet.

(d) Percentage occurrence of gland cells on the whorl branchlets: Frequency of occurrence of gland cells expressed as the percentage of gland cells to whorl branchlet and pinnule cells. Data from the region of the plant at which measurements for (a), (b) and (c) above were obtained as described on page 48.

(e) Distribution of whorl branchlets: number of axial cells bearing 2, 3 or 4 whorl branchlets expressed as a percentage of the total number of cells examined. Data grouped by reducing to nearest 10 per cent interval and plotting this against its frequency of occurrence in the specimens examined.


Number of specimens
•=1 O=2 ●=3 Δ=4
▲=5-9 ■=10-15
Dimensions of largest axial cells (a)
CELL LENGTH (µm)
CELL DIAMETER (µm)
Dimensions of whorl branchlet basal cells (b)
CELL LENGTH (µm)
Dimensions of longest whorl branchlet cells (c)
CELL LENGTH µm
CELL DIAMETER (µm)
Percentage occurrence of gland cells on the whorl branchlets (d)
NUMBER OF SPECIMENS
GLAND CELL PERCENTAGE
(e) Distribution of whorl branchlets
NUMBER OF SPECIMENS
PERCENTAGE BRANCHLETS IN WHORLS OF TWO (X)
PERCENTAGE BRANCHLETS IN WHORLS OF FOUR (Y)
PERCENTAGE BRANCHLETS IN WHORLS OF THREE = 100-(X or Y)

a single plant in which 60% of the branchlets were in whorls of four and the remainder in whorls of three (4:60%, 3:40%). There is an almost complete spread between these extremes with the largest number of plants bearing two whorl branchlets (2:100%).

The gland cell data (Figure 5d) show a similar spread: no gland cells could be detected in five of the specimens examined (St. 73.1, AW 412; St. 101.2, AW 856; St. 124.3, AW 814; St. 135.2, AW 813; St. 171.5, AW 854), and in large numbers of plants gland cells occurred with a frequency of less than one percent. At the other extreme, in a single specimen (St. 98.2, AW 809) 32% of the whorl branchlet and pinnule cells bore gland cells. Of special interest are the two specimens originating from the Baltic Sea (St. 262, AW 314; St. 263, AW 304) the former labelled *A. boreale* f. *baltica;* both possess gland cells.

Preliminary Observations on Morphological Variation in Culture

The examination of field and herbarium material revealed a complete spread of data, and extreme forms showed very different morphologies which would previously have been described under separate specific names. It is impossible to tell from material collected in the field whether these morphological differences have a genetic basis, or are merely environmentally induced. Vegetative fragments of plants were therefore grown in culture under defined conditions.

Initial culture experiments with plant apices showed that the algae underwent considerable morphological change particularly in branching pattern and cell size, the characters used for specific

delimitation.

Figure 6a shows an extreme example of this change in culture (ER 10:16-8:150), in a specimen (St.124.14) which, prior to culture, had pinnate branchlets borne in whorls of three with the cells of these branchlets two to three times as long as broad. A transition zone can be seen separating the two distinctive morphologies of field and culture. The morphology produced in culture is different from that initially exhibited in that the whorl branchlets are borne in groups of two and three and show irregular arrangement of the pinnules, the cells of the whorl branchlets and the pinnules are also considerably narrower.

A number of algae selected initially for their wide and distinctive morphological ranges were cultured in this manner and the cell size and branching pattern analysed before and after culture. The characters chosen for analysis were:

i. The number of whorl branchlets on each axial cell.

ii. The dimensions of the thirtieth axial cell from the apex of the plant.

iii. The form of the largest whorl branchlet borne on this cell.

iv. The dimensions of the longest cell of this whorl branchlet.

The material used consisted of the first twenty to forty cells of an apex of the plant, which was cultured (ER or ES 10:16-8:500) for a period of between thirty and forty days. In addition the largest axial cell of the parent plant and the longest cell of the largest whorl branchlet borne on this, were also measured for comparison with the herbarium material. The whorl branchlet morphologies are assigned to one of five descriptive categories: simple, secund, irregular,

FIGURE 6

SCAGELIA PYLAISAEI

(a) Apical fragment of Form A (St. 124.14, Bay Bulls, February 1971) after culture (ER 10:16-8:500) showing transition (TZ transition zone) from field morphology to culture morphology.

(b) Form A (St. 124.24, Bay Bulls, October 1971) branchlets in whorls of two and three, pinnules secund or irregular, cells have high length to diameter ratios.

(c) Form A (St. 124.21, Bay Bulls, July 1971), branchlets in whorls of two and three, pinnules irregular or pinnate.

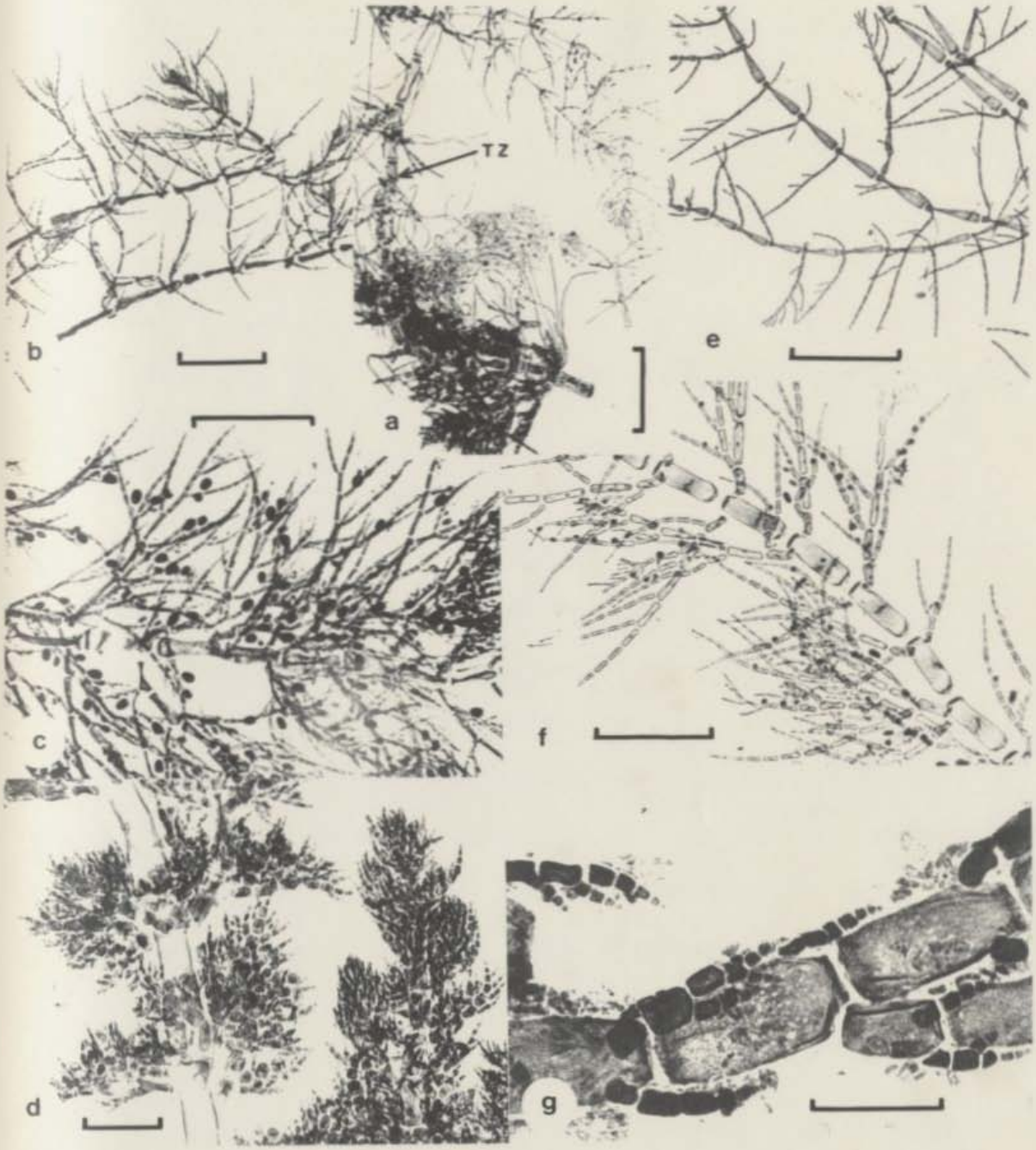
(d) Form A (St. 124.16, Bay Bulls, March 1971), branchlets in whorls of three and four, pinnules pinnate and bipinnate, cells have low length to diameter ratios.

(e) Form B (St. 104.17, St. Bernard, October 1971) branchlets in whorls of two, pinnules adaxially secund, cells have high length to diameter ratios.

(f) Form B (St. 104.14, St. Bernard, July 1971), branchlets in whorls of two, pinnules secund or irregular.

(g) Form B (St. 104.21, St. Bernard, March 1972), branchlets in whorls of two, pinnules irregular or pinnate. Cells have low length to diameter ratios.

All scales throughout = 250 µm


TZ
a
b
c
d
e
f
g

pinnate and bipinnate. Simple branchlets have no pinnules, secund bear them only on one side, irregular on both sides but not arranged opposite and paired on each cell as in the pinnate form. Bipinnate is an extreme form where the pinnules bear secondary pinnules in a pinnate manner.

Apical fragments from thirty-one specimens were cultured; the station numbers of the localities where these obtained together with pre- and post- culture data are given in Appendix IV. The distribution of the whorl branchlets is shown in Figure 7a-c in the same manner as the herbarium material. Figure 7c shows the distribution before and after culture.

Prior to culture there is an almost complete spread of numbers of whorl branchlets from paired to a specimen with 40% of its branchlets in whorls of four. After culture a complete segregation occurs into two populations one with all the whorl branchlets in groups of two, the other with the whorl branchlets in twos and threes ranging from 2:50%; 3:50% to 2:10%; 3:90%. The former group when superimposed on the original field data shows that this tendency to a reduced number of whorl branchlets is also apparent in the field material, but is obscured by the natural variation. The specimens which, after culture, have their whorl branchlets in groups of two and three will be referred to as "Form A", those with their branchlets in whorls of two as "Form B".

The cell measurements are also plotted (Figure 7d-g). Open points denote specimens having Form A and solid points Form B.

Figure 7d shows the data for the largest axial cell prior to the excision of the apical region for culture. There is a general

FIGURE 7

MORPHOLOGICAL CHANGES IN CULTURED APICAL FRAGMENTS

OF *SCAGELIA PYLAISAEI*

Summary of the data presented in Appendix IV of morphological changes in culture (ER or ES 10:16-8:500 for 30 to 40 days) of excised vegetative apices of *Scagelia pylaisaei*.

(a) Whorl branchlet distribution prior to culture: Frequency of occurrence in whorls of 2, 3 or 4 for each plant expressed as a percentage of the total number of axial cells examined. Data grouped by reducing to nearest 10 percent interval.

(b) Whorl branchlet distribution after culture: Data presented in same manner as for (a).

(c) Whorl branchlet distribution prior to culture; with *S. pylaisaei* Form B superimposed: *S. pylaisaei* Form B in culture only bears branchlets in whorls of two. The plants of this form after culture are identified on the original material as the shaded area.

(d) Dimensions of largest axial cell prior to culture: Scatter diagram of length to diameter of largest axial cell on plants prior to excision of the apical region for culture.

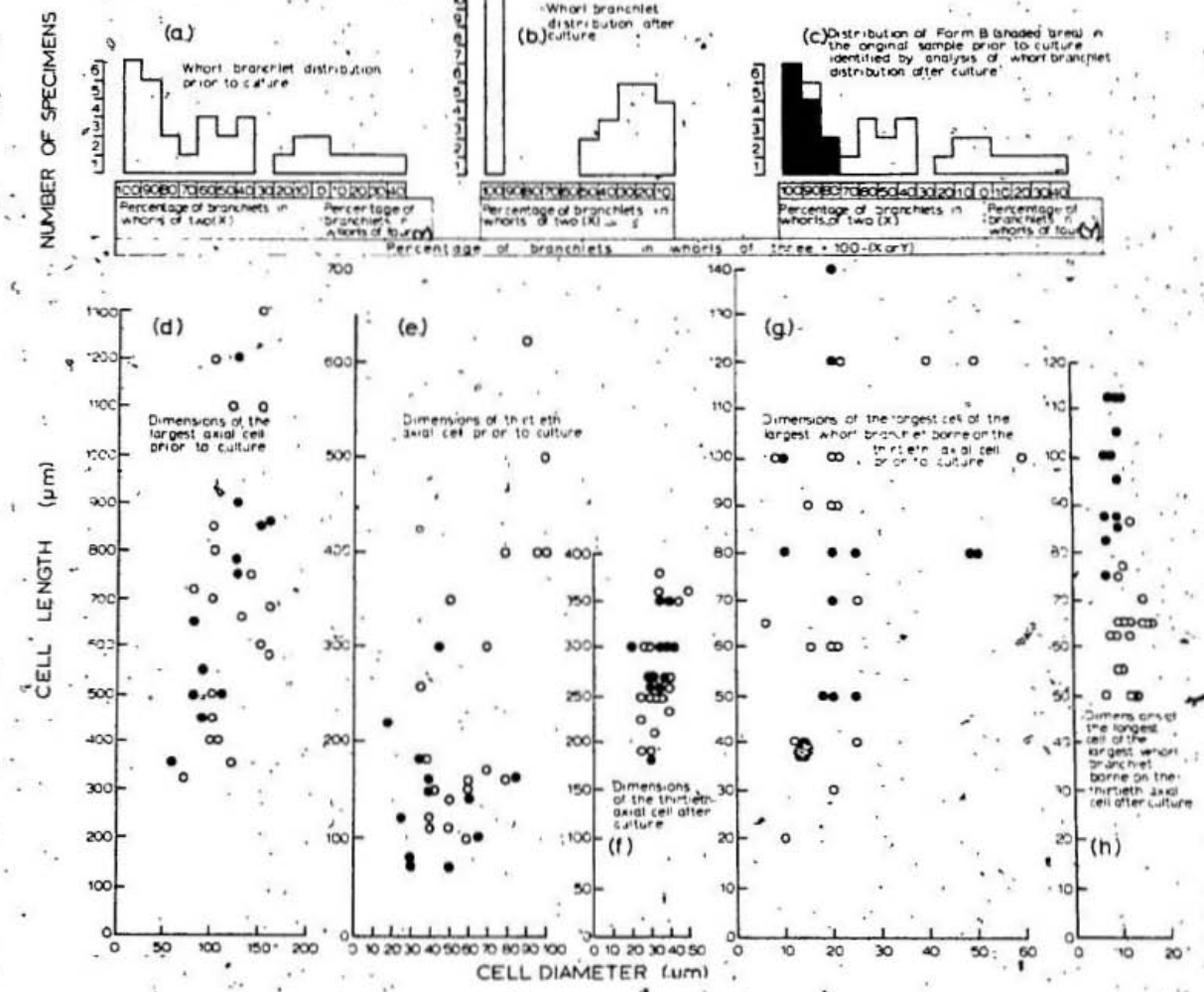
(e) Dimensions of thirtieth axial cell prior to culture: as for (d) above but for 30th axial cell.

(f) Dimensions of thirtieth axial cell after culture: as for (e) above but after culture.

(g) Dimensions of longest cell of largest whorl branchlet borne on the thirtieth axial cell prior to culture: Scatter diagram of cell length to cell diameter in plants prior to culture.

(h) Dimensions of longest cell of largest whorl branchlet borne on the thirtieth axial cell after culture: as for (g) above but after culture.

For scatter diagrams (d) to (h) open points are for *S. pylaisaei* Form A and solid points for *S. pylaisaei* Form B identified by their whorl branchlet distribution as in (c) above.


NUMBER OF SPECIMENS
(a)
Whorl branchlet distribution prior to culture
(b) Whorl branchlet distribution after culture
(c) Distribution of Form B (shaded area) in the original sample prior to culture identified by analysis of whorl branchlet distribution after culture
Percentage of branchlets in whorls of two (X)
Percentage of branchlets in whorls of four (Y)
Percentage of branchlets in whorls of three = 100-(X or Y)
CELL LENGTH (µm)
(d)
Dimensions of the largest axial cell prior to culture
(e)
Dimensions of thirteenth axial cell prior to culture
(f)
Dimensions of the thirteenth axial cell after culture
(g)
Dimensions of the largest cell of the largest whorl branchlet borne on the thirteenth axial cell prior to culture
(h)
Dimensions of the largest cell of the largest whorl branchlet borne on the thirteenth axial cell after culture
CELL DIAMETER (µm)

spread of the data corresponding in range and magnitude with the spread of the herbarium data (Figure 5a), with no segregation of Forms A and B. Figure 7e, g shows the same data, but for the thirtieth axial cell and the corresponding whorl branchlet cell. While both the dimensions and the range are considerably reduced in comparison with the data on the largest cell, there is still not any segregation of the two forms. After culture (Figure 7f, h) both the range of the dimensions of the thirtieth axial cell and associated whorl branchlet cells are considerably reduced. There is, however, still no segregation of forms on the basis of axial cell dimensions, but the whorl branchlet cell gives a complete separation. Form A has shorter and broader (Length : Diameter 4-7.1:1) cells than Form B (Length : Diameter 8.7-12.75:1).

The whorl branchlet morphologies (Appendix IV) also show some separation of the forms after culture. In Form A, they are secund to irregular but in Form B simple to barely secund.

Seasonal Variation in Vegetative Morphology of Form A and Form B

In view of the wide morphological range shown by the herbarium material it was decided to study populations of both Form A and Form B to detect any seasonal changes which might occur. Samples were therefore taken at the two major study sites Bay Bulls (St. 124) for Form A and St. Bernard (St. 104) for Form B. Both forms occurred abundantly throughout the sampling period, and with exception of a single collection appeared healthy, but at St Bernard in August (St. 104.15) the

majority of plants were partially bleached and several were obviously dead.

Form A was collected from a vertical rock face at depths between two and five metres, and Form B from similar depths on stable boulders. The specimens from these limited areas showed considerable uniformity within each collection, and the detailed examination of ten specimens was found sufficient to adequately reflect the morphological variation.

The mature portion of the axis of each specimen was examined and the proportion of the number of whorl branchlets on each axial cell determined in the same manner as the herbarium material. The largest branchlet in the whorl on every other axial cell between cells thirty and forty were examined and each cell on the branchlet coded on the number of pinnules that it bore (0, 1 or 2). The data from all the plants in a sample were combined, and the number of cells bearing either 0, 1 or 2 pinnules expressed as a percentage of the total number of cells examined. The length and diameter of the basal cell and the longest cell of each branchlet were measured, and the mean dimensions of the cells, fifty in each sample, calculated. The percentage of the whorl branchlet and pinnule cells which bore gland cells was calculated in the same manner as for the herbarium material.

Form A.

Figure 8a shows the percentage of axial cells bearing one, two, three and four whorl branchlets. Throughout the greater part of the year these are found in whorls of three. In the earlier months of

FIGURE 8

SEASONAL VARIATION IN MORPHOLOGY OF *SCAGELIA PYLAISAEI* FORM A

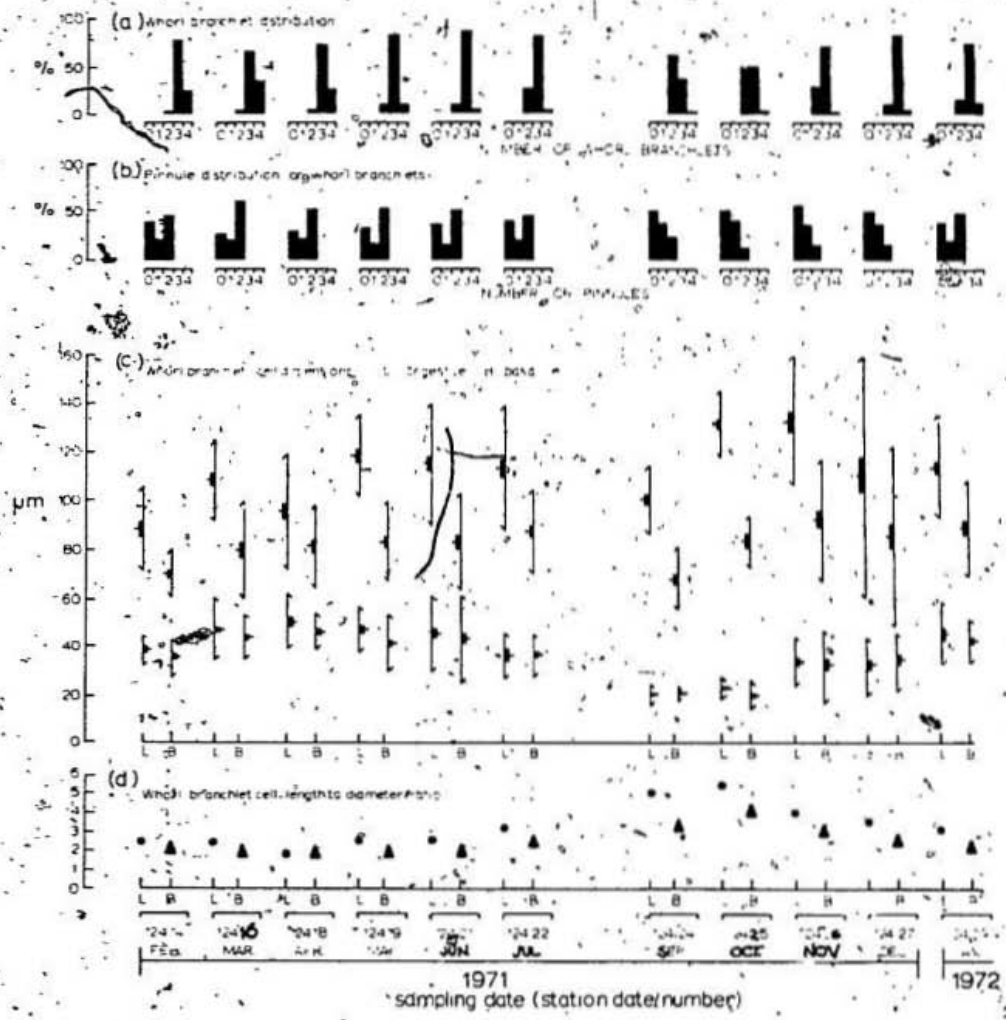
(a) Whorl branchlet distribution: Percentage of axial cells in the mature regions of the plants bearing whorl branchlets in whorls of 2, 3 or 4.

(b) Pinnule distribution on whorl branchlets: Percentage of whorl branchlet cells from the mature regions of the plants bearing 0, 1 or 2 pinnules.

(c) Whorl branchlet cell dimensions: Length and diameter of the longest (L) and basal (B) whorl branchlet cells in mature regions of the plants. Data are obtained in each instance from 5 cells on each of 10 plants, and are presented as a mean ± standard error (solid bar) and ± standard deviation (vertical line). For each pair of measurements presented on the same vertical line the larger is the cell length, the smaller the cell diameter.

(d) Whorl branchlet cell:length to diameter ratio: Ratio of mean length to mean diameter of longest (L) and basal (B) whorl branchlet cells, from data presented in (c) above.

All data are from a mean of 10 plants in each sample obtained from Bay Bulls (St. 124) between February 1971 and January 1972.


(a)
%
100
50
0
0 1 2 3 4
(b)
%
100
50
0
0 1 2 3 4
(c)
µm
160
140
120
100
80
60
40
20
0
L B
(d)
6
5
4
3
2
1
0
L B
24 10
MAR
24 19
JUN
24 22
JUL
24 27
NOV
1971
1972
sampling date (station date/number)

the year there are significant numbers of four branchlets; but this number is reduced in summer, and in fall the proportion of the branchlets in whorls of two reaches a maximum. Towards the end of the year there is a reduction in the number of whorls of two branchlets and an increase in the number of axial cells with whorls of three and four branchlets.

The arrangement of the pinnules on the whorl branchlets (Figure 8b) also shows a marked seasonal change. In the early part of the year the majority of whorl branchlet cells bear two opposed pinnules, giving the branchlet a pinnate appearance. The remaining whorl branchlet cells either completely lack or rarely bear a single pinnule. After July the majority of whorl branchlet cells either lack pinnules or bear them singly; the branchlets thus have a secund or irregular appearance.

The whorl branchlet cell dimensions are given in Figure 8c ,d. In the early months of the year the length of the longest cells in the branchlets show no apparent change, but a small decrease in September is followed by a significant increase in October and November. The cells produced in December are shorter, but there is considerable variation in the sample.

The diameter of the longest cells also shows seasonal variation. A slight increase occurs between February and June, followed by a marked decrease after July and this diameter is then maintained until October, when an increase again occurs.

These changes have a profound effect on the ratio of cell length to diameter. The cells are twice as long as broad in the period between

February and April and the ratio increases to reach a maximum in October of five and a half times as long as broad. The basal cells of the branchlets show the same trends as the longest cells and while they are shorter, their diameter does not differ significantly from that of the longest cells. The length to diameter ratio is thus smaller.

Gland cells were present and common in all specimens examined at all times of the year (Table 2). In most months there is considerably greater variation in gland cell number between specimens in the same collection than between separate collections, and no significant seasonal trends are evident.

Form B.

The variation in whorl branchlet arrangement on the axial cells is shown in Figure 9a , as for Form A. All the specimens examined showed a preponderance of two whorl branchlets on each axial cell with one to three branchlets occurring only rarely during certain months. Single branchlets were absent between Mar[illegible] and July. Three branchlet whorls were not detected in October, November, and December and whorls of four branchlets were never observed.

The arrangement of pinnules on the whorl branchlets (Figure 9b) differs from that displayed by Form A. There is considerable seasonal variation, but never a preponderance of cells bearing two pinnules. A number of branchlets can, however, be found in the early months of the year (February to April) with pinnately arranged pinnules. In the summer months (June, July) there is a decrease in the incidence of

TABLE 2

SEASONAL CHANGE IN OCCURRENCE OF GLAND CELLS ON

S. PYLAISAEI

Seasonal change in the frequency of gland cells of *S. pylaisaei* Form A at Bay Bulls (St. 124) between February 1971 and January 1972, and on *S. pylaisaei* Form B at St. Bernard (St. 124) between November 1970 and January 1972. Data is expressed as the percentage of gland cells to whorl branchlet and pinnule cells in the mature regions of 10 individual plants in each sample.

Collection Date	Station/Date Number	Individual Plant Number 1	2	3	4	5	6	7	8	9	10
S. pylaisaei Form A, Bay Bulls St. 124											
Feb. 1971	124.14	10	10	10	9	9	8	8	7	7	7
March 1971	.16	14	12	12	8	5	5	5	4	3	2
April 1971	.18	13	11	10	9	8	7	7	6	5	3
May 1971	.19	13	12	11	9	8	7	7	5	4	2
June 1971	.21	15	15	14	14	13	12	12	10	8	4
July 1971	.22	16	12	11	10	8	8	8	5	5	4
Sept. 1971	.24	16	14	9	9	7	5	4	4	4	2
Oct. 1971	.25	12	12	11	8	8	7	5	4	3	3
Nov. 1971	.26	14	12	10	9	9	9	6	5	4	3
Dec. 1971	.27	15	14	12	12	12	10	8	8	8	6
Jan. 1972	.29	18	17	16	15	15	14	13	13	12	10
S. pylaisaei Form B, St. Bernard St. 104											
Nov. 1970	104.7	5	3	2	2	2	1	1	0	0	0
Feb. 1971	.10	7	7	6	6	5	3	1	1	1	1
March 1971	.11	12	8	7	5	4	4	4	4	2	2
April 1971	.12	10	8	6	6	4	4	4	3	3	3
June 1971	.13	7	6	5	5	4	4	3	2	1	1
July 1971	.14	7	4	3	2	2	1	1	1	1	0
Sept. 1971	.16	4	2	2	1	1	1	0	0	0	0
Oct. 1971	.17	3	1	1	1	1	0	0	0	0	0
Dec. 1971	.18	6	5	4	3	3	2	2	1	1	0
Jan. 1972	.19	8	7	6	5	4	2	1	1	1	1

FIGURE 9

SEASONAL VARIATION IN MORPHOLOGY OF

SCAGELIA PYLAISAEI

FORM B

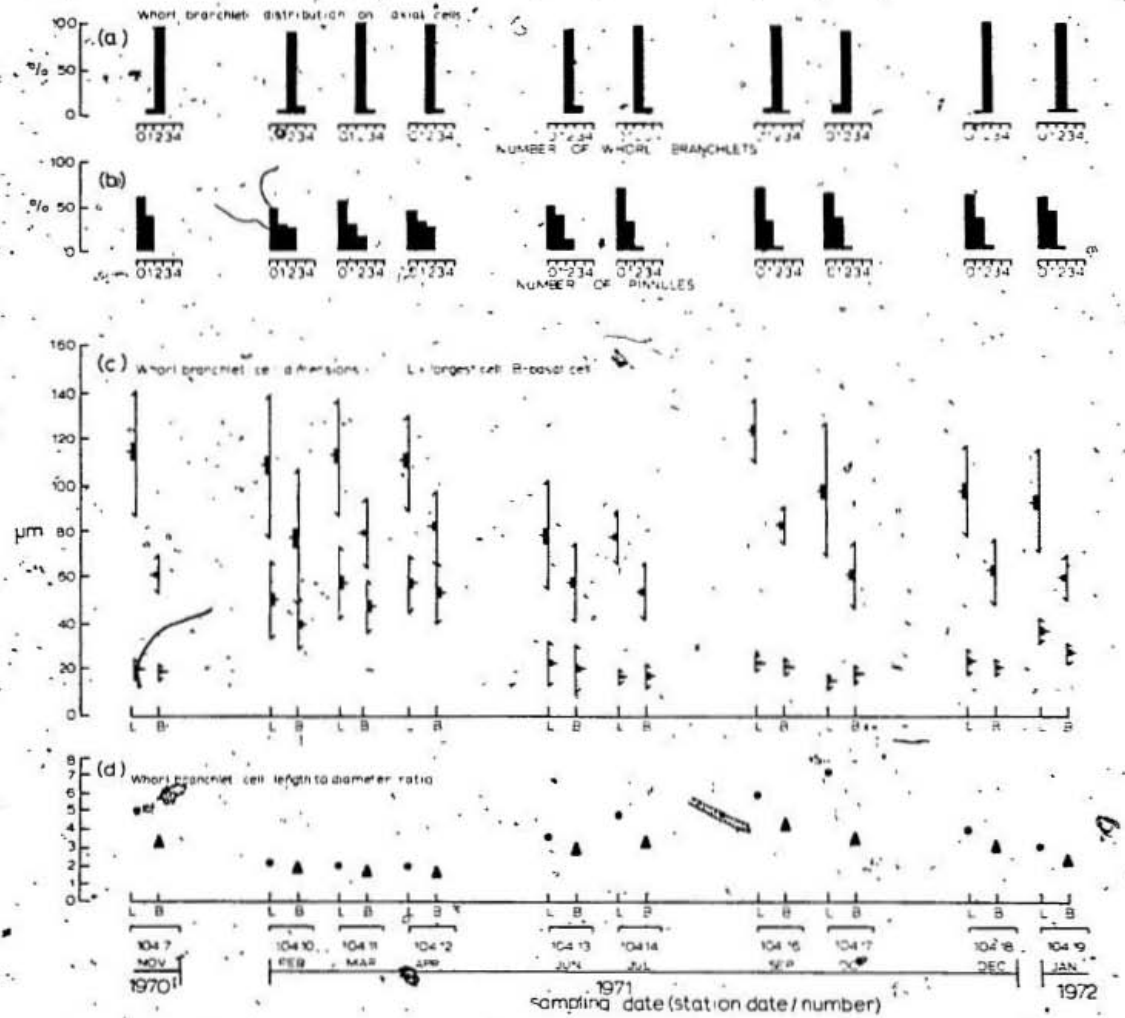
(a) Whorl branchlet distribution: Percentage of axial cells in the mature regions of the plants bearing whorl branchlets in whorls of 2, 3 or 4.

(b) Pinnule distribution on whorl branchlets: Percentage of whorl branchlet cells from the mature regions of the plants bearing 0, 1 or 2 pinnules.

(c) Whorl branchlet cell dimensions: Length and diameter of the longest (L) and basal (B) whorl branchlet cells in mature regions of the plants. Data are obtained in each instance from 5 cells on each of 10 plants, and are presented as a mean ± standard error (solid bar) and ± standard deviation (vertical line). For each pair of measurements presented on the same vertical line the larger is the cell length, the smaller the cell diameter.

(d) Whorl branchlet cell:length to diameter ratio: Ratio of mean length to mean diameter of longest (L) and basal (B) whorl branchlet cells, from data presented in (c) above.

All data are from a mean of 10 plants in each sample obtained from St. Bernard (St. 104) between November 1970 and January 1972.


(a)
%
100
50
0
01234
NUMBER OF WHORL BRANCHLETS
(b)
NUMBER OF PINNULES
(c)
μm
160
140
120
100
80
60
40
20
0
L B
(d)
8
7
6
5
4
3
2
1
0
104 7
NOV
1970
104 10
FEB
104 11
MAR
104 12
APR
104 13
JUN
104 14
JUL
104 15
SEP
104 17
DEC
104 18
104 19
JAN
1972
1971
sampling date (station date / number)

pinnate branching and a corresponding increase in the number of whorl branchlet cells bearing only one or no pinnules. This trend is continued in the fall to the virtual exclusion of all the oppositely arranged pinnules and the form of the branching is at this time predominantly secund or irregular.

The seasonal variations in the dimensions of the branchlet cells (Figure 9c,d) show obvious similarities with those of Form A (Figure 8c,d). In the early months of the year the cell lengths show no significant changes, but an abrupt decrease occurs in June and July. An increase occurs by September and this trend continues until November. Maximum cell diameters occur in March and April with a considerable decrease in June and July, but unlike their lengths the cell diameters do not increase again in the fall. An identical pattern of variation is shown by the basal cells though these are always shorter than the longest cell.

The seasonal variation in the ratio of length to diameter is more marked than in Form A, the longest cells are approximately twice as long as broad in February, March and in April and this ratio increases to reach a maximum of seven and a half in October. In both Forms A and B, it is the seasonal variation in diameter of the cells, rather than in length which significantly affects the ratio of the dimensions.

Unlike Form A, Form B shows considerable seasonal changes in the number of gland cells present on the plants (Table 2). There is, however, considerable variation in the samples, but gland cells are generally fewer than in Form A. Gland cells are most abundant in the

early months of the year with a small decrease in number occurring between February and July, but in September the percentage of gland cells decreases and this is maintained in October and November. Several plants were observed during this period which apparently lacked gland cells.

The seasonal morphological variation shown by Form A is illustrated in Figure 6b-d, and by Form B in Figure 6e-g.

Morphological Variation in Culture

In view of the marked seasonal changes in morphology observed in both Forms A and B, a number of cultures were initiated and incubated under a variety of controlled conditions in an attempt to elucidate some of the physical factors controlling the morphology of the algae. The factors chosen for study were light intensity, temperature and daylength.

Establishment of Cultures.

Four culture series were established, obtained from spores released in each instance from a single plant.

Culture series (i) Form A, tetraspores, from a plant obtained at Bay Bulls (St. 124.20).

Culture series (ii) Form B, tetraspores from a plant obtained at Grand le Pierre (St. 101.3). This plant was initially sterile and developed tetrasporangia in culture (ES 10:16-8:500).

Culture series (iii) Form A, carpospores, from a plant obtained at Bay Bulls (St. 124.22).

Culture series (iv) Form B, carpospores, from a plant obtained at St. Bernard (St. 104.18).

The plants were placed in culture (ES 10:16-8: 150), and spore discharge and germination occured within 24 hrs. Coverslips with adhering spores, but free from other algal contaminants were then transferred to new cultures and incubated under the desired conditions.

Spore Germination.

Carpospores and tetraspores, of both Form A and Form B germinated in an identical manner, but two patterns of germination were observed in all culture series. The commonest pattern was the bipolar *Ceramium*-type of germination (Chemin,1937), but an aberrant unipolar type also occurred.

Bipolar germination: At the time of transverse division the carpospores and tetraspores measured 30-35 µm in diameter. The two cells divided again, in the same plane, one to form an upright vegetative filament, the other to produce an attaching rhizoid (Figure 10a).

The polarity of germination was unaffected by the direction of the incident light, but as the vegetative filament increased in length, it became positively phototropic.

Unipolar germination: Prior to germination the discharged spores were 45-60 µm in diameter, and the initial division was into two unequal cells (Figure 10b). The smaller divided again to produce what at first appeared to be a normal, vegetative filament (Figure 10b) of two or three cells. The terminal cell of this filament, however, became elongated, with reduced pigmentation and developed into

FIGURE 10

SCAGELIA PYLAISAEI

(a) Normal bipolar type of spore germination producing a rhizoid (RZ) and a vegetative axial filament (AF). Scale = 100 µm

(b) Aberrant unipolar germination, no apical growth but a filament of cells terminating in a rhizoid (RZ) produced basally. Scale = 100 µm

(c) Cell proximal to the spore divides laterally to produce the vegetative axial filament while the rhizoid (RZ) develops in the normal manner. Scale = 100 µm

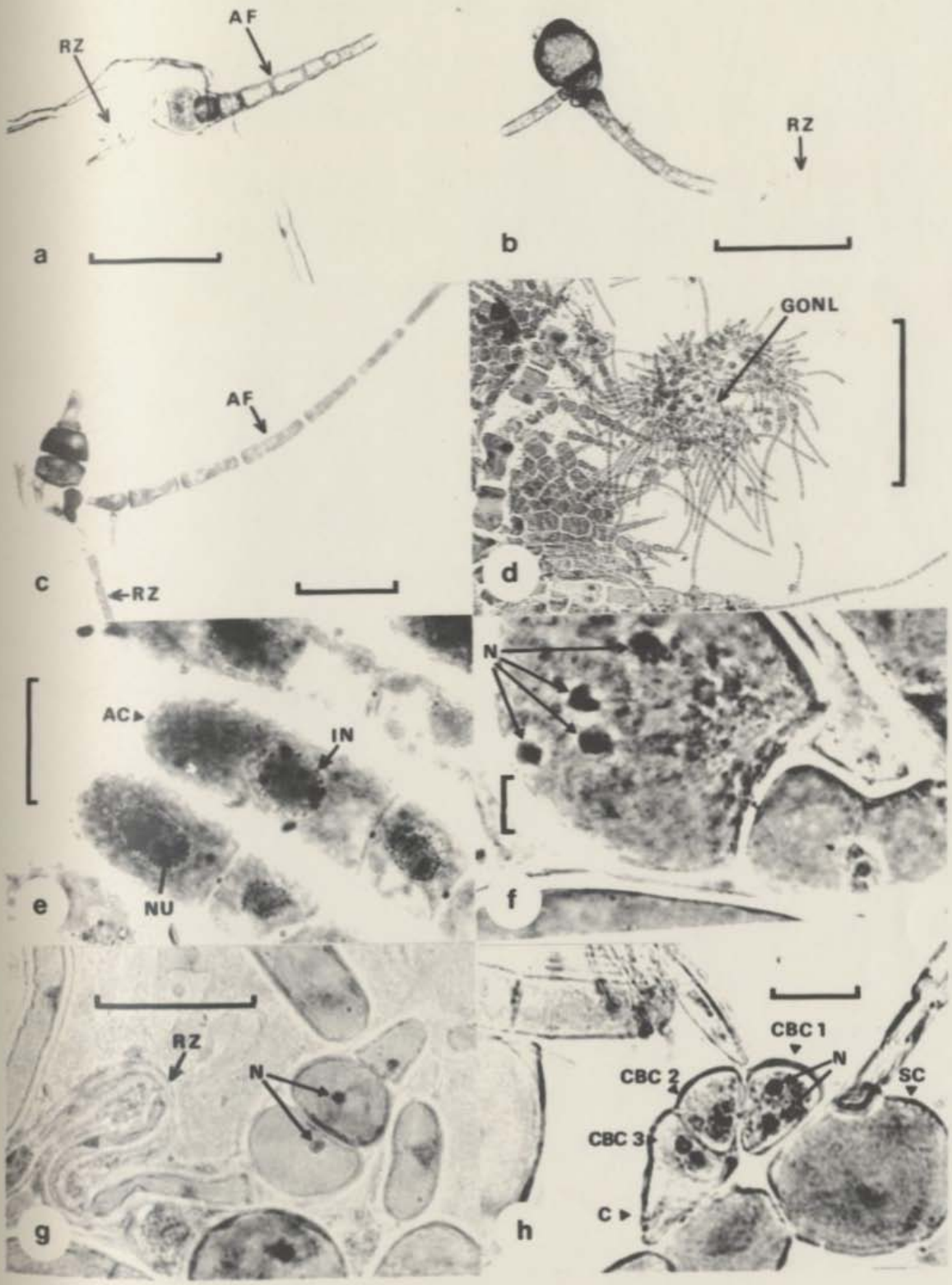
(d) Gonimolobe with carpospore germinating *in situ*, all vegetative axial filaments radiate outwards. Scale = 500 µm

(e) Interphase nucleus (IN) in an apical cell (AC) with prominent nucleolus (NU). Stained with acetocarmine. Scale = 10 µm

(f) Spore with four nuclei (N) showing aberrant unipolar germination pattern. Stained with acetocarmine. Scale = 50 µm

(g) Normal spore germination with uninucleate (N) cell producing apical growth and a rhizoid (RZ). Stained with acetocarmine. Scale = 50 µm

(h) Binucleate (N) condition of three carpogonial branch cells (CBC), the single carpogonium (C) nucleus is not visible. SC = supporting cell. Stained with acetocarmine. Scale = 10 µm


RZ
AF
a
b
RZ
AF
c
RZ
GONL
d
AC
IN
NU
e
N
f
RZ
N
g
CBC 1
N
CBC 2
SC
CBC 3
C
h

a rhizoid. The cell proximal to the spore then divided laterally, and the branch thus formed developed into a normal upright axis (Figure 10c).

In situ germination: A single gonimolobe of Form A, culture series (iii) did not release its carpospores and these were observed to have germinated *in situ*. The germination was bipolar, the rhizoidal pole directed toward the centre of the gonimolobe, the axial pole toward the periphery (Figure 10d).

Culture Conditions.

Culture series (i-iv) were incubated under the conditions given in Table 3 . ES medium was used throughout, and was changed at approximately weekly intervals.

Results were not obtained from all conditions investigated, either because of culture chamber failures, or because of insufficient material.

Examination of Cultures.

Cultures were examined for growth rate, morphology and gland cell production.

Growth rates: Growth rates in culture were measured by cell counts, either directly using a binocular dissecting microscope, or by the removal of a sample from each culture and observing this after mounting in lactophenol-cotton blue. The latter method was frequently used as it permitted more accurate counts. All the counts are of vegetative cells, including the initial spore cell, but excluding rhizoid cells, gland cells, and any cell of reproductive structures. Two counts were obtained from each plant: one of the number of cells

TABLE 3

CONDITIONS UNDER WHICH CULTURES OF FORM A AND FORM B OF *S. PYLAISAEI* HAVE BEEN GROWN.

i = CULTURES FROM TETRASPORES OF FORM A.
ii = CULTURES FROM TETRASPORES OF FORM B.
iii = CULTURES FROM CARPOSPORES OF FORM A.
iv = CULTURES FROM CARPOSPORES OF FORM B.

Culture series	Light intensity lx	Temperature, °C: Daylength (light-dark), hours						
		2:8-16	2:16-8	5:8-16	5:16-8	10:8-16	10:16-8	15:16-8
i	1200		+		+		+	+
	500	+		+	+	+	+	+
	150	+	+	+	+	+	+	+
ii	1200		+	+	+	+	+	
	500		+	+	+	+	+	
	150		+		+	+	+	
iii	1200				+		+	+
	500	+			+	+	+	+
	150	+			+	+	+	+
iv	1200		+	+	+		+	
	500		+	+	+		+	
	150		+		+		+	

in the main axis, the other of the total number of cells.

Total cell counts were obtained up to approximately one hundred cells, after which they became subject to excessive errors. It was not feasible to remove a sample of a fixed number of plants for each observation, hence data are presented as a mean together with standard deviation and standard error of the mean.

Detailed cell counts were obtained from culture series (i), (ii) and (iii).

Morphological measurements: Plants showed identical morphologies, under fixed conditions, irrespective of whether they had been derived from carpospores or tetraspores. Morphological measurements of Form A and Form B were made from culture series (i) and (ii) from plants which possessed a minimum of fifty main axial cells. They were therefore of different ages, depending on the culture conditions employed. Each set of measurements was obtained from ten plants. The following measurements were made:

(a) The length, diameter, and ratio of length to diameter of the 2nd, 4th, 8th, 10th, 12th, 15th, 20th, and 25th axial cells.

(b) The numbers of whorl branchlets per axial cell, in the region between the apical cell and the 25th axial cell. This data has, for convenience, been divided into five groups:

Group I. the apical cell to axial cell 5 inclusive.

Group II. axial cell 6 to axial cell 10 inclusive.

Group III. axial cell 11 to axial cell 15 inclusive.

Group IV. axial cell 16 to axial cell 20 inclusive.

Group V. axial cell 21 to axial cell 25 inclusive.

Each group consists of five axial cells from ten plants, making a total of fifty axial cells in each group, for each culture condition examined. Each axial cell was examined and the percentage bearing one, two, three or four whorl branchlets calculated.

(c) The length, diameter, and ratio of length to diameter, of the basal cell and the longest cell of the whorl branchlets.

(d) The arrangement of pinnules on the whorl branchlets calculated in the same manner as for the field data.

Measurements (c) and (d) were obtained from five whorl branchlets on each plant. The branchlets chosen were, the largest of the whorl on axial cells 28, 30, 32, 34, and 36. When an indeterminate branch was encountered in any whorl, the largest whorl branchlet on the next distal axial cell was measured, and on alternate cells after this, until five branchlets on each plant has been examined.

Mature whorl branchlets: The whorl branchlets, for measurements (c) and (d), were initially chosen because they appeared to have reached their maximum development, both in cell size and pinnule arrangement. To confirm this decision measurements (c) and (d) were made on every 5th axial cell, between number 5 and 50 inclusive, in ten plants of Form A from culture series (i) at 2:16-8:1200 and 15:16-8:1200. These are two of the more extreme conditions employed.

The data for cell measurements (c) and pinnule arrangement (d) are presented in Figure 11. Both sets of data show the same trends: a rapid increase in cell size and numbers of pinnules up to the whorl branchlet on axial cell 20, a slight increase in the branchlet borne on cell 25, and no significant increases distal to this point. Similar

FIGURE 11

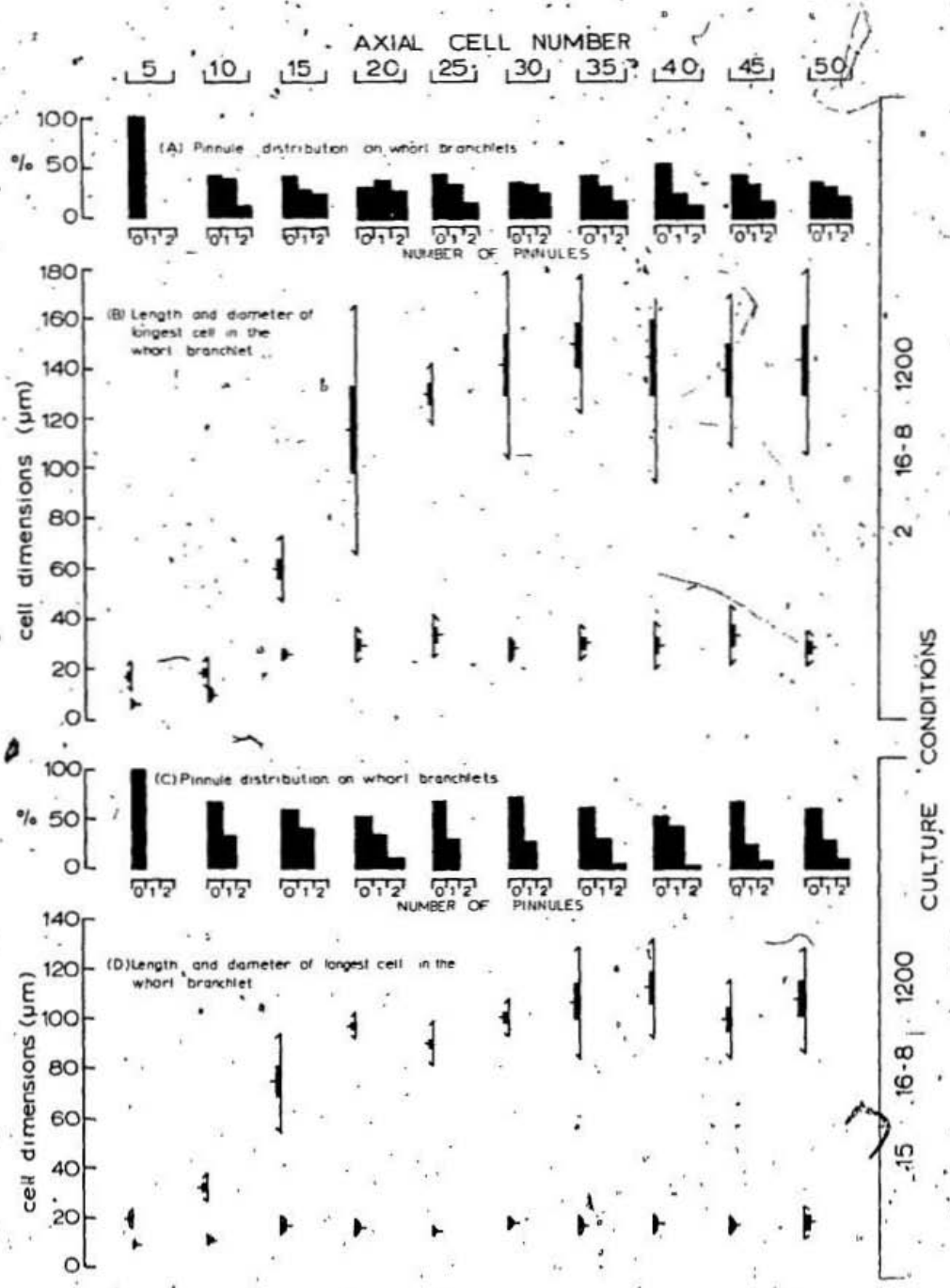
MORPHOLOGICAL VARIATION OF WHORL BRANCHLETS WITH POSITION ON THE AXIS, IN CULTURES OF *SCAGELIA PYLAISAEI*

FORM A

Data are obtained from the largest whorl branchlets borne on axial cells (numbered from apex i.e. apical cell = 1) 5, 10, 15, 20, 25, 30, 35, 40, 45 and 50; as a mean of 10 plants in each sample. Two extreme culture conditions are utilized ES 2:16-8:1200 (for A and B) and 15:16-8:1200 (for C and D).

(A and C) Pinnule distribution on whorl branchlets: Percentage of whorl branchlet cells bearing 0, 1 or 2 pinnules.

(B and D) Length and diameter of longest cell in the whorl branchlet: Data are presented as a mean ± standard error (solid bar) and ± standard deviation (vertical line). For each pair measurements presented on the same vertical line the larger is the cell length the smaller the cell diameter.


AXIAL CELL NUMBER
5
10
15
20
25
30
35
40
45
50
(A) Pinnule distribution on whorl branchlets
%
100
50
0
0 1 2
NUMBER OF PINNULES
(B) Length and diameter of longest cell in the whorl branchlet
cell dimensions (µm)
180
160
140
120
100
80
60
40
20
0
(C) Pinnule distribution on whorl branchlets
(D) Length and diameter of longest cell in the whorl branchlet
140
120
100
80
60
40
20
0
2 16-8 1200
15 16-8 1200
CULTURE CONDITIONS

data were obtained for Form B from culture series (ii). No detailed measurements were made at other conditions, but visual observations confirmed the above findings. The whorl branchlets chosen for measurements, on axial cells between 28 and 36 are thus mature.

Gland cells: It was found impossible to adequately compare the numbers of gland cells, produced under different culture conditions.

Initially, the ratio of gland cells to whorl branchlet and pinnule cells was calculated in the same manner as for the field material. Considerable variation was found within single cultures, which was often greater than the variation between cultures. Subsequent visual examination of cultures, derived from other sources, showed that the numbers of gland cells appeared dependent on the age of the culture rather than on any specific incubation condition. High proportions of gland cells were also found in cultures in which the medium had not been frequently changed.

Variation in Form A.

Growth rates: The data for the growth rates of plants in culture series (i), with conditions employed are given in Figure 12. There is an initial lag period in the development of the young plants, which is independent of culture conditions.

After seven days there is little significant difference in the numbers of cells produced in any of the samples. After fourteen days, the higher growth rates are in the long day plants at the higher temperatures, and this is obvious both in the axial and total cell counts. There is, however, little difference in the effects of light intensity when other conditions remain constant. The short day plants

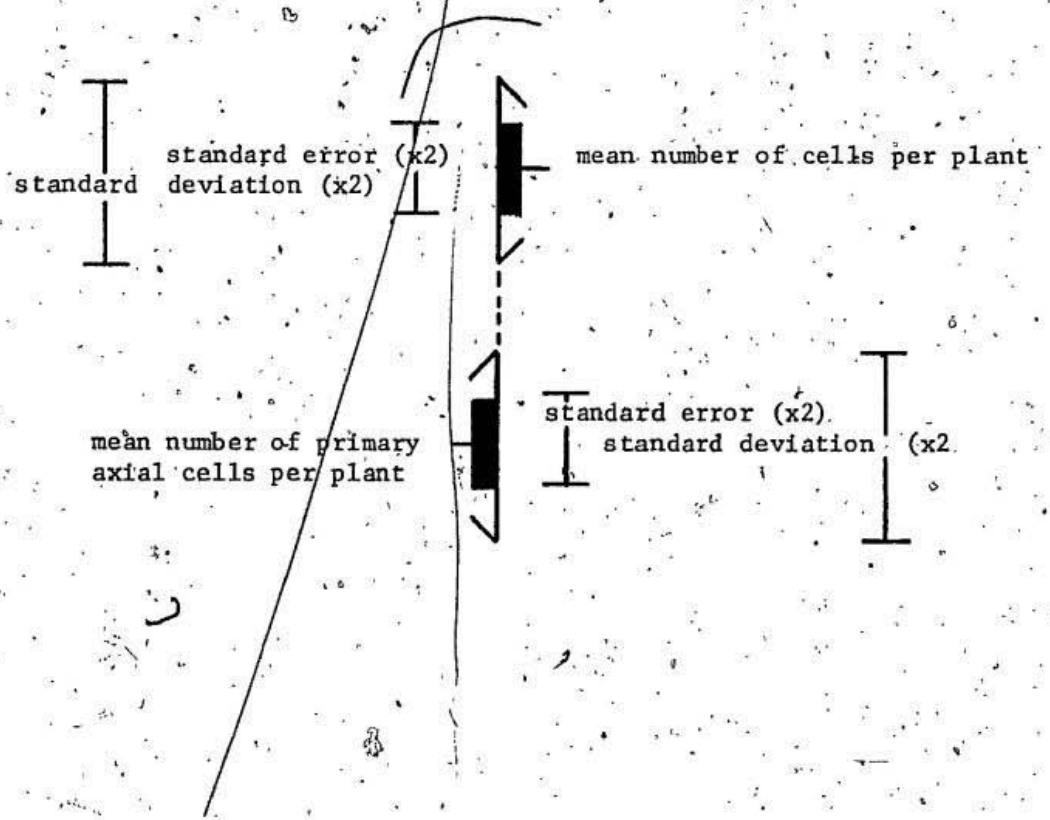
FIGURE 12

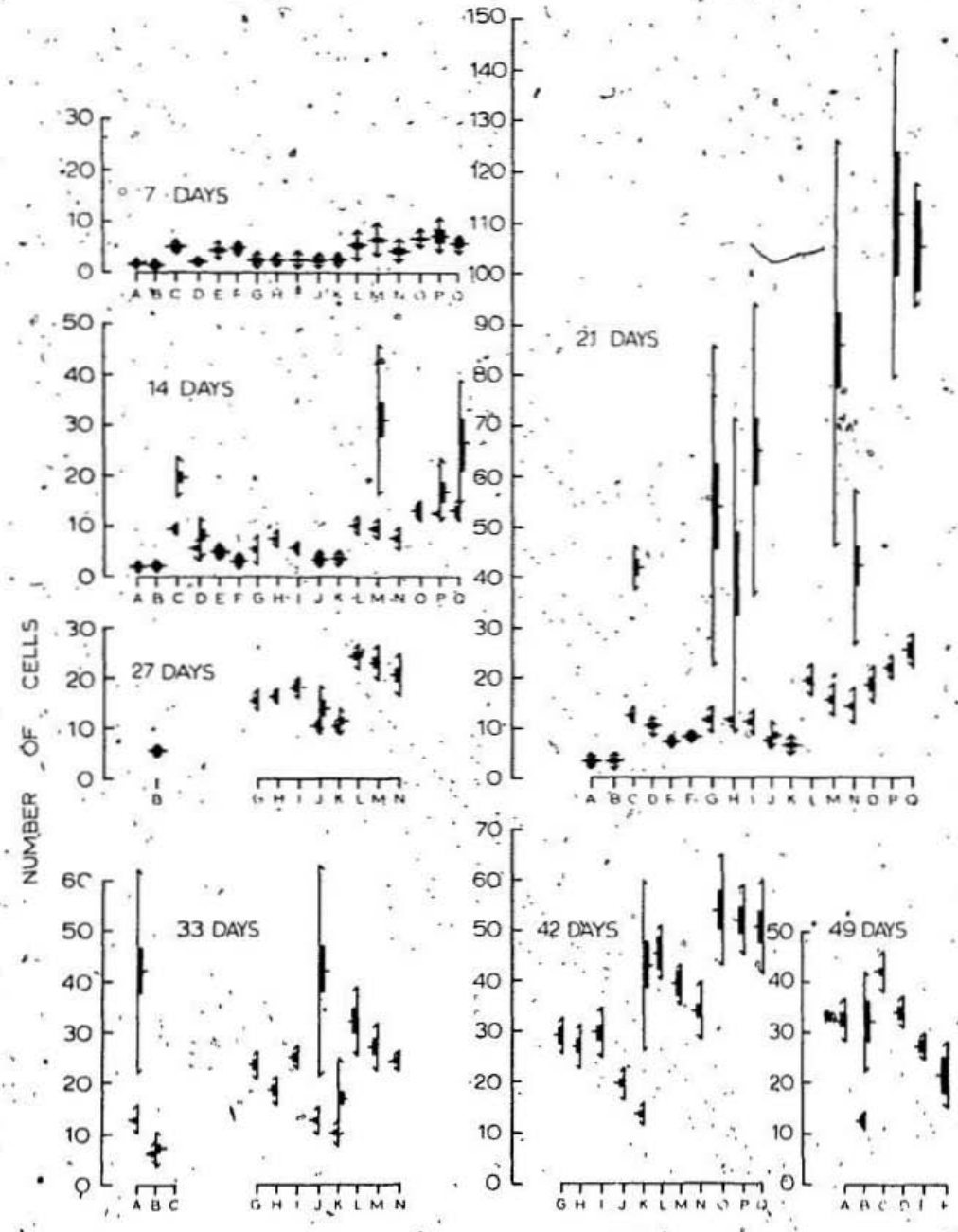
GROWTH RATES OF *SCAGELIA PYLAISAEI*

IN CULTURE I

Growth rates at several culture conditions of *S. pylaisaei*, culture series (i), derived from tetraspores of Form A. Measured as the mean number of cells produced per plant, and the mean number of axial cells produced per plant, after 7, 14, 21, 27, 33, 42 and 49 days in culture.

Culture Conditions	ES		
A	2:8-16:1200	J	10:8-16:500
B	2:8-16:150	K	10:8-16:150
C	5:16-8:500	L	10:16-8:1200
D	5:16-8:150	M	10:16-8:500
E	5:8-16:500	N	10:16-8:150
F	5:8-16:150	O	15:16-8:1200
G	5:16-8:1200	P	15:16-8:500
H	5:16-8:500	Q	15:16-8:150
I	5:16-8:150		




7 DAYS
14 DAYS
21 DAYS
27 DAYS
33 DAYS
42 DAYS
49 DAYS
NUMBER OF CELLS
CULTURE CONDITIONS

show the slowest growth rates, being lower than for the long day plants under comparable conditions. After twenty-one days, the differences between cultures increase, the most obvious being the reduced rate of growth in the short daylength plants, which is especially marked at the lower temperatures where the plants remain unbranched.

The trends outlined above are continued in the later samples (33, 42, 49 days), with the major difference being the commencement of branching in the slower growing cultures. Thus it would appear that the principal factors affecting the rate of cell division are temperature and daylength, with light intensity, especially at the higher temperatures, having the least effect.

Figure 13 shows the growth rate in culture series (iii), obtained from carpospores. The trends are the same as those in culture series (i), and no significant differences in the rates of cell division in plants formed from the two types of spore.

Axial cell morphology: Axial cell morphology is dependent on the rate of cell enlargement and the age of the cell. The cells chosen for comparison are distinguished by their position in relation to the apical cell, the rate of division of which is dependent on the incubation conditions. The compared cells may thus be of different ages. The data can therefore be used for static morphological studies, but cannot be used directly to give comparative data on the rates of cell elongation.

The cell length data are given in Figure 14 . In all cultures at 2°C the cells show an almost identical pattern, remaining short and

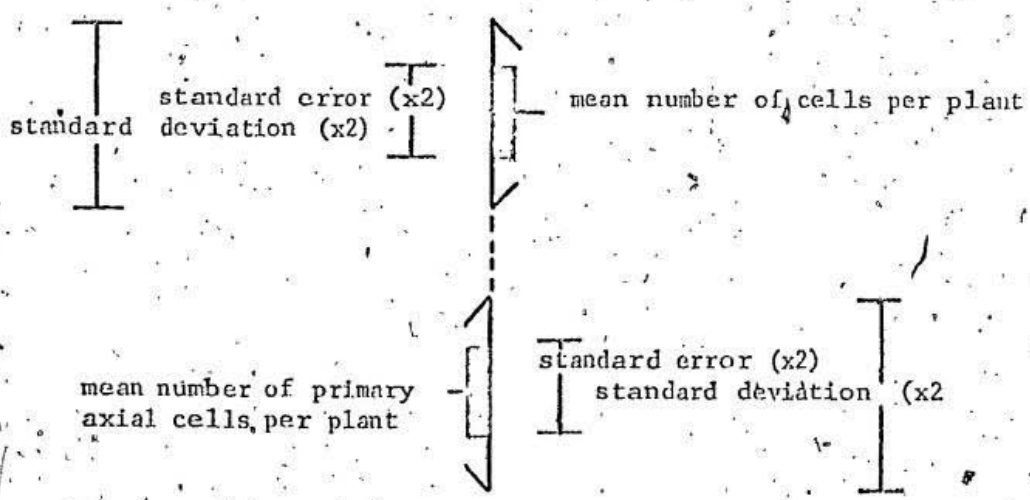
FIGURE 13

GROWTH RATES OF *SCAGELIA PYLAISAEI*
IN CULTURE II

Growth rates at several culture conditions of *S. pylaisaei*, culture series (iii), derived from carpospores of Form A and culture series (ii) derived from tetraspores of Form B. Measured as the mean number of cells produced per plant, and the mean number of axial cells produced per plant after 7 and 21 days of culture.

Culture Conditions ES

A	2:8-16:500	J	10:8-16:150
B	2:8-16:150	K	10:16-8:1200
C	5:16-8:1200	L	10:16-8:500
D	5:16-8:500	M	10:16-8:150
E	5:16-8:150	N	2:16-8:1200
F	10:8-16:500	O	2:16-8:150
G	10:8-16:150	P	5:8-16:500
H	10:16-8:1200	Q	5:8-16:150
I	10:16-8:500	R	10:8-16:1200



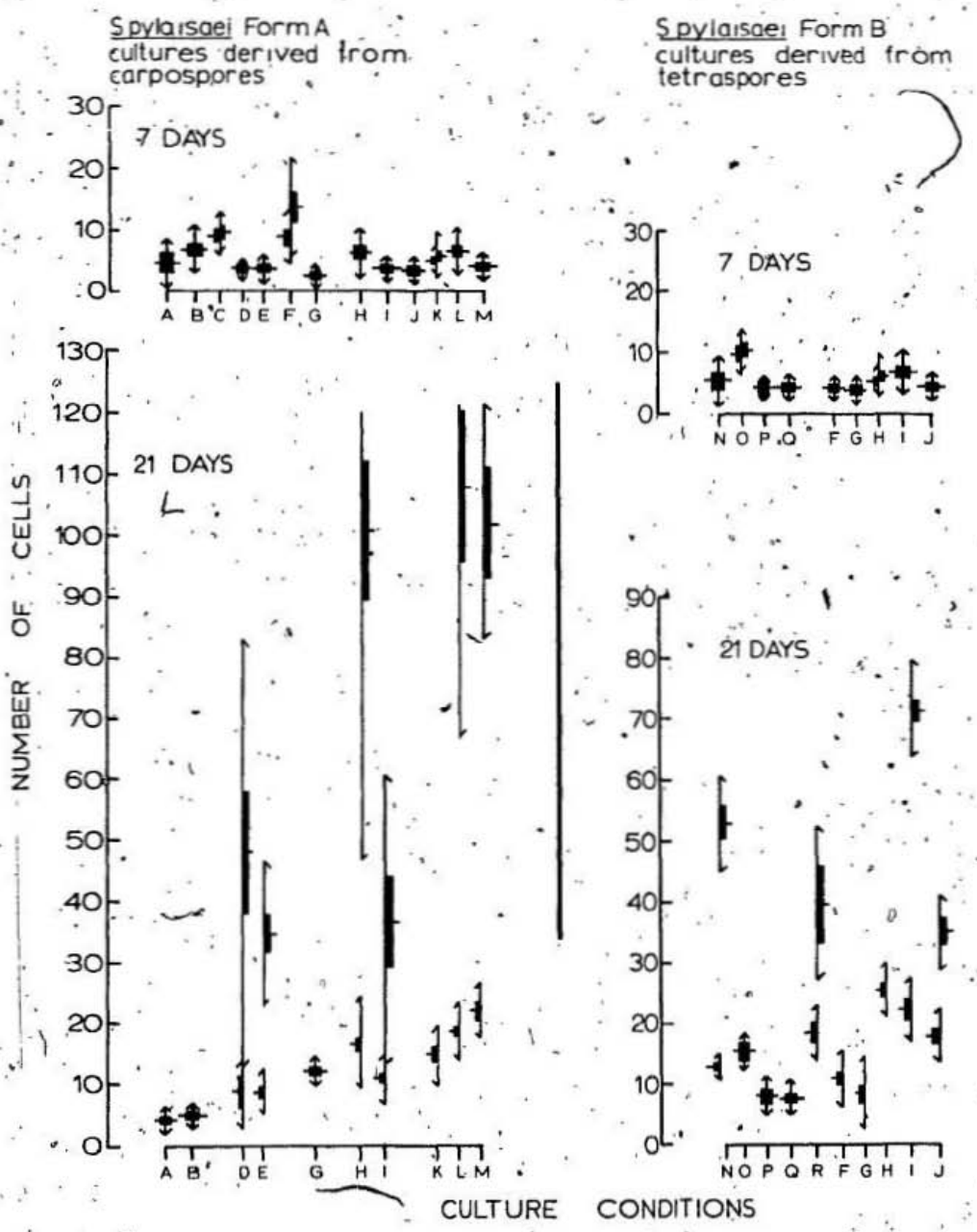
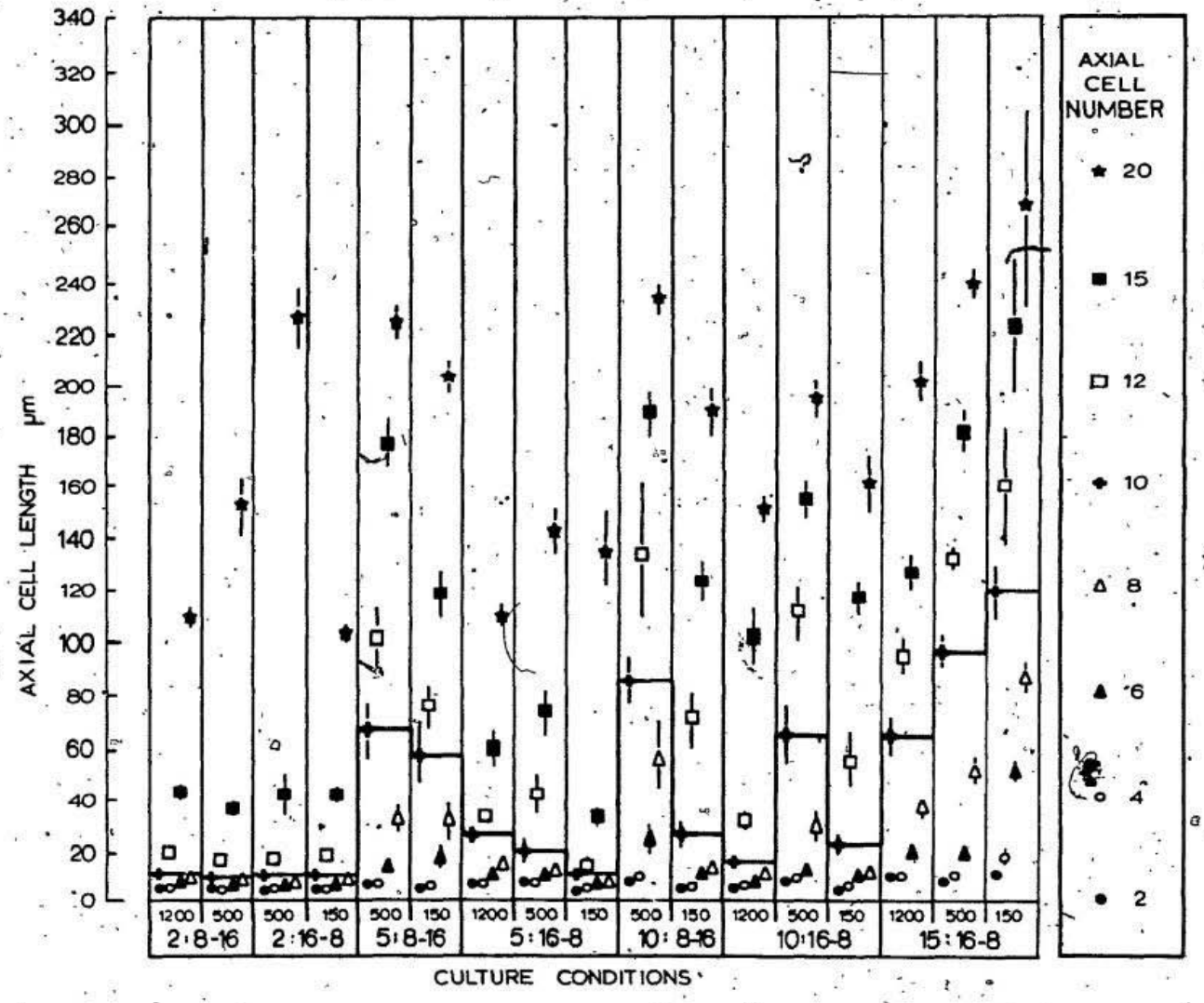

S.pylaisaei Form A
cultures derived from
carpospores
S.pylaisaei Form B
cultures derived from
tetraspores
7 DAYS
21 DAYS
NUMBER OF CELLS
CULTURE CONDITIONS
A B C D E F G H I J K L M
N O P Q R F G H I J

FIGURE 14

AXIAL CELL LENGTH OF *SCAGELIA PYLAISAEI* FORM A IN CULTURE

Mean length (± standard error) of axial cells number 2, 4, 6, 8, 10, 12, 15, 20 from the apex of *S. pylaisaei* Form A grown under several culture conditions. Each point is the mean of measurements from 10 plants.


AXIAL CELL LENGTH µm
340
320
300
280
260
240
220
200
180
160
140
120
100
80
60
40
20
0
1200 500 500 150 500 150 1200 500 150 500 150 1200 500 150 1200 500 150
2:8-16
2:16-8
5:8-16
5:16-8
10:8-16
10:16-8
15:16-8
CULTURE CONDITIONS
AXIAL CELL NUMBER
20
15
12
10
8
6
4
2

only twice as long as the subapical cell at cell number 10. At 5°C there is a marked difference in the cell lengths between short and long daylengths. This is most marked at the higher light intensities, but is not so obvious at 10°C. At 15°C plants have slightly longer cells than at all other conditions with the longest at the lower light intensities. This is in contrast to cultures at lower temperatures, where, when differences occur, plants at the lower light intensities have the shorter cells.

The data on cell diameters are not presented, as variations under different culture conditions are small in comparison with those for cell lengths. This indicates that the ratio of cell length to cell diameter is greatest at the higher temperatures and at the short daylengths.

Arrangement of the whorl branchlets on the axial cells: The percentage of the axial cells bearing whorls of 0, 1, 2, 3, or 4 cells are given as a series of histograms (Figure 15). The axial cells develop their first and second whorl branchlets in Group I (apex to cell number 5), but the majority of cells lack branchlets. Two cells in this first group have whorls of three branchlets, but the majority of plants which bear whorls of three branchlets first form them on the cells located in Group II (cells 6 to 10 inclusive) and it is also in this region that fourth whorl branchlets, if formed, develop. The maximum development of four whorl branchlets takes place in Group III (cells 11-15 inclusive).

The greatest number of whorl branchlets are produced at the lower temperatures and long daylengths. At the lower temperatures there

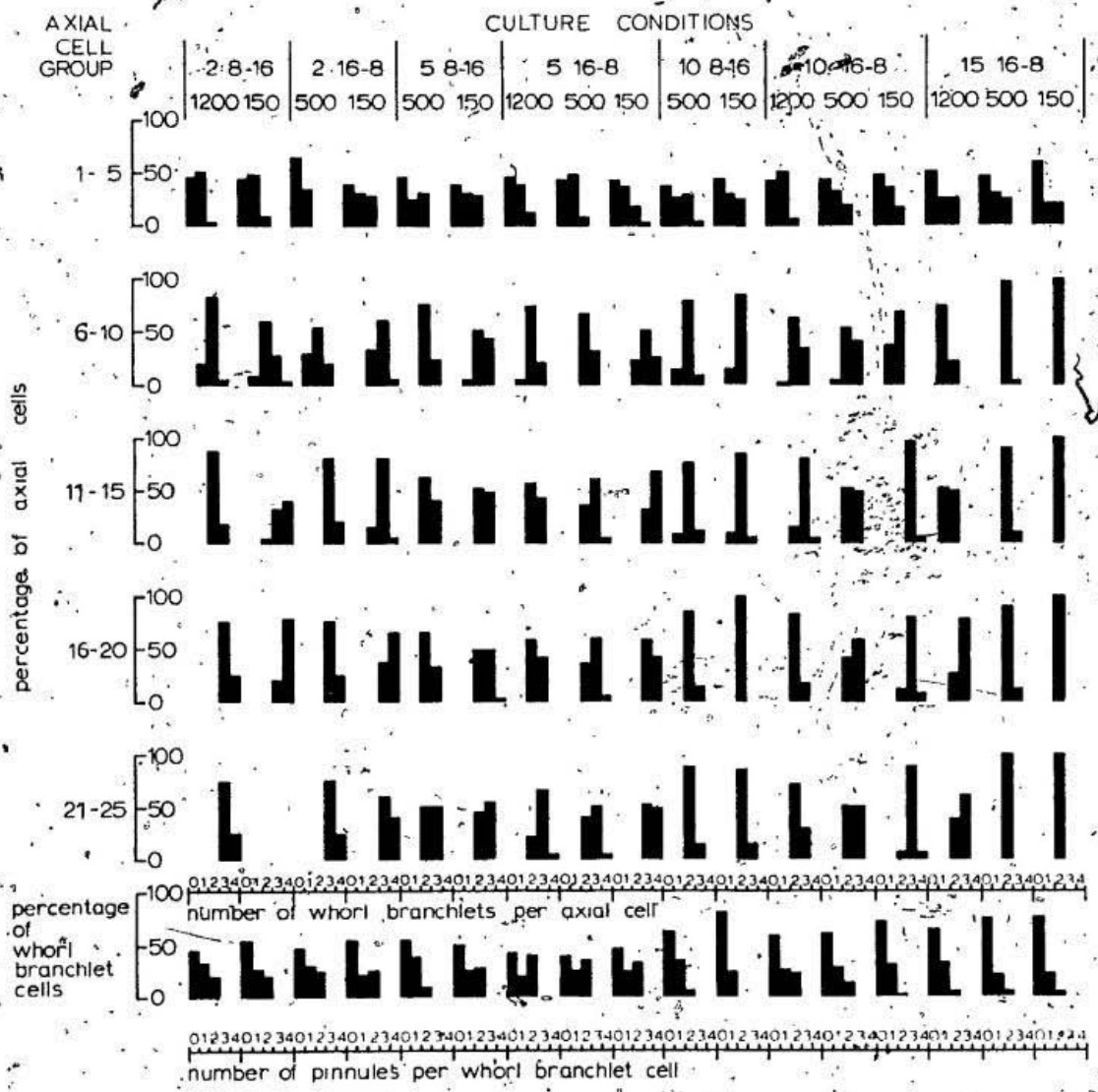
FIGURE 15

WHORL BRANCHLET AND PINNULE ARRANGEMENT ON
SCAGELIA PYLAISAEI FORM A IN CULTURE

Number of whorl branchlets per axial cell: Percentage of whorl branchlets occurring in whorls of 1, 2, 3 or 4 in axial cell groups, 1 (apical-5), 6-10, 11-15, 16-20, 21-25; under several culture conditions.

Number of pinnules per whorl branchlet cell: Percentage of whorl branchlet cells from mature regions of the plants bearing 0, 1 or 2 pinnules.

Each block is data from 10 plants.


AXIAL CELL GROUP
CULTURE CONDITIONS
2 8-16 1200 150
2 16-8 500 150
5 8-16 500 150
5 16-8 1200 500 150
10 8-16 500 150
10 16-8 1200 500 150
15 16-8 1200 500 150
1-5
6-10
11-15
16-20
21-25
100
50
0
percentage of axial cells
0 1 2 3 4
number of whorl branchlets per axial cell
percentage of whorl branchlet cells
number of pinnules per whorl branchlet cell

is an increase in the number of branchlets with decrease in light intensity, but the reverse trend is shown under short daylengths where plants produce fewer whorl branchlets. The reduction in number of whorl branchlets is more marked with increase in temperature. Plants bearing whorls of four branchlets were not found at 15°C, and four whorl branchlets were also rare at 10°C. Under a single culture condition (15:16-8:150) all axial cells bore only pairs of branchlets.

Arrangement of pinnules on the whorl branchlets: The percentage of the whorl branchlet cells bearing 0, 1 or 2 pinnules are shown in Figure 15. The range of variation is not as marked as in the arrangement of the whorl branchlets on the axial cells. Two major trends are, however, apparent: there is reduction in the total number of pinnules and in the number of cells bearing two pinnules with increase in temperature. There are also fewer pinnules produced at lower light intensities and shorter daylengths.

Pinnule cell morphology: There is little difference in the length between the longest pinnule cells under most conditions (Figure 16b). At lower temperatures under short daylengths, however, the cells are longest at high light intensities. The diameters of these cells show little difference under all culture conditions.

The variations in length and diameter of the basal cells (Figure 16a) follow the same patterns as those of the longest cells, but the trends are clearer at the higher temperatures where the cells are longest under the higher light intensities, just as they are at lower temperatures in short daylengths.

The basal cell diameters show no significant differences between

FIGURE 16

VARIATION IN WHORL BRANCHLET CELL DIMENSIONS

IN CULTURES OF *SCAGELIA PYLAISAEI*

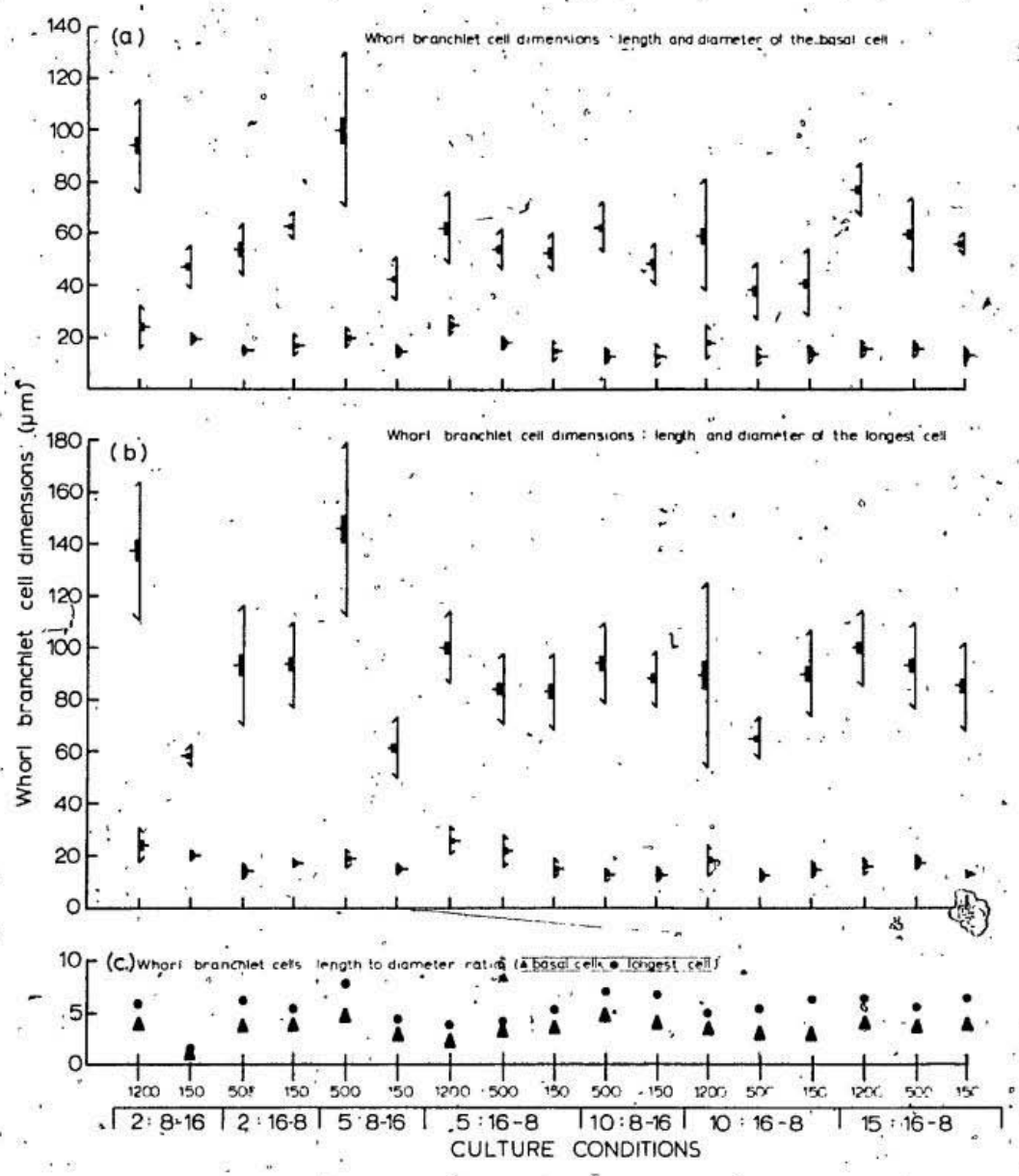
FORM A

(a) Whorl branchlet cell dimensions: Length and diameter of the basal cell of the whorl branchlets in mature regions of the plants, grown under several culture conditions.

(b) Whorl branchlet cell dimensions: Length and diameter of the longest cell of the whorl branchlets in mature regions of the plants, grown under several culture conditions.

Data for (a) and (b) are obtained in each instance from 5 cells on each of 10 plants and are presented as a mean ± standard error (solid bar) and ± standard deviation (vertical line). For each pair measurements presented on the same vertical line the larger is the cell length and the smaller the cell diameter.

(c) Whorl branchlet cells:length to diameter ratios: Ratio of mean length to mean diameter of longest (L) and basal (B) whorl branchlet cells, from data presented in (a) and (b) above.


(a)
Whorl branchlet cell dimensions : length and diameter of the basal cell
(b)
Whorl branchlet cell dimensions : length and diameter of the longest cell
Whorl branchlet cell dimensions (µm)
(c) Whorl branchlet cells length to diameter ratios (▲ basal cell, ● longest cell)
1200 150 500 150 500 150 1200 500 150 500 150 1200 500 150 1200 500 150
2 : 8-16
2 : 16-8
5 : 8-16
5 : 16-8
10 : 8-16
10 : 16-8
15 : 16-8
CULTURE CONDITIONS

culture conditions. The ratio of length to diameter of both the basal and the longest cell of whorl branchlets is greatest at the higher light intensities and at short daylengths, but these differences are not very marked (Figure 16c).

Variation in Form B.

Growth rates: The growth rates presented in Figure 13 are for culture series (ii) derived from tetraspores of Form B. No data are presented for culture series (iv), derived from carpospores of Form B, but visual observation revealed no differences between this and culture series (ii).

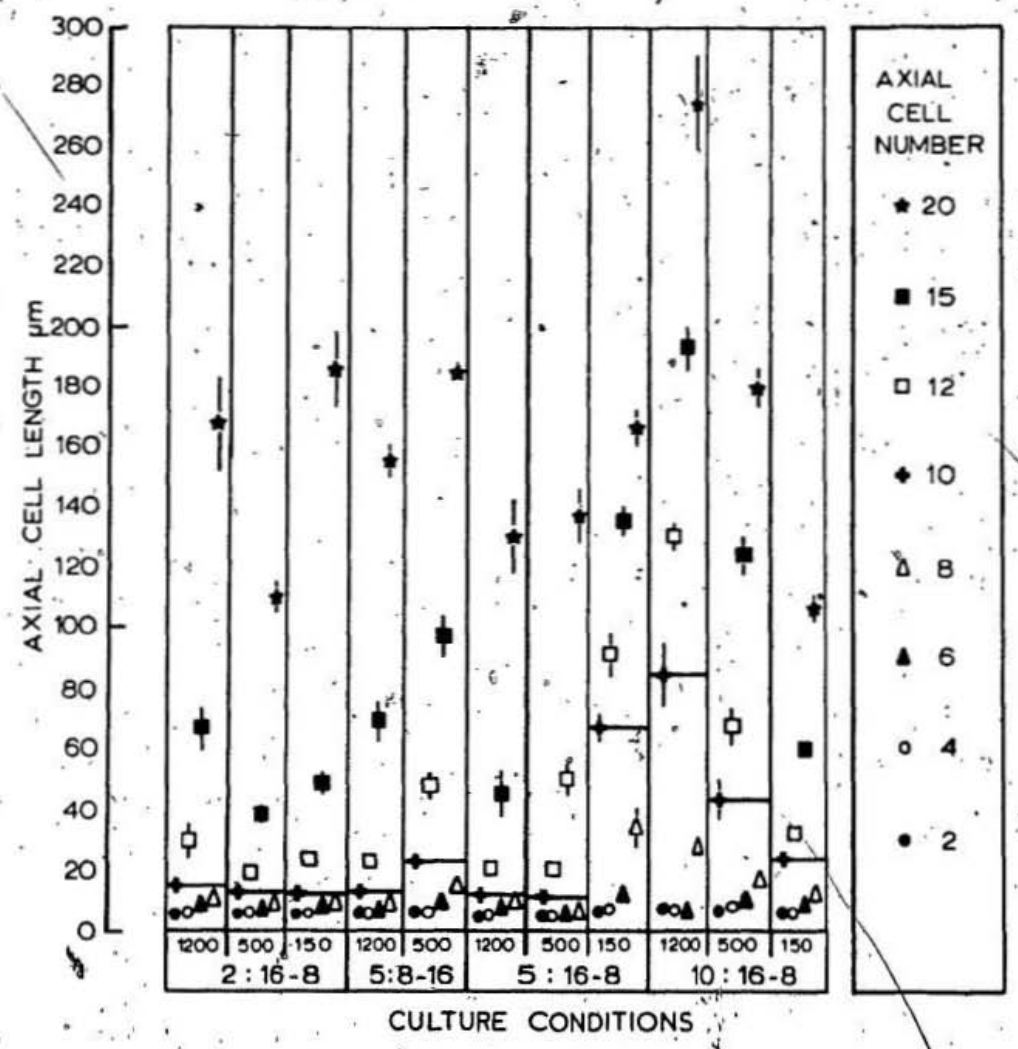
The growth rates are similar to those of culture series (i) showing the same rates of cell division under corresponding culture conditions and hence the same general trends between cultures. These may be summarized as an increase in the rate of cell division with an increase in temperature, and with significantly higher rates under long day conditions than short days at the same temperature and light intensities.

Axial cell morphology: The data on the axial cell lengths (Figure 17) do not show the same degree of variation between cultures as in Form A, and differences in length at all light intensities at 2°C, 5°C and short daylength and the higher light intensities at 5°C and long daylength are insignificant. The cell lengths at 5:16-8:150 are much greater and are comparable to those at high light intensities at 10°C. At 10°C the longest cells are found at the highest light intensities, in contrast with the trends shown at lower temperatures.

FIGURE 17

AXIAL CELL LENGTH OF *SCAGELIA PYLAISAEI* FORM B IN CULTURE

Mean length (± standard error) of axial cells number 2, 4, 6, 8, 10, 12, 15, 20 from the apex of *S. pylaisaei* Form B grown under several culture conditions. Each point is the mean of measurements from 10 plants.


AXIAL CELL LENGTH µm
300
280
260
240
220
200
180
160
140
120
100
80
60
40
20
0
1200
500
150
2 : 16-8
5:8-16
5 : 16-8
10 : 16-8
CULTURE CONDITIONS
AXIAL CELL NUMBER
20
15
12
10
8
6
4
2

The axial cells of Form B are significantly longer than comparable cells of Form A produced under the same conditions.

Arrangement of whorl branchlets on the axial cells: At all culture conditions Form B shows a greatly reduced number of whorl branchlets, in comparison with Form A (Figure 18). Under no conditions are whorls of four branchlets formed, whorls of three are rare and confined to the higher light intensities at 2°C. The majority of axial cells bear only two whorls of branchlets and a significant number, especially at lower light intensities and high temperatures, bear only single branchlets.

The first whorl branchlets are cut off the axial cells of Group I (apical cell to cell 5 inclusive) though this group shows a preponderance of cells lacking branchlets. It is not until Group II (cells 6 - 10 inclusive) that a majority of cells bear pairs of branchlets. Thus, in culture, Form B differs from Form A in that there is a considerable reduction in the number of whorl branchlets, and these are cut off at a greater distance from the apical cell.

Arrangement of pinnules on the whorl branchlets: The data on the number of pinnules borne on the whorl branchlet cells are presented in Figure 18 . In all the cultures of Form B the whorl branchlets either lack pinnules and are simple, or possess them arranged in a secund or irregular manner, but they are never predominantly pinnate. Under all conditions the majority of cells bear no pinnules, and in only three culture conditions (2:16-8:1200, 5:16-8:1200, 10:16-8:1200) are any cells found bearing two pinnules. Under the other conditions some cells bear only single pinnules and these reach their greatest number

FIGURE 18

WHORL BRANCHLET AND PINNULE ARRANGEMENT ON

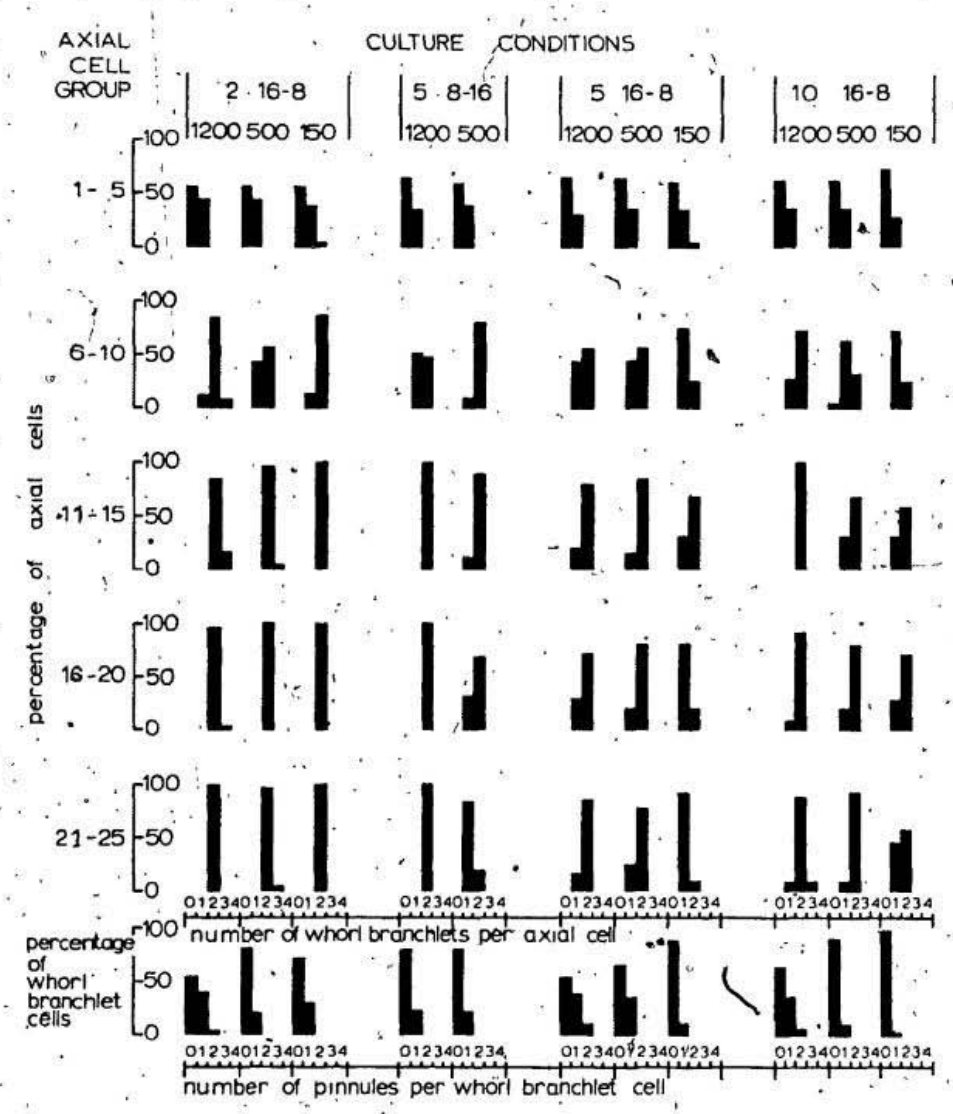
SCAGELIA PYLAISAEI FORM B

IN CULTURE

Number of whorl branchlets per axial cell: Percentage of whorl branchlets occurring in whorls of 1, 2, 3 or 4 in axial cell groups, 1 (apical-5), 6-10, 11-15, 16-20, 21-25; under several culture conditions.

Number of pinnules per whorl branchlet cell: Percentage of whorl branchlet cells from mature regions of the plants bearing 0, 1 or 2 pinnules.

Each block is data from 10 plants.


AXIAL CELL GROUP
CULTURE CONDITIONS
2 16-8
5 8-16
5 16-8
10 16-8
1200 500 150
1200 500
1200 500 150
1200 500 150
1-5
6-10
11-15
16-20
21-25
100
50
0
percentage of axial cells
0123401234
number of whorl branchlets per axial cell
percentage of whorl branchlet cells
number of pinnules per whorl branchlet cell

at the high light intensities at the lower temperatures, and are conversely least common at the lower light intensities at higher temperatures. Thus, the pinnule arrangement shows the same general trends as Form A, but with a considerable reduction in number under all conditions.

Pinnule cell morphology: The dimensions of the pinnule cells are presented in Figure 19. There are only small differences between cell lengths at 2°C under all light intensities and between these and cells at 5°C at long daylengths at high intensities. At 5°C under low light intensities and short daylengths the cells are shorter. At 10°C all lengths are reduced under low light conditions.

The cell diameters are significantly smaller at 10°C than at 2°C, and cell length: diameter ratios are greater under all conditions at 10°C in spite of a reduction in cell length at the lower light intensities. The basal cells show the same trends as the longest cells.

For both Forms A and B, the basal cells are always significantly shorter than the longest cell in the whorl branchlet.

Effects of salinity on growth rate and gland cell formation.

Scagelia pylaisaei has been recorded from the Baltic Sea (as *Antithamnion boreale* f. *baltica*, Reinke, 1889), a region of reduced salinity, where it reportedly lacks gland cells. It was decided therefore to investigate the effects of salinity, on growth rate and gland cell formation of both Form A and Form B. The salinities chosen were $27^{o}/_{oo}$, $24^{o}/_{oo}$, $21^{o}/_{oo}$, $18^{o}/_{oo}$, $15^{o}/_{oo}$, and $10^{o}/_{oo}$, and control cultures were grown at $30^{o}/_{oo}$ as "full" salinity. Both culture series

FIGURE 19

VARIATION IN WHORL BRANCHLET CELL DIMENSIONS

IN CULTURES OF *SCAGELIA PYLAISAEI*

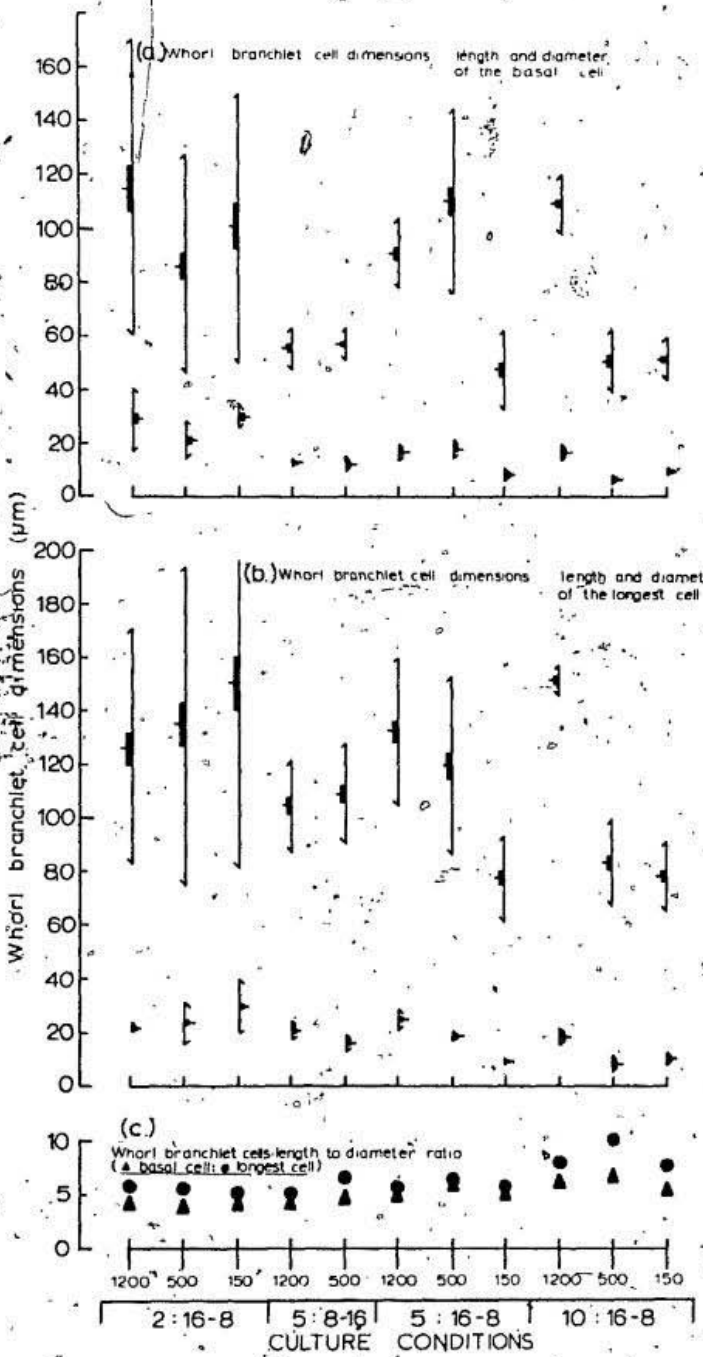
FORM B

(a) Whorl branchlet cell dimensions: Length and diameter of the basal cell of the whorl branchlets in mature regions of the plants, grown under several culture conditions.

(b) Whorl branchlet cell dimensions: Length and diameter of the longest cell of the whorl branchlets in mature regions of the plants, grown under several culture conditions.

Data for (a) and (b) are obtained in each instance from 5 cells on each of 10 plants and are presented as a mean ± standard error (solid bar) and ± standard deviation (vertical line). For each pair of measurements presented on the vertical line the larger is the cell length and the smaller the cell diameter.

(c) Whorl branchlet cells:length to diameter ratios: Ratio of mean length to mean diameter of longest (L) and basal (B) whorl branchlet cells, from data presented in (a) and (b) above.


(a.) Whorl branchlet cell dimensions length and diameter of the basal cell
(b.) Whorl branchlet cell dimensions length and diameter of the longest cell
Whorl branchlet cell dimensions (µm)
(c.)
Whorl branchlet cells-length to diameter ratio
(▲ basal cell; ● longest cell)
1200 500 150 1200 500 1200 500 150 1200 500 150
2:16-8
5:8-16
5:16-8
10:16-8
CULTURE CONDITIONS

were established from tetraspores of field collected material (Form A, Bay Bulls, St. 124.30; Form B, Grand le Pierre, St. 101.6).

The spores were discharged in culture at 10:16-8:150 in full salinity ES medium, transferred to 2:16-8:150, allowed to germinate and become established. Form A was kept under this condition for 12 days, Form B for 7 days. These were subcultured into the salinity series and placed under 10:16-8:500. Culture medium was changed at approximately seven day intervals. Samples were taken for cell counts after 14 and 23 days of growth. The cultures were harvested after 54 days, and the mature regions of the plants examined for gland cells in the same manner as the herbarium and field material. The data from these cultures are presented in Figure 20. The plants, when transferred to the salinity series, were simple filaments and the initial growth on transfer was in the development of whorl branchlets, with only a limited increase in the number of axial cells in the first fourteen days.

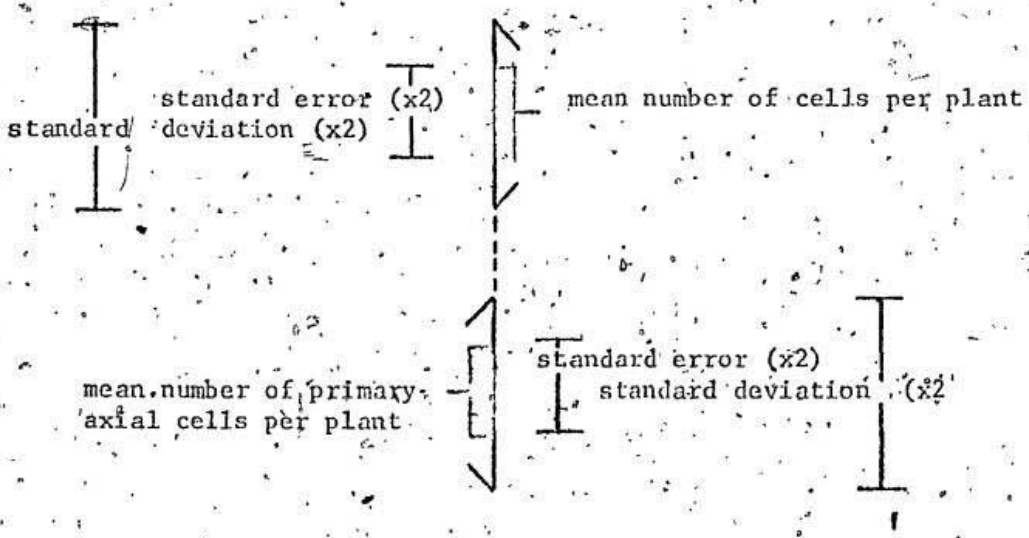
Form A: There are no significant differences in the total number of cells over the salinity range $30^{o}/_{oo}$ - $15^{o}/_{oo}$ after 14 days in culture. No growth occurred at $10^{o}/_{oo}$, and the apical cells of these plants were bleached. At 23 days there are no significant differences over the salinity range $30^{o}/_{oo}$ - $21^{o}/_{oo}$, but there is a reduction in growth, more apparent in the total number of cells than in the number of axial cells, at $18^{o}/_{oo}$ and $15^{o}/_{oo}$ salinity. No further growth had occurred at $10^{o}/_{oo}$, and all the cells in the plants had bleached. There is a reduction in the number of gland cells formed with a decrease in salinity and at the lowest level tested, at which the plants grew

FIGURE 20

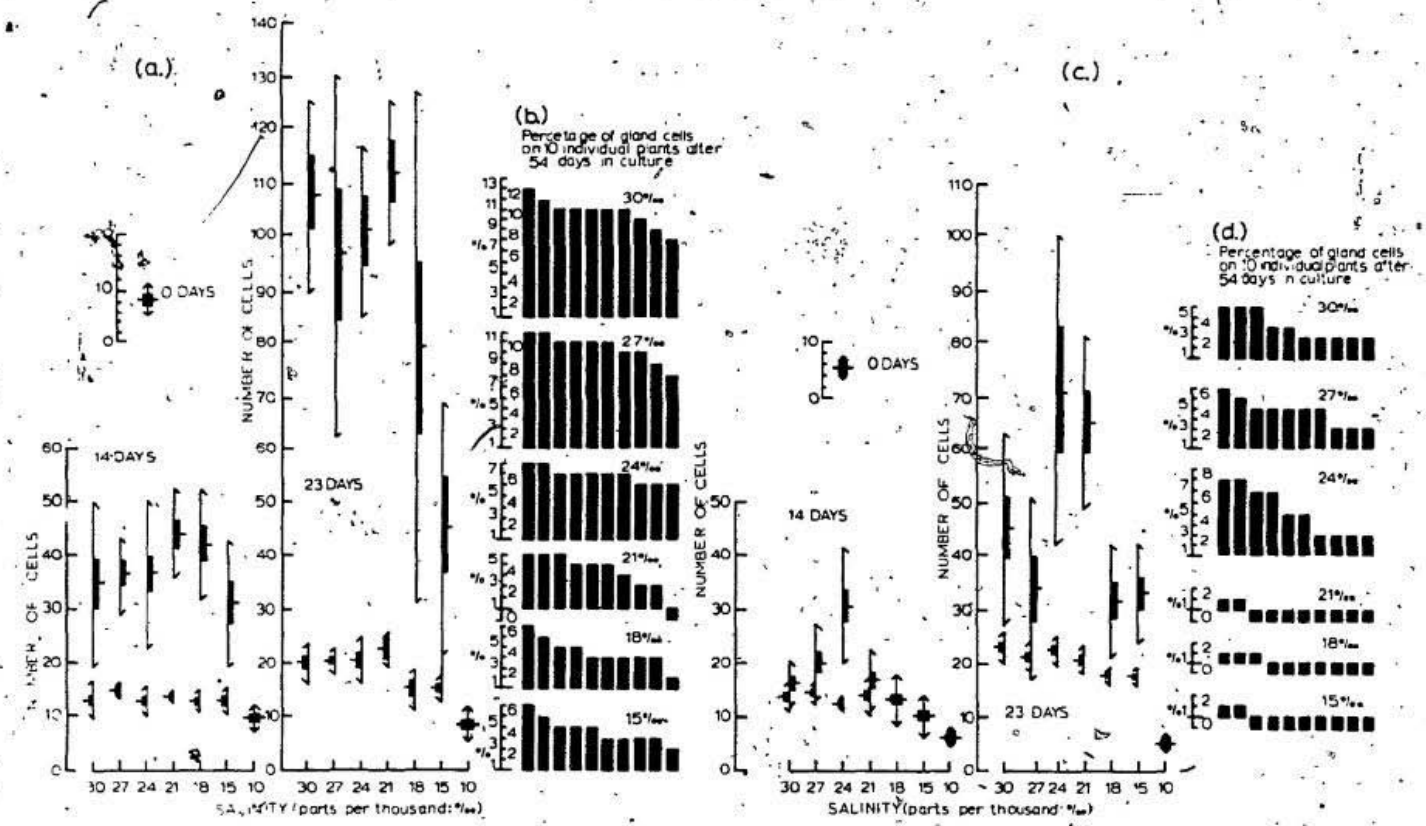
EFFECTS OF SALINITY ON GROWTH AND GLAND CELL DEVELOPMENT OF *SCAGELIA PYLAISAEI*

Growth rates of gametophyte sporelings of (a) Form A and (c) Form B at 10:16-8:500 under several salinity conditions. Measured as the mean number of cells produced per plant and the mean number of axial cells produced per plant at 14 and 23 days. Measurement at 0 days are from sporelings at the beginning of the experiment.

Frequency of gland cells after 54 days in culture of (b) Form A and (d) Form B. Data are presented for 10 individual plants as the percentage of whorl branchlet and pinnule cells in the mature regions of the plants which bear gland cells.



FORM A SCAGELIA PYLAISAEI FORM B



($15^{o}/_{oo}$), gland cells are less than half as abundant as at full salinity.

Form B: The Form B plants show similar trends to those of Form A. There are no significant differences in the number of axial cells formed at 14 and 23 days over the salinity range $30^{o}/_{oo}$ - $15^{o}/_{oo}$. The maximum total number of cells produced is at $24^{o}/_{oo}$ and $21^{o}/_{oo}$, apparent in both the 14 and 21 day sample, with a significant reduction in the total number of cells produced at $18^{o}/_{oo}$ and $15^{o}/_{oo}$ salinity. No growth occurred at $10^{o}/_{oo}$ salinity, and all the plants were bleached and dead.

Form B produces fewer gland cells than Form A under all comparable conditions. The greatest numbers are found at the higher salinities and are most abundant at $24^{o}/_{oo}$, with a reduction in number at $21^{o}/_{oo}$ salinity. There are no significant differences in gland cell number between $21^{o}/_{oo}$ and $15^{o}/_{oo}$, and in the majority of plants examined at these salinities they are absent.

Reproduction and Life History

Reproductive Periodicity.

The samples collected to determine the reproductive periodicity of the two forms of *Scagelia pylaisaei*, were divided into four categories:

I. Female gametophytes bearing mature carposporophytes.

II. Fertile male gametophytes.

III. Fertile tetrasporophytes.

IV. Sterile plants.

The data are presented in histograms of the percentages of the four categories together with the number of specimens in each sample.

Form A: (Figure 21) The data were obtained from Bay Bulls (St. 124). All reproductive structures are present at all times of the year, and in all except one sample there is a preponderance of tetrasporophytes; fertile male gametophytes were the least frequently observed category. Sterile plants are most abundant in the winter months and appear to be rare or absent in the late summer and fall.

Form B: The data obtained from St. Bernard (St. 104) (Figure 22) show the same seasonal trends as Form A, but these are considerably more marked. Tetrasporophytes can be found at all times of the year, but are rare in the winter months. Sterile plants show almost the reverse trends of the tetrasporophytes, being most common in winter and absent in the fall. Of the fertile plants, the tetrasporophytes show an even greater preponderance over the gametophytes than is shown in Form A. Both fertile male and female gametophytes bearing carposporophytes are most abundant in the fall, and almost completely absent in the winter months.

None of the plants obtained from these two sites showed any reproductive anomalies. However, at other sites, on three occasions, plants were collected bearing both tetrasporangia and gametophytic reproductive organs. Two plants of Form A were obtained from Portugal Cove (St. 135.9) and from New Chelsea (St. 145.1), both of which bore tetrasporangia together with mature carposporophytes. A plant of Form B was obtained from Brookside (St. 112.1) bearing tetrasporangia and spermatangia.

FIGURE 21

REPRODUCTIVE PERIODICITY OF
SCAGELIA PYLAISAEI
FORM A

Reproductive periodicity of *S. pylaisaei* Form A at Bay Bulls (St. 124) between October 1970 and May 1972. Data are shown as percentage of total number of specimens examined for four categories of plant: sterile plants, female gametophytes with carposporophytes, fertile male gametophytes, fertile tetrasporophytes.

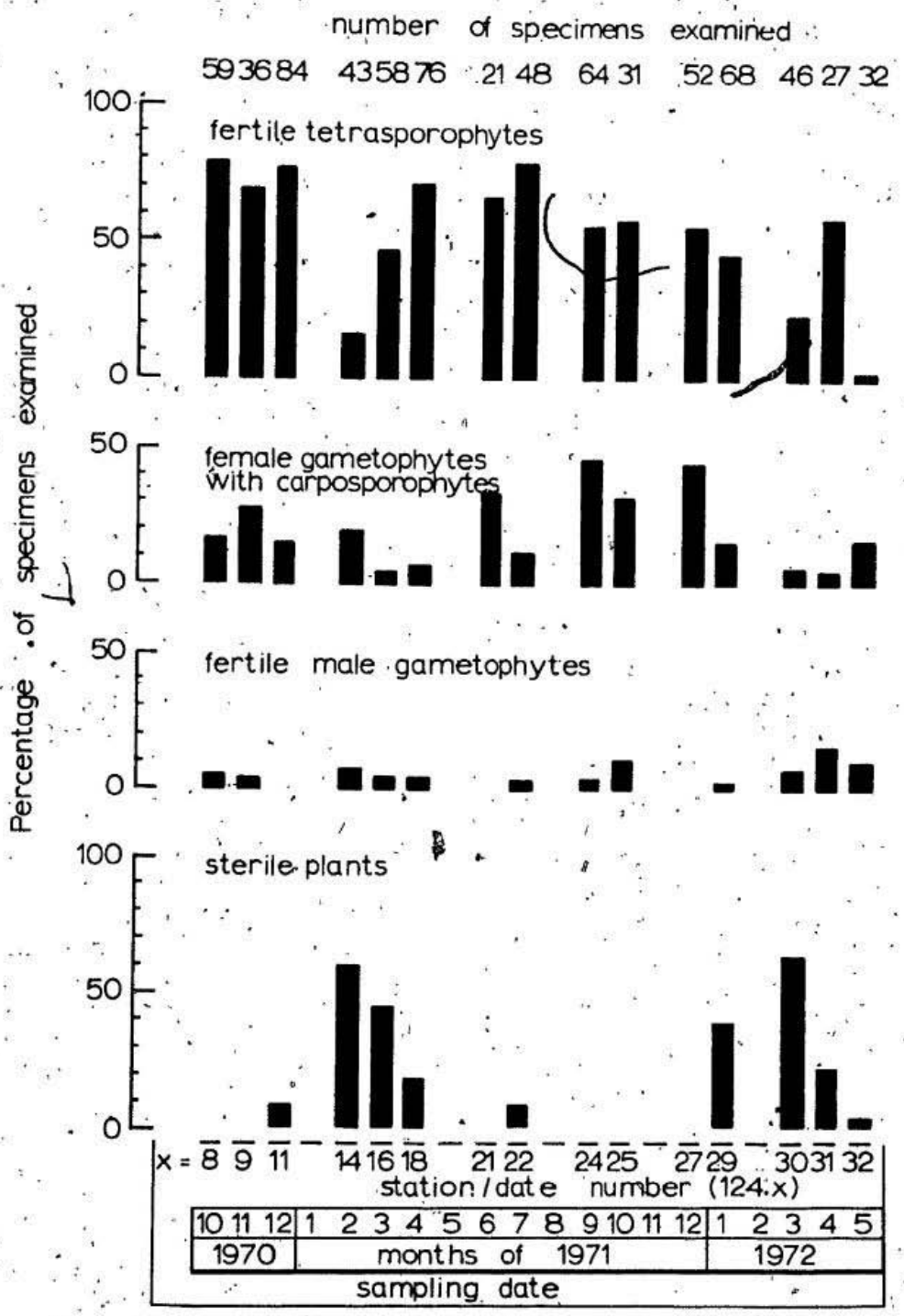

number of specimens examined
59 36 84 43 58 76 21 48 64 31 52 68 46 27 32
Percentage of specimens examined
fertile tetrasporophytes
female gametophytes with carposporophytes
fertile male gametophytes
sterile plants
100
50
0
x = 8 9 11 14 16 18 21 22 24 25 27 29 30 31 32
station / date number (124.x)
10 11 12 1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5
1970
months of 1971
1972
sampling date

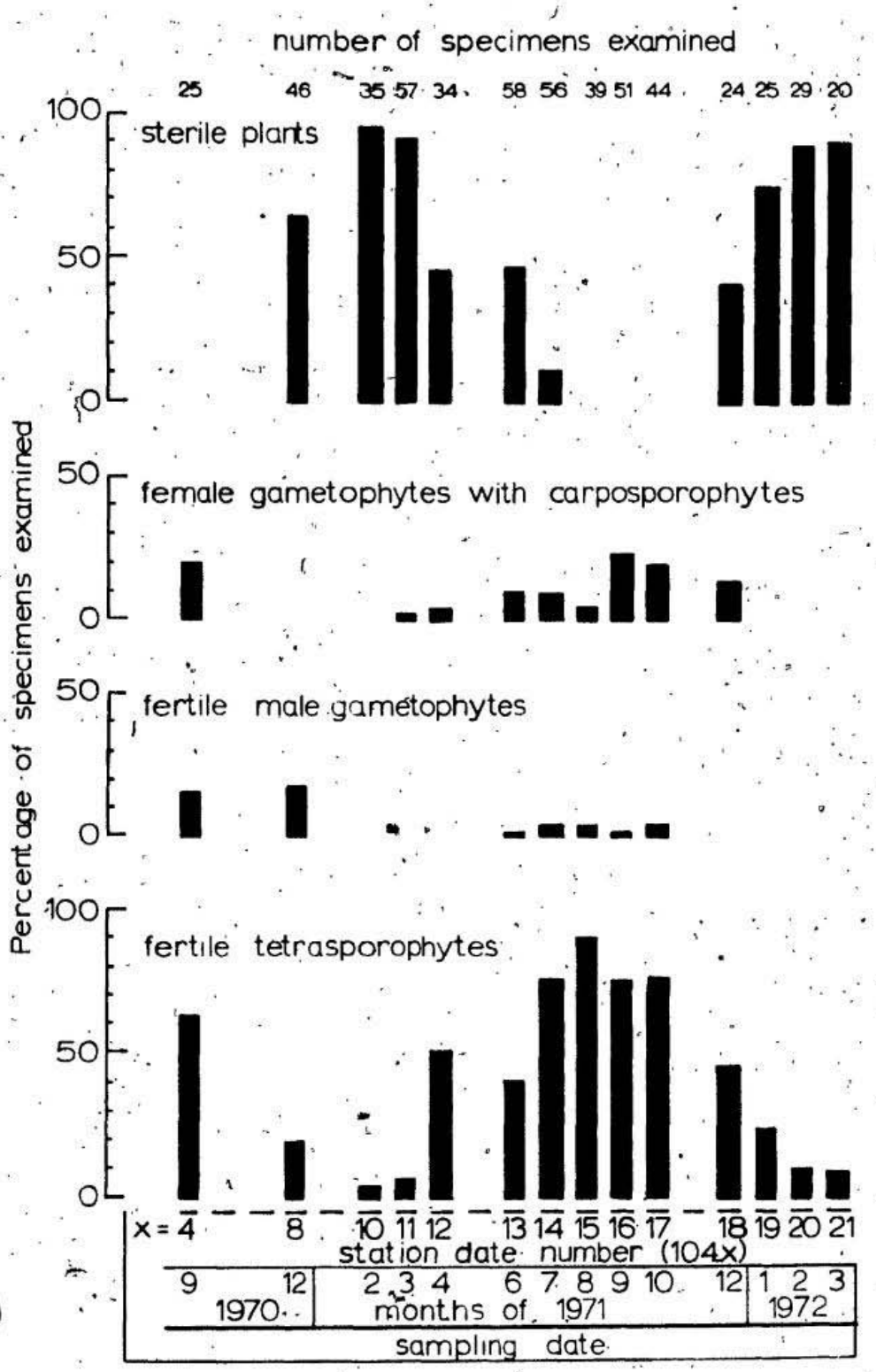
FIGURE 22

REPRODUCTIVE PERIODICITY OF

SCAGELIA PYLAISAEI

FORM B

Reproductive periodicity of *S. pylaisaei* Form B at St. Bernard (St. 104) between September 1970 and March 1972. Data are shown as percentage of total number of specimens examined for four categories of plant: sterile plants, female gametophytes with carposporophytes, fertile male gametophytes, fertile tetrasporophytes.


number of specimens examined
25 46 35 57 34 58 56 39 51 44 24 25 29 20
sterile plants
female gametophytes with carposporophytes
fertile male gametophytes
fertile tetrasporophytes
Percentage of specimens examined
100
50
0
x = 4 8 10 11 12 13 14 15 16 17 18 19 20 21
station date number (104x)
9 12 2 3 4 6 7 8 9 10 12 1 2 3
1970 months of 1971 1972
sampling date

Life History in Culture.

The occurrence of tetrasporophytes, gametophytes and carposporophytes of both forms of *Scagelia pylaisaei* suggest, that in the field, they have a *Polysiphonia*-type of life history. Discrepencies have, however, been observed. Tetrasporangial plants predominate in both forms and tetrasporangia have been found on plants together with either carposporophytes or spermatangia. The life histories of both Form A and Form B were therefore investigated in culture.

Spores released from forty three individual plants, collected in the field were germinated and the sporelings grown to reproductive maturity. All cultures were maintained at 10:16-8:500, and took between thirty and fifty days to become fertile. Cultures derived from spores obtained from field material are termed primary cultures, and their results together with the source of the spores and the culture media employed are presented in Table 4 for Form A, and Table 5 for Form B.

When tetrasporangia and carposporphytes occurred on the same plants, separate cultures of tetraspores and carpospores were established. The mature carposporophytes were removed using fine forceps and a micropipette, and inoculated into culture. Branchlets bearing tetrasporangia, but no carposporophytes, were placed in culture where they released tetraspores.

On many occasions fertilizations occurred spontaneously in gametophyte cultures, but special cross ferilization experiments were also conducted. Plants were removed from culture prior to maturity and cultured individually until they either produced procarps or spermatangia. Male and female gametophytes were then brought together in 50ml culture

TABLE 4

SUMMARY OF THE LIFE HISTORY DATA OBTAINED FROM CULTURES

OF *S. PYLAISAEI* FORM A

Primary cultures were derived from spores obtained from plants collected in the field, their source is indicated by the station date number. Primary cultures are divided into six categories (I-VI) based on the spores cultured and the reproductive bodies formed on the resulting plants. Secondary cultures were derived from spores obtained from plants produced in primary culture, their source is indicated by a superscript in the results section of the primary cultures.

The results show the types of reproductive plants obtained, together with their approximate percentages.

All cultures were grown at 10 : 16-8: 500 for periods of 30-50 days, the cultures utilised either ER or ES media, the former have their station/date numbers underscored.

Primary cultures in categories V and VI are from plants which bore both carpospores and tetraspores.

ABBREVIATIONS

T. tetraspores and tetrasporophytes
C. carpospores
A. vegetative apical region
M. male gametophytes
F. female gametophytes

PRIMARY CULTURES OF FORM A

Category	Sources (Station/Date Number)	Spore Type	Result of Culture	
I.	121.1, 122.1, 124.8, 124.27, 128.8, 158.2	T ⟶	$M^1:F^2$	50:50%
II.	124.4, 124.6, 124.17, 124.27, 131.1, 133.2	T ⟶	$T^3F^4:T^5M^6$	50:50%
III.	122,1, 124.4, 124.6, 124.8, 124.21, 124.27, 128.12, 131.1, 145.1, 158.2	C ⟶	T^7	100%
IV.	124.22	C ⟶	$T^8M^9:T^9$	50:50%
V.	145.1	T ⟶	F^{10}	100%
		C ⟶	T^{11}	100%
		A ⟶	F^{10}	
VI.	135.9	T ⟶	no germination	
		C ⟶	no germination	
		A ⟶	F^{14}	

SECONDARY CULTURES OF FORM A

Products of Primary Culture	Result of Culture	
M^1xF^2 ⟶	C ——— T	100%
T^3 ⟶	F^{12}	100%
T^7 ⟶	M:F	50:50%
F^2xM^9 ⟶	no fertilization	
T^{11} ⟶	M:F	50:50%
M^6xF^4 ⟶	C ——— T	100%
T^5 ⟶	M^{13}	100%
T^8 ⟶	M:F	50:50%
$F^{10}xM^1$ ⟶	C ——— T	100%
$F^{12}xM^{13}$ ⟶	C ——— T	100%

TABLE 5

SUMMARY OF LIFE HISTORY DATA ON FORM B OBTAINED FROM CULTURE

Culture conditions, the lay out of the data and the abbreviations are as for Form A in Table

Category IV Culture is from a plant bearing tetrasporangia and spermatangia

PRIMARY CULTURE OF FORM B

Category	Sources (Station/Date Number)	Spore Type	Result of Culture	
I.	101.3, 101.5, 103.2, 104.4, 104.5, 104.8, 104.12, 104.18, 171.1, 171.4	T ⟶	$M^1T^2:F^3T^4$	50:50%
II.	104.16	T ⟶	$M^5:F^6$	50:50%
III.	101.3, 104.4, 104.5, 104.16, 104.18, 171.1	C ⟶	T^7	100%
IV.	112.1	T ⟶	M	100%
		M		

SECONDARY CULTURES OF FORM B

Products of Primary Culture	Result of Culture		
M^1xF^3 ⟶	C ⟶	T	100%
T^2 ⟶	M		100%
T^7 ⟶	M:F		50:50%
M^5xF^6 ⟶	C ⟶	T	100%
T^4 ⟶	F		100%

vessels, it was found that the vibrations occurring in the culture cabinet were adequate to facilitate the release and transfer of spermatia. All fertilizations were duplicated and control cultures of procarpial plants also established. The controls never produced carposporophytes.

The carpospores and tetraspores obtained in culture have been germinated and grown to maturity, they are termed secondary cultures and the results are presented in Table 4, for Form A, and Table 5 for Form B.

Primary cultures of Form A: Primary cultures of Form A have been divided into six categories (I-VI). Tetraspores (Category I and II) produced progeny, approximately half of which bore spermatangia (M^1 and M^6), and half procarps (F^2 and F^4). In several cultures (Category II) tetrasporangia (T^2 and T^4) developed on both male (M^6) and female plants (F^4). Tetraspores from a plant (Category V), which also bore mature carposporophytes, developed only into procarpial plants.

Carpospores (Categories III, IV and V) produced tetrasporangial (T^7, T^8 and T^9) progeny, irrespective of whether the plants from which they were derived bore other reproductive organs (Category V). On a single occasion (Category IV) half of the tetrasporangial plants (T^8) also produced spermatangia (M^9).

On two occasions plants were found (Category V and VI) bearing both tetrasporangia and mature carposporophytes. Their excised apical regions (A) produced procarpial plants (F^{10} and F^{14}). In one instance (Category VI) tetraspores and carpospores were released, but bleached

and did not germinate.

Secondary cultures of Form A: On all but a single occasion male plants (M^1 and M^6) proved capable of fertilizing female plants (F^2, F^4 and F^{10}) to produce carposporophytes irrespective of whether either parent also bore tetrasporangia. No success was achieved in the attempt to fertilize a female plant (F^2) with a male, which also bore tetrasporangia (T^8 M^9), derived from Category IV, primary culture of carpospores.

Progeny from tetraspores (T^3) occurring on female plants (F^4) were all female (F^{12}), and (T^5) from male plants (M^6) all male (M^{13}). F^{12} females could be fertilized by M^{13} males. The production of tetrasporangia on spermatangial and procarpial plants (Category II, T^3 and T^5) occurred most frequently in crowded cultures and could be inhibited by vegetative subculture to fresh medium. Not all crowded cultures produced tetrasporangia, and they did not always appear on all plants in the same culture. On several occasions tetrasporangia did not occur on male and female plants, but arose on subsequent generations derived from these plants. An attempt to fertilize a female (F^2) lacking tetrasporangia with a male (M^6) with tetrasporangia was successful, but the result was invalidated when the female parent produced tetrasporangia and became a F^4 female subsequent to fertilization.

Tetraspores (T^7, T^8 and T^{11}) from plants, including those obtained in Category IV (T^8) which also bore spermatangia, germinated to produce equal numbers of male and female plants.

All carpospores produced in culture germinated to produce tetrasporangial plants.

Life cycle of Form A: From the results of primary and secondary cultures it is possible to establish the life cycle of *Scagelia pylaisaei* Form A as it occurs in culture. This is presented in Figure 23 , it is basically of the *Polysiphonia*-type with the addition of accessory tetrasporangia on the male and female plants, which reproduce the parent.

The spermatangia produced on tetrasporangial plants (Category IV) do not appear to function in the life cycle.

Primary cultures of Form B: Primary cultures of Form B are divided into four categories. Tetraspores (Categories I and II) produced equal numbers of male (M^1 and M^5) and female (F^3 and F^6) plants and on all but a single occasion (Category II), they also bore tetrasporangia (T^2 and T^4). Tetraspores (Category IV) from a plant which also bore spermatangia produced only male plants.

Carpospores (Category III) produced all tetrasporangial (T^7) plants.

Secondary cultures of Form B: All attempted fertilizations between male (M^1 and M^5) and female (F^3 and F^6) plants were successful, and the carpospores produced gave rise to tetrasporangial plants.

Tetraspores (T^2) occurring on male plants (M^6) produced all male plants, and those (T^4) on female plants produced all female plants. Tetraspores (T^7) derived from primary cultures of carpospores produced equal numbers of male and female plants.

Life cycle of Form B: The life cycle of Form B, as shown by primary and secondary cultures is presented in Figure 23 . It is essentially the same as that of Form A with accessory tetrasporangia

FIGURE 23

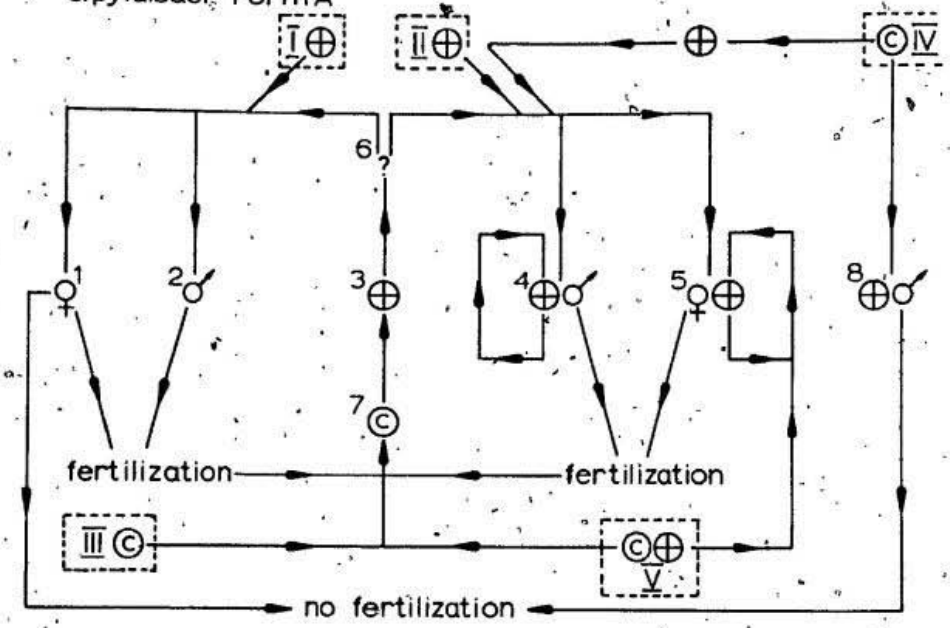
LIFE CYCLE OF *SCAGELIA PYLAISAEI*

In both Form A and Form B haploid male (2) and female (1) gametophytes produce diploid carposporophytes bearing carpospores (7) which germinate to give tetrasporophytes bearing meiotic tetrasporangia and producing haploid tetraspores (3). These regenerate the male (2) and female (1) gametophytes. In some instances the male (4) and female (5) gametophytes also bear apomeiotic tetrasporangia, but the factors (6) initiating their development remain unknown. Spermatangia (8) produced on tetrasporophytes do not appear to function in the life cycle.

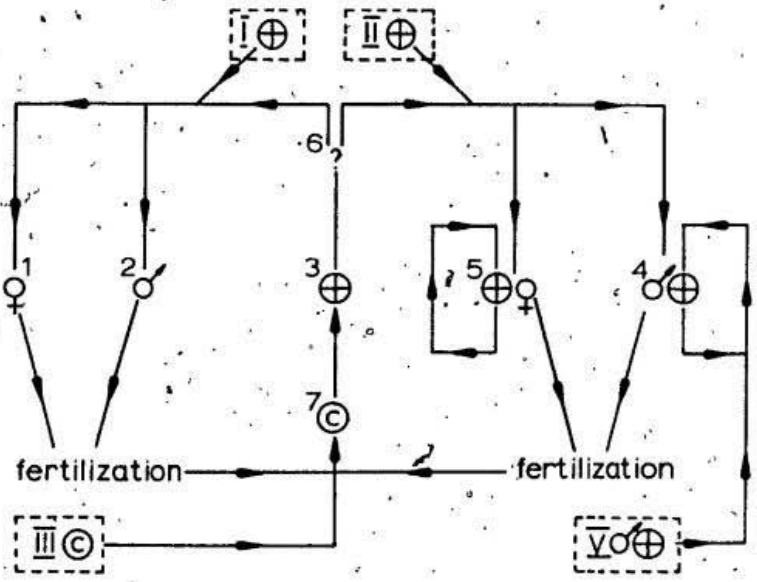
Form A: I, II, III, IV, V are spore sources from field material and refer to the culture categories listed in Table 4.

Form B: I, II, III, V are spore sources from field material and refer to the culture categories listed in Table 5.

S. pylaisaei Form A



S. pylaisaei Form B



occurring on male and female plants.

The Effects of Incubation Conditions on Reproduction in Culture.

Cultures of Form A and Form B, derived from both tetraspores and carpospores, were grown under a range of culture conditions to investigate their effects on reproduction and provide information on the factors controlling reproductive periodicity in nature. Culture series (i - iv), also used to determine growth rates in culture, were utilized. Cultures were sampled at intervals, but it was not possible to remove and examine a constant number of specimens on all occasions. Data are therefore presented as the actual number of specimens found in each sample to bear tetrasporangia (T), spermatangia (M), procarps (F) or to be sterile (S).

Form A: The results of culture of tetraspores of Form A together with the incubation conditions employed are presented in Table 6 . The plants eventually became fertile under all incubation conditions tested. Plants bearing spermatangia were the first to become fertile and these were followed by plants bearing procarps. Under all conditions procarpial and spermatangial plants were formed in approximately equal numbers. At 10° and 15°C, procarpial and spermatangial plants also produced tetrasporangia.

The time required for the plants to become fertile appear to be controlled by the same factors which regulate the growth rate. Light intensity has the least effect, and plants first become fertile at the higher temperatures and long daylengths.

Data on the growth of carpospores of Form A are presented in

TABLE 6

CULTURES OBTAINED FROM TETRASPORES OF *S. PYLAISAEI* FORM A.

COLLECTED ST. 124.20

Culture conditions ES		Days in culture after germination							
		15	21	27	33	42	49	84	104
2 16-8	1200	Sterile	Sterile	Sterile	Sterile	11M22S	ND	9M6F4S	
	150	"	"	"	"	Sterile	ND	10M1F11S	
2 8-16	500	"	"	"	"	"	Sterile	No data	4M1F4S
	150	"	"	"	"	"	3M8S	No data	3M4F
5 8-16	500	"	"	"	"	1M8S	8M1F12S	10M12F3S	
	150	"	"	"	"	3M6S	6M5S	6M4F3S	
5 16-8	1200	"	"	"	10M8S	8M8S	7M1F6S	15M12F	
	500	"	"	"	Sterile	5M6S	22M26S	16M1F11S	
	150	"	"	"	7M34S	13M11S	8M7S	9M9S	9M6F4S
10 8-16	500	"	"	"	Sterile	2M8S	13M6F8S	14M17F	14M8F2FT
	150	"	"	"	"	2M33S	3M2F1S	11M12F	16M15F
10 16-8	1200	"	"	8M1F9S	9M10F	4M4F1S	8M10F	4MT6FT	
	500	"	12M9S	9M11S	10M9F2S	10M11F1FT	5M6F1FT	2M6MT10FT	
	150	"	1M78S	8M16S	6M1F5S	18M16F	10M12F	4M6F	
15 16-8	1200	"	14M40S	No data	10M12F	4M6F5MT3FT	10MT8FT		
	500	"	3M28S	6M1F7S	8M10F	12M9F6FT	22MT18FT		
	150	"	Sterile	5M7S	6M8F	16M8F10FT	12FT14MT		

M = fertile male gametophyte. F = fertile female gametophyte. S = sterile plant
FT = female gametophyte bearing tetraspores, MT male gametophyte bearing tetraspores.
Each code is preceded by the number of plants bearing these attributes in the sample.

Table 7. These have not been grown under the same number of conditions as have the plants from tetraspores. Under all conditions the plants produced tetrasporangia and in all comparable conditions they require slightly longer than the plants raised from tetraspores to become fertile. Daylength has a considerable effect and plants under short daylength take longer to become fertile than plants under comparable conditions at long daylengths.

Form B: The data from the culture of tetraspores of Form B are presented in Table 8. The same trends as described for Form A are shown with approximately equal numbers of male and female plants being produced. At long daylength at 10° C the plants eventually also produced tetrasporangia. The reduced number of culture conditions and the different ages of the samples do not permit detailed comparison of the two Forms A and B. Plants of Form B, however, take longer to mature than those of Form A. Culture of carpospores of Form B (Table 9) produces plants all of which eventually bear tetrasporangia.

Culture of Apical Fragments of Winter Sterile Plants.

A number of cultures were also set up from apical fragments of sterile plants of both Form A and Form B collected at Bay Bulls (St. 124.29) and St. Bernard (St. 104.21) respectively. The purpose of this culture series was to establish whether both tetrasporophytes and gametophytes were present in the sterile populations found in the winter months. Apical fragments of 20 separate plants from each site were cultured (ES 10:16-8: 500) for 42 days, the

TABLE 7

CULTURES OBTAINED FROM CARPOSPORES OF *S. PYLAISAEI* FORM A COLLECTED ST. 124.22

Culture conditions ES		Days in culture after germination				
		20	32	53	72	89
2 8-16	500	Sterile	Sterile	Sterile	8T1S	15T
	150	"	"	"	10T5S	18T
5 16-8	1200	"	1T32S	22T		
	500	"	3T23S	32T		
	150	"	Sterile	8T1S		
10 8-16	500	"	"	14T		
	150	"	"	8T1S		
10 16-8	1200	"	7T4S	14T		
	500	"	14T2S	18T		
	150	"	2T8S	13T		
15 16-8	1200	"	18T1S	22T		
	500	"	15T	26T		
	150	"	23T3S	12T		

T = fertile tetrasporophytes S = sterile plants
Each code is preceded by the number of the plants bearing these attributes in the sample.

TABLE 8

CULTURES OBTAINED FROM TETRASPORES OF *S. PYLAISAEI* FORM B

COLLECTED ST. 101.3

Culture conditions ES			Days in culture after germination			
			21	28	58	65
2	16-8	1200	Sterile	Sterile	27M23F	5M5F
		500	"	"	4M2F5S	56M53F
		150	"	"	10M1F12S	5M4F
5	8-16	1200	"	"	7M8S	5M1F4S
		500	"	"	Sterile	1M5S
5	16-8	1200	"	"	10M10F	6M6F1S
		500	"	"	50M34F22S	10M6F4S
		150	"	"	10M12F23S	10M8F6S
10	8-16	1200	"	"	18M6F21S	No data
		500	"	"	9M6F11S	"
		150	"	"	22M4F26S	"
10	16-8	1200	"	3M4S	2M2MT3FT	8M4MT6F9FT
		500	"	14M40S	16M18F1S	10M7F2FT
		150	"	Sterile	1M1F1S	No data

M = fertile male gametophyte, F = fertile female gametophyte, S = sterile plant
MT = fertile male gametophyte bearing tetraspores, FT = fertile female gametophyte bearing tetraspores. Each code is preceded by the number of the plants bearing these attributes in the sample.

TABLE 9

CULTURES OBTAINED FROM CARPOSPORES OF *S. PYLAISAEI* FORM B

COLLECTED ST. 104.18

Culture conditions ES		Days in culture after germination			
		21	34	56	65
2 16-8	1200	Sterile	1T16S	7T14S	18T
	500	"	Sterile	2T5S	7T
	150	"	"	6T8S	11T2S
5 8-16	1200	"	"	14T13S	22T
	500	"	"	6T8S	16T
5 16-8	1200	"	2T18S	18T	
	500	"	4T17S	26T	
	150	"	Sterile	14T	
10 16-8	1200	"	17T	10T	
	500	"	12T	10T	
	150	"	14T3S		

T = fertile tetrasporophyte, S = sterile plant
Each code is preceded by the number of plants bearing these attributes in the sample.

results are presented in Table 10.

Table 10.

	Pre-culture	Post culture, 42 days
Form A	20 sterile	23 tetrasporophytes 4 female gametophytes
Form B	20 sterile	16 tetrasporophytes 2 female gametophytes 1 male gametophyte

It is not possible to establish precise ratios of numbers of gametophytes to tetrasporophytes because a number of the apical fragments were not viable whilst others grew rapidly and fragmented, hence the anomalies in the numbers of plants reported before and after culture. It is apparent, however, that sterile populations are made up of both tetrasporophytes and gametophytes with a preponderance of the former.

Hybridization.

Approximately twenty sporelings, derived from tetraspores, were removed from cultures (ES 10:16-8:500) of Form A (St. 124.27) and Form B (St. 104.18) after 18 and 24 days of growth respectively. The plants were not fertile; each was placed in a separate culture vessel and transferred to ES 10:8-16:500 and allowed to reach reproductive maturity, when they produced either procarps or

spermatangia. The cultures were maintained by apical subculture.

Although spontaneous fertilizations had occurred previously in mixed cultures of gametophytes, it was thought necessary to optimize the chance of this occurrence, and the plants were brought together on a shaking device. Duplicate cultures of each combination were tested, with control cultures of procarpial material. The combinations tested and the results obtained are presented in Table 11.

Fertilizations were obtained from Form A (1), with carposporophyte development occurring at 21 days; carpospores matured and were released after 35 days. Carposporophyte development in Form B (4) was observed at 30 days, with carpospore release at 42 days. No hybridization occurred between Forms A and B (2 and 3) and the control female gametophytes did not develop carposporophytes.

Cytological Studies

All cytological studies have been confined to the examination of acetocarmine stained nuclei of Forms A and B which have been found to be identical and will be described together. With the exception of dividing cells, discharged spores, and the first three cells of the carpogonial branch, all cells observed were uninucleate.

Interphase.

The interphase nuclei contain a prominent single nucleolus (Figure 10e) surrounded by a granular cytoplasm enclosed in a barely discernible nuclear membrane. Interphase nuclei vary in size and shape, depending on their position in the plants. In axial cells in

TABLE 11

HYBRIDIZATION EXPERIMENTS BETWEEN *SCAGELIA PYLAISAEI* FORM A AND FORM B

		Male Gametophyte		Female Gametophyte	Results (2 cultures)	
Attempted Hybridizations	1.	Form A	X	Form A	+	+
	2.	Form A	X	Form B	-	-
	3.	Form B	X	Form A	-	-
	4.	Form B	X	Form B	+	+
Controls	5.			Form A	-	-
	6.			Form B	-	-

the apical region they are spherical and occupy a central position in the cell (Figure 10e), but in mature axial cells they assume a lenticular shape and are displaced to the side of the cell, presumably as a consequence of vacuolation.

The nuclei of the apical cells vary in size depending on their state of division. In interphase they measure ca. 5 µm diameter. Nuclear size in the axial cells varies from 4-5 µm diameter in the subapical cells to 40-60 µm in a mature axial cell. The nucleoli also vary considerably in size and increase with nuclear size.

The multinucleate condition has been observed in germinating tetraspores and carpospores (Figure 10f), but occurs only in the atypical, unipolar germinations, while those which have germinated normally are uninucleate (Figure 10g).

Atypical sporelings are most commonly found to have germinated epiphytically on the parent plant, or to be free-floating in the culture medium. Spores which were firmly attached to the substrate were predominantly uninucleate. The first three cells of the carpogonial branch (Figure 10h) are binucleate, but the supporting cell and the carpogonium are uninucleate.

Mitosis.

Mitotic cell divisions have been observed in the apical axial cell, axial cells producing whorl branchlets, whorl branchlet cells producing pinnules, spermatangial mother cells, and in supporting cells producing auxiliary cells; they are identical in all details except nuclear dimensions.

In the apical cell of the axis the nucleus increases in size and becomes more deeply staining, a large number of small granular bodies appear in early prophase and during late prophase coalesce to form chromosomes (Figure 24a). The chromosomes appear irregular in form, but due to their small size it is impossible to describe their morphology. The nucleolus and nuclear membrane disappear immediately prior to metaphase. The chromosomes in metaphase (Figure 24b) are closely aggregated and individually indistinguishable, in equatorial view they appear as a solid bar across the cell. No spindle fibres or polar bodies were seen.

In anaphase (Figure 24c) the two sets of chromosomes separate as tightly packed masses and in telophase the nuclei are reformed (Figure 24d) without the chromosomes becoming individually recognisable.

Meiosis.

Meiosis was only observed in tetrasporangia. Cytological preparations of tetrasporangia were more difficult to obtain than those of apical cells. Tetrasporangia at first division are larger than apical cells, but are equally difficult to squash, and the cytoplasm stains densely, making good differentiation imperative. In addition a number of chromosome-like artifacts are produced, even in inter-phase nuclei, which increase the difficulty of interpreting the events occurring in divisions.

The tetrasporangial mother cell, as cut off the whorl branchlet cell, is ovoid in form and contains a single nucleus (Figure 24e).

FIGURE 24

SCAGELIA PYLAISAEI

(a) Mitotic prophase, showing individual chromosomes, in a supporting cell (SC) prior to auxiliary cell formation. CBC, 1, 2, 3, = carpogonial branch cells.

(b) Mitotic metaphase (MP) in an apical cell.

(c) Mitotic anaphase in an apical cell with two distinct chromosome plates (CP).

(d) Apical cell, nucleus in telophase (TN) prior to cytokinesis.

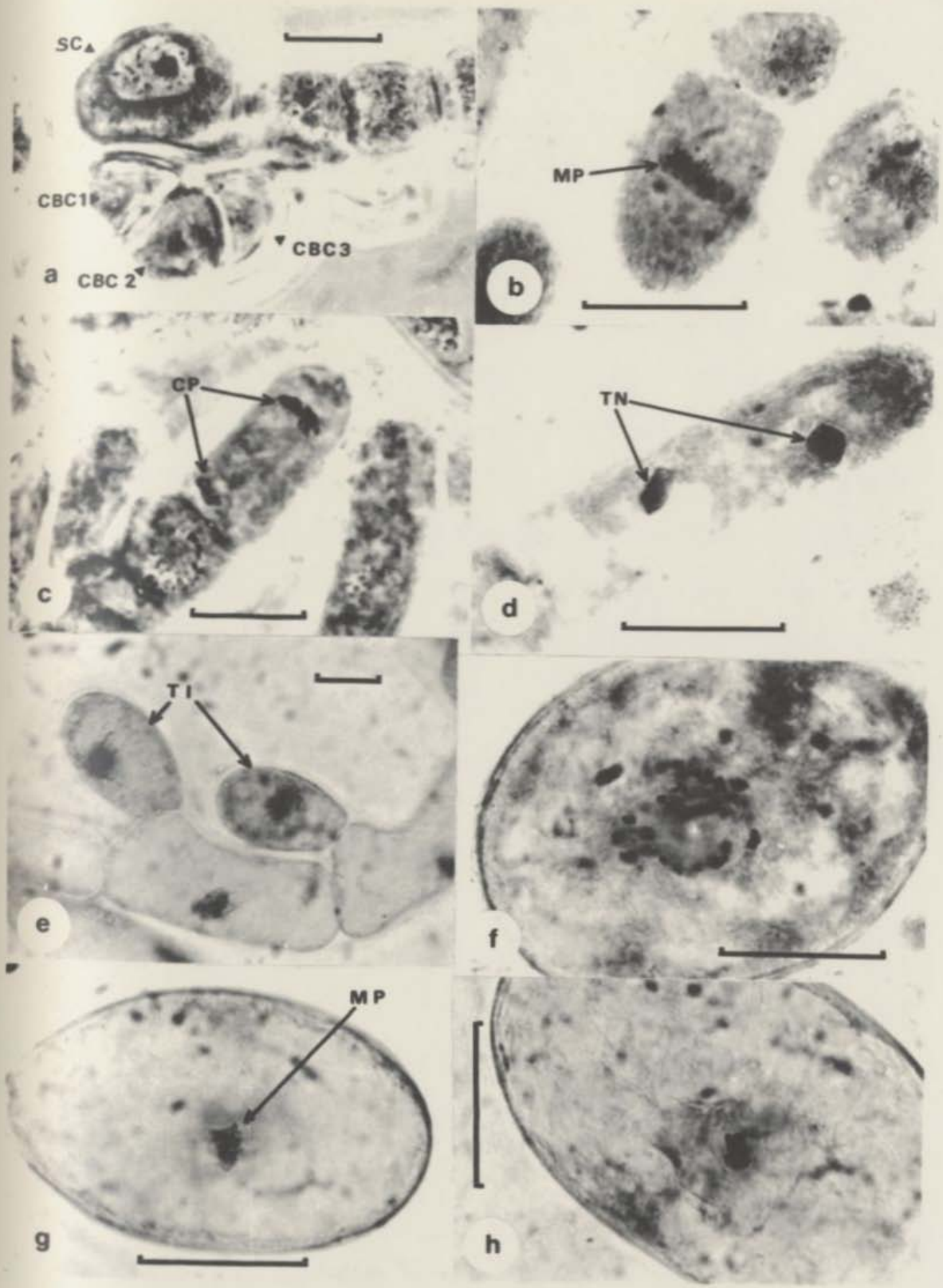
(e) Ovoid tetrasporangial initial (TI) with single centrally located nucleus.

(f) Tetrasporangium, nucleus in diakinesis with approximately 26 chromosome bivalents.

(g) Tetrasporangium with first metaphase plate (MP).

(h) Tetrasporangium in early anaphase, chromosome plates commencing separation.

All stained with acetocarmine. Scale = 10 µm throughout.


SC
CBC1
CBC3
a
CBC 2
MP
b
CP
c
TN
d
TI
e
f
MP
g
h

The cell enlarges and nuclear division commences. No division figures prior to the leptotene stage of prophase have been observed and the chromosomes in early leptotene are poorly staining and barely discernible. As the division proceeds into diakinesis the chromosomes shorten to produce deeply staining almost globular bivalents (Figure 24f). The nucleolus persists through diakinesis and disappears as the bivalents aggregate to form the metaphase plate (Figure 24g).

No spindle fibres or polar bodies have been observed and individual chromatids are not apparent at any stage of prophase. The chromosomes on the metaphase plate are more loosely aggregated than in mitotic metaphase, but are still individually indiscernible. The two groups of chromosomes separate as a mass in anaphase (Figure 24h) and in telophase (Figure 25a) they re-organize into the nucleus without becoming individually recognisable.

The cytoplasm cleaves along the short axis of the tetrasporangium at the site of the metaphase plate and a bisporangium, each cell containing a single nucleus, is formed (Figure 25b). Each bispore nucleus undergoes what is apparently a normal mitotic division, but the chromosomes appear less spread in prophase than they are in the mitosis of an apical cell. The metaphase plates (Figure 25c) are orientated along the long axis of the tetrasporangium, but may be rotated in this plane in respect to each other. If they lie in the same plane a regular cruciate tetrasporangium is formed (Figure 25d), but commonly the arrangement of the spores produced by this second division is offset (Figure 25d).

FIGURE 25

SCAGELIA PYLAISAEI

(a) Tetrasporangium with first telophase nuclei (1°TN). Stained with acetocarmine. Scale = 10 µm

(b) Bispore stage of tetrasporogenesis with uninucleate spores. Stained with acetocarmine. Scale = 50 µm

(c) Tetrasporangium at second metaphase showing orientation of metaphase plates (2°MP). Stained with acetocarmine. Scale = 10 µm

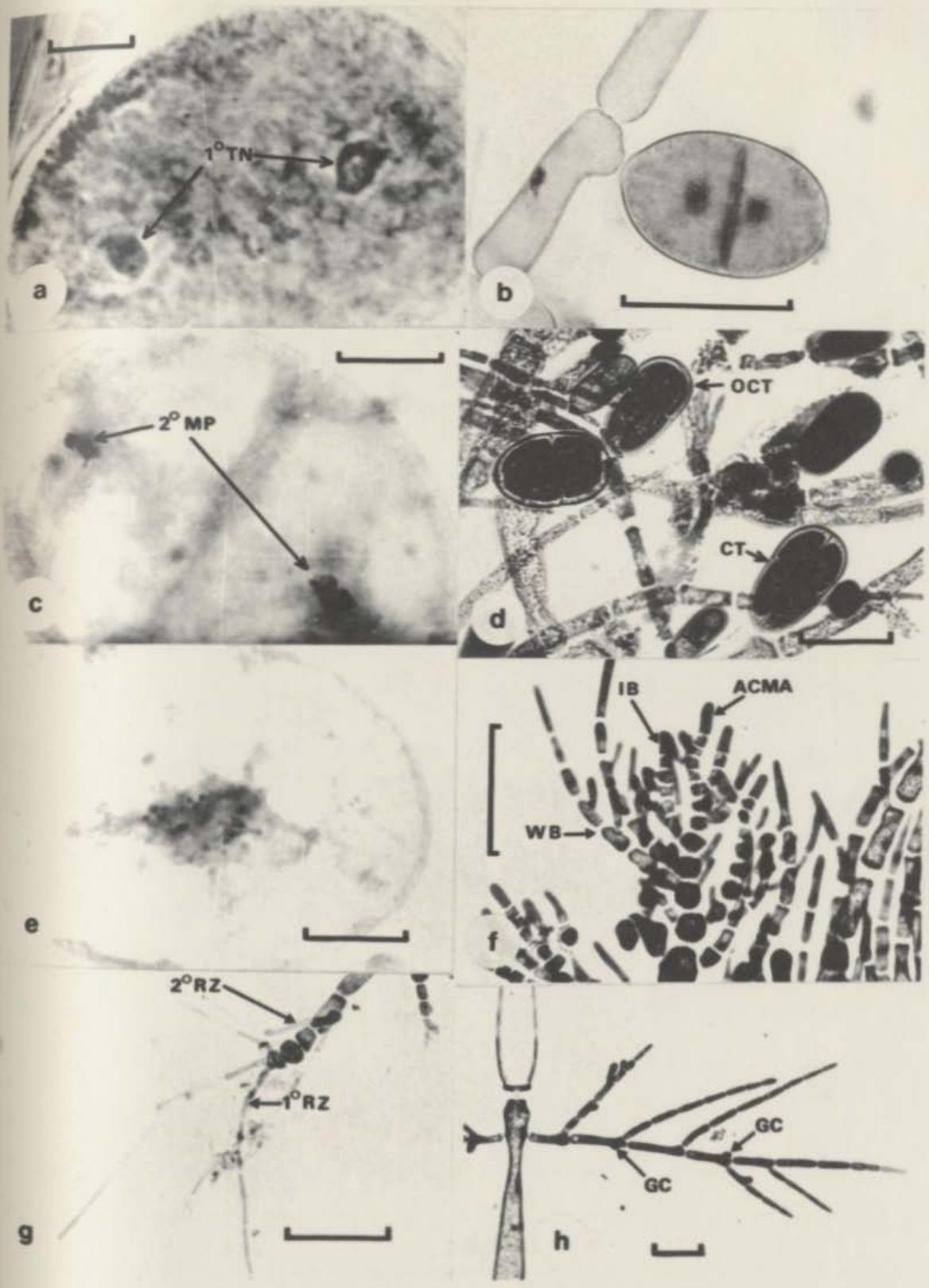
(d) Mature tetrasporangia showing cruciate (CT) and offset cruciate (OCT). Scale = 50 µm

(e) Apomeiotic tetrasporangium in prophase. Chromosomes do not occur as bivalents. Stained with acetocarmine. Scale = 10 µm

(f) Apical region with curvature of main axis behind the apical cell (ACMA), the development of whorl branchlets (WB) and indeterminate branches (IB). Scale = 10 µm

(g) Basal region with initial primary rhizoid (1°RZ) and secondary (2°RZ) re-inforcing rhizoids developing on basal axial cells. Scale = 100 µm

(h) Whorl branchlet with irregular pinnule arrangement. Gland cells (GC) are borne on whorl branchlets, but may occur together with a pinnule. Scale = 100 µm


1°TN
a
b
2°MP
c
OCT
CT
d
e
IB
ACMA
WB
f
2°RZ
1°RZ
g
GC
GC
h

Apomeiosis.

The cytology of tetrasporangia produced on functional gametophytes obtained in culture from tetraspores of both Forms A and B has been investigated. With the exception of the prophase, the processes appear identical with those described for normal meiosis. No early stages of prophase have been observed, but in the stage equivalent to diakinesis a haploid number of 20-26 individual chromosomes occurs (Figure 25e), which do not appear as bivalents. The later stages of tetraspore formation proceed in the same manner as in the meiotic tetrasporangia, and four uninucleate spores are produced.

Chromosome Numbers.

The small size of the chromosomes, the necessity of examination of these in late prophase and the difficulties of squashing the cells make precise chromosome counts impossible. Even when good preparations have been obtained chromosome counts have often differed between cells on the same plant.

The data obtained from the field material, together with its source, are given in Table 12 for Forms A and B. The culture data are presented in Table 13 , with the sources which refer to the results section of Tables 4 and 5 for cultures A and B respectively.

The frequency of chromosome numbers for all material examined from all mitotic sources is shown in Figure 26a . Bivalent numbers occurring at diakinesis in tetrasporangia are presented in a similar manner in Figure 26b. Although there is a considerable spread of data,

TABLE 12

CHROMOSOME COUNTS OBTAINED FROM FIELD MATERIAL OF FORMS A AND B OF *S. PYLAISAEI*

	Apical cells F. gametophytes		Apical cells Tetrasporophytes		Bivalents Tetrasporangia		Apical cells Sterile plants	
	Source	Number	Source	Number	Source	Number	Source	Number
Form A	124.5	18	121.1	43-47	124.24	24-26	128.8	46-52
	124.8	24-28	122.1	52	124.25	24-27	134.2	48
	124.25	26	124.5	44-50				
	124.26	20-26	124.8	51				
	145.1	23-27	124.24	48-50				
	158.2	30	124.25	46-52				
			124.26	49				
Form B	101.3	24	101.3	46-50	104.19	22-24	101.4	20-23, 46-49
	104.5	22-30	103.2	44-49			101.6	43-52
	104.6	23-26	104.5	47-54			101.10	48
	171.1	25	104.13	49			171.4	46-48

Source refers to the station/date number of the collection site.
Number refers to the chromosome number obtained except in meiotic counts where it refers to the number of bivalents observed.

TABLE 13

CHROMOSOME COUNTS FROM CULTURED MATERIAL OF *S. PYLAISAEI*

Form A

Culture result Category	Source of Material		Mitotic (a) Prophase	Tetrasporangial Prophase
I	124.21	$M^1:F^2$	21-26	
II	124.27	$T^3F^4:T^5M^6$	20-27	26[c]
III	128.12	T^7	46-53	22-25[b]
IV	124.22	T^8	49	24[b]
V	145.1	F^{10}	25	
V	145.1	T^{11}	48	

Form B

I	101.3, 104.8	$M^1T^2:F^3T^4$	22-27	
I	104.18	MT^2		23-26[c]
III	104.18	T^7	46-52	25-26[b]

a. counts obtained from vegetative apical cells, spermatangial mother cells and developing auxiliary cells

b. bivalents present at diakinesis

c. single chromosomes present in late prophase of tetrasporangium.

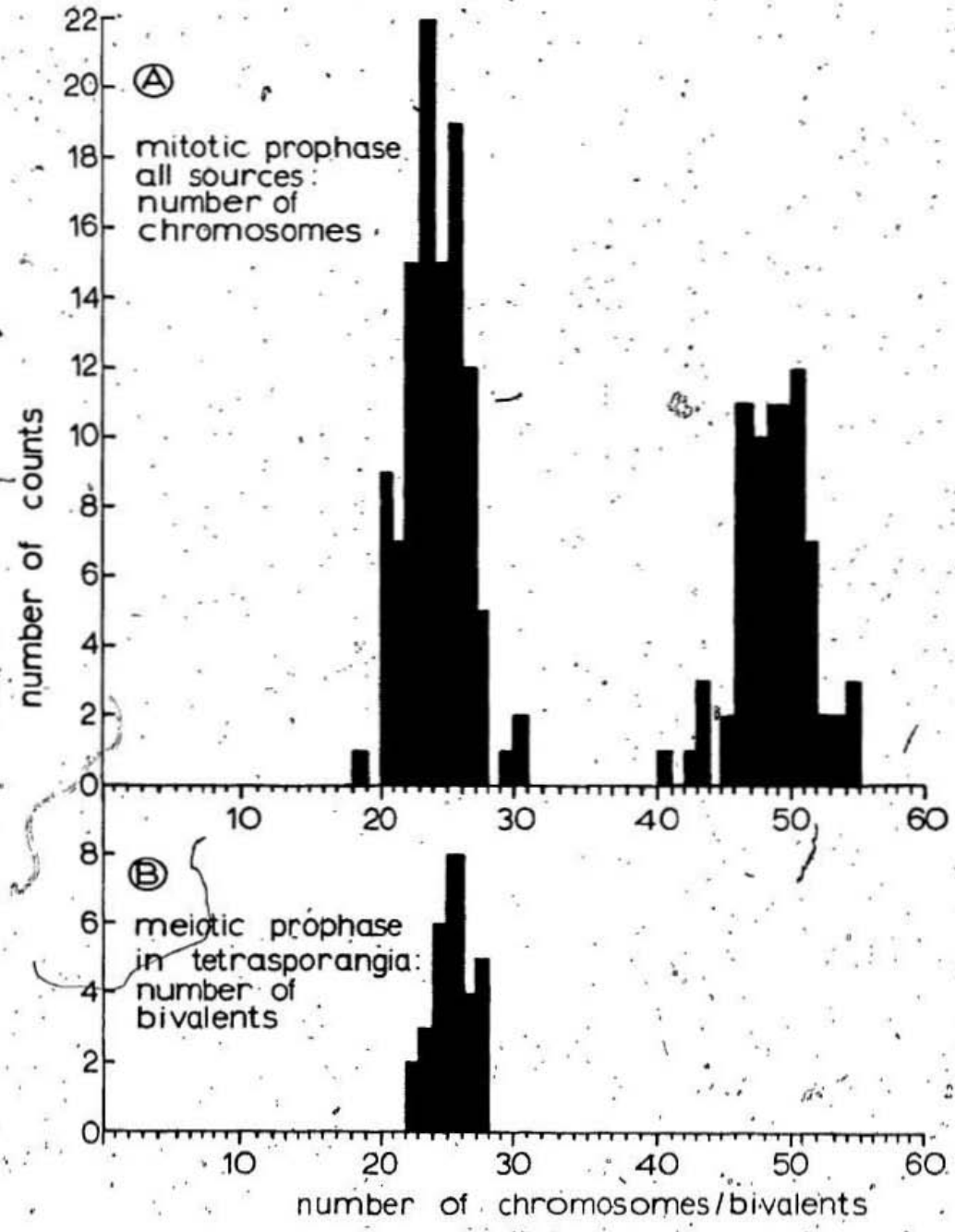
Culture result category and source of material refer to Table 4 Primary Cultures of Form A and to Table 5 Primary Cultures of Form B.

FIGURE 26

CHROMOSOME COUNTS IN

SCAGELIA PYLAISAEI

Distribution of chromosome counts from A. mitotic prophases and B. distribution of bivalent counts from meiotic prophases of tetrasporogenesis, obtained from both field and culture specimens.


A
mitotic prophase
all sources:
number of
chromosomes
B
meiotic prophase
in tetrasporangia:
number of
bivalents
number of counts
number of chromosomes/bivalents

two distinct groups of counts are apparent, the first ranges from 18-30 chromosomes with the maximum number of counts for 24-26 chromosomes; a second group shows a slightly greater spread, 40-55 chromosomes with a peak frequency between 47-52 chromosomes. The number of bivalents observed in meiosis ranges from 22-27 with a peak frequency at 25. There are no significant differences in chromosome numbers obtained from plants of Form A and Form B. Thus it would appear that the haploid chromosome number n = ca. 25, and a diploid number 2n = ca. 50.

In the field (Table 12) female gametophytes are haploid while tetrasporangial material is diploid, both haploid and diploid sterile plants have been observed. In Form A material from culture, male and female gametophytes are haploid (Table 13) as are those of Category II which possess apomeiotic tetrasporangia. Tetrasporophytes (Category III) are diploid, and bear meiotic tetrasporangia. The plants obtained in Category IV cultures bearing tetrasporangia and spermatangia are diploid with meiotic tetrasporangia, no counts have been obtained from spermatangial mother cells of this material. In Category IV the plants produced from the tetraspores (F^{10}) are haploid whilst those from the carpospores (T^{11}) are diploid, no cytological data have been obtained from the tetrasporangia borne on these plants. Form B (Table 12) shows a similar chromosome distribution, in Category I the male and female gametophytes are haploid and their tetrasporangia are apomeiotic. The tetrasporophytes (Category III) are diploid and have meiotic tetrasporangia.

Description of *Scagelia pylaisaei*

The specific epithets which are brought into synonymy as *Scagelia pylaisaei* were applied to several different morphological forms and these were often incompletely described. There is for instance no detailed report on the development of the carposporophyte. It is necessary therefore that *S. pylaisaei* be described. The following description is based entirely on field material and includes the complete morphological range observed in this study of both Form A and Form B.

Vegetative Morphology.

Main axis: *Scagelia pylaisaei* is erect and shows no tendency to a prostrate habit. Attachment is by rhizoids, initially from the basal cell of the main axis (Figure 10a) and subsequently re-enforced by others (Figure 25g) from the lower cells of the main axis and the basal cells of the whorl branchlets. The apical cell produces axial cells by transverse division and these enlarge, principally by elongation. Axial cell dimensions from herbarium material examined in this study are given in Figure 5a.

Whorl branchlets: Branchlets occur in whorls of two, three and four. They are formed by the lateral division of axial cells in the apical region. The first branchlets often occur secundly on two or three adjacent axial cells, and this produces a curvature of the axis in the apical region (Figure 25f). Whorl branchlets are initially simple (Figure 25f), but at maturity each cell may bear one or two pinnules. Pinnule arrangement varies being, secund

(Figure 6e) on the adaxial face of the whorl branchlet, irregular (Figure 25h) or pinnate (Figure 27a). Pinnules may also bear pinnules (Figure 27b) and in extreme instances whorl branchlets are bipinnate. Pinnules when arranged secundly or irregularly are found on the ab- and adaxial side of the whorl branchlets, but pinnately arranged pinnules are borne laterally.

There is a correlation between the ratio of length to diameter of the whorl branchlet cells and the pinnule arrangement. Branchlets of cells with high ratios usually have few pinnules and these are arranged in a secund or irregular manner. Cells with low ratios have predominantly pinnately arranged pinnules. Dimensions of the longest branchlet cells found in the herbarium material examined in this study are given in Figure 5c .

Mature paired whorl branchlets are usually of the same size (Figure 27c), but when arranged in whorls of three or four, one or two branchlets (Figure 27a) are often reduced.

Lateral indeterminate branches: Lateral indeterminate branches are borne on every 4th to 6th axial cell and develop into vegetative axes indistinguishable from the primary axis. They arise in the apical regions (Figure 25f) in an identical manner to the whorl branchlets which they replace. Whorl branchlets may arise when the branch is as few as four cells in length (Figure 25f) and initially are secund on the abaxial face. Branches may also replace pinnules on whorl branchlets (Figure 27d) and are usually formed on the basal cells.

Gland cells: Gland cells (Figure 25h) overlie individual cells of whorl branchlets and pinnules. They replace pinnules on the

FIGURE 27

SCAGELIA PYLAISAEI

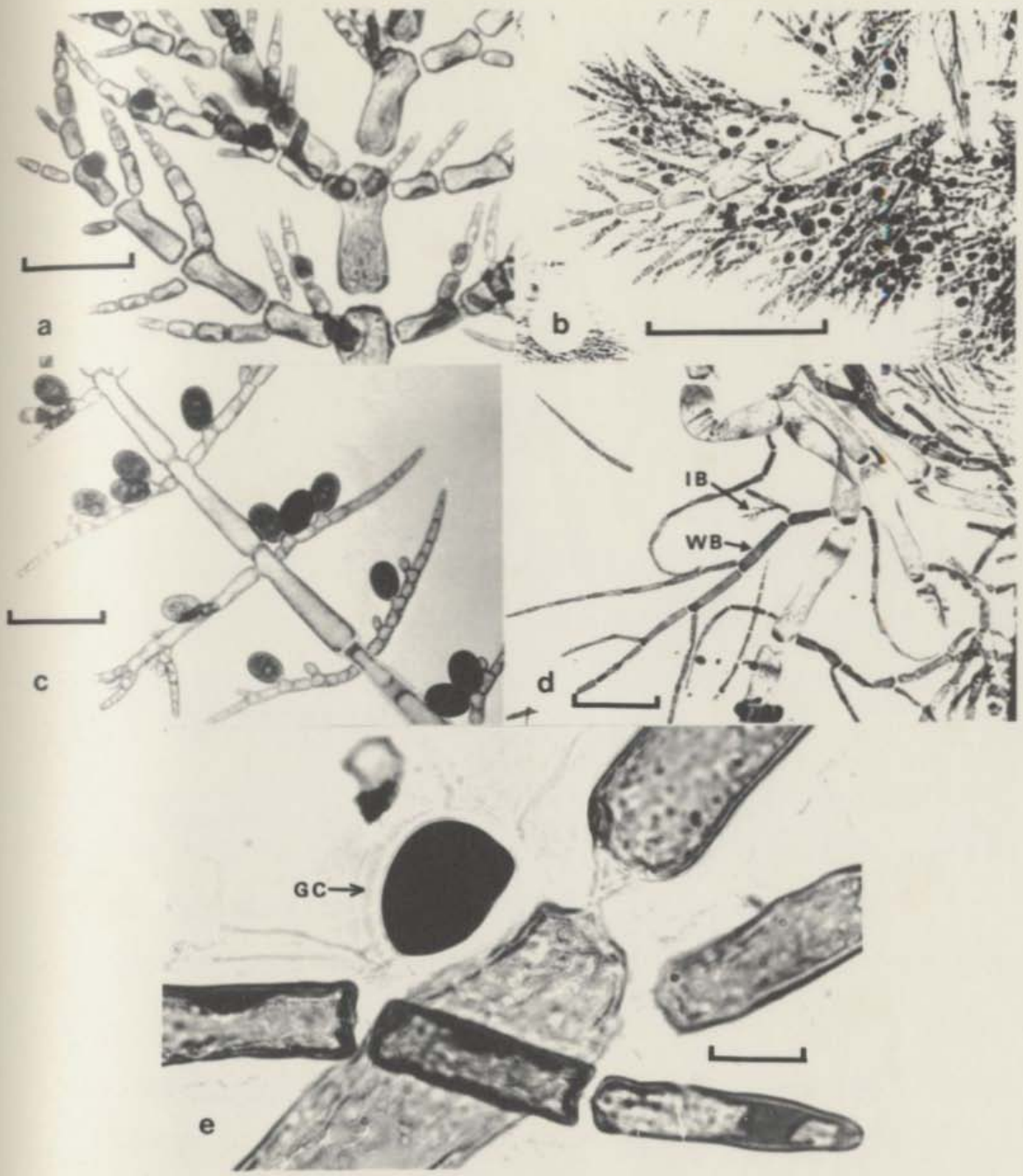
(a) Branchlets in whorls of three, two of similar size, the third reduced. Scale = 100 µm

(b) Whorl branchlets with bipinnately arranged pinnules. Scale = 500 µm

(c) Paired, opposite whorl branchlets of similar size, tetrasporangia, single and paired, are sessile on whorl branchlet cells. Scale = 100 µm

(d) Developing indeterminate branch (IB) replacing pinnules on whorl branchlets (WB). Scale = 100 µm

(e) Mature gland cell (GC) lacks pit connection with parent cell. Stained with acetocarmine. Scale = 10 µm


a
b
c
d
IB
WB
GC
e

whorl branchlet cells, often occurring together with a single pinnule (Figure 25h), but never found in addition to two pinnules. Two gland cells have not been seen on a single cell. Mature gland cells are discoid, measuring 10 x 5 µm to 35 x 35 µm (major diameter x depth) and have no pit connection with their parent cell. They have a refractive appearance and stain uniformly with acetocarmine (Figure 27e). The gland cell initial arises in the same manner as a pinnule and staining with acetocarmine revealed a nucleus (Figure 28a) and a pit connection, but as the cell matures it loses its pigmentation and the pit connection degenerates.

Morphology and Development of Reproductive Organs.

Tetrasporangia: Mature tetrasporangia are ovoid and cruciately divided (Figure 25d), but the vertical division is often offset giving an appearance of tetrahedral division (Figure 25d). They are borne singly or paired (Figure 27c), adaxially on whorl branchlet and pinnule cells. Measurements of mature tetrasporangia for the herbarium material examined are given in Appendix III, at maximum they measure 80 x 56 µm. The tetrasporangial initial is ovoid (Figure 24e) and divides transversely to form a bispore (Figure 25b), the bispore cells divide at right angles to the plane of the first division to form four spores.

Spermatangia: Whorls of 1 - 4 spermatangial branches (Figure 28b) are borne on whorl branchlet and pinnule cells. Each spermatangial branch is of 2-5 cells each bearing whorls of 1-4 branches composed of 1 or 2 cells. The ultimate cells are the spermatangial mother cells and each may form up to four spermatangia.

FIGURE 28

SCAGELIA PYLAISAEI

(a) Developing gland cell (GC) has pit connection (PC) with parent cell. Stained with acetocarmine. Scale = 10 μm

(b) Spermatangial branches (SC) borne on the whorl branchlets, releasing spermatia (S). Scale = 50 μm

(c) Procarp, carpogonial branch (CB) attached to enlarged supporting cell (Su.C) prior to auxiliary cell formation. Spermatia (S) are attached to the trichogyne (T). Scale = 50 μm

(d) Fungal infection of terminal cell of a rhizoid (RZ), the mature fungal sporangium (FS) has a single discharge tube (DT). Scale = 50 μm


PC
GC
a
S
SC
b
T
S
CB
Su.C
c
DT
FS
RZ
d

Procarps: Carpogonial branches (Figure 28c) develop on the basal cells of whorl branchlets in the apical regions of the axes. The whorl branchlet develops normally except that its basal cell produces a cell on its abaxial side which develops into a four celled carpogonial branch, the last cell is the carpogonium with an elongated trichogyne.

Development of the carposporophyte: Spermatia were observed attached to trichogynes (Figure 28c). The trichogyne subsequently degenerates and the basal cell of the whorl branchlet cuts off the auxiliary cell (Figure 29) on its adaxial face. The carpogonium develops a connection with the auxiliary cell, but from the material examined it was impossible to tell whether this connection is direct or through the intermediary of a connecting cell. A fusion cell forms (Figure 29), consisting of the auxiliary cell, the basal cell of the whorl branchlet and the axial cell on which this is borne. A gonimoblast initial (Figure 29) develops on, and remains partially fused with, the upper face of the auxiliarly cell. This initial produces four or five irregularly placed cells and each ultimately forms a group of carpospores aggregated into sequentially developing gonimolobes (Figure 29). The mature carposporophytes are not surrounded by whorl branchlets and the fertile axis continues vegetative growth and may subsequently bear other carposporophytes.

Fungal Parasites.

No fungal infections were seen on field material, but were found in a single culture of Form A. The culture (ES 10:16-8:150) was of apical fragments of a tetrasporangial plant from Portugal Cove

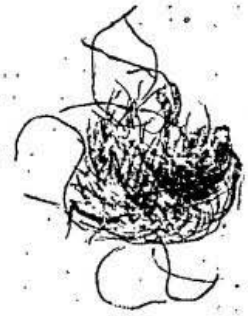


FIGURE 29

DEVELOPMENT OF THE CARPOSPOROPHYTE OF *SCAGELIA PYLAISAEI*

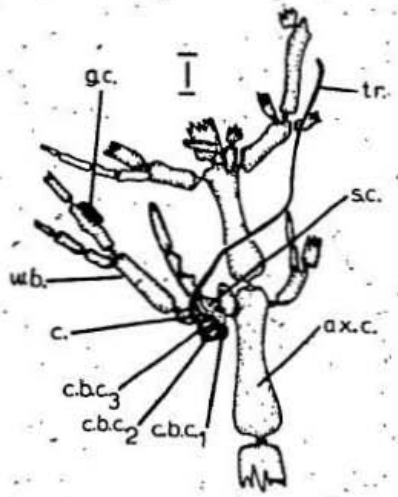
I. Development of the procarp, with the basal cell of a whorl branchlet functioning as the supporting cell bearing a three celled carpogonial branch plus the carpogonium with its elongate trichogyne.

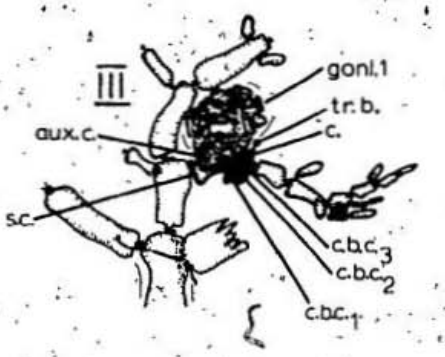
II. Immediate post-fertilization stage, the supporting cell has divided to produce the auxiliary cell and the trichogyne has partially degenerated, but no connection has developed between the auxiliary cell and the carpogonium.

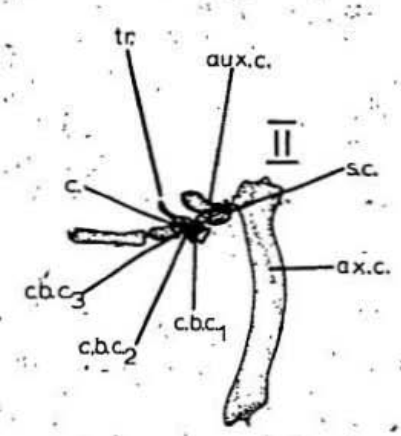
III. Initial development of the carposporophyte with a single gonimolobe. Partial fusion has occurred between the carpogonium, the auxiliary cell, the supporting cell and the axial cell bearing the fertile whorl branchlet.

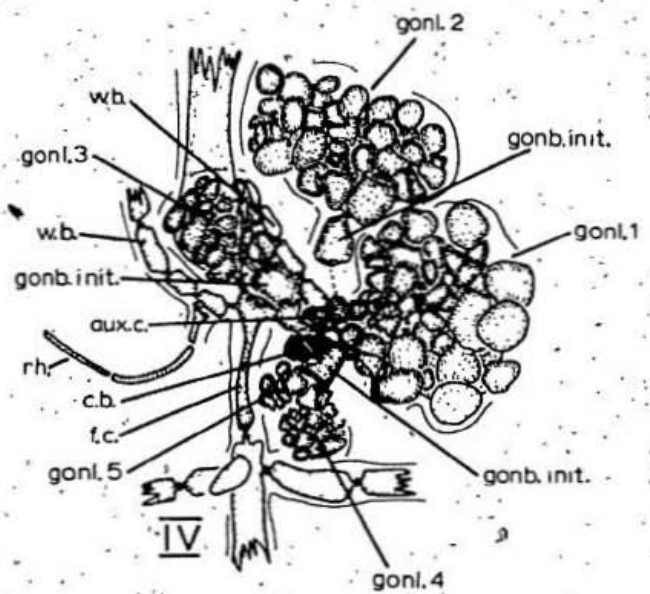
IV. Structure of the mature carposporophyte. Five gonimolobes are developing each on a gonimoblast initial cell. A prominent fusion cell has formed consisting of the axial cell, the supporting cell, the auxiliary cell and the carpogonium. The lower cells of the carpogonial branch persist.

aux.c. = auxiliary cell; ax.c. = axial cell; c. = carpogonium; c.b.c. = carpogonial branch cell; f.c. = fusion cell; g.c. = gland cell; gonl. = gonimolobe; gonb. init. = gonimoblast initial; rh. = rhizoid; s.c. = supporting cell; tr. = trichogyne; w.b. = whorl branchlet.


g.c.
I
tr.
s.c.
w.b.
c.
a.x.c.
c.b.c.3
c.b.c.2
c.b.c.1


III
gonl.1
tr.b.
aux.c.
c.
s.c.
c.b.c.3
c.b.c.2
c.b.c.1


tr.
aux.c.
II
s.c.
c.
a.x.c.
c.b.c.3
c.b.c.1
c.b.c.2


gonl.2
w.b.
gonb.init.
gonl.3
w.b.
gonl.1
gonb.init.
aux.c.
rh.
c.b.
f.c.
gonl.5
gonb.init.
IV
gonl.4

(St. 135.10) and was cytologically fixed before the fungus was found. Mature sporangia (Figure 28d) occurred in the apical cells of the axes, and in terminal cells of rhizoids. The contents of the infected cells were destroyed, but the adjacent cells appeared normal. The sporangia were completely contained within the host cell and measured (22) 30-40 (45) x (12) 22-30 (37) µm, they possessed single discharge tubes measuring 5-8 x 5-8 µm (length x diameter). No planonts were observed.

Habitat.

Both Forms A and B, where these were identified, occur in sheltered and exposed localities. Scattered specimens are found in the lower littoral, especially in rock pools, but they occur most commonly in the immediate sublittoral, both are found to the lower limit (Approx. 40 m), from which collections have been made. Both forms grow on bedrock, stable boulders, and commonly as epiphytes on larger algae in exposed localities. In sheltered regions they also occur on loose gravel.

No detailed morphological studies were undertaken with respect to depth, but plants from deep water are usually smaller than those from the immediate sublittoral. Changes in cellular morphology and branching pattern with depth, at least over the ranges examined here, appear insignificant in comparison to seasonal changes.

ANTITHAMNIONELLA FLOCCOSA (O. F. MÜLL.) NOV. COMB.

Introduction

Taxonomic Introduction

A. floccosa was first described from Norway by Müller (1782) as *Conferva floccosa*, and the currently accepted name is *Antithamnion floccosum* (O. F. Müll.) Kleen (Parke and Dixon, 1968; South and Cardinal, 1970). This study has shown that the species does not fall within the circumscription of the genus *Antithamnion* Nägeli (1847) as outlined by Wollaston (1968, 1971), and its transfer to the genus *Antithamnionella* Lyle is proposed. The species will thus be named *Antithamnionella floccosa* (O. F. Müll.) nov. comb. and will include in synonymy the following:

Conferva floccosa O. F. Müller (1782)

Callithamnion plumula var. *pusilla* Lyngbye (1819)

Callithamnion floccosum (O. F. Müll.) C. Ag. (1828)

Callithamnion pollexfenii Harvey (1844)

Pterothamnion floccosum Nägeli (1855)

Antithamnion floccosum (O. F. Müll.) Kleen (1874)

Callithamnion floccosum var. *atlanticum* J. Ag. (1876)

Antithamnion plumula var. *floccosum* Rosenvinge (1893)

Geographical Distribution

A. floccosa has been reported from the North Atlantic and the North Pacific; in the former it occurs on both the American and European coasts. Its recorded range in eastern North America is from Massachusetts (Taylor, 1957) northwards to southern Labrador (South

and Hooper, 1972); reports of its occurrence in eastern Canada have been listed by Cardinal (1968) and subsequent to this it has been recorded from Newfoundland (South, 1970; Whittick and South, 1971, 1972). In Europe it occurs in Scotland (Batters, 1902), the Faeroes (Børgesen, 1902) and northern Norway (Kleen, 1874; Foslie, 1890; Jaasund, 1965), but is apparently absent from southern Scandinavia. Zinova (1955) reports its occurrence in the Murman Sea, it is present in Iceland (Jønsson, 1901) and southern Greenland (Rosenvinge, 1899), but has not been reported from Spitzbergen. Its occurrence on the Pacific coast of North America (Kylin, 1925; Scagel, 1957) has been questioned (Wollaston, 1971).

Vertical Distribution

A. floccosa is frequently reported from the lower littoral (Foslie, 1890; Jønsson, 1901; Børgesen, 1902; Taylor, 1957), but has been found sublittorally to depths of 20 m (Jaasund, 1965) in Norway, and to 35+ m in Eastern Canada (Edelstein *et al.*, 1969).

Reproduction and Life History

No experimental work on the life history of *A. floccosa* has been reported. Tetrasporangia have been frequently recorded in the field (Foslie, 1890; Jønsson, 1901; Børgesen, 1902; Newton, 1931; Taylor, 1957; Jaasund, 1965), but there are no reports of male gametophytes. Female gametophytes, with carposporophytes, have been recorded on a single occasion (Foslie, 1890). There are no descriptions of the carposporophyte; the report by Daines (1913) is from a species currently recognised as *Antithamnionella pacifica* (Harv.) Wollaston

(Kylin, 1925). Edelstein and McLachlan (1966) have observed juvenile plants of *A. floccosa* between January and March in Nova Scotia, and have reported tetrasporangial plants in January, February, May, November and December (Edelstein *et al.*, 1970).

Fungal Infections

A. floccosa, in Newfoundland, is attacked by a species of *Olpidiopsis* Cornu (Oomycetes, Olpidiopsidaceae) which was initially identified as *O. magnusii* Feldmann and Feldmann (Whittick and South, 1971), but later described as a new species, *O. antithamnionis* Whittick and South (1972).

Aims of the Study

The principal aims of this study of *A. floccosa* were:

i. to provide a detailed description of the species with special reference to the development of the carposporophyte.

ii. to determine its reproductive periodicity at the Bay Bulls (St. 124) study site.

iii. to determine its life history in culture.

iv. to provide cytological confirmation of its life history.

v. to report on an incidence of fungal parasitism.

Observations and Results

Description of *Antithamnionella floccosa*

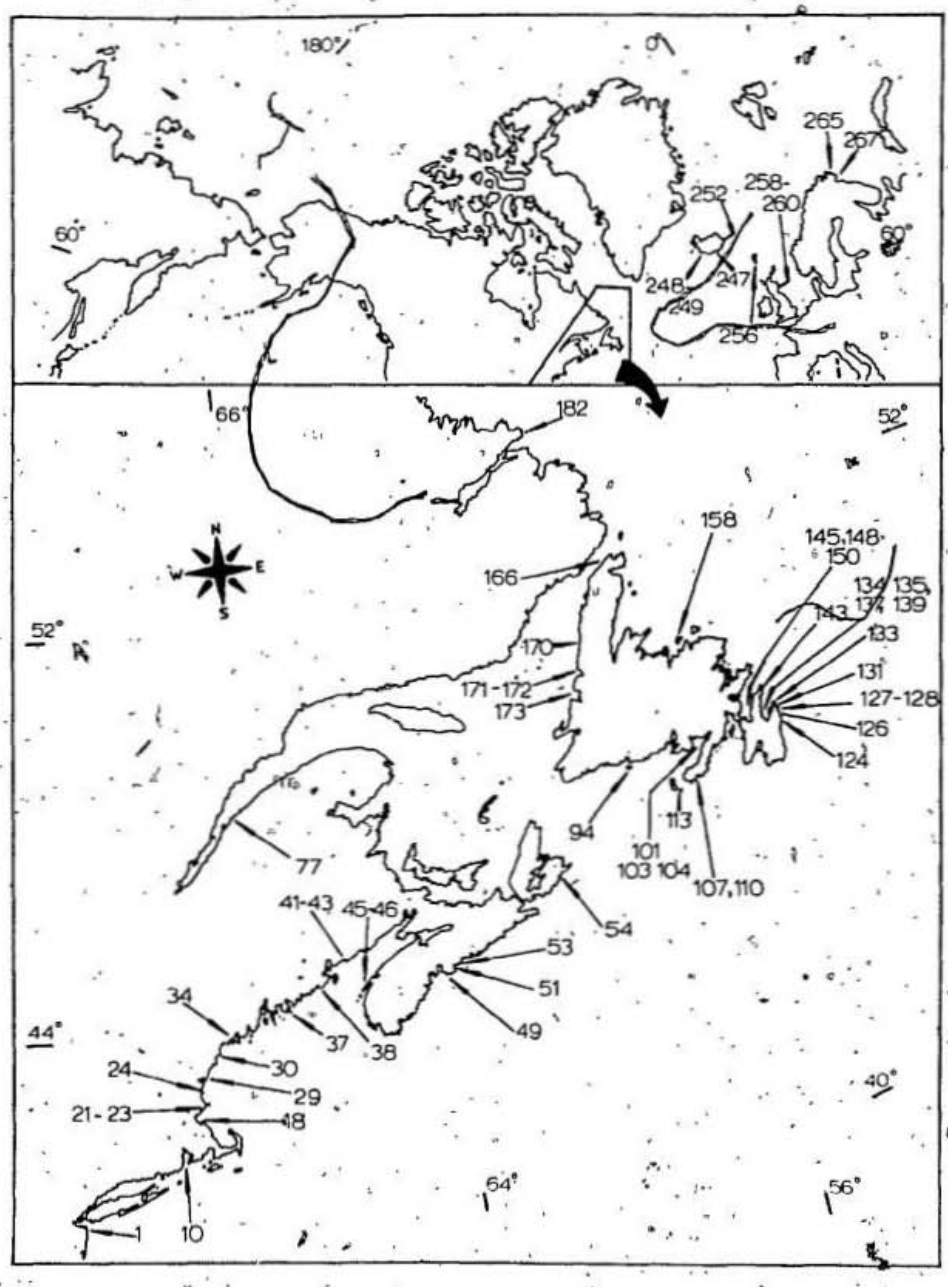
This description is based on an examination of herbarium material (from the sites given in Appendix II, and illustrated in Figure 30), and on extensive collections from Bay Bulls (St. 124).

FIGURE 30

COLLECTION SITES OF EXAMINED SPECIMENS OF

ANTITHAMNIONELLA FLOCCOSA

Localities from which specimens of *A. floccosa* examined in this study were obtained. The localities indicated by the station numbers are given in Appendix II.


180°
60°
265
267
252
258-
260
60°
248
247
249
256
66°
182
52°
158
145,148
150
166
134
135
139
143
137
133
52°
170
131
171-172
127-128
173
126
124
94
113
101
103 104
107,110
77
41-43
45-46
54
53
51
34
49
44°
37
38
24
30
29
21-23
48
40°
64°
56°
1
10

The herbarium material confirms the distribution of the species as given in the literature and extends the range southward in North America to northern New Jersey (St. 1.1). Specimens from southern Greenland (Rosenvinge, 1899) have not been seen.

Vegetative Morphology.

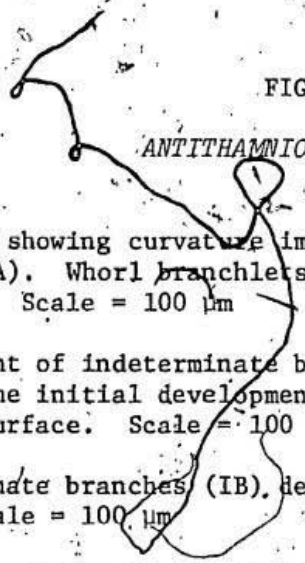
A. floccosa has a prostrate habit, but the tips of the axes are free and erect. Axial cells vary in size depending on their position; the smallest is the immediate subapical cell (4-7 x 8-10 µm), and in the mature axis they may measure 2000 x 150 µm. Each axial cell bears a pair of subequal, opposite, simple, subulate whorl branchlets, which in the mature part of the thallus consist of ten to fifteen cells. The largest of the whorl branchlet cells may measure 65 x 30 µm. The whorl branchlets are arranged distichously on the axis, and arise in the apical region in a regular manner. The 3rd, 4th, 5th, and occasionally 6th axial cells from the apex divide simultaneously (Figure 31a), each producing a single, secund whorl branchlet. The axial cells immediately below develop a similar secund whorl branchlet series, but on the opposite side of the axis, and they divide again to produce the second whorl branchlet (Figure 31a).

Whorl branchlets reach their maximum size on the 15th to 25th axial cells; they are erecto-patent to the axis, rarely become recurved and are never uncinate.

Indeterminate lateral branches arise in an identical manner to the whorl branchlets (Figure 31b) which they replace. They are borne alternately on every 3rd to 6th axial cell. On occasion

FIGURE 31

ANTITHAMNIONELLA FLOCCOSA



(a) Main axis showing curvature immediately posterior to the apical cell (ACMA). Whorl branchlets (WB) develop secundly in groups of three. Scale = 100 µm

(b) Development of indeterminate branches (IB) in the apical region showing the initial development of whorl branchlets on the abaxial surface. Scale = 100 µm

(c) Indeterminate branches (IB) developing on the whorl branchlets (WB). Scale = 100 µm

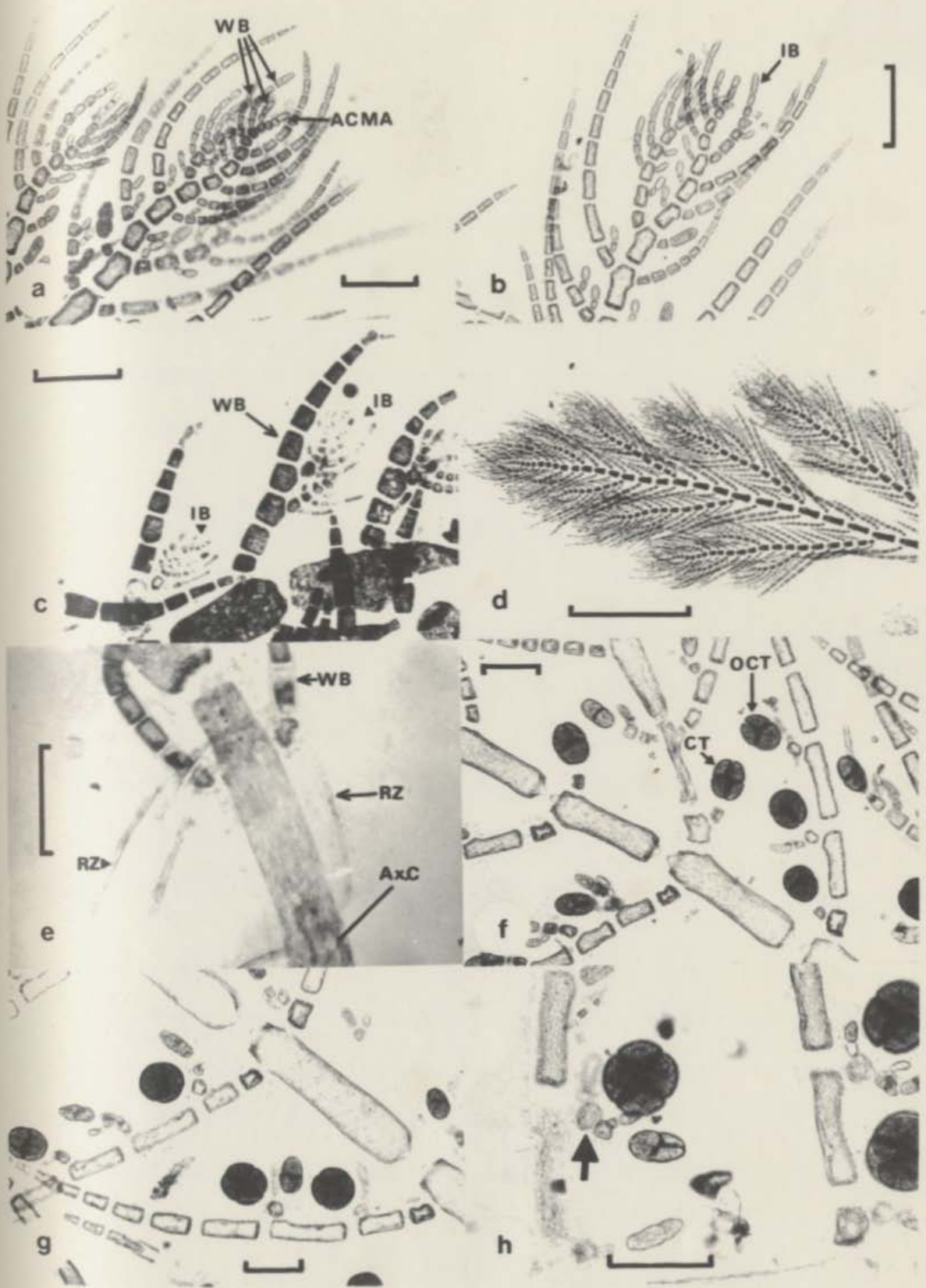
(d) Tufted appearance of the apical region. Scale = 500 µm

(e) Rhizoids (RZ) developing on cells of whorl branchlets (WB) in proximity to the axial cells (Ax.C). Scale = 100 µm

(f) Cruciate (CT) and offset cruciate tetrasporangia (OCT) pedicellate on a single cell or developing terminally on a two to four celled pinnule. Scale = 100 µm

(g) Tetrasporangia occurring in clusters of two and three on a single cell. Scale = 100 µm

(h) Cell bearing the tetrasporangia may also produce a two to four celled branch on which other tetrasporangia may form. Scale = 100 µm


WB
ACMA
a
IB
b
WB
IB
IB
c
d
WB
RZ
RZ
AxC
e
OCT
CT
f
g
h

indeterminate branches also develop on whorl branchlet cells (Figure 31c).

The relationship between axial cell size, their position, and the length of the whorl branchlets which they bear, is shown in Figure 32 for a typical plant of *A. floccosa*. Axial cell length increases regularly with distance from the apex. After the 20th axial cell the length of the whorl branchlets does not increase, and the 50th and 60th axial cells are approximately the same length as their whorl branchlets. In the basal regions of the plants, axial cells may be four to five times as long as their whorl branchlets. As a result of this growth pattern, whorl branchlets, and indeterminate branches with their whorl branchlets, are clustered in the apical regions. The basal regions, with their elongated axial cells, appear sparsely branched, giving the apical region of *A. floccosa* a distinctive tufted appearance (Figure 31d).

As the axis grows, its basal regions become prostrate and attached to the substrate by rhizoids, which develop on the whorl branchlet cells proximal to the axis (Figure 31e).

Reproductive Morphology.

Tetrasporangia: Tetrasporangia are borne on the adaxial face of a whorl branchlet, they are never sessile, but usually pedicellate on a single cell (Figure 31f). On occasion they are terminal on a two- to four-celled pinnule (Figure 31f). The tetrasporangia are usually solitary, but may be borne in clusters of two or three on a single cell (Figure 31g). The cell which bears the tetrasporangium

FIGURE 32

COMPARATIVE MORPHOLOGY OF
ANTITHAMNIONELLA FLOCCOSA
AND *A. PACIFICA*

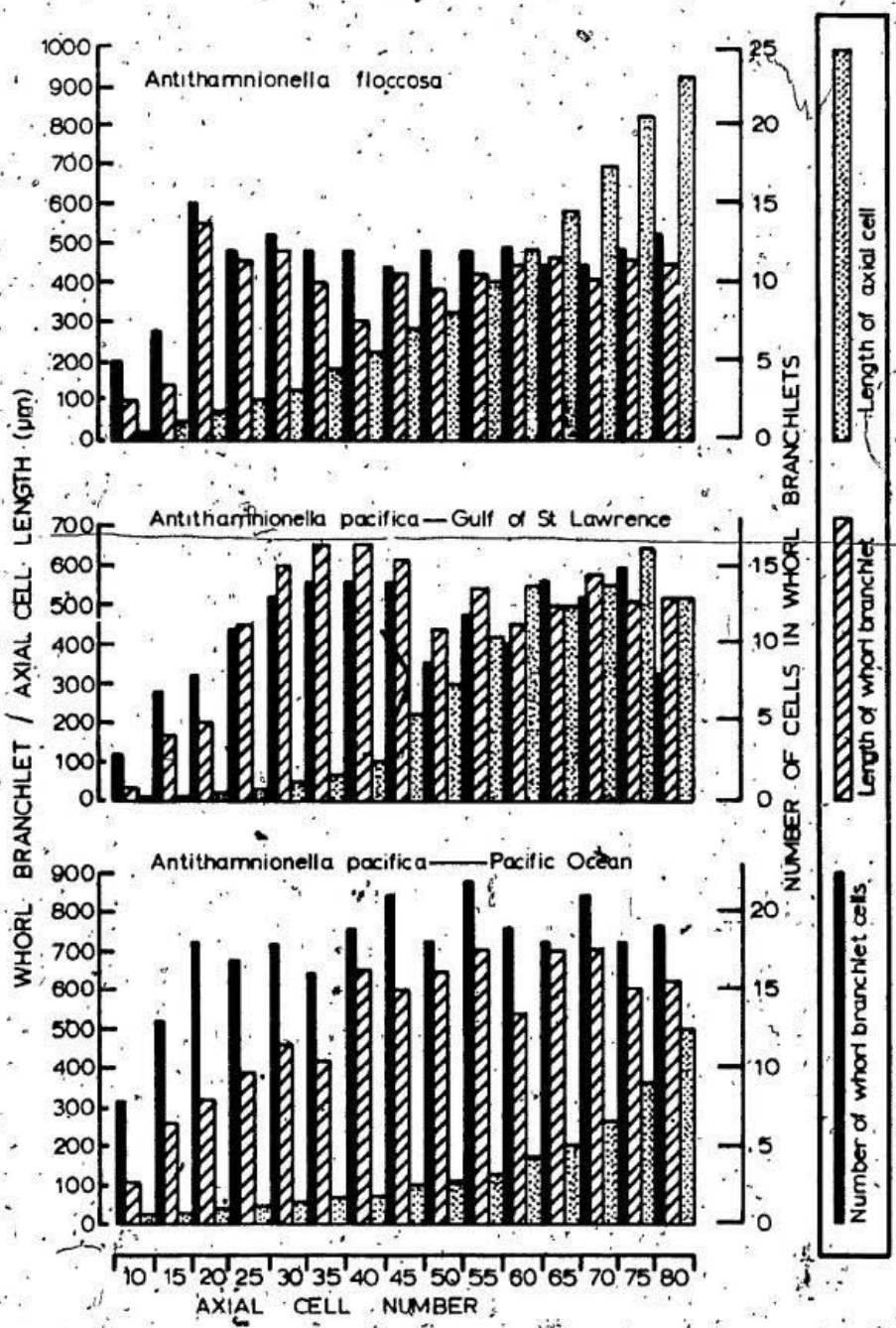
Comparison of the length of every fifth axial cell in the main axis, together with the length and the number of cells, of the longest whorl branchlet borne on this axial cell for three species of *Antithamnionella*.

A. floccosa (St. 124.26, Bay Bulls, November 1971)

A. pacifica (St. 77.1, St. Fabien-sur-Mer, Gulf of St. Lawrence, September 1966)

A. pacifica (Pacific Grove, California; *fide* Wollaston)

All data has been obtained from a single specimen in each instance.


Antithamnionella floccosa
Antithamnionella pacifica—Gulf of St Lawrence
Antithamnionella pacifica——Pacific Ocean
WHORL BRANCHLET / AXIAL CELL LENGTH (µm)
NUMBER OF CELLS IN WHORL BRANCHLETS
AXIAL CELL NUMBER
Length of axial cell
Length of whorl branchlet
Number of whorl branchlet cells

may divide to produce a short two to three celled branch (Figure 31h) on which other tetrasporangia may form.

The developing tetrasporangium enlarges to 50-60 x 25-30 µm prior to the first division which is across the narrow axis to form a bispore (Figure 33a); a second vertical division produces the tetraspore. Three types of division are evident in the mature tetrasporangia: a regular cruciate division (Figure 31f), an offset cruciate division (Figure 31f), and what appears to be a normal tetrahedral division (Figure 33b); all may be found on the same plant.

Clusters of undivided sporangia-like bodies (Figure 33c) have been frequently observed, and are particularly common in the prostrate basal regions of the plants. They occasionally appear to be cruciately divided (Figure 33c), and it is possible that they are abortive tetrasporangia. Similar structures were reported by Jaasund (1965) for *A. floccosa* (as *Antithamnion floccosum*). It is not known if they are viable and if so whether they function as meiotic tetrasporangia or mitotic monosporangia.

Spermatangia: Short two to five celled branches develop, either singly, or in groups of two or three on the adaxial side of the whorl branchlets (Figure 33d). Each cell of the short branches may either bear a whorl of two to four spermatangia, or develop a short, one to three celled branch, each cell of which bears two to four spermatangia.

Procarps: The first cell of a whorl branchlet is cut off from an axial cell in the apical region of the axis. This single whorl

FIGURE 33

ANTITHAMNIONELLA FLOCCOSA

(a) Cytokinesis of tetrasporangium showing initial bispore formation. Scale = 10 µm

(b) Mature tetrahedrally divided tetrasporangium (TT). Scale = 50 µm

(c) Clusters of monosporangia (MC) with a single developing tetrasporangium (T). Scale = 50 µm

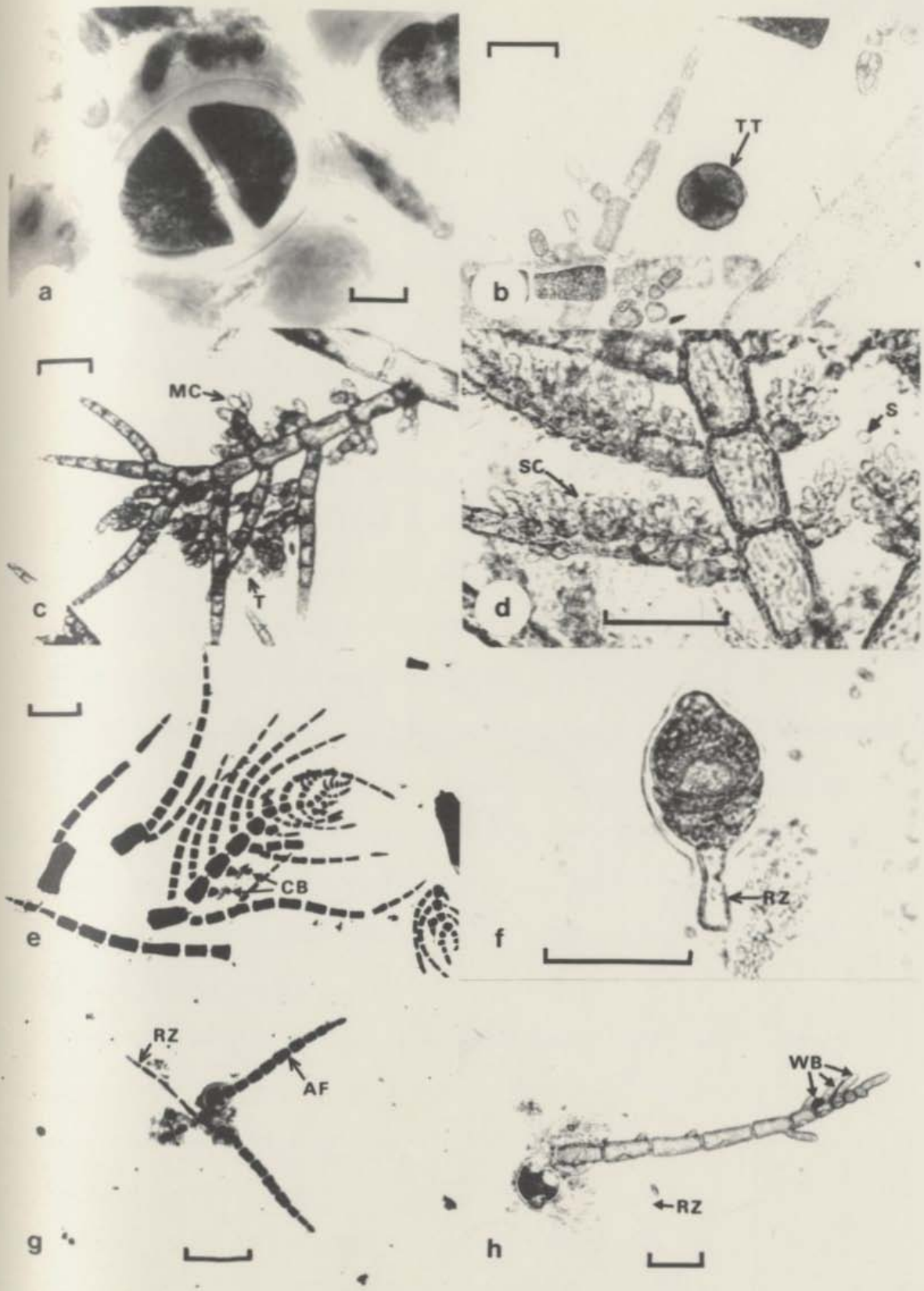
(d) Spermatangial clusters (SC) on adaxial surface of whorl branchlets, releasing spermatia (S). Scale = 50 µm

(e) Apical region of female gametophyte with carpogonial branches (CB) on basal cells of reduced whorl branchlets remaining unfertilized. Axis continues normal vegetative growth. Scale = 50 µm

(f) Germinating tetraspore producing a rhizoid (RZ). Scale = 50 µm

(g) Late stage of spore germination with a rhizoid (RZ) and a simple axial filament (AF). Scale = 100 µm

(h) Formation of first whorl branchlets (WB) on an axial filament. Rhizoid (RZ) continues growth. Scale = 50 µm


a
b
TT
MC
T
c
SC
S
d
CB
e
RZ
f
RZ
AF
g
WB
RZ
h

branchlet cell is the supporting cell, and divides to produce a cell on its abaxial face (Figure 34) to form a four celled carpogonial branch. The terminal carpogonium is elongated to form a trichogyne (Figure 34). The whorl branchlet cell then divides again, but the cell produced undergoes no further division, thus a fertile whorl branchlet consists of two cells (Figure 34).

If fertilization does not occur the trichogyne degenerates, the vegetative axis continues growth, but no further development of the whorl branchlet occurs (Figure 33e).

Development of the carposporophyte: After fertilization, the basal portion of the trichogyne persists (Figure 34). The carpogonium produces a connecting cell (Figure 34), which fuses with the auxiliary cell, formed on the adaxial face of the supporting cell. During development of the carposporophyte, the auxiliary cell, the supporting cell, and the axial cell bearing the fertile whorl branchlet fuse. This fusion cell is also partially fused with the gonimoblast initial (Figure 34), which is cut off from the upper surface of the auxiliary cell. The gonimoblast initial produces two to five cells, each producing carpospores aggregated into sequentially developing gonimolobes (Figure 34).

Growth of the fertile axial apex ceases after fertilization and is replaced (Figure 34) by the accelerated growth of a lateral branch. The development of the carposporophyte stimulates division of the axial cells immediately distal to the fusion cell. In addition to their paired distichous whorl branchlets they develop one or two further whorl branchlets (Figure 34), which form a loose

FIGURE 34

DEVELOPMENT OF THE CARPOSPOROPHYTE OF *ANTITHAMNIONELLA FLOCCOSA*

I. Development of the procarp on the basal cell of a developing whorl branchlet in the apical region of the plant.

II. Four celled carpogonial branch, including carpogonium with elongated trichogyne.

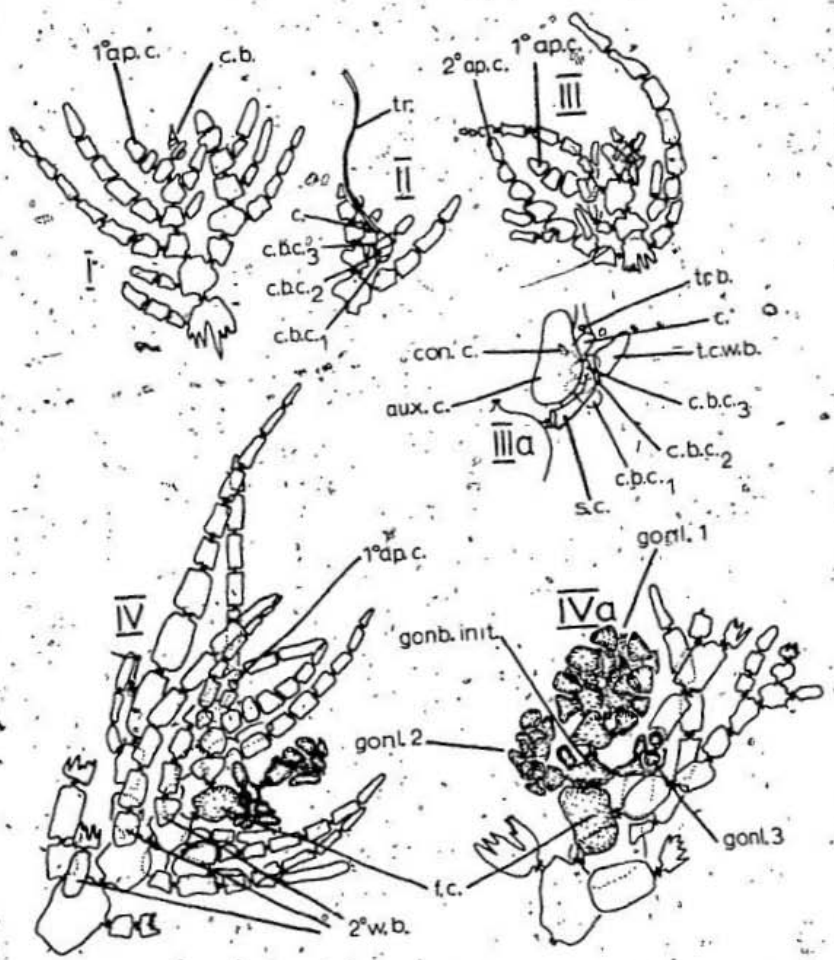
III. Immediate post-fertilization stage. The growth of the main axis by division of the primary apical cell is supressed and is replaced by a secondary apical cell of an indeterminate lateral branch.

IIIa. Detail of immediate post-fertilization stage. The fertile whorl branchlet does not continue vegetative growth and consists only of the basal supporting cell and second terminal cell. The supporting cell divides to produce the auxiliary cell on its adaxial face which becomes joined with the carpogonium via a connecting cell. The trichogyne degenerates, but the basal portion persists separate from the carpogonium.

IV. Developing carposporophyte. A fusion cell forms from the axial cell bearing the fertile whorl branchlet, the supporting cell, the carpogonium, the auxiliary cell and the gonimoblast initial developing from this cell. The axial cells basal to the fusion cell divide laterally to produce secondary whorl branchlets, which form a loose involucre around the developing carposporophyte.

IVa. Detail of the developing carposporophyte. The fusion cell produces a gonimoblast initial producing cells which develop into a series of sequentially developing gonimolobes.

ap.c = apical cell; aux.c = auxiliary cell; c. = carpogonium; c.b. = carpogonial branch; c.b.c. = carpogonial branch cell; conc.c = connecting cell; f.c. = fusion cell; gonl. = gonimolobe; gonb. init. = gonimoblast initial; s.c. = supporting cell; tr. = trichogyne; tr.b. = trichogyne base; t.c.w.b. = terminal cell of whorl branchlet; w.b. = whorl branchlet.


1°ap.c.
c.b.
tr.
II
c.
c.b.c.3
c.b.c.2
c.b.c.1
I
2°ap.c.
1°ap.c.
III
tr.b.
c.
con. c.
t.c.w.b.
aux. c.
c.b.c.3
IIIa
c.b.c.2
c.b.c.1
s.c.
1°ap.c.
IV
gonl. 1
IVa
gonb. init.
gonl. 2
gonl. 3
t.c.
2°w.b.

filamentous involucre around the carposporophyte.

Habitat.

In Newfoundland, *A. floccosa* occurs in rock pools on the lower littoral and extends to depths of 15 metres. It is most common at depths of 2-5 metres, where it grows abundantly on solid rock substrate in both sheltered and exposed localities. *A. floccosa* rarely grows epiphytically, but small plants have on occasion been found on *Ptilota serrata* Kütz.

Reproduction and Life History

Reproductive Periodicity.

Data on reproductive periodicity are summarized in Figure 35. Sterile plants predominate, except at two periods: in June and July fertile tetrasporophytes are most abundant, and between November and March tetrasporophytes and fertile gametophytes are found. Fertile male gametophytes, and female gametophytes bearing carposporophytes, are most abundant between November and January, and at other times of the year only isolated plants are found. Tetrasporophytes predominate in June and July to the virtual exclusion of all other plants, and throughout the year are more abundant than gametophytes.

Life History in Culture.

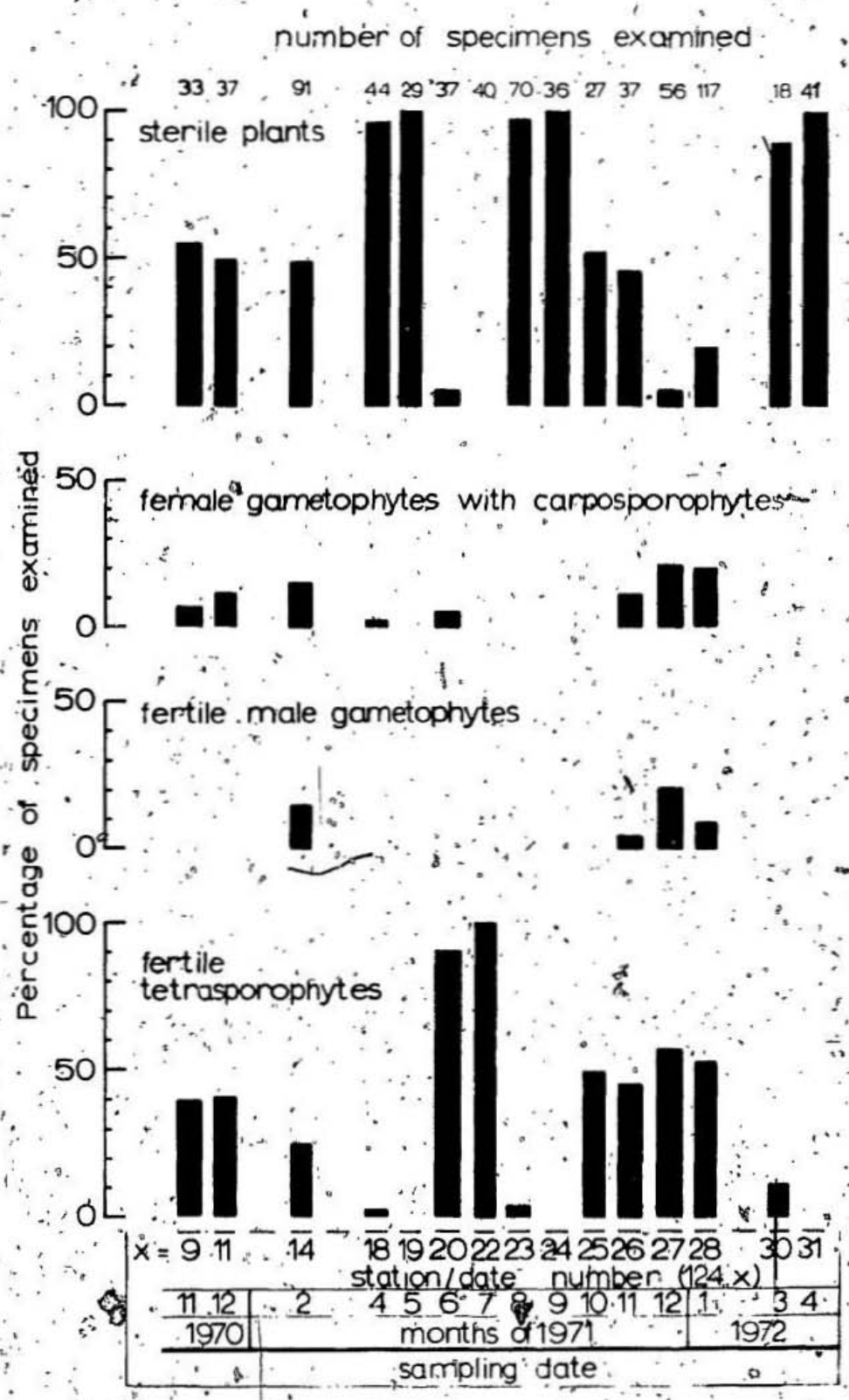
Cultures were derived from spores of plants collected at the following localities: carpospores St. 104.8, St. 131.1, St. 135.11, tetraspores St. 104.13, St. 124.20, St. 128.9, and were grown in ER 10:16-8:1200 or 10:16-8:500. The spores germinated approximately

FIGURE 35

REPRODUCTIVE PERIODICITY OF

ANTITHAMNIONELLA FLOCCOSA

Reproductive periodicity of *A. floccosa* at Bay Bulls (St. 124) between September 1970 and April 1972. Data are shown as percentage of total number of specimens examined for four categories of plant: sterile plants, female gametophytes with carposporophytes, fertile male gametophytes and fertile tetrasporophytes.


number of specimens examined
33 37 91 44 29 37 40 70 36 27 37 56 117 18 41
100
50
0
sterile plants
50
0
female gametophytes with carposporophytes
50
0
fertile male gametophytes
Percentage of specimens examined
100
50
0
fertile tetrasporophytes
x = 9 11 14 18 19 20 22 23 24 25 26 27 28 30 31
station/date number (124 x)
11 12 2 4 5 6 7 8 9 10 11 12 1 3 4
1970
months of 1971
1972
sampling date

24 hrs after discharge. They enlarged to ca. 60 µm diameter, divided transversely, a protrusion formed at the rhizoidal pole, and a rhizoid (Figure 33f) of elongate colorless cells (ca. 100 x 10 µm) developed.

The apical pole of the spore produced a simple filament of 6-8 cells (Figure 33g). Formation of whorl branchlets commenced at this stage (Figure 33h). Carpospores and tetraspores germinated in an identical manner; no aberrant germination patterns were seen. The plants were maintained in culture, when necessary by apical subculture, for periods of up to six months; they never became fertile.

Two culture series were set up, one from tetraspores derived from plants collected at New Chelsea (St. 145.1), the other from carpospores of plants obtained from Bay Bulls (St. 124.26). They were grown in ES under the following conditions:

2:8-16:1200,500,150

5:8-16:1200,500,150

5:16-8:1200,500,150

10:8-16:1200,500,

10:16-8:2300,1200,500,150

15:16-8:2300,1200,500

Spores germinated and the plants grew under all the conditions. No detailed measurements of growth rate were made, but visual observation revealed that:

i. the rate of cell division is greatest at high temperature.

ii. the rate of cell division is reduced under short daylength conditions in comparison with similar conditions at long daylength, even when compensation was made for lower total

illuminance.

iii. the light intensity at low temperatures has little effect on the rate of cell division, but at 10°C and 15°C is greatest at high light intensities.

At 10:8-16:500 and 10:16-8:150 an aberrant growth form occurred, and the axial cells bore only single whorl branchlets. They were arranged in alternate secund groups of three to four branchlets (Figure 36a). All cultures were maintained for periods in excess of six months, and did not become fertile under any conditions.

In an attempt to induce the formation of reproductive organs, cultures were transferred:

i. from ES to sterile seawater, which was changed at 48 h intervals; plants were maintained in this manner at 10:16-8:1200 for 28 days and remained healthy.

ii. from 15:16-8:500 to 5:8-16:500, and 5:16-8:500.

iii. from 5:16-8:500 and 5:8-16:500 to 15:16-8:500

iv. from 10:16-8:1200 and 5:16-8:1200 to total darkness for five days, and then returned to the original conditions.

Development of reproductive organs was not induced by any of the above conditions, though normal vegetative growth continued.

Cytological Studies

Interphase Nuclei.

A. floccosa has uninucleate cells, except for the first three cells of the carpogonial branch, which are binucleate. The nuclei

FIGURE 36

ANTITHAMNIONELLA FLOCCOSA

(a) Aberrant axial development showing alternate secund groups of whorl branchlets. Scale = 100 µm

(b) Mitotic prophase in a haploid apical cell with ca. 25 chromosomes. Stained with acetocarmine. Scale = 10 µm

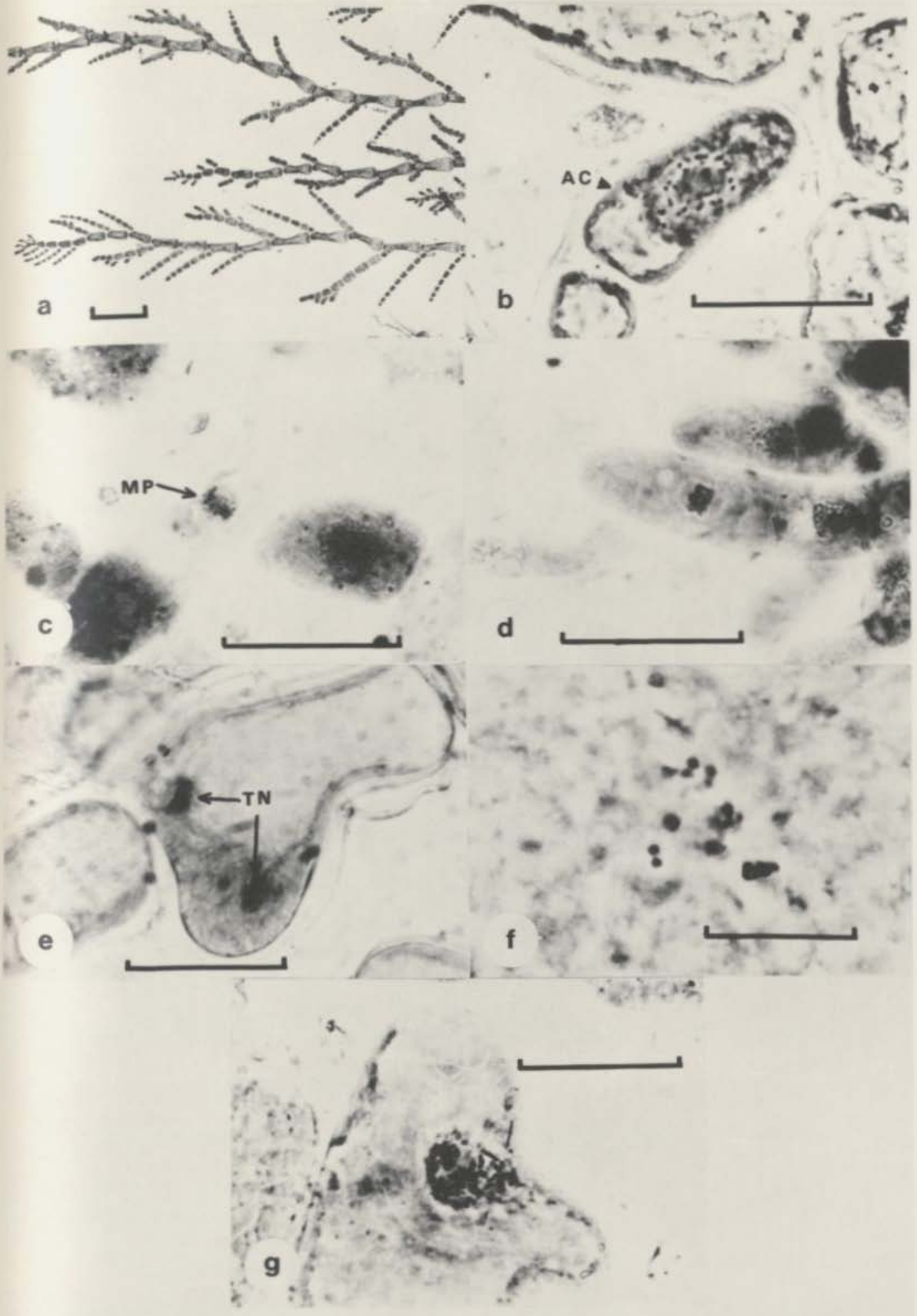
(c) Mitotic metaphase plate (MP). Stained with acetocarmine. Scale = 25 µm

(d) Mitotic anaphase. Stained with acetocarmine. Scale = 10 µm

(e) Mitotic telophase. Stained with acetocarmine. Scale = 10 µm

(f) Diakinesis stage of meiotic prophase in a tetrasporangium. Stained with acetocarmine. Scale = 10 µm

(g) Mitotic prophase in a diploid cell. Approximately 50 chromosomes. Scale = 10 µm


a
b
AC
c
MP
d
e
TN
f
g

vary in size with their position in the plant. In the axial cells they are smallest in the immediate subapical cell, measuring ca. 4 µm diameter with a 2.5 µm diameter nucleolus. In mature axial cells the nucleus is displaced to the side of the cell, has a lenticular form and may measure up to 80 µm in largest diameter.

Mitosis.

Mitotic divisions have been observed in apical cells producing whorl branchlets, and in whorl branchlet cells. They are similar, except for differences in nuclear size. In the apical cell the nucleus enlarges to 6-7 µm diameter prior to division. The process of division through prophase (Figure 36b), metaphase (Figure 36c), anaphase (Figure 36d), and telophase (Figure 36e) is identical to that described for *Scagelia pylaisaei*.

Meiosis.

The site of meiosis is located in the tetrasporangia. The early stages of the meiotic prophase are weakly stained, but in diakinesis the bivalents are clearly visible (Figure 36f). The remainder of the division is identical to that described for *Scagelia pylaisaei*, with cytokinesis immediately following the first nuclear division. Thus irrespective of its final appearance, the ontogeny of the tetrasporangium is cruciate.

No irregular or apomeiotic divisions have been observed.

Chromosome Numbers.

All chromosome counts have been obtained from plants collected at Bay Bulls (St. 124). Counts from tetrasporophytes; male gametophytes

and female gametophytes are presented in Figure 37. Tetrasporophytes are diploid, with 44-52 chromosomes (Figure 36g); gametophytes haploid with 21-27 chromosomes (Figure 36b). Twenty-two to twenty-four bivalents are found in late meiotic prophase.

Thirty-three chromosome counts were obtained from eighteen sterile plants collected at Bay Bulls (St. 124.31) in April 1972. These are presented in Figure 37c. The plants are diploid, with counts ranging between 44 and 54.

Olpidiopsis antithamnionis Whittick and South

A fungal infection was observed in *A. floccosa* collected at three sites, Bay Bulls (St. 124.8), Portugal Cove (St. 135.11) and Logy Bay (St. 128.12) during October and November 1971. In the Bay Bulls collection (St. 124.8) approximately 60% of the host plants were found to be infected.

Heat treated seawater, into which fungal planonts had been released, was used as an inoculum to infect cultures derived from tetraspores of an uninfected plant of *A. floccosa*. In addition attempts were made to infect cultures of *Scagelia pylaisaei* var. *pylaisaei* and the *Trailliella* phase of *Bonnemaisonia hamifera* Hariot. All cultures of infected material were maintained in ER at 10:16-8:500.

Description of *Olpidiopsis antithamnionis*.

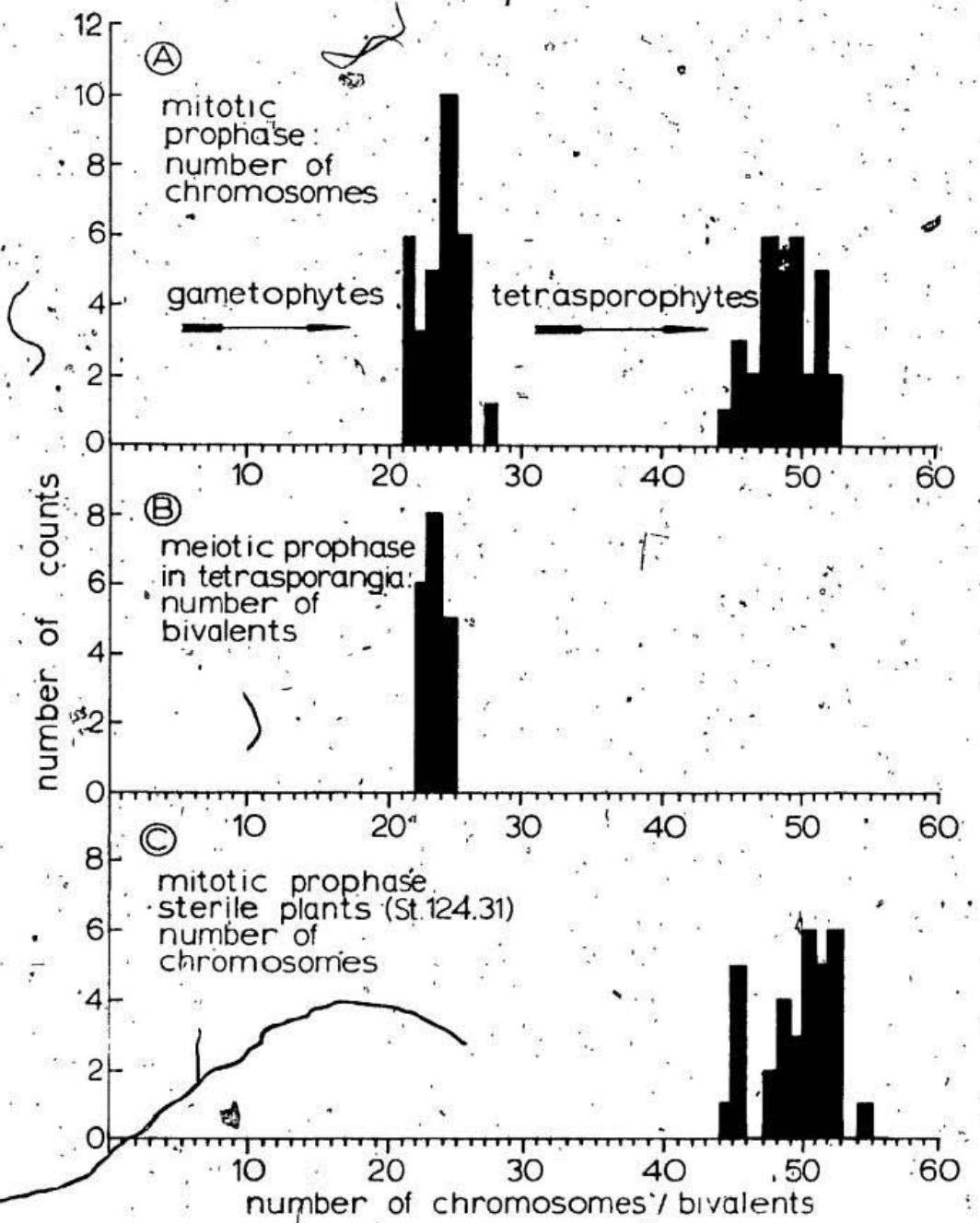
The mature fungal sporangia are smooth-walled and either spherical or ellipsoidal. The spherical sporangia measure (5) 20 - 40 µm in diameter and the ellipsoidal sporangia 40 - 80 (100) µm x 20 - 50 (80) µm. They usually develop a single cylindrical discharge

FIGURE 37

CHROMOSOME COUNTS IN

ANTITHAMNIONELLA FLOCCOSA

Distribution of chromosome counts obtained from A. mitotic prophases of fertile gametophytes and fertile tetrasporophytes and B. distribution of chromosome counts obtained from meiotic prophases of tetrasporogenesis. C. Distribution of chromosome counts obtained from 18 sterile plants collected in April 1972 at Bay Bulls (St. 124.31).


Ⓐ
mitotic prophase: number of chromosomes
gametophytes
tetrasporophytes
Ⓑ
meiotic prophase in tetrasporangia: number of bivalents
Ⓒ
mitotic prophase sterile plants (St.124.31) number of chromosomes
number of counts
number of chromosomes / bivalents

tube 5 - 10 (20) µm long by 5 - 12 (20) µm diameter, but on occasion sporangia with two or three discharge tubes were observed. The fungal planonts have an irregular pyriform shape and measure 5 x 3 µm, they contain a single, prominent, refractive body and are laterally biflagellate. The anteriorly directed flagellum appears shorter than the posteriorly directed one. No resting spores have been observed.

Site of Infection.

The most frequent sites of infection of the host are the cells of the main axis and those of the whorl branchlets (Figure 38a). The host cell may be completely or only partially taken over by the fungus. Consecutive axial cells are frequently attacked and multiple infections of single cells are not uncommon (Figure 38b). There is no correlation between sporangium size and the initial size of the host cell. In field material apical cells and tetrasporangia are only rarely infected and rhizoids are completely free from infection. In contrast to this, in the cultured plants the discharged tetraspores are very prone to attack and a number of infected rhizoids were also seen.

Mode of Infection and Sporangium Development.

In culture the posterior flagellum of the planont is observed to make contact with the cell wall of the host, it then enters a period of rapid movement which ceases as the planont body comes to lie against the host. The entire contents of the planont pass into the cell, however no penetration tube was observed and the empty cyst is only rarely evident after infection has occurred. Discoloration and hypertrophy of the host cell follow infection and partial or total

FIGURE 38

ANTITHAMNIONELLA FLOCCOSA

(a) *Olpidiopsis antithamnionis*, mature fungal sporangium (FS) with discharge tubes (DT) in whorl branchlet and axial cells. Scale = 50 µm

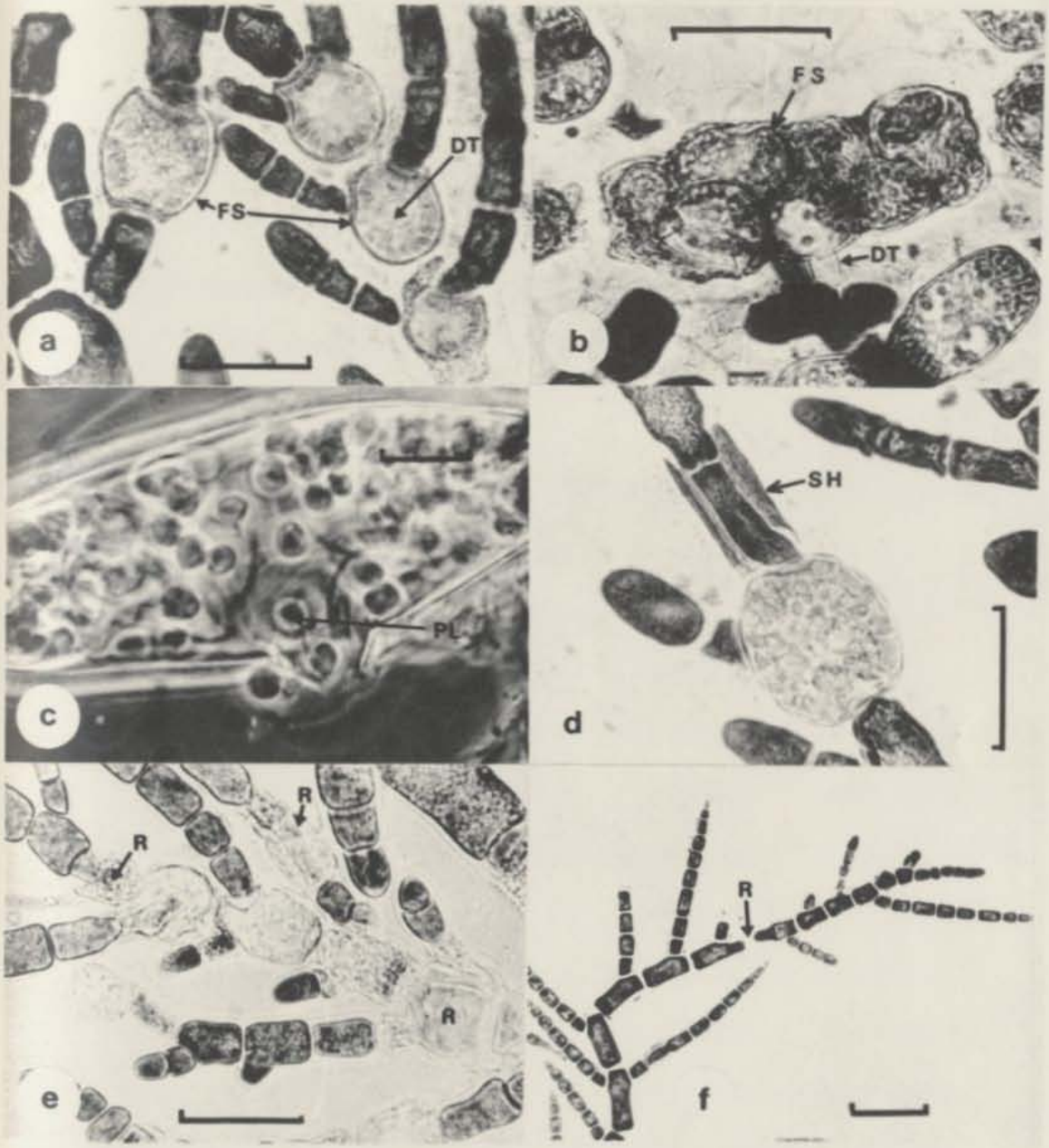
(b) *O. antithamnionis*, multiple sporangia (FS) with discharge tubes (DT) in a single axial cell. Scale = 50 µm

(c) Planonts of *O. antithamnionis* (PL) become motile and randomly distributed within the sporangium before release through the discharge tube. Scale = 10 µm

(d) *O. antithamnionis* infection with a sheating effect (SH) produced by thickening of the wall in the adjacent cell. Scale = 50 µm

(e) Regeneration (R) of the host by protrusion arising from uninfected cells, apical to the site of infection and growing basally within the walls of the previously infected cells. Scale = 50 µm

(f) Regeneration (R) of a previously infected axial cell by outgrowths from both adjacent cells. Scale = 100 µm


a
FS
DT
b
FS
DT
c
PL
d
SH
e
R
R
R
f
R

disintergation of the host plastids takes place. The enlarged fungal cell becomes a well defined area containing greyish masses of protoplasm. A distinct wall forms around this fungal body to produce the sporangium. Planonts are formed peripherally within the sporangium but become randomly distributed at maturity and are motile before release through the discharge tube (Figure 38c). Formation of sporangia may result in the necrosis of the adjacent host cells without direct infection, stimulating the contraction of the protoplasm and a thickening of the cell wall to produce a sheathing effect (Figure 38d).

Host Regeneration

Regeneration of the infected cells was only observed in field material, in culture every cell of the alga eventually became infected resulting in its death. The process of regeneration appears to take place by two distinct mechanisms dependant on the degree of infection of the host cell. In the instance where the protoplasm of the cell has not been totally destroyed by the fungus, where the sporangium has occupied only part of the cell, the sporangium wall degenerates, the host plastids regain their colour and the protoplasm reoccupies the whole of the cell. Only the thickened wall remains as evidence of infection. When the contents of the infected cell are completely destroyed by the fungus and the planonts have been released the sporangium degenerates. The lumen of the cell is reoccupied by cytoplasmic outgrowths from the neighbouring cells (Figure 38e) usually from the cell distal to the

site of infection. In some instances, however, regeneration occurs from both adjacent cells (Figure 38f) and the resulting protoplasmic protrusions may fuse on contact. Cell walls separating the regenerating cell from their neighbours may form in a number of places, at the original site of the walls prior to fungal infection, at the point of initiation of the protrusion or at the point of fusion of two protrusions. After regeneration the host wall remains thickened at the site of the infection, and it would appear from an examination of field material that this regeneration is a common phenomenon.

Host Specificity.

An examination of *S. pylaisaei* and the *Trailliella*-phase of *Bonnemaisonia hamifera* growing in close proximity to the heavily infected *A. floccosum* at the Bay Bulls site showed that they were free from the fungus. Attempts to infect those species in culture proved completely unsuccessful, even though successful re-infection of *A. floccosum* could be induced.

ANTITHAMNIONELLA PACIFICA (HARV.) WOLLASTON

Introduction

Cardinal (1967) and Cardinal and Villalard (1971) have reported *Antithamnionella pacifica* (as *Antithamnion pacificum*) from the Gulf of St. Lawrence, the first record of this species from eastern North America. Its previous recorded range was from Pacific Mexico (Dawson, 1944) northwards to British Columbia (Wollaston, 1971) and Alaska (Saunders, 1901). In view of the apparent disjunction in the distribution, the material from the Gulf of St. Lawrence was re-examined to verify the identification.

A. pacifica was first described from Vancouver Island as *Callithamnion floccosum* var. *pacificum* by Harvey (1862). Its synonymy is:

Callithamnion floccosum var. *pacificum* Harvey (1862)

Antithamnion floccosum var. *pacificum* (Harv.) Setchell and Gardner (1903)

Antithamnion pacificum (Harv.) Kylin (1925)

Wollaston (1971) has placed *Antithamnion uncinatum* Gardner, a species supposedly separated from *A. pacifica* by its uncinate whorl branchlets, within the circumscription of *Antithamnionella pacifica* as var. *uncinata*. The conspecificity of *Antithamnionella pacifica* (as *Antithamnion pacificum*) and *Antithamnion uncinatum* had been suggested by Capt (1930).

Personal examination of herbarium material held in NY has revealed an intergradation between these taxa, as was reported by

Wollaston (1971). The type material of *Callithamnion floccosum* var. *pacificum* held in TCD was also examined; the whorl branchlets in the lower part of the axis were recurved. It seems probable that var. *uncinata* is merely a morphological variant of *A. pacifica*.

Harvey (1862) described *Callithamnion floccosum* var. *pacificum* "Much more densely branched and with more longer pinnae than the usual Atlantic variety . . . ."

This vague distinction was refined by Agardh (1876) who described *C. floccosum* from the Atlantic as var. *atlanticum*. Its whorl branchlets were shorter than their articulations (axial cells) in contrast to those of *C. floccosum* var. *pacificum* which were three to four times as long. The character was also cited by Kylin (1925) when he raised *C. floccosa* var. *pacificum* to specific status.

The tendency to form recurved whorl branchlets in *A. pacifica*, which become uncinate in extreme examples, distinguish this species from *A. floccosa*.

Observations and Results

Three specimens of *A. pacifica* (QAC 4240, QAC 5291, QAC 4336) held in the personal herbarium of Dr. A. Cardinal have been examined. They were obtained from St. Fabien sur Mer on two occasions (St. 77.1, St. 77.2). The specimens were superficially identical, and resembled a delicate form of *A. floccosa*. The whorl branchlets were never recurved, and in the basal regions were either equal in length to, or slightly longer than, their supporting axial cells. A single specimen (QAC 5291) was examined in detail. The length of every fifth axial

cell, and the length of, and the numbers of cells in the longest whorl branchlet borne on this cell, were measured (Figure 32). A specimen of *A. pacifica* (NFLD 8648) from Pacific Grove, California identified by Dr. E. Wollaston has been treated in a similar manner (Figure 32).

The *A. floccosa* and the Pacific *A. pacifica* differ in four characters:

(i) the equivalent axial cells are approximately half as long in *A. pacifica* as in *A. floccosa*.

(ii) throughout the plant, the whorl branchlets of *A. pacifica* are longer than their axial cells, but in *A. floccosa* the axial cells in the basal regions are longer than the whorl branchlets.

(iii) mature whorl branchlets of *A. floccosa* are composed of fewer cells than those of *A. pacifica*.

(iv) the lower whorl branchlets of *A. pacifica* have slightly recurved tips while those of *A. floccosa* are straight.

The St. Lawrence *A. pacifica* resembles *A. floccosa*. This is particularly evident in the numbers of cells in the whorl branchlets, and in ratio of axial cell length to whorl branchlet length, in mid and basal regions of the plant. They differ in that the axial cells are shorter in the apical region of the St. Lawrence *A. pacifica*.

A detailed morphological study of the range of form in *A. pacifica* and *A. floccosa* is desirable, but from the information presented here, they are distinct. *A. pacifica* from the Gulf of St. Lawrence has closer affinities with *A. floccosa* than with the Pacific coast *A. pacifica*. The record of *A. pacifica* from the Gulf of St. Lawrence must therefore be rejected as a misidentification of *A. floccosa*.

ANTITHAMNION CRUCIATUM (C.) AG.

Introduction

The vegetative and reproductive anatomy of *Antithamnion cruciatum* and a number of forms and varieties of the species have been described in detail by L'Hardy-Halos (1968). It is clearly distinguished from other species and from related genera which occur in eastern Canada by the following:

(i) the whorl branchlets are borne paired and opposite, decussately arranged on alternate axial cells.

(ii) the gland cells are borne on short pinnules, and are applied to the adaxial face of two or three cells.

A. cruciatum has been recorded from eastern Canada on several occasions, which are listed in Table 14 .

Preliminary investigation of Newfoundland specimens held in NFLD and identified as *A. cruciatum* revealed that they were *Scagelia pylaisaei*. An attempt was therefore made to trace voucher specimens for other eastern Canadian records to verify their identity.

Observations

Ref. Nos. refer to Table 14 of the reported occurrence of *A. cruciatum* in eastern Canada.

Ref. No. 1 and 2: No specimens have been located for these records.

Ref. No. 3, 5 and 8: Five specimens labelled *A. cruciatum* held in ARL have been examined:

TABLE 14

REPORTED OCCURRENCE OF *ANTITHAMNION CRUCIATUM* (C.Ag.) Näg. IN EASTERN CANADA*

Ref. No.	Authors	Collection Location
1	Bell and MacFarlane 1933	Atlantic N.S. and P.E.I.
2	MacFarlane and Bell 1934	Halifax N.S.
3	Edelstein and McLachlan 1966	Atlantic Coast of N.S.
4	Cardinal 1967	Iles de la Madeleine, Que. (St. 59)
5	Edelstein *et al.* 1969	Halifax Co. N.S.
6	Lee 1969	Kelly's Island, Nfld. (St. 136)
7	Mathieson *et al.* 1969	Marystown, Nfld.
8	Edelstein *et al.* 1970	Digby Neck, N.S.
9	Stone *et al.* 1970	Campobello Island, N.B.

*The occurrence of *A. cruciatum* in eastern Canada, based on preceding records, has also been reported by: MacFarlane and Milligan, 1966; Cardinal, 1968; South and Cardinal, 1970.

(i) ARL 1727 Sandy Cove, N.S. (St. 45.3) is *A. floccosa.*

(ii) ARL 1361 Peggy Cove, N.S. (St. 49.2) is *A. floccosa.*

(iii) ARL 1242 Lunenberg Co., N.S. (St. 48.1) is *Scagelia pylaisaei.*

(iv) ARL 1426 Pt. Lepreau, N.B. (St. 43.1) is *A. floccosa.*

(v) ARL Cranberry Cove, Halifax, 16th April, 1967 is *A. floccosa.*

Ref. No. 4: Two specimens (QAC 4231 and QAC 4227) from the Iles de la Madeleine (St. 59.1, 59.2) both labelled *Antithamnion* sp. have been located in the herbarium of Dr. A. Cardinal. They are *Scagelia pylaisaei.*

Ref. No. 6: A voucher specimen for this record is held in CANA (CANA 2148g); it is *Scagelia pylaisaei.*

Ref. No. 7 and 9: voucher specimens for these records are held in the herbarium of the University of New Hampshire; they are *Scagelia pylaisaei.*

Though not all voucher specimens have been traced it appears that eastern Canadian records of *A. cruciatum* are based on misidentifications. However, a genuine specimen of *A. cruciatum* from eastern Canada was located held in ARL (ARL 3379), labelled as *A. americanum* and collected at Monk Head N.S. (St. 57.1) 4th October 1968.

ANTITHAMNION PLUMULA (ELLIS) THUR. IN LE JOL.

The vegetative and reproductive morphology of *Antithamnion plumula* have been reported in detail (Feldmann-Mazoyer, 1940; L'Hardy-Halos, 1968) and the development of a carposporophyte was studied by Kylin (1923). It has a *Polysiphonia*-type of life history in culture (Sundene, 1959). Magne (1964) has reported n = 23 and 2n = 46 chromosomes, and has demonstrated the occurrence of meiosis in the tetrasporangia. Numerous varieties and forms of this species are described (L'Hardy-Halos, 1968) and two unnamed, morphologically distinct strains could not be hybridized (Sundene, 1959).

In Europe, *A. plumula* occurs from the Mediterranean (Feldmann-Mazoyer, 1940) northwards to southern Scandinavia (Kylin, 1907; Rosenvinge, 1923-1924; Printz, 1926; Sundene 1953; Pankow, 1971). It is reported from the United Kingdom (Parke and Dixon, 1968) and the Faeroes (Børgesen, 1902), but records from Iceland (Jønsson, 1901), Greenland (Rosenvinge, 1893) and Spitzbergen (Agardh, 1868) are of *Scagelia pylaisaei*, as reported earlier in this work.

In eastern North America it occurs northwards to southern Massachusetts (Taylor, 1957), and Hehre and Mathieson (1970) have reported a single specimen from New Hampshire which was personally examined and found to be correctly identified. *A. plumula* reported from the Pacific coast of North America (Saunders, 1901; Dawson, 1962), has not been considered by Wollaston (1971). There is a single record from eastern Canada (South and Cardinal, 1970) based on a personal communication from Miss C. I. MacFarlane. The voucher specimen has

not been examined and its identification cannot be confirmed; it does, however, represent a considerable extension of the previously reported range of the species.

In eastern Canada *A. plumula* can only be confused with *Scagelia pylaisaei*. Both species have whorl branchlets which may be arranged irregularly on the axis, and both possess gland cells borne on single whorl branchlet or pinnule cells. They can be separated in that *A. plumula* has pinnules arranged secundly on the adaxial face of the whorl branchlets, and by the tetrasporangia, which are pedicellate on single cells borne on the whorl branchlets and pinnules.

THE GENUS *CALLITHAMNION*

The genus *Callithamnion* was erected by Lyngbye (1819) and subsequently has undergone changes in circumscription, coupled with the addition and deletion of species. Harris (1962) has reviewed the taxonomic history of the genus and has rejected, together with Boddeke (1958), its division by Feldmann-Mazoyer (1940). Feldmann-Mazoyer (1940) proposed that the species previously referred to *Callithamnion* which possessed uninucleate cells, irregular gonimolobes, and zig-zag carpogonial branches, should be placed in a new genus *Aglaothamnion* Feldmann-Mazoyer. Boddeke (1958) questioned the value of the shape of the gonimolobe as a taxonomic character, and noted the impracticality of estimating the number of nuclei in cells of herbarium material. Harris (1962) also found variability in the form of the carpogonial branch and supported Boddeke's (1958) conclusions.

The genus *Callithamnion* (including *Aglaothamnion*) contains approximately sixty species (Kylin, 1956) of which many are ill-defined. It is apparent from the literature and from examination of herbarium material that opinions differ in the delimitation of many species of *Callithamnion*. The principal characters used for separation of species (Harris, 1962; Halos, 1964) are:

(i) gross morphology.

(ii) branch morphology.

(iii) origin and growth rate of lateral branches in relation to the main apex.

(iv) arrangement of the branches on the main apex.

(v) vegetative cell dimensions.

(vi) dimensions of tetrasporangia.

(vii) degree of cortication.

(viii) presence or absence of terminal hairs.

(ix) morphology of the spermatangial branches.

(x) the shape of the carpogonial branch.

(xi) the form of the gonimolobes.

Many of these characters are susceptible to environmental influence and this, coupled with the lack of critical typification in the genus, has led to considerable confusion.

Only four species of *Callithamnion* occur in the study area: *C. byssoides* Arnott ex Harv. in Hook.; *C. roseum* sensu Harvey; *C. corymbosum* (Sm.) Lyngbye and *C. tetragonum* (With.) C. Ag. (including *C. baileyi* Harv.). With the exception of *C. roseum* they are reasonably well defined. These species are also found in the British Isles (Parke and Dixon, 1968) and a revision of the British species of *Callithamnion* is currently in progress (Price, unpublished); for this reason no taxonomic treatment has been attempted in this study. The names applied to the taxa are therefore tentative and are based on previous literature descriptions, principally those of Rosenvinge (1923-1924) and Halos (1964).

Studies have been limited to the phenology of the species as they occur in Newfoundland, their life history in culture, and to their cytology.

C. byssoides was not examined and although reported from

eastern Canada (Taylor, 1957; McFarlane and Milligan, 1966; McLachlan and Edelstein, 1970-71) it has not been found in Newfoundland. Voucher specimens for the eastern Canadian reports of this species have not been examined.

CALLITHAMNION ROSEUM 'SENSU' HARVEY

Introduction

The combination *Callithamnion roseum*, first used by Lyngbye (1819) has the basonym *Ceramium roseum* Roth (1798) but the currently accepted delimitation of this species is that of Harvey (1849) who did not examine any Roth specimens. Parke and Dixon (1968) suggest that *Callithamnion roseum* (Roth) Lyngbye and Harvey's *Callithamnion roseum* are not conspecific.

The species examined here resembles Harvey's (1849) illustration of *C. roseum* and agrees with subsequent descriptions (Farlow, 1881; Rosenvinge, 1923-1924; Taylor, 1957; Boddeke, 1958; Konrad-Hawkins, 1964a, 1964b, 1968, 1972; Halos, 1964) based on Harvey's concept of the species. It has thus been named *Callithamnion roseum* 'sensu' Harvey.

The vegetative and reproductive anatomy, including development of the carposporophyte, has been thoroughly described by Rosenvinge (1923-1924) and Halos (1964). Newfoundland material of *C. roseum* differs from the previous descriptions only in minor details of overall size, cell size and degree of cortication. Konrad-Hawkins (1964a, 1964b, 1968, 1972) has reported several detailed morphogenetic studies from both regenerating fragments and tetraspores of *C. roseum* in culture, but did not complete its life history. The only previous cytological study is that of Harris (1962) who obtained a haploid chromosome number n = 39. *C. roseum*, as reported by Harris (1962, 1966) is multinucleate and thus is not conspecific with the *C. roseum*

'sensu' Harvey of this study. It is apparent from this, and from examination of herbarium material labelled *C. roseum*, that opinions differ on the delimitation of the species. No attempt has therefore been made to assess the distribution and the seasonal reproductive periodicity of the species from previous reports except, as in the instance of Rosenvinge (1923-1924) and Halos (1964), where they are accompanied by a detailed description or illustration.

Callithamnion roseum has been reported from eastern Canada on a single occasion (Bell and MacFarlane, 1933) and was not previously found in Newfoundland. It was obtained from two localities in insular Newfoundland, St. Bernard (St. 104) where it was studied in detail, and on a single occasion from Bonne Bay (St. 171). At St. Bernard it is an inconspicuous alga, rarely exceeding 2 cm in height, growing epiphytically on *Cladophora rupestris* (L.) Kütz., *Polysiphonia lanosa* (L.) Tandy and *Plumaria elegans* under a cover of *Ascophyllum nodosum* (L.) Le Jol. on vertical rock faces at low water mark. It was rarely recognised in the field and collections were made by gathering large quantities of *Cladophora rupestris*, from areas where *C. roseum* occurred, and examining these in the laboratory.

Aims of the Study

The principal aims of this study of *C. roseum* were to:

(i) investigate its seasonal changes in morphology,

(ii) determine its reproductive periodicity.

(iii) establish its life history in culture and to determine the factors affecting the development of reproductive organs.

(iv) obtain cytological confirmation of the life history observed in culture.

Observations and Results

Seasonal Changes in Morphology

C. roseum showed seasonal changes in vegetative morphology with extreme forms occurring in March (St. 104.11) (Figure 39a) and in August (St. 104.15) (Figure 39b). The most noticeable changes were in cell size, overall size, the arrangement of the branches on the axis and their degree of crowding in the apical region. These characters for two typical plants of the extreme forms are given in Table 15 .

Table 15

Morphology of two extreme, seasonal, forms of *C. roseum* at St. Bernard

Morphological character	Date collected March 1971 (St. 104.11)	Date collected August 1971 (St. 104.15)
Maximum height of plants	less than 0.5 cm	2 cms
Maximum axial cell size	50 x 25 µm	300 x 60 µm
Apex of axis	indistinct: obscured by crowded lateral branches	distinct: lateral branches not crowded in apical region
Branching pattern	sub-distichous	spiral, angle of divergence 90-120°

FIGURE 39

CALLITHAMNION ROSEUM

(a) Specimen (St. 104.11 St. Bernard, March 1971) showing short celled, densely branched winter morphology. Scale = 100 µm

(b) Specimen (St. 104.15 St. Bernard, August 1971) showing long celled, diffuse branched summer morphology. Scale = 500 µm

(c) Sporeling produced from tetraspore with rhizoid (RZ) and axial filament (AF). Scale = 100 µm

(d) Procarps with carpogonial branch (CB) and trichogyne (T). Scale = 200 µm

(e) Spermatangial clusters (SC) borne on adaxial face of branches. Scale = 100 µm

(f) Young carposporophyte with a single developing gonimolobe. (GL). Scale = 100 µm


a
b
AF
RZ
c
CB
T
d
SC
e
GL
f

Reproductive Periodicity

Data on reproductive periodicity are presented in Figure 40 . *C. roseum* at St. Bernard was only fertile in summer and fall, and sterile plants predominated at all times of the year. Tetrasporophytes were first observed in July (St. 104.14), and in August (St. 104.15) fertile male gametophytes and carposporophytes were also present. The fertile plants persisted until October (St. 104.17), but in December (St. 104.18) all plants were sterile. Tetrasporophytes and gametophytes appeared to be present in approximately equal numbers.

Culture Studies

Cultures of *C. roseum* were established from tetraspores, carpospores, and excised apices of sterile plants.

Growth Rates.

A plant bearing tetrasporangia collected at St. Bernard (St. 104.16) in September 1971 was placed in culture (ES 10:16-8:150). Spores were released within 48 hrs, after which the parent plant was removed. Germination occurred immediately (Figure 39c) and was of the *Ceramium*-type (Chemin, 1937) as described by Konrad-Hawkins (1972), no aberrant unipolar germination patterns were observed. After 8 days coverslips bearing young sporelings were transferred to cultures under the conditions given in Figure 41 , where the results obtained are also reported.

Growth occurred under all conditions, but was greatest at the higher temperatures. Light intensity had little effect on the rate of cell production under any culture condition, except at the very low

FIGURE 40

REPRODUCTIVE PERIODICITY OF *CALLITHAMNION ROSEUM*

Reproductive periodicity of *C. roseum* at St. Bernard (St. 104) between March 1971 and March 1972. Data are shown as percentage of total number of specimens examined for four categories of plant: sterile plants, female gametophytes with carposporophytes, fertile male gametophytes and fertile tetrasporophytes.

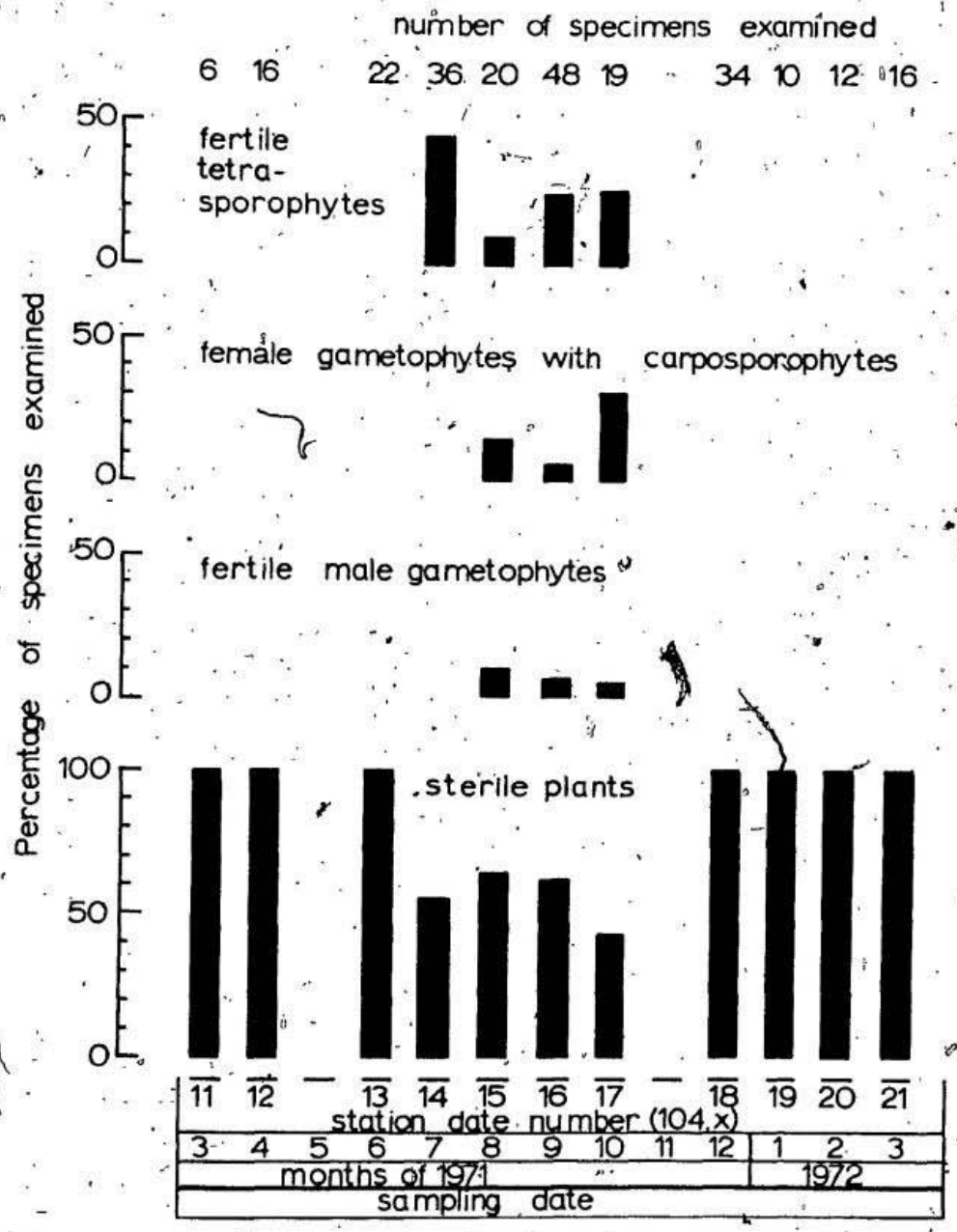
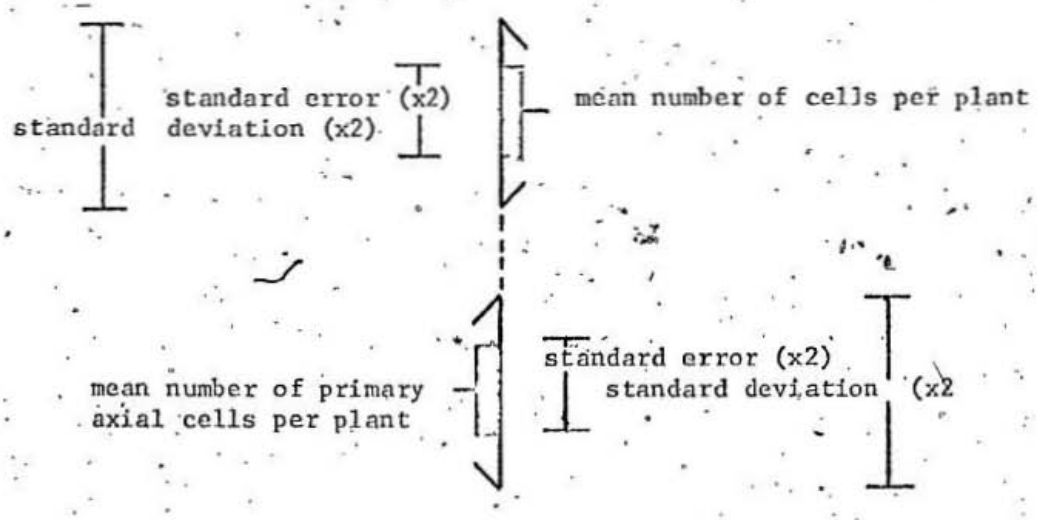
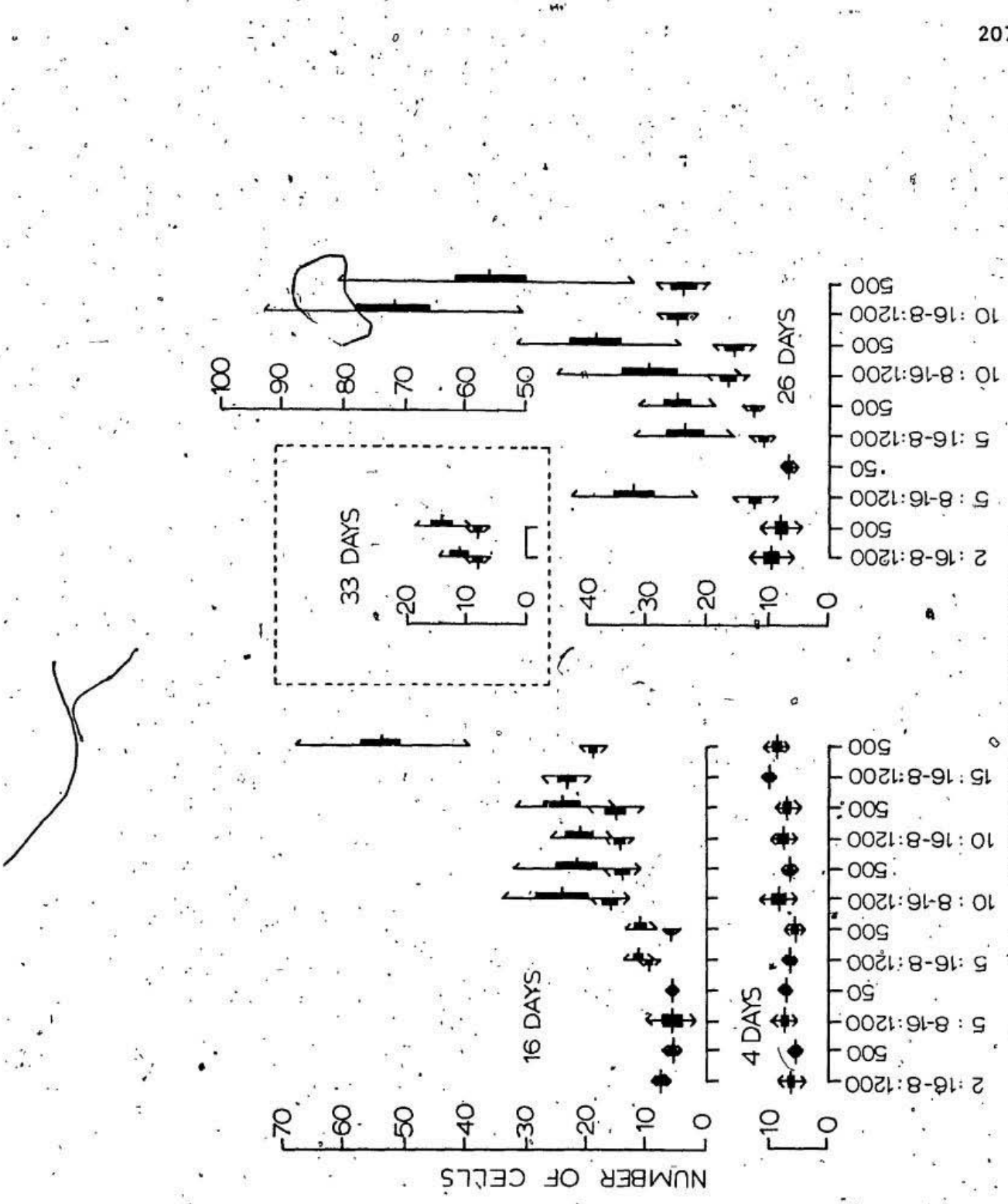

number of specimens examined
6 16 22 36 20 48 19 34 10 12 16
50
0
fertile tetra-sporophytes
50
0
female gametophytes with carposporophytes
50
0
fertile male gametophytes
Percentage of specimens examined
100
50
0
sterile plants
11 12 13 14 15 16 17 18 19 20 21
station date number (104.x)
3 4 5 6 7 8 9 10 11 12 1 2 3
months of 1971 1972
sampling date

FIGURE 41

GROWTH RATES OF *CALLITHAMNION ROSEUM* IN CULTURE

Growth rates at several culture conditions measured as the mean number of cells produced per plant and the mean number of axial cells produced per plant, of gametophytes derived from tetraspores after 4, 16, 26 and 33 days of culture.




NUMBER OF CELLS
4 DAYS
16 DAYS
33 DAYS
26 DAYS
CULTURE CONDITIONS
2 :16-8:1200
5 : 8-16:1200
50
5 :16-8:1200
500
10 : 8-16:1200
500
10 :16-8:1200
500
15 :16-8:1200
500
2 :16-8:1200
500
5 : 8-16:1200
50
5 :16-8:1200
500
10 : 8-16:1200
500
10 :16-8:1200
500

light intensity (5:8-16:50) where slow growth occurred.

In comparison with the results obtained for *Scagelia pylaisaei* daylength had little effect on the rate of cell division. Plants at 10°C grew at a slightly faster rate under long daylengths than under short daylengths, but at 5°C no differences were observed.

Because of the limited material no comparative data of the growth of sporelings from carpospores were obtained.

Life History in Culture.

The cultures, obtained from tetraspores and used for growth rate experiments were grown to reproductive maturity: the results are presented in Table 16 .

Fertile cultures contained approximately equal numbers of procarpial (Figure 39d) and spermatangial plants (Figure 39e). Cultures under short daylengths and at 2°C were maintained for 134 days and, although the plants exceeded the size at which long daylength plants had become fertile, they remained sterile.

Sterile plants transferred from 10:8-16:500 to 10:16-8:500 produced spermatangia and procarps in four days. Plants transferred from 10:8-16:500 to 10:16-8:500 for 1, 2 or 3 complete 24 h cycles and returned to 10:8-16:500 remained sterile. After procarps and spermatangia were formed, their production continued when plants were returned to 10:8-16:500.

A developing carposporophyte (Figure 35f) was observed in culture at 10:16-8:1200 seven days after the first appearance of procarps and spermatangia. The female gametophyte on which it was

TABLE 16

RESULTS OF EXPERIMENTS TO DETERMINE THE EFFECT OF CULTURE CONDITIONS ON THE FORMATION OF REPRODUCTIVE ORGANS BY SPORELINGS OBTAINED FROM TETRASPORES OF *CALLITHAMNION ROSEUM*

Culture conditions-ES medium	Days in culture before the first appearance of reproductive organs
15:16-8:1200	Procarps and spermatangia at 33 days
" " 500	"
10:16-8:1200	Procarps and spermatangia at 46 days
" " 500	"
10:8-16:1200	No reproductive organs formed
" " 500	"
5:16-8:1200	Spermatangia formed after 74 days,
" " 500	procarps after 82 days
5:8-16:1200	No reproductive organs formed after 134 days
" " 50	"
2:16-8:1200	"
" " 500	"

formed was isolated, under the same culture conditions. The carpospores matured and were discharged after a further 12 days, and were then transferred to cultures under the conditions given in Table 17 . Germination occurred in the same manner as for the tetraspores.

Plants at 10°C and 15°C under long daylength produced tetraspores. Growth occurred under short days at 10°C, but the plants did not become fertile even though they remained in culture for 75 days and exceeded the size at which plants became fertile under long daylengths. Plants transferred from 10:8-16:500 to 10:16-8:500 produced tetrasporangia within 48 hrs.

The life history of *C. roseum* in culture was completed through two successive cycles; no deviations from the sequence of tetrasporophytes, gametophytes and carposporophytes was observed. The life cycle of *C. roseum* in culture is thus of the *Polysiphonia*-type and the formation of reproductive organs appears to be induced by long daylengths.

Culture of Excised Apices of Sterile Plants.

Excised apical regions, consisting of approximately 20 axial cells from plants collected at St. Bernard in July (St. 104.14) and February (St. 104.20) were cultured in ES at 10:16-8:1200 for 48 and 52 days respectively. All plants became fertile. The results of these cultures are presented in Table 18 .

The sterile field population on both occasions proved to consist of gametophytes and tetrasporophytes, but the former predominated in July (St. 104.14), when tetrasporophytes have become

TABLE 17

RESULTS OF EXPERIMENTS TO DETERMINE THE EFFECT OF CULTURE CONDITIONS ON THE FORMATION OF TETRASPORANGIA ON SPORELINGS OBTAINED FROM CARPOSPORES OF *CALLITHAMNION ROSEUM*

Culture conditions ES medium	Days in culture before first appearance of tetrasporangia
15:16-8:1200	28
" " 500	31
10:16-8:1200	36
" " 500	36
10:8-16:1200	No tetrasporangia formed after 75 days
" " 500	"

TABLE 18

RESULTS OF CULTURE OF EXCISED APICES OF STERILE PLANTS OF *CALLITHAMNION ROSEUM*

Source	Pre-culture	Post-culture
St.104.14 St. Bernard 4 - 7 - 1971	17 sterile plants	8 male gametophytes, 7 female gametophytes 2 tetrasporophytes
St.104.20 St. Bernard 10 - 3 - 1972	10 sterile plants	2 male gametophytes 4 female gametophytes 4 tetrasporophytes

fertile in nature.

Cytological Studies

Limited cytological observations were made, entirely on cultured material. Great difficulty was experienced in staining the nuclei of *C. roseum*, few preparations of dividing nuclei were obtained and none was of sufficient quality to allow chromosome counting.

Interphase nucleus.

All the vegetative cells of *C. roseum* are uninucleate (Figure 42a); cells of the carpogonial branch were not examined. The interphase nucleus in the apical cell (Figure 42b) is ca. 6-8 µm diameter and occupies the centre of the cell. The nucleus does not increase in size with increase in cell size, but is displaced to the periphery of the cell. (Figure 42c).

Mitosis.

Very few mitotic preparations have been obtained and were either weakly stained or poorly differentiated. No deviations from the normal mitotic processes were observed.

Meiosis.

Tetrasporangial initials are uninucleate and enlarge to ca. 40 x 30 µm prior to the first nuclear division. Few early prophase stages were seen, but a distinct diakinesis (Figure 42d) with approximately 30 bivalents was observed. No other nuclear stages of tetrasporogenesis were found, but four nuclei (Figure 42e) are present in the tetrasporangium before cytokinesis. Cleavage of the

FIGURE 42

CALLITHAMNION ROSEUM

(a) Uninucleate axial cells. Stained with acetocarmine. Scale = 100 µm

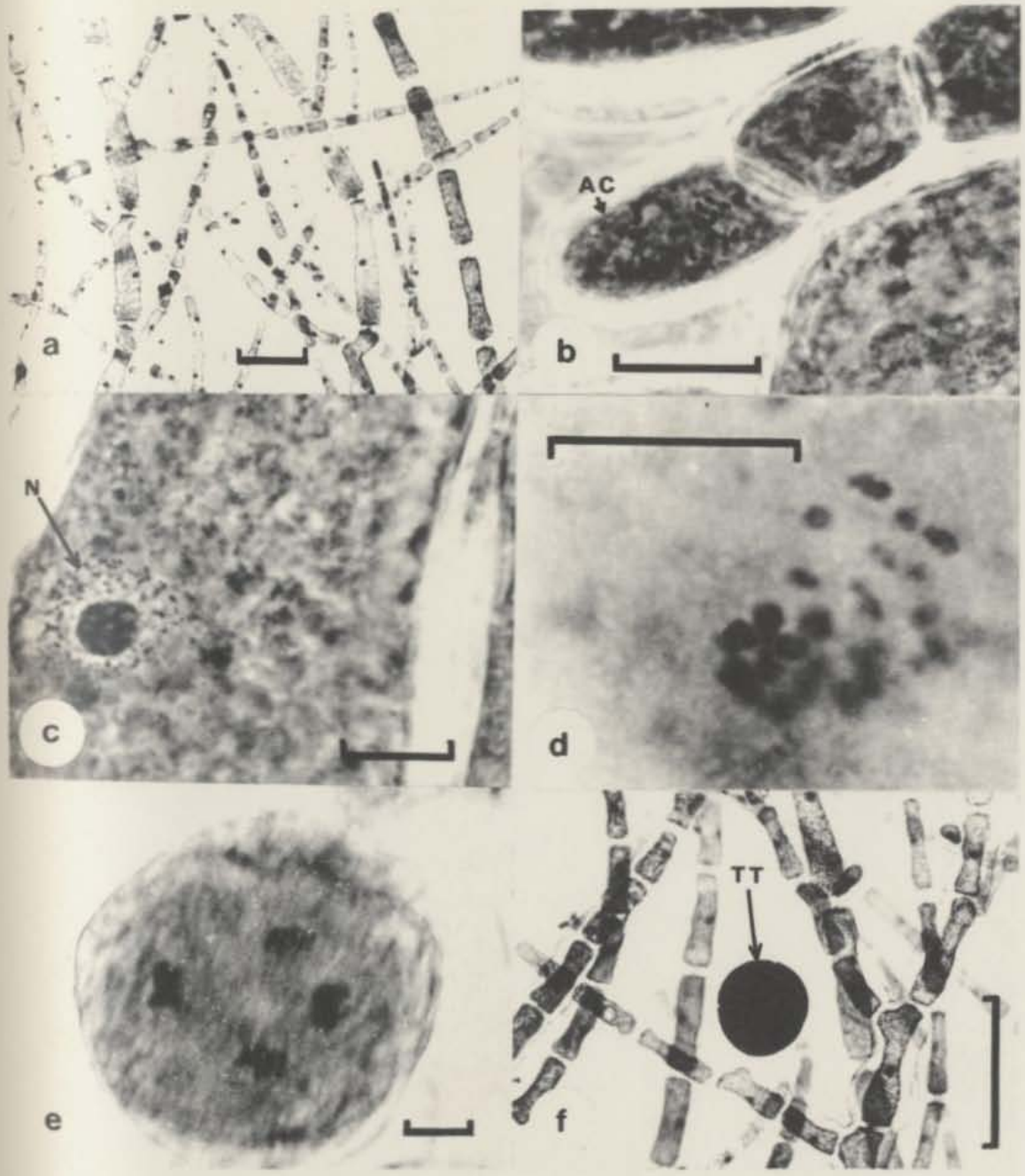
(b) Centrally located interphase nucleus in apical cells (AC). Stained with acetocarmine. Scale = 100 µm

(c) Interphase nucleus (N) in main axis displaced to periphery of the cell. Stained with acetocarmine. Scale = 10 µm

(d) Tetrasporangium, meiotic prophase in diakinesis showing approximately 30 bivalents. Stained with acetocarmine. Scale = 10 µm

(e) Undivided tetrasporangium showing quadrinucleate condition prior to cytokinesis. Stained with acetocarmine. Scale = 50 µm

(f) Mature tetrasporangium showing tetrahedral cleavage (TT). Stained with acetocarmine. Scale = 100 µm


a
AC
b
N
c
d
e
TT
f

cytoplasm is tetrahedral to form four tetraspores (Figure 42f.).

Chromosome Numbers.

Apart from the single observation of approximately 30 bivalents in diakinesis, no other chromosome counts were obtained.

CALLITHAMNION CORYMBOSUM (SM.) LYNGBYE

Introduction

Callithamnion corymbosum is readily distinguished from other northeastern American species of *Callithamnion* by its corymbose apical branching pattern (Figure 43a). The vegetative and reproductive anatomy has been described on a number of occasions and the following are particularly significant, Thuret and Bornet (1878), Oltmanns (1898), Kylin (1907), Rosenvinge (1923-1924), Feldmann-Mazoyer (1940) and Halos (1964). Tetrasporophytes, dioecious gametophytes and carposporophytes have been recorded. Tetrasporangia have been reported on plants together with spermatangia and carposporophytes (Thuret in Le Jolis, 1864; Thuret and Bornet, 1878; Børgesen, 1902); such plants have been named *C. corymbosum* var. *amphicarpa* Thur. in Le Jol.

C. corymbosum has a wide geographic distribution, occurring in the Black Sea (Zinova, 1967), the Mediterranean (Hauck, 1885; Feldmann-Mazoyer, 1940), the Canary Islands (Børgesen, 1930) and throughout Europe to northwestern Norway (Kleen, 1874). Its range in the western Atlantic is from Brazil (Taylor, 1960) to eastern Canada (Cardinal, 1968), and it has recently been reported from Newfoundland (South, 1971). There are no records of its occurrence in Iceland or Greenland.

At its northernmost locations in Europe *C. corymbosum* is a sublittoral alga (Kleen, 1874; Børgesen, 1902; Printz, 1926), found as an epiphyte on larger algae. In Nordland (Kleen, 1874) only sterile

FIGURE 43

CALLITHAMNION CORYMBOSUM

(a) Apical region showing corymbose branching pattern. Scale = 50 µm

(b) Sterile fragments found in algal detritus (St. 104.11 St. Bernard, March 1971). Scale = 400 µm

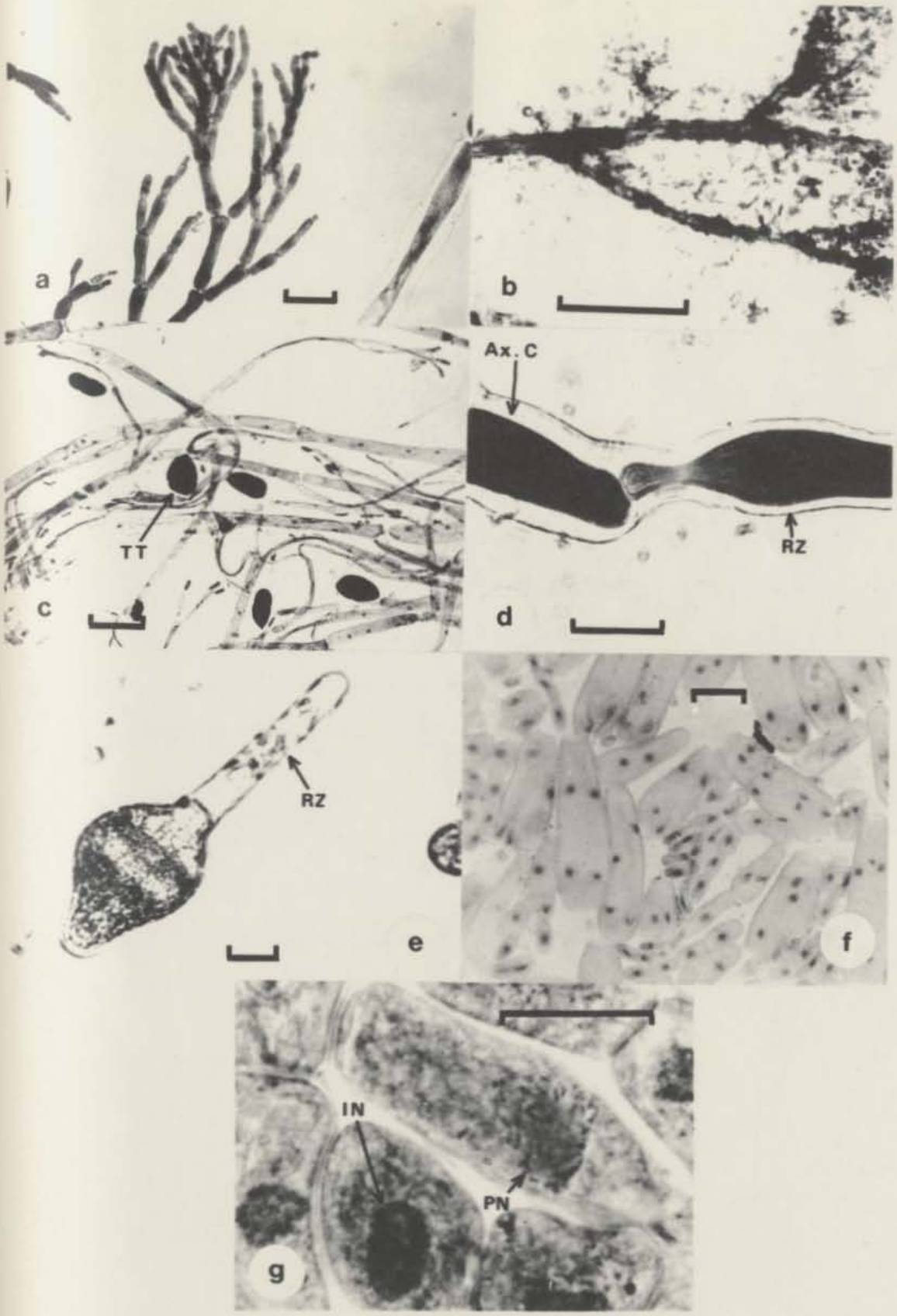
(c) Tetrahedrally divided tetrasporangia (TT) in apical region. Stained with acetocarmine. Scale = 100 µm

(d) Development of a rhizoid (RZ) from an axial cell (Ax.C) in the basal region of a fragmented plant. Scale = 25 µm

(e) Germination of a tetraspore with developing rhizoid (RZ). Scale = 10 µm

(f) Multinucleate axial cells. Stained with acetocarmine. Scale = 100 µm

(g) Uninucleate cells in apical region with interphase nuclei (N) and a nucleus in late mitotic prophase (PN). Stained with acetocarmine. Scale = 10 µm


a
b
Ax. C
TT
RZ
c
d
RZ
e
f
IN
PN
g

plants have been found. Printz (1926) reported tetrasporophytes and carposporophytes from the Trondheim Fjord and Børgesen (1902) reported var. *amphicarpa* from the Faeroes.

Hassinger-Huizinga (1952) has cultured *C. corymbosum* through nine successive generations and the *Polysiphonia*-type of life history predominated. Occasionally tetrasporangia occurred on a plant together with either spermatangia or procarps, and the tetraspores produced tetrasporophytes. It was claimed that the aberrant tetrasporophytes resulted from the presence of two or four chromosomes, additional to the normal diploid complement (2n = 60). Dixon (1970a) has rightly stated that this cytological data must be regarded with caution. To conclusively establish the addition or deletion of two chromosomes in sixty from a nucleus of ca. 5 μm diameter requires cytological preparations of higher standards than have ever been reported for the Rhodophyta.

C. corymbosum was found at six localities (St. 95, St. 98, St. 99, St. 101, St. 104, St. 171) in Newfoundland during the study period, it occurred from low water mark to depths of ca. 10 metres on rock and as an epiphyte on larger algae. The species has only been studied in detail at St. Bernard (St. 104).

Aims of the Study

The principal aims of the study were:

(i) to establish the phenology of the species.

(ii) to obtain its life history in culture.

(iii) to establish the factors controlling reproduction in culture.

(iv) to obtain cytological confirmation of its life history.

Observations and Results

Phenology

Callithamnion corymbosum was first found at St. Bernard in September 1970 (St. 104.4) and was one of the commonest components of the sublittoral flora. Data on its occurrence and reproductive periodicity between September 1970 and March 1972 are presented in Figure 44. Tetrasporangia were observed in October (St. 104.6) and by November (St. 104.7) occurred on all plants. *C. corymbosum* was still common in December (St. 104.8) and some plants still fertile; however, in the immediate sublittoral (0-2 metres depth) they had become bleached, and were breaking down. In January (St. 104.9) the species was no longer obvious, but fragmented plants, some bearing tetrasporangia, were found amongst the diatoms and the *Trailliella*-phase of *Bonnemaisonia hamifera* which are the major components of the understorey algae.

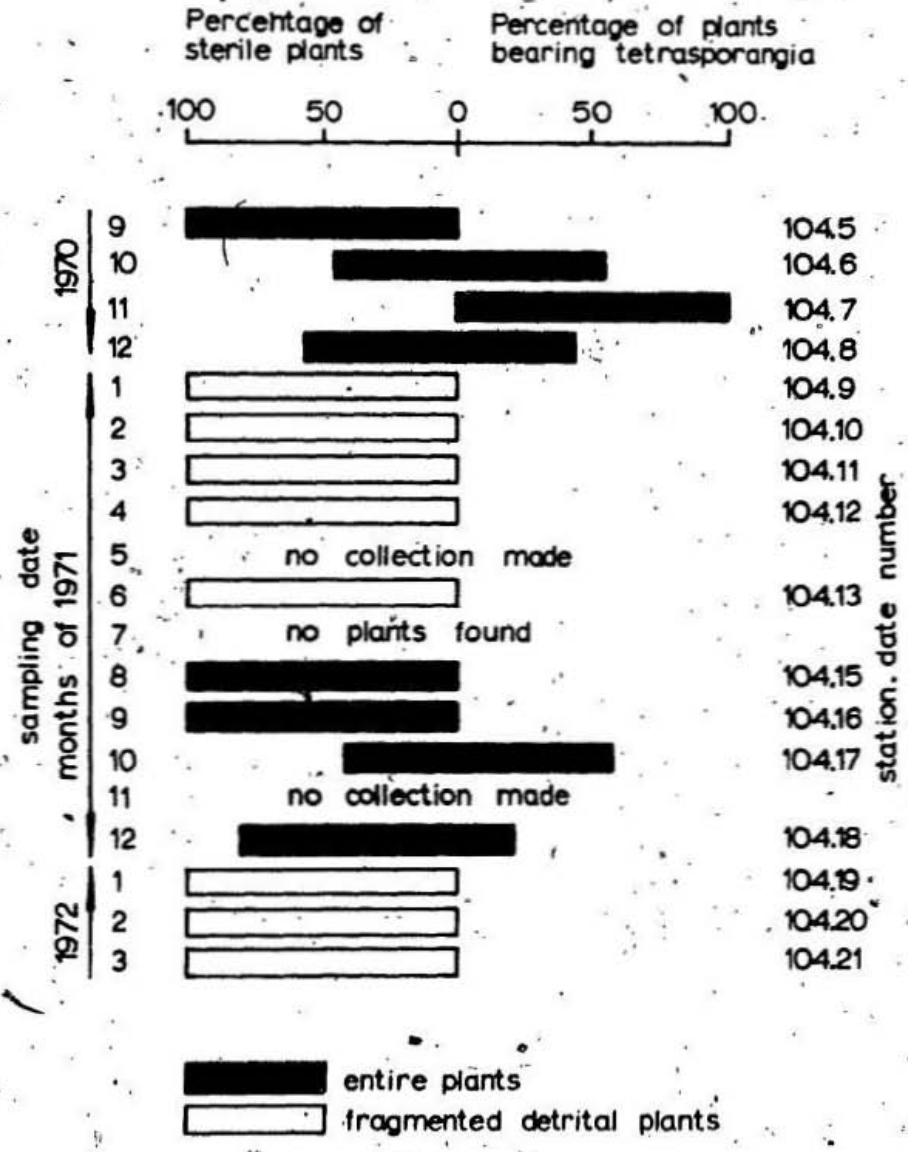
Sterile fragments (Figure 43b) were observed throughout the spring and early summer, but could not be found in July (St. 104.14). In August (St. 104.15) large sterile plants were commonly found and by September (St. 104.16) the species was again a dominant part of the flora. Tetrasporangia (Figure 43c) were produced in October (St. 104.17) and found again in December (St. 104.18). Only detrital fragments of the species could be found in the early months of 1972.

Gametophytes and carposporophytes were never observed at St. Bernard, nor have they ever been found at any other sites in

FIGURE 44

PHENOLOGY OF *CALLITHAMNION CORYMBOSUM*

Phenology of *C. corymbosum* at St. Bernard (St. 104) between September 1970 and March 1972, showing the percentage of fertile tetrasporophytes and the periods when plants could only be found as detrital fragments.


Percentage of sterile plants
Percentage of plants bearing tetrasporangia
100
50
0
50
100
1970
1972
sampling date months of 1971
9
10
11
12
1
2
3
4
5
6
7
8
9
10
11
12
1
2
3
no collection made
no plants found
no collection made
104.5
104.6
104.7
104.8
104.9
104.10
104.11
104.12
104.13
104.15
104.16
104.17
104.18
104.19
104.20
104.21
station. date number
entire plants
fragmented detrital plants

Newfoundland.

In August 1971 (St. 104.15) two large rocks were removed from above the high water mark and placed in the immediate sublittoral, in an area where a dense growth of *C. corymbosum* occurred. In September (St. 104.16) the rocks were covered with young plants of *C. corymbosum*. Tetrasporangia had not then developed in the population, and vegetative propagation must have occurred.

Two other sites, Grand le Pierre (St. 101) and Bonne Bay (St. 171), where populations of *C. corymbosum* occur, were visited at irregular intervals. No detailed collections were made, but observations revealed that a similar seasonal pattern occurred. At Grand le Pierre large populations of plants were found in June (St. 101.1), and were fertile in August (St. 101.2). At Bonne Bay (St. 171.5) plants bore tetrasporangia in July. This earlier growth is possibly linked to the water temperatures (Appendix II) which were higher earlier in the year at these sites than at St. Bernard.

Culture Studies

The field studies revealed an apparent lack of gametophytes, the occurrence of vegetative propagation, and the cryptic nature of the species in winter. The fate of the tetrasporangia produced in nature is unknown. They may be:

(i) abortive.

(ii) apomeiotic, reproducing the tetrasporangial plants.

(iii) meiotic, but with the growth of the gametophytes suppressed by environmental factors.

In view of these observations the growth and reproduction of *C. corymbosum* was studied in culture.

Cultures from Tetraspores.

Tetrasporangial plants were collected at St. Bernard (St. 104.6) in October 1970 and placed in ER 10:16-8:500. No discharge of spores occurred, but the parent plant fragmented. Each fragment developed a basal rhizoid (Figure 43d) and continued apical growth. Sterile fragments were transferred to other cultures, where they continued growth and produced tetrasporangia. The tetraspores produced in culture were released and germinated (Figure 43e) showing the typical *Ceramium* pattern (Chemin, 1937). The coverslips on which they were growing were cleaned of vegetative fragments, placed in separate cultures and incubated at 15:16-8:1200, 500 and 10:16-8:1200, 500, 150.

After germination, no further growth occurred; at maximum three celled sporelings were produced and often spores only developed a simple rhizoid. After 28 days in culture sporelings appeared healthy, but no further growth had occurred.

On several subsequent occasions tetraspores produced in culture were isolated, but either produced only limited growth or did not germinate.

Cultures from Vegetative Fragments.

Detrital fragments of *C. corymbosum* collected from St. Bernard in February 1971 (St. 104.10) and April 1971 (St. 104.12) were cultured ER 10:16-8:500. They grew and produced tetrasporangia.

A single sterile plant collected at St. Bernard in September

1971 (St. 104:16) was allowed to fragment in culture (ES 10:16-8:150). Unattached fragments were inoculated into ES medium and placed under a number of conditions to determine the effects on growth and production of tetrasporangia. The culture conditions and results obtained are presented in Table 19.

Vigorous vegetative growth and production of tetrasporangia occurred at 10°C and 15°C under both long and short daylengths, but at lower temperatures there was little growth and no tetrasporangia were formed. With two exceptions light intensity had little effect on the cultures. Vegetative growth occurred at 15:16-8:2300, but production of tetrasporangia was inhibited. Plants transferred to 15:16-8:500 after 56 days at 15:16-8:2300 produced tetrasporangia in four days. High light intensities were lethal at 2°C, but at 150 lx the plants remained viable, though no obvious growth occurred. Fragments of *C. corymbosum* after 96 days at 2:8-16:150 were transferred to 10:16-8:500, where they produced tetrasporangia in 28 days.

Cytological Studies

All cytological studies were made on material obtained from cultures.

The vegetative cells of *C. corymbosum* are multinucleate (Figure 43f) and only the cells in the immediate apical region (Figure 43g) have a single nucleus. There is no increase in nuclear size with increase in cell size. Mitosis was observed on a number of occasions in apical and rhizoidal cells with no apparent deviation from the normal process. Chromosome counts were obtained from dividing

TABLE 19

RESULTS OF CULTURE OF VEGETATIVE FRAGMENTS OF *CALLITHAMNION CORYMBOSUM* OBTAINED FROM ST. BERNARD (ST.104.16)

Culture conditions ES medium	Vegetative growth	Production of tetrasporangia
15:16-8:2300	Vigorous growth	None produced in 56 days
" " 1200	"	Produced in 14 days
" " 500	"	"
" " 150	"	"
10:16-8:2300	"	Produced in 32 days
" " 1200	"	Produced in 23 days
" " 500	"	"
" " 150	"	"
10:8-16:1200	"	Produced in 32 days
" " 500	"	"
5:16-8:1200	Very slow growth	None produced in 94 days
" " 500	"	"
" " 150	"	"
5:8-16:1200	Very little growth	"
" " 500	but fragments	"
" " 150	remain alive	"
2:8-16:1200	Fragments bleached	"
" " 500	"	"
" " 150	No growth, fragments	"
	remain alive	

nuclei in late prophase (Figure 43g). The preparations were not well differentiated and accurate counting was difficult, counts ranged from 57-65 chromosomes with no obvious peak at any number.

No cytological preparations of dividing tetrasporangia or germinating tetraspores were obtained.

CALLITHAMNION TETRAGONUM (WITH.) C. AG.

Introduction

Rosenvinge (1923-1924) has given a detailed description of the vegetative and reproductive anatomy of *Callithamnion tetragonum*. He included within his concept of this entity four other species, *C. brachiatum* Bonnem., *C. fruticulosum* J. Ag., *C. baileyi* Harv. and *C. spiniferum* Kylin, the latter three being placed in *C. tetragonum* var. *fruticulosa* (J. Ag.) Rosenvinge. The delimitation of these species had previously been discussed by Kylin (1907) who concluded that they could be separated on cell dimensions.

The broadened concept of *C. tetragonum* (Rosenvinge, 1923-1924) has not been universally accepted, and in North America *C. baileyi* is still maintained as a separate species (Taylor, 1957; South and Cardinal, 1970). It is the only member of this group reported from eastern Canada (South and Cardinal, 1970). Although initially described by Harvey (in Bailey, 1848) as a separate species it is evident that he later (Harvey, 1853) had doubts about its separation from *C. tetragonum* and stated: ". . . the most robust forms with the shortest joints approach inconveniently near to *C. tetragonum*. . . ."

Farlow (1881) also maintained *C. baileyi* as a separate species but suggested: "We are inclined to believe that it would be better to consider the present species as delicate forms of *C. tetragonum*. . . ."

Taylor (1957) retained *C. baileyi* and *C. tetragonum* as separate species while admitting that they were not sharply distinguishable. He states that *C. tetragonum* is a coarser and more heavily corticated

species than *C. baileyi*.

The characters used for the separation of the two species: cell dimensions, gross morphology and degree of cortication, are subject to environmental influence (Harris, 1962) and have only limited taxonomic value in the genus *Callithamnion*.

Specimens identified as *C. tetragonum* or *C. baileyi* collected in North America and held in BM, TCD and NY have been examined; they show a complete intergradation. At one extreme the specimens resemble *C. tetragonum* as illustrated by Rosenvinge (1923-1924), with short barrel-shaped cells and branches with abruptly acuminate tips. At the other extreme they are more delicate, and the majority, identified as *C. baileyi*, are similar to *C. tetragonum* var. *fruticulosa* as described by Rosenvinge (1923-1924). Some specimens approach *C. spiniferum* as illustrated by Kylin (1907). Thus there appears to be no justification for maintaining *C. baileyi* as a separate species from *C. tetragonum*.

C. tetragonum has been recorded from the Mediterranean (Feldmann-Mazoyer, 1940), the Canary Islands (Børgesen, 1930) and throughout Europe to southern Scandinavia (Kylin, 1907; Rosenvinge, 1923-1924). It has not been reported from the Faeroes or from Iceland. In the western Atlantic it occurs from New Jersey (Taylor, 1957) northwards to Canada (as *C. baileyi*, Cardinal, 1968; South and Cardinal, 1970) and has recently been reported from Newfoundland (South and Hooper, 1972).

Plants with tetrasporangia, spermatangia, procarps and carposporophytes are recorded. The gametophytes have been reported to be monoecious (Farlow, 1881; Halos, 1964) or as either monoecious or

dioecious (Taylor, 1957). Tetrasporangia have frequently been reported on the same plant with either procarps, spermatangia or both (Kylin, 1907; Davis, 1910; Rosenvinge, 1923-1924; Knaggs, 1969).

Mathias (1927, 1928) has reported chromosome counts of n = 9-10 and 2n = 18-20 for *C. tetragonum* (as *C. brachiatum*), but this was criticised by Westbrook (1930, 1935). More recently Harris (1962) has claimed n = 28-33.

There are no reported culture studies of *C. tetragonum*.

C. tetragonum has been found at three sites in Newfoundland: Bonne Bay (St. 171), Grand le Pierre (St. 101) and St. Bernard (St. 104). It occurs from low-water mark to depths of ca. 10 metres. Plants grow on rocks and occur as epiphytes on larger algae. All Newfoundland material resembles Rosenvinge's (1923-1924) var. *fruticulosa*. Monoecious gametophytes, carposporophytes and tetrasporophytes have been found, but tetrasporangia were never seen in nature on the same plants as spermatangia and procarps.

Aims of the Study

The principal aims of the study of *C. tetragonum* were to:

(i) observe its reproductive periodicity in Newfoundland.

(ii) obtain its life history in culture and elucidate the factors affecting the formation of reproductive organs.

(iii) obtain cytological confirmation of the life history.

Observations and Results

Reproductive Periodicity

In Newfoundland *C. tetragonum* is only fertile in the latter half of the year. At Grand le Pierre, fertile monoecious gametophytes, tetrasporophytes and carposporophytes were found in November (St. 101.3) and December (St. 101.4). All plants were sterile in January (St. 101.5) and remained so until July (St. 101.8) when tetrasporophytes and gametophytes were again fertile. A single plant found in March (St. 104.21) at St. Bernard was sterile. At Bonne Bay (St. 171.6) a single tetrasporophyte was found in October, and several sterile plants were collected in April (St. 171.7).

Culture Studies

Cultures (ES 10:16-8:150) were established from carpospores and tetraspores from plants obtained at Grand le Pierre (St. 101.3) in November 1971. Germination (Figure 45a) was immediate and was of the *Ceramium*-type (Chemin, 1937). After seven days at 10:16-8:150 two culture series, one from carpospores and one from tetraspores, were set up and incubated under the conditions given in Figure 46 .

Growth Rates.

Samples were removed from all cultures after 21 days, and the number of axial cells and the total number of cells per plant were counted. No fixed number of plants was examined, but there was a minimum of ten in each sample. The means of the counts together with standard deviations and standard errors of the means, are presented

FIGURE 45

CALLITHAMNION TETRAGONUM

(a) Germination of a tetraspore, with a simple axial filament (AF) and a rhizoid (RZ). Scale = 100 µm

(b) Apical region of a tetrasporophyte with tetrasporangia (T). Scale = 500 µm

(c) Monoecious gametophyte with a procarp (P) and spermatangial cluster (SC). Scale = 100

(d) Mature carposporophyte with several developing gonimolobes. Scale = 500 µm

(e) Tetrasporangium (T) and spermatangial cluster on adjacent cells of a branch. Scale = 100 µm

(f) Uninucleate apical and adjacent cells. Cells on which lateral branches are initiated are also uninucleate. Stained with acetocarmine. Scale = 10 µm

(g) Multinucleate axial cells (Ax.C) in basal portions of the plants surrounded by corticating filaments (CF). Stained with acetocarmine. Scale = 100 µm

(h) Metaphase plates (MP) of four synchronously dividing nuclei in a tetranucleate axial cell. Stained with acetocarmine. Scale = 10 µm

(i) Binucleate cell in a lateral branch producing a further branch (Y). The nuclei, in metaphase (MP) are dividing synchronously and the daughter nucleus from nucleus 1 will become the nucleus of the new cell. Stained with acetocarmine. Scale = 10 µm

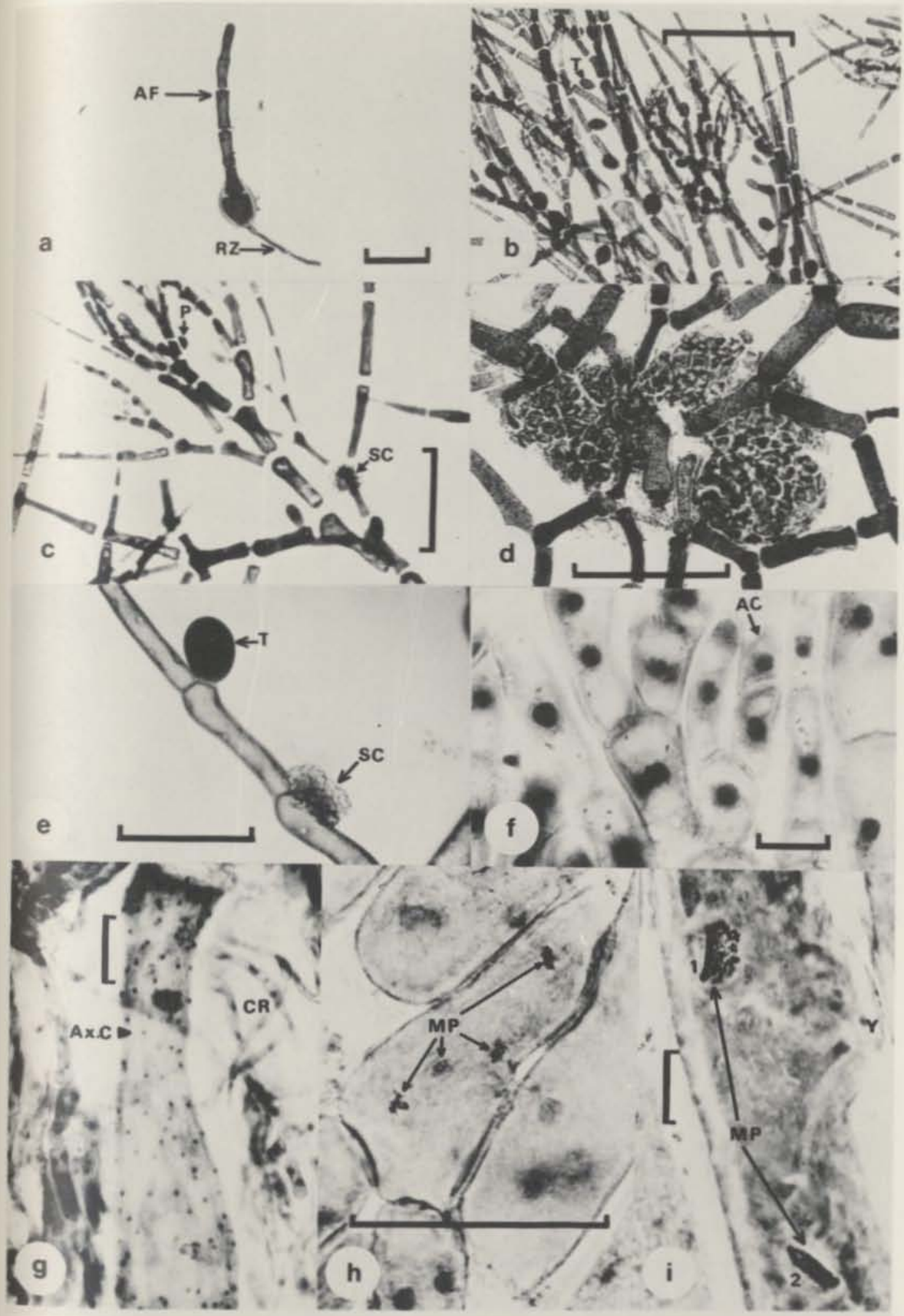
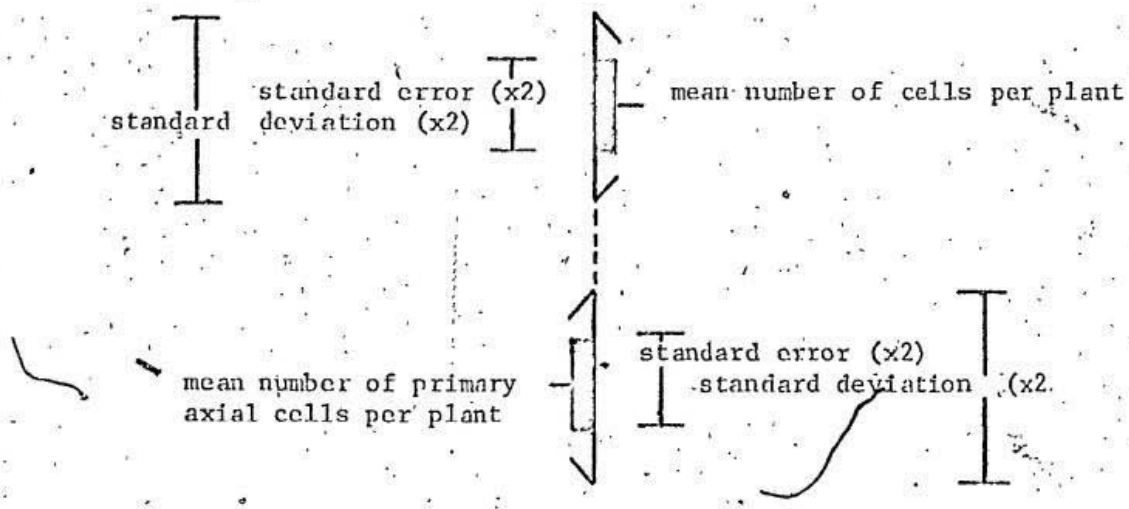

AF
RZ
a
b
P
SC
c
d
T
SC
e
AC
f
Ax.C
CR
g
MP
h
MP
Y
i
2

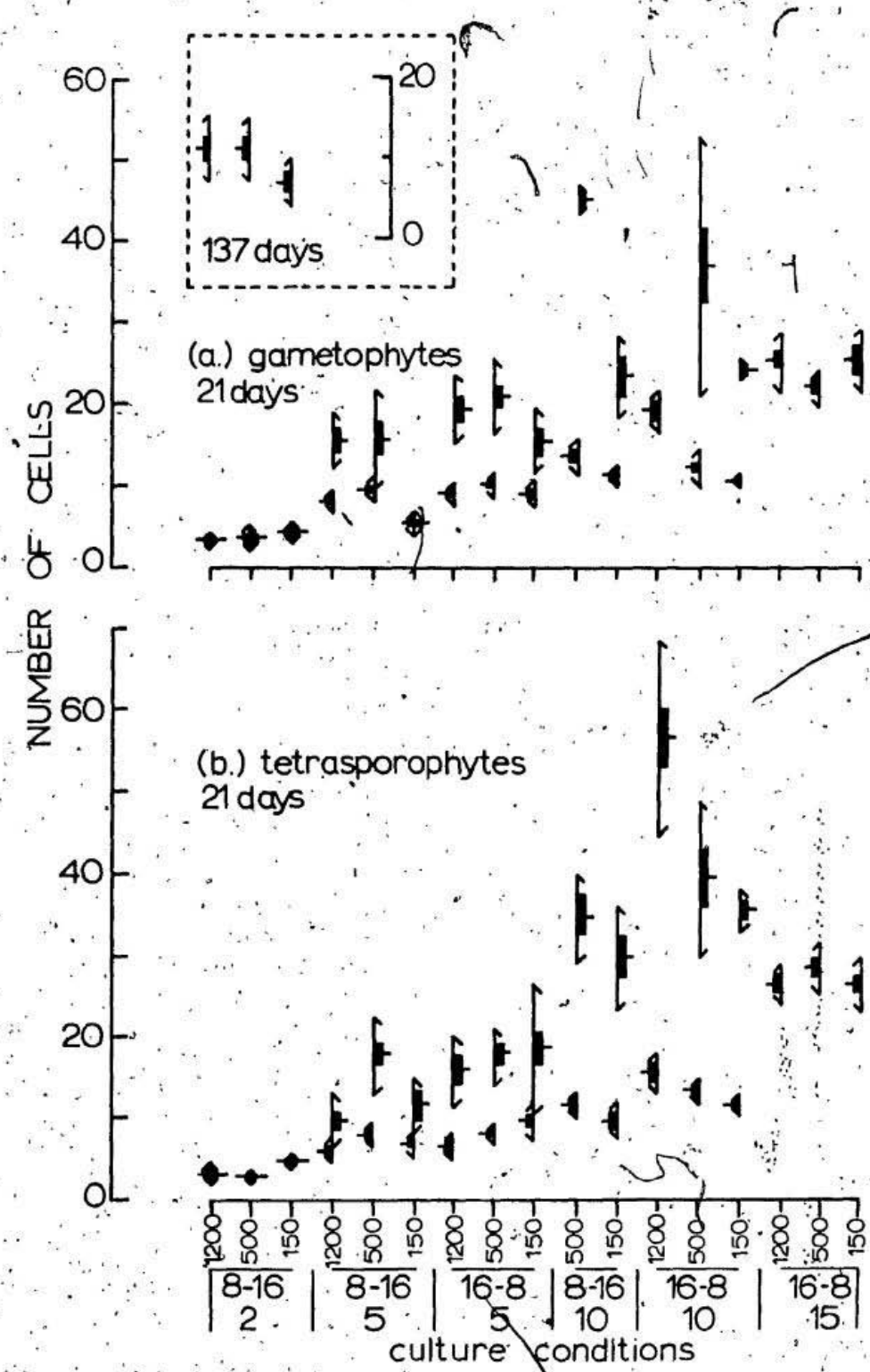
FIGURE 46

GROWTH RATES OF *CALLITHAMNION TETRAGONUM*

IN CULTURE

Growth rates at several culture conditions measured as the mean number of cells produced per plant and the mean number of axial cells produced per plant of: (a) gametophytes, derived from tetraspores after 21 days and 137 days of culture. (b) tetrasporophytes, derived from carpospores after 21 days of culture.




NUMBER OF CELLS
60
40
20
0
20
0
137 days
(a.) gametophytes
21 days
(b.) tetrasporophytes
21 days
1200
500
150
8-16
2
8-16
5
16-8
5
8-16
10
16-8
10
16-8
15
culture conditions

in Figure 46.

In the tetraspore cultures, growth rate was greatest at high temperatures, and daylength and light intensity have little effect at any one temperature. No noticeable growth occurred at 2:8-16 at any light intensity, and the cultures were again sampled at 137 days. The sporelings had grown, and were of similar size at the three light intensities. The cultures derived from carpospores do not show any significant differences in growth rate compared to those from tetraspores.

Life History in Culture.

The cultures used to assess the growth rate were continued until the sporelings produced reproductive organs. Cultures derived from carpospores produced tetrasporophytes (Figure 45b) and those from tetraspores produced monoecious gametophytes (Figure 45c).

The incubation periods required for the formation of reproductive organs under the different culture conditions are presented in Table 20. Under all conditions formation of spermatangia, tetrasporangia and procarps required similar periods of culture, although spermatangia were frequently the first formed. Light intensity had little effect on the induction period, which was shortest at the higher temperatures. At 10° cultures under short daylength took slightly longer to become fertile than those under equivalent conditions at long daylengths. Under long day conditions the formation period at 5°C was more than three times that required at 10°C. Cultures at 2°C and 5°C under short daylengths were continued for 137 days and no reproductive organs were produced, though plants exceeded the size

TABLE 20

INDUCTION OF REPRODUCTIVE ORGANS OF *CALLITHAMNION TETRAGONUM* IN CULTURES DERIVED FROM TETRASPORES AND CARPOSPORES

Culture conditions ES medium	Carpospore cultures	Tetraspore cultures	
	Days to first formation of Tetrasporangia	Days to first formation of Spermatangia	Procarps
2:8-16:1200	No induction	No induction	No induction
" " 500	"	"	"
" " 150	"	"	"
5:8-16:1200	"	"	"
" " 500	"	"	"
" " 150	"	"	"
5:16-8:1200	71	71	76
" " 500	76	71	76
" " 150	76	76	84
10:8-16: 500	31	25	31
" " 150	31	25	31
10:16-8:1200	25	21	25
" " 500	21	21	25
" " 150	25	21	25
15:16-8:1200	21	21	21
" " 500	21	21	21
" " 150	21	21	21

at which they became fertile at higher temperatures.

Tetrasporangia produced in culture germinated to produce monoecious gametophytes. Fertilizations occurred in culture, carposporophytes were formed (Figure 45d) and the carpospores germinated to produce sporelings which bore tetrasporangia. Single gametophytes were isolated into separate cultures (10:16-8:500) before they became fertile, and produced spermatangia and procarps. Developing carposporophytes were observed four days after the formation of the procarps, and they matured and released carpospores after a further eight days.

Tetrasporophyte cultures at 10:16-8:1200 and 10:16-8:500 were allowed to continue growth after the formation of tetrasporangia. At forty-four days a number of plants had produced spermatangia and procarps in addition to tetrasporangia (Figure 45e), and a single carposporophyte was also observed. The plant bearing the developing carposporophyte was transferred to a separate culture (ES 10:16-8:500), but bleached out and died before the carpospores matured. Six other plants bearing procarps, spermatangia and tetrasporangia were isolated in separate cultures. They continued growth and production of all three types of reproductive organs, but no fertilizations were achieved. The tetraspores germinated and produced monoecious gametophytes which were allowed to remain in culture with the parent plant. Numerous carposporophytes developed on the gametophytes, but none were observed on the parent plant.

The life history of *C. tetragonum* in culture is of the *Polysiphonia*-type, but with the modification of monoecious gametophytes.

The tetrasporophytes are also capable of producing spermatangia and procarps, and from the occurrence of a single carposporophyte these appear functional. The ultimate fate of the carpospores produced by this carposporophyte is unknown.

Cytological Studies

All cytological examinations were carried out on material from culture. Numerous instances of dividing nuclei were observed, but no preparations of sufficient quality to allow chromosome counting were obtained. No nuclear divisions were seen in tetrasporangia.

Interphase nuclei in vegetative cells are of constant size throughout the plant, and measure 6-7 µm in diameter. The cells at the apex of the plant are uninucleate (Figure 45f), but become multinucleate in the more mature regions (Figure 45g).

The number of nuclei found in the main axial cells of a tetrasporophyte cultured in ES 10:16-8:1200 in relation to cell size and position is presented in Table 21. Synchronous nuclear division occurs in the multinucleate axial cells (Figure 45h) resulting in nuclear number increasing in a geometric series. Up to the 8 nucleus stage [redacted] deviations occur, at the 16 nucleus stage and beyond fewer nuclei are found than would be theoretically predicted. Failure of a few nuclei to divide synchronously would account for such discrepancies. Cells with more than 64 nuclei were observed, but these were obscured by corticating rhizoids (Figure 45g) and precise counts were impossible.

Lateral branch development on the main axis does not interfere with the geometric sequence. Such branches are initiated in the

TABLE 21

RELATIONSHIP BETWEEN NUMBER OF NUCLEI, AXIAL CELL SIZE AND POSITION IN *CALLITHAMNION TETRAGONUM*

Axial Cell Position in relation to apical cell	Cell Dimensions length x diameter µm	Number of Nuclei in the cell
Apical cell	17.5 x 12.5	1
2	20 x 12.5	1
3	25 x 15	1
4	40 x 22.5	1
5	30 x 30	1
6	32.5 x 35	2
7	40 x 40	2
8	37.5 x 42.5	4
9	50 x 50	4
10	75 x 62.5	8
11	87.5 x 62.5	8
12	112 x 67	15
13	125 x 70	16
14	163 x 75	16
15	163 x 75	16
16	187 x 80	15
17	225 x 87	29
18	250 x 87	29

TABLE 21 (CONTINUED)

Axial Cell Position in relation to apical cell	Cell Dimensions length x diameter µm	Number of Nuclei in the cell
19	328 x 100	29
20	320 x 100	31
21	320 x 100	29
22	332 x 104	32
23	340 x 112	63
24	376 x 104	58
25	400 x 108	56
26	400 x 120	60
27	400 x 120	59
28	400 x 120	59
29	400 x 130	57
30	400 x 120	58
31	420 x 120	60
32	400 x 100	57

immediate apical region (Figure 45f) when the parent cells are uninucleate.

The number of nuclei in the lateral branches does not show any pattern. The cells of the branches may divide when they are multinucleate (Figure 45f), and as the nuclear divisions are synchronous, the transfer of a single nucleus to the developing structure interupts the geometric series.

PLUMARIA ELEGANS (BONNEM.)SCHMITZ

Introduction

Plumaria elegans is a widespread alga of the North Atlantic. It occurs throughout Europe from the Rio de Vigo in Spain (Hamel, 1929) to northern Norway (Jaasund, 1965). In North America it is found from New Jersey (Taylor, 1957) to Newfoundland (Mathieson *et al.*, 1969). It has been reported from the Faeroes (Børgesen, 1902) and from Iceland (Jønsson, 1901), but is apparently absent from Greenland.

The vegetative anatomy of the species is thoroughly described (Nägeli, 1847; Cramer, 1864; Rosenvinge, 1923-1924), and details of the structure and development of the reproductive organs and the carposporophyte are given by Suneson (1938) and Drew (1939).

P. elegans possesses, in addition to a haploid gametophyte (n = 31) generation and a diploid tetrasporophyte (2n = 62) generation, a triploid phase (3n = 93) (Drew,1939). This is genetically isolated from the haploid and diploid generations and reproduces by paraspores. Rueness (1968) has shown in culture that paraspores produce paraspore-bearing plants, confirming the life history suggested by Drew (1939) on the basis of field and cytological studies. Drew(1939) and Rueness(1968) have discussed the European distribtuion of *P. elegans* in relation to its reproductive structures. At its northern localities only parasporophytes are reported and at the southern limits only haploid and diploid plants occur. In midrange all three generations are present, which led

Drew (1939) to speculate that the triploid generation is an adaptation to life in cold waters. The situation is complicated by the reported occurrence of tetrasporangia and parasporangia on the same plants (Rosenvinge, 1923-1924; Drew, 1939). Drew (1939) showed that the tetrasporangia occur on the triploid generation, but did not find parasporangia on the diploid tetrasporophytes. She has suggested that tetrasporangia on the triploid plants signify an attempted meiosis, but there is no cytological evidence and their function is unknown.

There is no detailed account of the distribution of the three generations in North America. Taylor (1957) reports the occurrence of gametophytes, tetrasporophytes and parasporophytes, but all the fertile eastern Canadian material examined in this study was parasporangial.

Parasporangia occur throughout the year in southern Scotland (Blackler, 1956), but are absent in the spring in Danish waters (Rosenvinge, 1923-1924). More northerly records of parasporangia, sometimes erroneously reported as cystocarps (Rueness, 1968), are mainly for the summer months (Foslie, 1890; Jønsson, 1901; Børgesen, 1902; Jaasund, 1965).

P. elegans has been found at nine sites in Newfoundland (St. 94, St. 100, St. 101, St. 103, St. 104, St. 105, St. 106, St. 107, St. 171) where it occurs from the lower littoral to depths of ca. 14 metres. It is especially abundant on vertical rock faces in the immediate sublittoral. Detailed studies were made at St. Bernard (St. 104) where it occurs in the lower littoral and immediate

sublittoral on rock faces overhung with *Ascophyllum nodosum*. All fertile plants bore parasporangia, but tetrasporangia were occasionally seen.

Aims of the Study

There are no experimental studies of *P. elegans* from its northernmost localities in Europe, and no life history or cytological studies are reported from North American material. The principal aims of this study were:

(i) to assess the phenology at St. Bernard.

(ii) to establish the life history in culture of parasporangial plants, and to confirm the work of Rueness (1968).

(iii) to cytologically examine material from field and culture, and confirm the existence of a triploid generation in North America.

(iv) to establish the role of tetrasporangia in the life history of parasporangial plants.

Observations and Results

Phenology

P. elegans is a perennial alga at St. Bernard and parasporangia are found throughout the year. The distribution and degree of development of the parasporangia does, however, show considerable seasonal variation and these data are presented in Table 22.

In September 1970 (St. 104.4) all plants bore mature parasporangia consisting of up to 15 spores. The parasporangia were found throughout the plant, this situation persisted until December

TABLE 22

PHENOLOGICAL DATA OF *PLUMARIA ELEGANS* AT ST. BERNARD (ST. 104) BETWEEN SEPTEMBER 1970 AND MARCH 1972

	Collection Date																	
	1970				1971											1972		
	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M
Station/Date number (St. 104.x)x=	4	6	7	8	9	10	11	12	NO DATA	13	14	15	16	17	NO DATA	18	19	20	21
Parasporangia in apical region	+	+	+	+							+	+	+	+					
Parasporangia in basal region	+	+	+	+	+	+	+	+		+	+	+	+	+		+	+	+	+
In situ germination of parasporangia								+		+									
Plants bleached in the littoral						+	+											+	+

(St. 104.8). In the early months of 1971 (St. 104.9 - .12) parasporangia in varying degrees of development were observed on the lower portions of the plants, but were absent in the apical regions. The sterile apices continued growth throughout the first half of the year, but no parasporangia were produced. The parasporangia on the basal regions remain quiescent until April (St. 104.12), when a number of spores were observed to have germinated *in situ* (Figure 47a). In June (St. 104.13) all the paraspores showed *in situ* germination, but a number of undivided parasporangial initials were also present. The *in situ* germination produces an irregular branching pattern, giving the lower regions of the plant a distinctive appearance (Figure 47b). In July (St. 104.14) mature parasporangia were found in the basal regions of the plants, presumably developing from preformed initials seen throughout the earlier part of the year. Developing parasporangia were also found in the apical regions (Figure 47c), though few of these appeared mature. In August (St. 104.15) mature parasporangia were abundant on all parts of the plants and the irregular branching pattern in the basal region was obscured by the subsequent vegetative growth. In the latter part of the study, from September 1971 to March 1972 (St. 104.16 - .21) the sequence of events was identical to that reported for the previous year.

Several plants were found bearing tetrasporangia in September (St. 104.16) and October (St. 104.17).

Sublittoral populations were present throughout the year and were most abundant in the latter part of summer. The majority of

FIGURE 47

PLUMARIA ELEGANS

(a) *In situ* germination of paraspores (GP) within the parasporangium. Scale = 100 µm

(b) Branch with new growth (NG) at apex lacking paraspores and region basal to this with paraspores germinating *in situ* (1GP). Scale = 500 µm

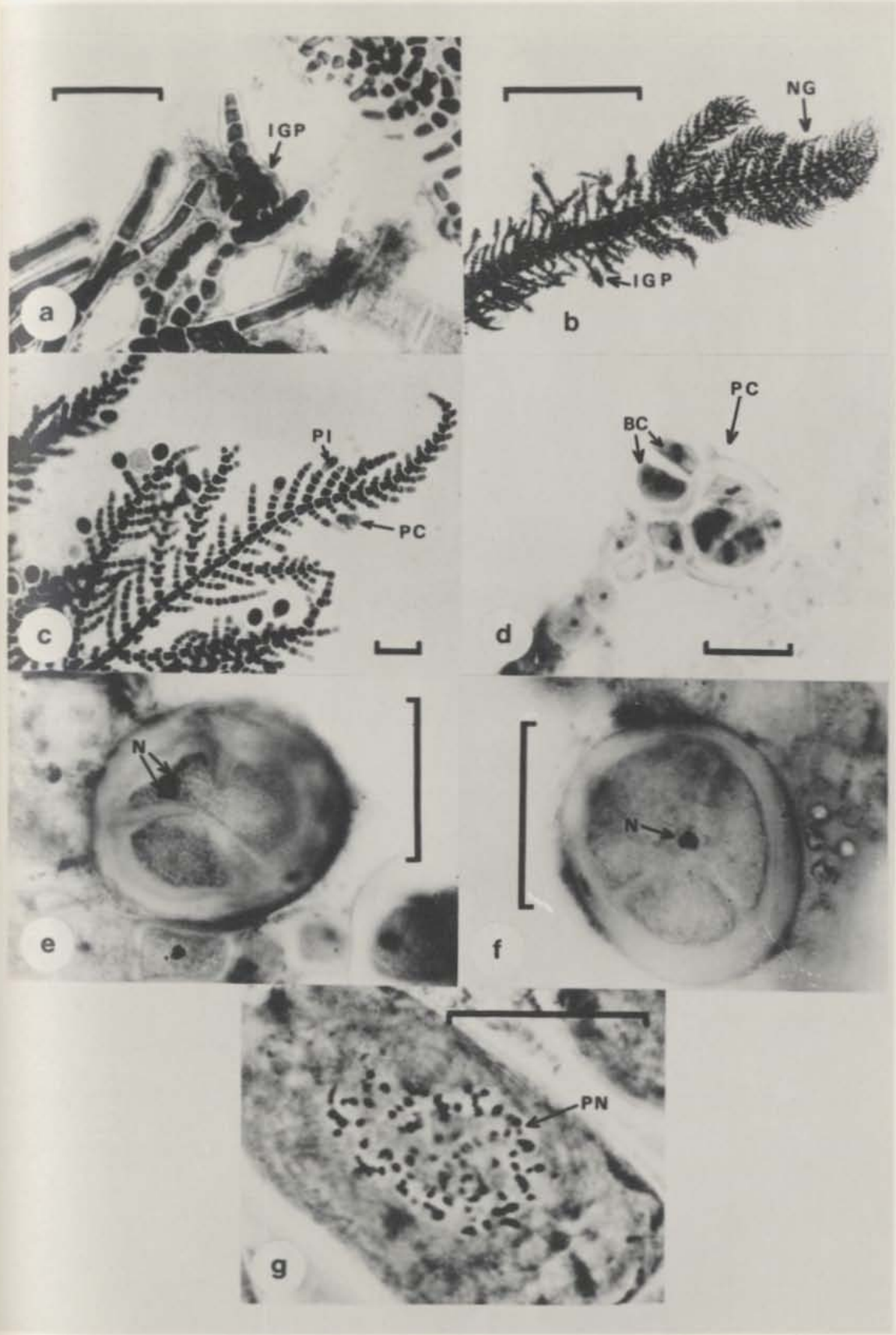
(c) Parasporangial initials (PI) and developing parasporangial clusters (PC) in apical region of a plant. Scale = 100 µm

(d) Parasporangial cluster (PC) with binucleate cells (BC). Stained with acetocarmine. Scale = 50 µm

(e) Tetrasporangium with two nuclei (N) showing incomplete cytokinesis. Stained with acetocarmine. Scale = 50 µm

(f) Tetrasporangium with a single nucleus (N) and complete tetrahedral cytokinesis. Stained with acetocarmine. Scale = 50 µm

(g) Mitotic prophase nucleus (PN) in an apical cell. Scale = 10 µm


IGP
a
NG
IGP
b
PI
PC
c
PC
BC
d
N
e
N
f
PN
g

intertidal plants, however, disappeared in the winter months and were observed to be bleached in February and March of both 1970 and 1971.

Culture Studies

Cultures, derived from discharged paraspores and vegetative fragments of sterile plants, were used to determine growth rates and the factors affecting the formation of reproductive organs.

Growth Rates.

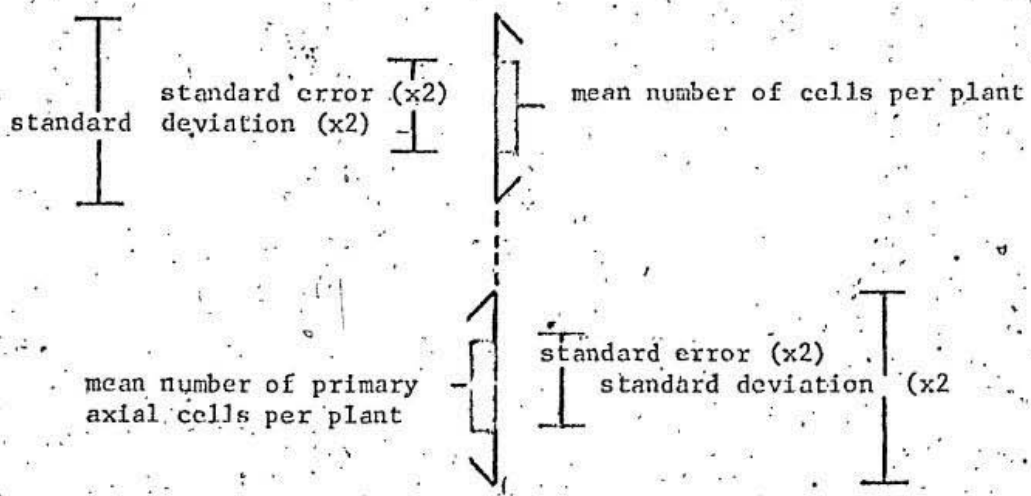
Cultures were established from paraspores released from plants collected at St. Bernard (St. 104.16) in September 1971. Apical regions, bearing parasporangia, were excised and rinsed free of adhering contaminants. The fragments were placed in culture (ES 10:16-8:150) for seven days, paraspores were released and the majority germinated. Coverslips bearing paraspores were placed in separate cultures and incubated under the conditions given in Figure 48. The cultures were sampled after 6 and 7 days growth and those at 2°C were sampled again at 151 days. No fixed number of plants were counted; means of axial cell numbers and total number of cells in each plant, together with standard deviations and standard errors of the mean are presented in Figure 48.

The growth rate is greatest at high temperatures. Light intensity at 2°C and 5°C has little effect on growth rate, at 10°C axial cell counts are similar at all intensities, but the total number of cells is reduced under low illumination. At 15°C the numbers of axial cells is greatest at high intensities. The growth rates appear little affected by daylength at 10°C when compensation is made for

FIGURE 48

GROWTH RATES OF *PLUMARIA ELEGANS* IN CULTURE

Growth rates at several culture conditions measured as the mean number of cells produced per plant and the mean number of axial cells produced per plant of sporelings produced from paraspores after (a) 6 days, (b) 17 days, (c) 151 days of culture.



NUMBER OF CELLS
(a.)
6 Days
(b.)
17 Days
(c.)
151 Days
0
10
20
30
40
50
60
2:8:16:1200
500
150
5:16:8:1200
500
150
10:16:8:1200
500
10:16:8:1200
500
150
15:16:8:1200
500
150
Culture conditions

the reduction in total illuminance.

Life History in Culture.

The cultures used for the determination of growth rates were continued for 151 days or until the sporelings became fertile. They were examined at approximately weekly intervals and the culture period required for the formation of parasporangia is given in Table 23.

Only plants under long daylengths at 10°C and 15°C became fertile. Sporelings after 151 days in culture at 2°C and 5°C did not reach the size at which they became fertile at 10°C and 15°C. At 10°C under short daylengths the plants were apparently large enough to produce parasporangia, but these were not observed.

Sterile apices consisting of approximately 40 axial cells were excised from plants collected at St. Bernard in June 1971 (St. 104.13). They were rinsed in medium (ES) and cultured under the conditions given in Table 24 where the results of these cultures are also presented.

Parasporangia were first formed at 15°C, but were also produced at 10°C under long and short daylengths. Light intensity and daylength have no significant effect on the time required for their formation. Cultures at 2°C and 5°C were maintained for 113 days. No parasporangia were formed, though fragments continued vegetative growth.

Thus in culture paraspores from *Plumaria elegans* obtained from St. Bernard give rise to parasporangium bearing plants. The formation of parasporangia is apparently temperature dependent.

TABLE 23

FORMATION OF PARASPORANGIA IN CULTURE ON PLANTS OBTAINED FROM PARASPORES OF *PLUMARIA ELEGANS*

Culture conditions ES medium	Culture period required from germination to formation of parasporangia
2:8-16:1200	No formation at 151 days
" " 500	"
" " 150	"
5:16-8:1200	"
" " 500	"
" " 150	"
10:8-16:1200	"
" " 500	"
10:16-8:1200	101 days
" " 500	"
" " 150	"
15:16-8:1200	68 days
" " 500	"

TABLE 24

FORMATION OF PARASPORANGIA IN CULTURES OF STERILE APICES OF *PLUMARIA ELEGANS*

Culture conditions ES medium	Culture period required for the formation of parasporangia
2:8-16:1200	No induction at 113 days
" " 500	"
" " 150	"
5:8-16:1200	"
" " 500	"
" " 150	"
5:16-8:1200	"
" " 500	"
" " 150	"
10:8-16:1200	44 days
" " 500	"
10:16-8:1200	42 days
" " 500	38 days
" " 150	42 days
15:16-8:1200	29 days
" " 500	"

An apical fragment bearing developing parasporangia was transferred from 15:16-8:500 to 2:16-8:500 and cultured for 28 days. The paraspores germinated *in situ*, but none were released. Fragments maintained at 15:16-8:500 continued maturation and release of paraspores.

Cytological Studies

Mitotic divisions were observed in apical cells, corticating cells and in developing parasporangia, and showed no deviations from the normal pattern of division. In some instances of paraspore formation cytokinesis lags behind karyokinesis, and results in the formation of a number of multinucleate cells within the parasporangial clusters (Figure 47d).

A number of tetrasporangia were also examined, but no dividing nuclei were seen. The mature tetrasporangia had undergone cytokinesis, but in many instances (Figure 47e) this was incomplete. One tetrasporangium was divided into four spores, but only one of these contained a nucleus (Figure 47f). In another (Figure 47e), two nuclei were formed in an incompletely divided cell. In no instances have four uninculeate spores been found in a tetrasporangium.

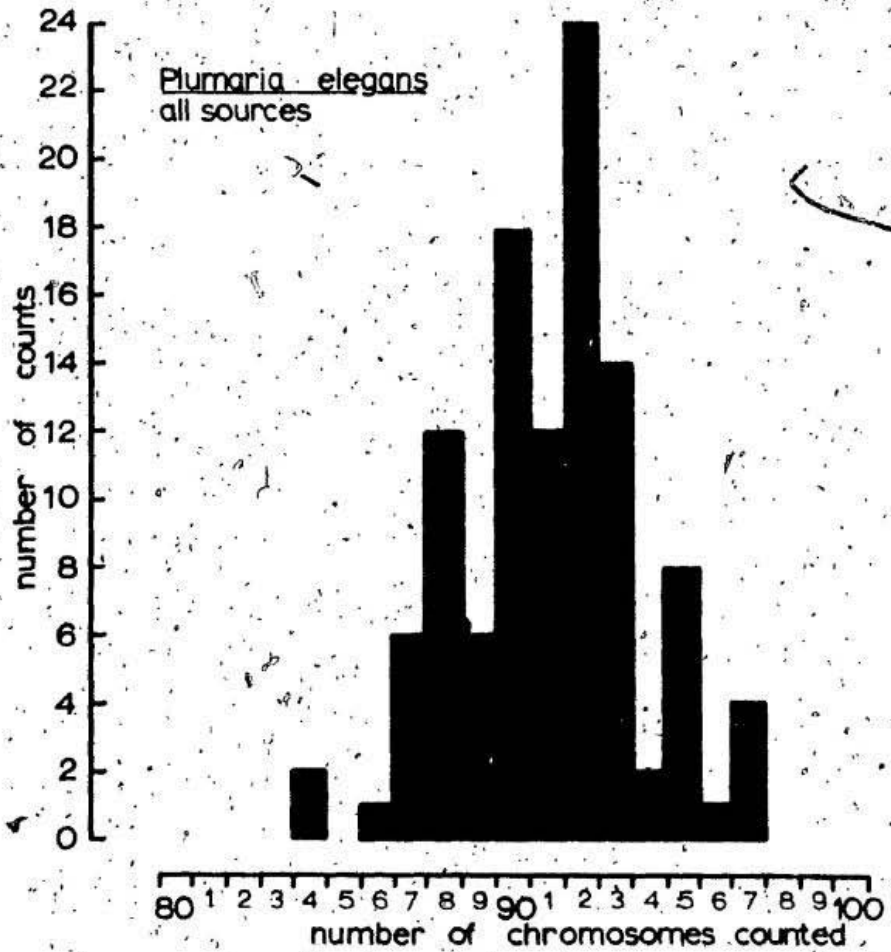
Chromosome Numbers.

Chromosome counts were made from mitotic divisions in late prophase (Figure 47g). Counts ranging between 84 and 97 were obtained, with the maximum number between 90 and 93; these are presented in Figure 49 . These counts are in agreement with those given by Drew (1939) for triploid parasporangial plants from Europe.

FIGURE 49

CHROMOSOME COUNTS IN
PLUMARIA ELEGANS

Distribution of chromosome counts obtained from mitotic prophases of *P. elegans* from both vegetative cell divisions and from parasporogenesis.


Plumaria elegans
all sources
number of counts
0
2
4
6
8
10
12
14
16
18
20
22
24
80 1 2 3 4 5 6 7 8 9 90 1 2 3 4 5 6 7 8 9 100
number of chromosomes counted

DISCUSSION

Taxonomy

Wollaston (1968) has redefined the circumscription of the genus *Antithamnion* on the basis of examination of large collections of hitherto unknown or under-described southern Australian species of this and related genera. She has shown that many of the species in the previously accepted concept of *Antithamnion* are the products of distinct and separate evolutionary lines. Wollaston (1968) distinguishes the genus *Antithamnion* in its possession of the following characters:

(i) All axes prostrate and indeterminate, occasionally free and distinct only at the tips of the branches.

(ii) Axes completely lacking rhizoidal cortication.

(iii) Whorl branchlets of similar morphology and arranged in opposite pairs, either distichous or decussate; each whorl branchlet has a small basal cell which does not bear pinnules.

(iv) Gland cells borne on special short two to four celled branches.

(v) Tetrasporangia cruciately divided, usually ovoid when mature.

(vi) Carpogonial branches borne singly on the basal cells of the whorl branchlets at the branch apices, although a number of (4-20) procarps may develop on each axis only a single carposporophyte matures.

Wollaston (1971) has subsequently established the genus *Scagelia* with its type species *Antithamnion occidentale* Kylin. The

diagnostic features of the genus are:

(i) An erect axis, with a pronounced curvature in the immediate apical region.

(ii) Two to four whorl branchlets, often of unequal length on each axial cell.

(iii) Gland cells borne on single cells of unmodified whorl branchlets and pinnules.

(iv) Carpogonial branches are borne on the basal cells of the whorl branchlets.

(v) The fertile axis and the whorl branchlet bearing the carpogonial branch continue normal growth after fertilization.

The taxa described in this work, as Form A and Form B, which were formerly referred to *Antithamnion* do not agree with Wollaston's concept of this genus, but closely fit her description of *Scagelia*. The first available specific epithet is *pylaisaei* based on *Callithamnion pylaisaei* (Montagne, 1837), the combination *Scagelia pylaisaei* (Mont.) nov. comb. has therefore been proposed.

It is apparent from the description of *Antithamnionella floccosa* that it also could not be retained within the genus *Antithamnion* Näg. as delimited by Wollaston (1968).

Antithamnionella was first described by Lyle (1922) for a new species *A. sarniense* and distinguished from *Antithamnion* in possessing tetrahedrally divided tetrasporangia. Feldmann-Mazoyer (1940) rejected *Antithamnionella* and transferred *A. sarniense* to *Antithamnion sarniense* (Lyle) G. Feldmann. *A. sarniense* has subsequently been shown to be conspecific with *Antithamnion spirographidis* Schiffner (Sundene, 1964a),

and this epithet has priority.

Wollaston (1968) has examined *Antithamnion spirographidis* showing that it is incorrectly placed in *Antithamnion* Näg. and has thus transferred it to *Antithamnionella* Lyle as *Antithamnionella spirographidis* (Schiffner) Wollaston. Wollaston (1968) distinguishes *Antithamnionella* from *Antithamnion* in that:

(i) it has erect lateral branches with a prostrate axis.

(ii) lateral branches are produced in place of whorl branchlets.

(iii) there is inconsistency in the numbers of branchlets per whorl and in the branching of the whorl branchlets.

(iv) gland cells are sessile on single cells of the whorl branchlets.

(v) the tetrasporangia may be either tetrahedrally or cruciately divided.

(vi) spermatangial branches bear spermatangial mother cells laterally rather than terminally.

(vii) only 1-3 procarps are formed at any one branch apex each being borne on a reduced whorl branchlet of two cells.

The reproductive features (v-vii) exactly fit the description of *A. floccosa*, but the vegetative structure differs in details. *A. floccosa* lacks gland cells and in mature portions of the thallus regularly bears two simple whorl branchlets on each axial cell.

Wollaston (1971) transferred a further two species of *Antithamnion*, *A. glanduliferum* Kylin and *A. pacificum* (Harv.) Kylin to *Antithamnionella*. This has broadened the concept of the genus, as *A. pacifica* and *A. glandulifera* regularly bear two whorl branchlets

per axial cell and show a reduced prostrate axial system. In addition *A. pacifica* almost totally lacks gland cells. The reproductive features remain as initially described (Wollaston, 1968), but the concept of the vegetative features of the genus is sufficiently broadened to accept *A. floccosa*. There is, however, a nomenclatural problem concerning the genus *Pterothamnion* Nägeli as the combination *Pterothamnion floccosum* (O. F. Müll.) Näg. apparently has priority over the proposed combination.

Pterothamnion as initially described by Nägeli (1855) included, in addition to *P. floccosa*, *P. plumula* (Ellis) Näg. which is currently recognised as *Antithamnion plumula*. Nägeli (1861) later added a number of other species to *Pterothamnion* and erected a sub-genus *Haplocladium* to which *P. floccosa* was transferred while *P. plumula* was retained directly under *Pterothamnion*. It is thus evident that *P. plumula* rather than *P. floccosa* should be regarded as the type species of *Pterothamnion*. *Antithamnion plumula* has not been studied in detail in this work, but it is evident from previous reports (Kylin, 1923; L'Hardy-Halos, 1968) that it cannot be included within *Antithamnionella* Lyle. Thus *Antithamnionella floccosa* is the correct combination for the species previously named *Antithamnion floccosum*.

The systematic position of *Antithamnion plumula* obviously requires detailed study, as it is also evident that the species does not fall within the circumscription of the genus *Antithamnion* as defined by Wollaston (1968).

Of the seven species of *Antithamnion* listed for eastern Canada (South and Cardinal, 1970) only *A. cruciatum*, the type species, is

retained with confidence. *A. plumula* is tentatively retained, but its occurrence in eastern Canada and its systematic position require further study. The occurrence of *A. pacificum* (*Antithamnionella pacifica*) is rejected as a mis-identification of *A. floccosum*, which has been transferred to the genus *Antithamnionella*. *Antithamnion pylaisaei*, *A. americanum* and *A. boreale* are combined as *Scagelia pylaisaei*.

The four taxa, *Antithamnion cruciatum*, *A. plumula*, *Antithamnionella floccosa* and *Scagelia pylaisaei* are easily distinguished by the following key:

Artificial key to the taxa, formerly included in *Antithamnion*, which occur in eastern Canada

(1) Gland cells borne on specialised short pinnules and overlie 2 or 3 cells . . . . . *Antithamnion cruciatum*

(1) Gland cells either absent or borne in single cells of whorl branchlets and pinnules . . . . . (2)

(2) Gland cells absent; all whorl branchlets simple . . . . . *Antithamnionella floccosa*

(2) Gland cells, present or rarely absent, not all whorl branchlets simple . . . . . (3)

(3) Pinnules regularly secund on adaxial face of whorl branchlets, tetrasporangia pedicellate . . . . . *Antithamnion plumula*

(3) Pinnules irregularly or pinnately arranged rarely entirely secund, or absent, tetrasporangia sessile . . . . . *Scagelia pylaisaei*

The two Forms of *S. pylaisaei*, *S. pylaisaei* var. *boreale* and *S. pylaisaei* var. *pylaisaei* are not readily separable without resorting to culture techniques to distinguish between genotypic and ecotypic variation.

Variation in thallus morphology with respect to distributional and seasonal factors is one of the major difficulties of algal taxonomy. The early phycologists described species from herbarium material often on the basis of single specimens and had no knowledge of the algae in their natural habitats (Dixon, 1970b). In addition the ideas of fixity of specific form were strongly entrenched and it was not until the latter half of the nineteenth century that the concepts of evolution and inherent variation became accepted. The statement by Kjellman (1883) is especially relevant to this work:

> I am of the opinion that the genus *Antithamnion* is a young genus whose species are in the course of development, no marked differentiation being as yes (sic) established and the transitional forms not having disappeared.

It is significant that this statement was made by a phycologist who had an intimate knowledge of the form variation, over a large part of their environmental ranges, of the species he examined. It was inevitable therefore, that the earlier phycologists should regard minor morphological variations as sufficient to constitute separate species. The subsequent lack of critical study of type material, range of form, and an overreliance on previous descriptions, has led to extremely confused taxonomic situations amongst many groups of algae. Such a situation existed amongst the former taxa of *Antithamnion* for which the combination *Scagelia pylaisaei* is proposed.

The characters of cell size and branching pattern, formerly used as taxonomic criteria, are unreliable and do not, on the basis of experimental and long term field investigations, constitute acceptable delimitations within the proposed concept of *S. pylaisaei*. It appears from the variation shown in the herbarium material, and from an examination of the literature and type material that the various epithets combined under *S. pylaisaei* merely denote a number of ill defined morphological forms of a single species.

Reports of morphogenetic studies of the form of the Rhodophyta in nature are scanty (Dixon, 1963b, 1966b, 1970b). The use of cell measurements in field and in culture to provide a morphogenetic basis for the solution of taxonomic problems in the filamentous Rhodophyta, appears to be restricted to the work of Harris (1966) on *Callithamnion* spp. and the more extensive studies of Knaggs (1965, 1966b, 1966c) on *Rhodochorton purpureum* (Lightf.) Rosenvinge.

Dixon (1966b, 1970a) has stated that the external form of an algal thallus is determined by the disposition of the axes, the shape of the axes and the longevity of the plant. In a uniaxial, uniseriate, uncorticated thallus such as that of *Scagelia pylaisaei* the disposition and shape of the axis is dependent on a few easily measurable factors.

(i) the rate of division of the apical cell.

(ii) the subsequent enlargement of the axial cells.

(iii) the degree to which the axial cells divide laterally to produce whorl branchlets.

(iv) the degree to which the whorl branchlet cells enlarge and divide.

The age of the plant determines its overall size, but has little effect on its detailed anatomy.

This study has attempted to explain the seasonal changes in morphology by the use of cultures grown under defined physical conditions; it is not intended to be an intensive study of morphogenesis in the species.

The results of culture of apical fragments from plants of very different morphologies show separation into two distinct Forms (A and B), which are easily distinguished in culture by the form of their whorl branchlets and the dimensions of the whorl branchlet cells. The most striking difference, however, is that in Form B all the branchlets were borne in pairs, while those of Form A occurred in whorls of two and three. On the basis of whorl branchlet morphology the two Forms are inseparable in the field, and although the tendency to form paired whorl branchlets on the axial cells of Form B is quite marked in nature, it is not a rigid distinction.

Although the magnitude is different the numbers of whorl branchlets produced show the same seasonal patterns in both Form A and Form B. The greatest number are present in spring when the water temperature is low, and daylength and light intensity are increasing. Conversely, fewer whorl branchlets are found in the fall, the time of highest seawater temperature and shortening daylengths. The same phenomenon is shown in culture, with the greatest number of branchlets per axial cell produced under long daylengths at low temperatures.

The rates of growth of both Forms in culture show the same trends; they are lowest at low temperatures and at short daylengths.

A reduction in the rate of apical cell division under short daylengths also occurs in *Antithamnionella floccosa*, and has been reported by Dixon and Richardson (1970) for *Gallithamnion tetricum* (Dillw.) S.F. Gray, and for *Griffithsia pacifica* Kylin (Waaland and Cleland, 1972). In contrast no obvious effects have been observed in this study on *Callithamnion roseum*, *C. tetragonum* and *Plumaria elegans*.

The factors which initiate cell division in the Rhodophyta are unknown, but it has been shown in the field, by cytological study (Austin and Pringle, 1968), that cell division in *Rhodomela larix* (Turner) C.Ag. exhibits a diurnal rhythm. Such a rhythm has been shown by direct observation in cultures of *Griffithsia pacifica* (Waaland and Cleland, 1972) and confirmed as an endogenous phenomenon unaffected by transfer to continuous light conditions.

In *Griffithsia pacifica* daylength has little effect on cell elongation (Waaland and Cleland, 1972). No direct measurements have been made on the rate of cell elongation in *S. pylaisaei*, but these can be inferred from the axial cell measurements and the rate of division of the apical cells. The axial cells in the subapical region are longest at high temperatures under short daylengths and conversely are shorter at low temperatures under long daylengths.

The rate of cell division is reduced under short daylengths, thus if other factors remain constant, corresponding cells are older in short daylength than in long daylength plants. If the rate of cell elongation is unaffected by photoperiod, as in *G.pacifica*, the corresponding cells will be longer under short daylengths. The cells

are longest at high temperatures, indicating that although cell division is greatest at these temperatures the rate of cell elongation must also be accelerated.

As with the rate of cell division light intensity appears to have the least effect on cell size, and a similar observation was made for *Griffithsia pacifica* (Waaland and Cleland, 1972).

Under all equivalent conditions, cultured plants of Form B have longer cells in the immediate apical regions than plants of Form A. The rate of apical cell division in both forms is, however, similar under the same conditions, suggesting that one of the major differences between the two forms is the rate of cell elongation.

The rate of apical cell division and the elongation of the derivative cells appear to exert considerable influence on whorl branchlet production. The greatest number of whorl branchlets are formed on plants in which the axial cells remain short for the greatest distance behind the apical cell. Such a morphology results from rapid cell division accompanied by a reduced rate of elongation, and in culture occurs at low temperature and short daylengths. It is significant that the maximum numbers of whorl branchlets are found in nature in spring, when seawater temperatures are low, but when both daylength and total illumination are increasing. Conversely fewer whorl branchlets are found on plants which have long cells in the immediate subapical regions. Such plants are formed by high rates of cell elongation in relation to the rate of cell division and in culture occur at the higher temperatures especially under short day conditions. In nature such conditions, and such plant morphologies,

are found in the fall when seawater temperature is high, but daylength and illumination are reduced. Whorl branchlets are cut off the axial cells in sequence at two to five cell intervals behind the apical cell, and thus there appears to be a critical axial cell size above which lateral division does not take place. This has been confirmed by culture observations. Apical fragments of Form A, bearing only paired whorl branchlets, cultured under conditions promoting the formation of whorls of three or four branchlets produce these only on the cells in the immediate subapical region.

While it is proposed that the size of the axial cell in the immediate subapical region determines the number of whorl branchlets that it will ultimately bear, it is possible that the converse is true. Dixon (1971) has shown that the formation of lateral indeterminate branches in *Griffithsia flosculosa* (Ellis) Batt., *Ptilota plumosa* (Huds.) C. Ag. and *Ceramium rubrum* (Huds.) C. Ag. retards the elongation of the axial cell on which they are borne. Indeterminate branches of *S. pylaisaei* do not have this effect. It is possible, however, that a large number of whorl branchlets i.e., four instead of two, could retard the elongation of their supporting cell. The initial whorl branchlets are formed in the same sequence regardless of field or culture conditions, and would be expected to show equal inhibitory effects, but these have not been observed. Thus, the hypothesis that axial cell size determines the number of whorl branchlets appears correct.

The formation and growth of lateral branches has been examined in *Callithamnion roseum* (Konrad-Hawkins, 1964b) and in *Griffithsia*

pacifica (Duffield *et al.*, 1972). Development occurred in the same manner, and showed the same rate of cell division, as the main axis. No detailed measurements have been made, but visual observations suggest this is also true for lateral indeterminate branches of *S. pylaisaei*.

Dixon (1970a) has stated that marked physiological differences exist between branches of limited and unlimited growth. External factors would not, therefore, be expected to affect such branches in the same manner. The information on the production and growth of lateral branches of *Callithamnion roseum* (Konrad-Hawkins, 1964b) and *Griffithsia pacifica* (Duffield *et al.*, 1972) is thus not comparable with that obtained in this study for whorl branchlets of *S. pylaisaei*.

Whorl branchlets of *S. pylaisaei* develop in sequence and the first formed reaches its maximum size twenty to thirty axial cells behind the apex, regardless of external conditions. The basal cells are not the largest cells in the mature whorl branchlets, but show the same morphological trends as the largest cells.

Whorl branchlet morphology shows a seasonal change from a predominantly pinnate arrangement in the coldest months to an irregular or secund form in the late summer. A significant change in the morphology of the whorl branchlet cells accompanies this reduction in pinnule number. The length of the cells remains fairly constant, but there is a marked reduction in diameter, resulting in an increase in the length to diameter ratio. The change occurs in both Form A and Form B, but is more pronounced in the latter.

In culture Form B produces fewer pinnules than Form A under

the same conditions, and in both forms there is a reduction in pinnule number with increase in temperature. This reduction is especially evident at low light intensities and under short daylengths, and correlates with field observations. Whorl branchlet cell dimensions, especially in Form A, do not show the range under different culture conditions, that are observed in the field. Form B does, however, show a significant reduction in cell diameter in culture at the higher temperatures. Whorl branchlet cell dimensions are of the same order of magnitude in the field and in culture.

No direct measurements have been made on the rates of cell division and elongation in the whorl branchlets, and it is thus impossible to explain how these affect pinnule and gland cell production. There is, however, a distinct correlation between reduction in the number of pinnules and an increase in the ratio of the length to diameter of the whorl branchlet cells; this is shown in both field and culture. It has already been shown that whorl branchlet production and the dimensions of the developing axial cells are intimately linked, it is thus tempting to speculate that a similar relationship exists between whorl branchlet cell morphology and pinnule production.

Gland cells are apparently initiated in the same manner as pinnules, in that their formation is dependent on a lateral division of a whorl branchlet or pinnule cell. Morphogenetically, gland cells behave as pinnules, in that they replace them, and are never borne on a whorl branchlet cell together with two pinnules. Seasonal changes in environmental conditions do not appear to cause significant changes in the numbers of gland cells in Form A. In Form B, however, their

numbers show considerable reduction, and they are absent in some plants in the latter part of the year.

It is significant that of the taxa, now considered within the circumscription of *S. pylaisaei*, the two most often stated to lack gland cells are *Antithamnion americanum* and *A. boreale* f. *baltica*. In addition both have few irregularly placed pinnules and whorl branchlet cells with high length to diameter ratios. Both species occur at the southern limits of the range of *S. pylaisaei*, the former in North America and the latter in Europe, where summer seawater temperatures are highest.

In culture, under lowered salinity, both Forms A and B produce fewer gland cells at the limits of their salinity tolerance, and the reduction is more marked in Form B than in Form A. The lower salinity conditions also cause a reduction in the growth rate, and hence also in the numbers of whorl branchlets and pinnules. In addition, in Form B, fewer gland cells are produced at salinities which do not significantly affect the growth rate. It is possible that the reduced salinities in the Baltic Sea contribute to the lack of gland cells reported (Reinke, 1889; Pankow, 1971) in *S. pylaisaei* (as *Antithamnion boreale*).

Examination of herbarium material of *S. pylaisaei* has shown that the specimens labelled *Antithamnion americanum* and *A. pylaisaei* have been principally separated on the dimensions of the whorl branchlet cells, with no regard for the number of whorl branchlets borne on each axial cell. This criterion was used by Harvey (1853), as specimens in his herbarium bearing whorl branchlets paired, or in groups of three

on each axial cell have been identified as *Callithamnion americanum* if the branchlets were made up of long narrow flexuous cells. Specimens with stouter cells and more regular pinnate branchlets are labelled *C. pylaisaei*. One of the latter type, which I believe can be related to my Form B has been used for illustration of *Callithamnion pylaisaei* (Harvey, 1853).

The reliance on cell dimensions has been perpetuated in modern Floras (Zinova, 1955; Taylor, 1957) to distinguish between the alleged species *A. americanum* and *A. pylaisaei*.

In Europe morphologies resembling Form A and Form B of this study are treated as a single species, *A. boreale*, of which a number of taxonomic forms and varieties have been described (Kjellman, 1883; Reinke, 1889). Two major subspecific taxa are currently recognised, *A. boreale* var. *boreale* (var. *typica*) and *A. boreale* var. *corallina*. The latter is distinguished by bearing branchlets in whorls of three and by its stouter cells giving it a compact tufted appearance (Kjellman, 1883). The two varieties *A. boreale* var. *corallina* and *A. boreale* var. *boreale* are respectively comparable with Form A and Form B described in this work.

In Floras which have included the three species, *A. boreale* has been separated on the predominantly secund nature of the pinnules on the whorl branchlets (Zinova, 1955; Taylor, 1957), but this is a highly variable character of little taxonomic consequence. The separation of *A. boreale* from *A. plumula* by Pankow (1971) on the basis of the former lacking gland cells is also erroneous.

Sundene (1962) has shown that two morphologically dissimilar

strains of *A. boreale* retained their distinguishing features in culture under identical conditions and were thus genetically distinct. The illustrations of the material from culture of these strains, identified by Sundene (1962) as *A. boreale* var. *corallina* and *A. boreale* var. *boreale* (var. *typica*) show close similarities with cultured material of Form A and Form B respectively. The differing culture conditions do not however permit direct comparison.

The naming of the two forms of *S. pylaisaei* presents considerable problems. They are morphologically distinguishable in culture and on the basis of limited hybridization experiments intersterile, but the field material is not readily distinguishable and to give the two forms specific status would create confusion. I propose therefore to treat these as a single species and give varietal status to the two forms.

The lack of interbreeding of the two varieties is the most serious objection to this treatment. There is, however, a precedent in the genus *Antithamnion:* two morphologically distinct strains of *A. plumula* were cultured by Sundene (1959), both had a *Polysiphonia*-type of life history, but were intersterile. Sundene (1959) retained both strains as a single species, *A. plumula*. No subsequent separation has been made at the specific level, even though the range of morphology of *A. plumula* has subsequently been examined in detail, and numerous forms and varieties described (L'Hardy-Halos, 1968).

The present proposal has a number of advantages. The two varieties described in this work have been delimited on the basis of the culture of limited material from a restricted geographic area. It is possible that other as yet unrecognised, genetically distinct

entities occur, which could also be accommodated as varieties. It also allows the retention of reproductively distinct varieties e.g. *Antithamnion boreale* var. *droebachense* (Sundene, 1962) as *S. pylaisaei* var. *droebachense* (Sundene) nov. comb.

Examination of isotype material of *Callithamnion pylaisaei* held in TCD revealed that it bore a considerable number of its branchlets in whorls of three and this confirms the observations of Kützing (1861) on similar material. Form A is thus legitimately referred to *Scagelia pylaisaei*. The first available varietal name is var. *boreale* Gobi (1878), his and Kjellman's (1883) subsequent description agree with material described here as Form B. Sundene's (1962) concept of var. *boreale* (var. *typica*) also shows close agreement with my Form B. It is thus proposed that Form B be named *Scagelia pylaisaei* var. *boreale* (Gobi) nov. comb. The erection of a variety automatically confers varietal status on the parent species which is thus *Scagelia pylaisaei* var. *pylaisaei* (Mont.) nov. comb.

Wollaston (1971) has given a thorough description of the vegetative and reproductive morphology of *S. occidentale* based on an examination of the type material, as well as extensive collections on the Pacific coast of North America between California and southern British Columbia. The reproductive structures, with the exception of minor and probably insignificant differences in the degree of branching of the spermatangial clusters, are identical with those described for *S. pylaisaei* in this work. Differences in vegetative morphology are of degree; *S. pylaisaei* usually bears branchlets in whorls of two and three, *S. occidentale* bears them predominantly in whorls of three and

four. It also appears to possess greater numbers of gland cells and often a single cell produces two, a situation not observed in *S. pylaisaei*. Further studies should be undertaken to establish the relationship between *S. pylaisaei* and *S. occidentale*. These should include a detailed study of the seasonal and geographic changes in morphology of *S. occidentale*, its culture under a variety of conditions, and attempts at hybridization between the two species. Such studies may reveal that *S. occidentale* should be regarded as a variety of *S. pylaisaei*; however, for the present they should be retained as separate species.

Fungal Infections

Records of fungal parasitism in *Antithamnion* and related genera are limited: *Olpidium plumulae* (Cohn) Fischer, recorded from *Antithamnion plumula* (Cohn, 1865), and subsequently from *A. cruciatum* and *Scagelia pylaisaei* (as *A. pylaisaei*, Farlow, 1881), is now regarded as a misinterpretation of gland cells (Feldmann and Feldmann, 1955), and is excluded from *Olpidium* (Sparrow, 1960; Johnson and Sparrow, 1961). Sparrow (1969) has reported an infection of *Antithamnion defectum* Kylin by a species of *Olpidiopsis* which he stated might be referable to *O. feldmannii* Aleem. L'Hardy-Halos (1970) has recorded *Petersenia lobata* infecting *Antithamnionella spirographidis* (as *Antithamnion sarniense*).

Specific delimitation in *Olpidiopsis* infecting marine algae is based primarily on the identity of the host, sporangium shape and the number of discharge tubes (Sparrow, 1960; Johnson and Sparrow, 1961).

Four species of *Olpidiopsis* have been described from marine algae. Johnson and Sparrow (1961) list three: *O. andreii* (Lagerheim) Sparrow, *O. magnusii* Feldmann and Feldmann, and *O. feldmannii*. All may occur as parasites on members of the Rhodophyta. Feldmann and Feldmann (1967) tentatively referred a fungal parasite of *Radicilingua reptans* (Kylin) Papenfuss to the genus as *O.? dangeardii* Feldmann and Feldmann. The diagnostic features of these species are presented in Table 25.

O. antithamnionis most closely resembles *O. feldmannii* or *O. magnusii*. The more frequently reported *O. feldmannii* is confined in its hosts to members of the Bonnemaisoneaceae (Rhodophyta), infecting the *Trailliella*-phase of *Bonnemaisonia hamifera* and the *Falkenbergia*-phase of *Asparagopsis armata* Harv. (Aleem, 1952, 1953; Dixon, 1963c; Johnson and Howard, 1968). It is thus significant that *O. antithamnionis* would not infect the *Trailliella*-phase of *B. hamifera* in culture, and the sporangia and planont dimensions further distinguish it from *O. feldmannii*. *O. magnusii* as described by Feldmann and Feldmann (1955) is highly restricted in its host, being reported only from the rhizoids of *Ceramium flabelligerum* J. Ag. The dimensions of both the sporangia and planonts are similar to those of *O. antithamnionis*, though in *O. magnusii* only spherical sporangia have been reported. The planonts of *O. magnusii* are reniform, and while no mention of refractive bodies is made by Feldmann and Feldmann (1955) their illustration shows two inclusions at opposite ends of the planont. *O. andreii* has been reported, usually infecting members of the Chlorophyta and Phaeophyta (Johnson and Sparrow, 1961) and its occurrence in *Ceramium strictum* Harv. (Aleem, 1950) has been questioned

TABLE 25

DIAGNOSTIC FEATURES OF *OLPIDIOPSIS* SPECIES REPORTED TO INFECT MARINE ALGAE

	O. andreii[1] (Lagerheim) Sparrow	*O. magnusii* Feldmann and Feldmann 1955	*O. feldmannii* Aleem 1952	*O. dangeardii* Feldmann and Feldmann 1967
Sporangial shape	spherical or elipsoidal	spherical	spherical or oblong	spherical irregularly lobed
Number of sporangia formed in a single host cell	1-23	1-7	1-3	1(2)
Number of discharge tubes formed by each sporangium	1-7	1	1(3)	(1)2-3
Shape of discharge tube	cylindrical	cylindro-conical	conical	cylindrical
Discharge tube dimensions (length x breadth)	78 x 3-5 µm	? - 5.5 µm	5-10 x 2-4 µm	? x 4-5 µm
Dimensions of spherical sporangia (diam.)	5-39 µm	? - 45 µm	15-30(35) µm	25-40 µm
Dimensions of elongate sporangia (length x breadth)	15-25 x 8-15 µm	not reported	30-45(5) x 20-25 µm	not reported
Number and position of planont flagella	anteriorly biflagellate	laterally biflagellate	laterally biflagellate	not reported
Shape of planont	pyriform	reniform	rounded or pyriform	reniform
Planont dimensions (length x breadth)	4-5 x 3 µm	? x 5 µm	2-2.5 x 1.5-2 µm	3-4 µm (diam.)
Number of refractive bodies in planont	two	two[2]	one	unknown
Resting spores	present	unknown	present[3]	present

(1) Data from Sparrow 1960; all other data from original descriptions.
(2) From illustration, Feldmann and Feldmann 1955 Fig. 42.
(3) Not reported in original description but observed by Johnson and Howard 1968.

(Dixon, 1960). It differs from *O. antithamnionis* by the sporangia possessing numerous long narrow discharge tubes. In addition the planonts are anteriorly bi-flagellate and contain two refractive bodies. Feldmann and Feldmann (1967) only tentatively referred their fungus to the genus *Olpidiopsis*, they did not observe living planonts, and were unable to determine the number and position of the flagella. The description of the sporangia as irregularly lobed, most commonly with two to three discharge tubes, seems closer to the characteristics of the genus *Petersenia* Sparrow than to *Olpidiopsis*.

In so far as the culture and field observations were made *O. antithamnionis* appears to be host specific.

Host regeneration is a phenomenon not previously described following fungal infection of other filamentous benthic marine algae. The processes involved appear similar to those described by Feldmann and Feldmann (1967) occurring in the membranous thallus of *Radicilingua reptans*, however, they differ in some details. In *R. reptans*, attack by *O. dangeardii* always results in the death of the infected cells and the necrosis of the adjacent tissue, regeneration is by outgrowth of the surrounding healthy cells, which come to overlie, but do not grow within the walls of the parasitised cells. The fungal infection of *Antithamnionella floccosa* does not always result in the death of the infected cell and such cells are capable of regeneration. In the majority of instances, however, total destruction of cell contents and the death of the adjoining cell occurs; regeneration differs in that the outgrowths of the healthy cells occur within the walls of the dead cells. This is significant in a uniseriate filamentous alga, as

another form of regeneration could result in the loss of the distal portions of the plant.

It is impossible to identify the fungus in *Scagelia pylaisaei* as only empty sporangia were observed, but these closely resemble some of the sporangia produced by *O. antithamnionis*. The inability of the fungus to infect *S. pylaisaei* in culture and its freedom from infection in the field, whilst surrounded by a parasitised population of *Antithamnionella floccosa*, suggest that it is not *O. antithamnionis*.

Cytological Studies

Cytological examinations have been made of all the species cultured in this work, but although dividing nuclei were frequently observed it was often impossible to obtain chromosome counts. Difficulties were principally due to the small size of the nuclei and chromosomes, to poor differentiation of the stain and to inadequate squashing of the cells. Poor squashing is responsible for the apparently incomplete chromosome complements shown in some of the photographs. An attempt to overcome this problem was made by Newroth (1971) who presented photographs of nuclear prophases at several focal planes. This approach does not appear to be particularly effective as a chromosome may occur on more than one photograph, giving falsely high counts; the technique was not adopted in this study. In spite of these difficulties both meiotic and mitotic divisions were observed and appear as previously reported (Magne, 1964; Dixon, 1966a) similar to those occurring in higher plants. The nuclear divisions do, however, differ from higher plants in that the metaphase plates are highly

compacted, and individual chromosomes are indistinguishable.

The number of nuclei, their shape, size and arrangement in the cell vary considerably in the Rhodophyta (Dixon, 1966a). The shape of the nucleus in the species examined in this study is dependent on its position in the cell. In the cells of the apical regions the nucleus occupies a central position and is spherical, but in mature cells it is displaced by vacuolation and assumes a lenticular form. These observations agree with reports by Magne (1964).

The species examined in this study can be divided into three categories on the form and disposition of their nuclei:

(i) Uninucleate throughout, no significant increase in nuclear dimensions with increasing cell size and maturity . . . . . *Plumaria elegans, Callithamnion roseum*

(ii) Uninucleate throughout, manyfold increase in nuclear dimensions with increasing cell size and maturity . . . . . *Scagelia pylaisaei, Antithamnionella floccosa*

(iii) Uninucleate only in the apical regions, the more mature cells multinucleate, but with no significant increase in nuclear size . . . . . *Callithamnion corymbosum, Callithamnion tetragonum*

No detailed study of the number of nuclei in relation to cell position and maturity appears to have been previously undertaken. It has, however, been recognised in at least two species, *Griffithsia globulifera* Harv. (as *G. bornetiana*; Lewis, 1909) and *Pleonosporium borreri* (Dixon, 1966a) that the number of nuclei per cell increases with increase in cell size and maturity.

The occurrence of synchronous nuclear division in multinucleate cells has been illustrated by Magne (1964) for *Chrondrus crispus*, Stackh., and its occurrence in other members of the Rhodophyta is intimated by Dixon (1966a). Its potential significance in producing nuclear numbers which increase in a geometric series, as shown here for *C. tetragonum* does not appear to have been recognised. Two multinucleate members of the Ceramiaceae previously examined, *P. borreri* and *G. globulifera* are unlike *C. tetragonum* in that their apical cells contain an irregular number of nuclei, but are not uninucleate. The lack of constancy of nuclear number in apical cells between individual plants would tend to obscure any series which occurred within a plant.

Meiosis, demonstrated by the observation of bivalents in the diakinesis stage was seen in developing tetrasporangia of *S. pylaisaei*, *A. floccosa* and *C. roseum*. Tetrasporangia produced on haploid gametophytes of *S. pylaisaei* were shown to be apomeiotic. Paraspores of *P. elegans* are formed by mitotic division.

The cytology of both cruciately and tetrahedrally divided tetrasporangia was examined and the nuclear events found to be identical. The two types of sporangia do, however, differ in the pattern of cytoplasmic cleavage in relation to nuclear division, and in arrangement of the planes of the second nuclear divisions.

Tetrahedral division was only observed cytologically in *Callithamnion roseum* and the process agrees with previous reports (Magne, 1964; Dixon, 1966a). The planes of the second nuclear divisions are at right angles to each other and to the plane of the first division,

producing four nuclei each situated at the corners of a tetrahedron. Cytoplasmic cleavage commences after all nuclear divisions are complete.

Plumaria elegans also forms tetrahedrally divided tetrasporangia on the parasporangial plants, but only interphase nuclei were observed. Drew (1939) suggests that the occurrence of tetrasporangia on parasporangial plants represents an attempted meiotic division and speculates that it may be irregular. Her speculation is supported by the observations presented in this work, as the occurrence of only one or two nuclei in a sporangium undergoing cytokinesis is atypical of the tetrahedral form of tetrasporogenesis.

The formation of cruciate tetrasporangia, observed in *S. pylaisaei* and *A. floccosa*, differs in that cytoplasmic cleavage follows each nuclear division. The first cleavage is immediately after the first telophase, to form a bispore. The planes of the second nuclear divisions are at right angles to the plane of the first, but have irregular arrangement with respect to each other. The results are at variance with the claim (Dixon, 1966a) that cytoplasmic cleavage immediately following the first nuclear division is restricted to zonate tetrasporangia.

That a bipartite sporangium precedes the formation of cruciate tetrasporangia is evident throughout the Rhodophyta (Fritsch, 1945; Kylin, 1956), but whether this first cytoplasmic cleavage is prior to the second nuclear division is unclear. Hommersand (1963) claims that each nuclear division in both zonate and cruciate tetrasporangia, is followed by cytokinesis, which is contrary to the opinion of Fritsch (1945, p. 652), who based his description on the work of Yamanouchi

(1921) and Bauch (1937) on zonate tetrasporangia. Rosenvinge (1923-1924) states that in *Antithamnion*, tetraspore formation is by two separate bipartitions and suggests that nuclear division precedes each cytoplasmic cleavage.

It is evident that there is confusion in the literature and that further cytological examination of the ontogeny of cruciate sporangia from other Rhodophyta is necessary. Hommersand (1963) has suggested that bisporangia and cruciate tetrasporangia in the Ceramiales result from a failure of meiosis. The evidence presented in this study, together with that of Drew (1955), Sundene (1959, 1964a, 1964b) and Magne (1964) does not support such a suggestion.

All mature tetrasporangia of *S. pylaisaei* are cruciately divided and although in *A. floccosa* they occasionally appeared to be tetrahedral only the cruciate form of development was observed in this species. It would thus appear that, irrespective of the final form of division, ontogenetic observations are necessary before a tetrasporangium can be designated either cruciate or tetrahedral.

Apomeiosis in species formerly referred to *Antithamnion*, *S. pylaisaei* (as *A. boreale*; Sundene, 1962) and *S. occidentale* (as *A. occidentale*; West and Norris, 1966), has been demonstrated in culture, but has not been cytologically studied.

Two species of the Rhodophyta in which tetrasporangia are supposedly apomeiotic, *Rhodymenia palmata* (L.) Grev. and *Lomentaria orcadensis* (Harv.) Coll. ex Taylor (as *L. rosea*) have been previously cytologically examined. In the former Magne (1959, 1964) has shown that the somatic cells possess 14 chromosomes; but 14 bivalents occur

in the tetrasporangia which otherwise have an apparently normal meiosis. In *L. orcadensis* Svedelius (1935) reported that nuclear divisions in the tetrasporangia were mitotic. This species was re-investigated (Magne, 1964) and found to have normal meiosis, but specimens from different localities possessed either 10 or 20 bivalents. No somatic counts were obtained and the species requires further investigation.

The apomeiosis in *S. pylaisaei* differs from the previous reports in that chromosome bivalents did not occur in late prophase. Further observations on the form of condensation of the chromosomes in early prophase are necessary, but from the data obtained to date the division appears to be a normal mitotic one.

Chromosome counts have been obtained for *Scagelia pylaisaei*, *Antithamnionella floccosa*, *Callithamnion corymbosum*, *C. roseum*, and *Plumaria elegans*.

S. pylaisaei and *A. floccosa* are shown cytologically to have the basic *Polysiphonia*-type of life history, with the tetrasporophyte diploid with respect to the haploid male and female gametophytes. In addition it is shown that the apomeiotic tetrasporangia of *S. pylaisaei* are borne on the haploid phase. Both varieties of *S. pylaisaei* have similar chromosome numbers. Thus there is no evidence to suggest a polyploid series and the cytological study does not provide any information on the relationship or origin of the two varieties. The single chromosome count obtained in diakinesis for *C. roseum* (n = ca. 30) does not agree with that reported by Harris (1966) (n = 39), but it appears unlikely that the species reported by him as *C. roseum* and

the species examined in this study are conspecific. The counts obtained for *C. corymbosum* are similar to the range reported by Hassinger-Huizinga (1952) for diploid material. The parasporangial plants of *P. elegans* examined in this study contain ca. 90 chromosomes, with a range of counts similar to that reported by Drew (1939). This confirms the existence of the triploid strain of *P. elegans* in North America.

Previous chromosome counts obtained for members of the Ceramiaceae have been listed and reviewed by Dixon (1966a); haploid numbers range from 6-90+. Many of the early counts are contradicted by more modern examinations. The majority of modern counts range between n = 23 and n = 35, and the chromosome numbers obtained in this study fall within these limits.

Spore Germination

Germination of carpospores, tetraspores and paraspores was identical and predominantly of the bipolar-type considered typical for members of the Ceramiales (Killian, 1914; Kylin, 1917; Chemin, 1937); it has been termed the *Ceramium*-type of germination (Chemin, 1937). An exception was the unipolar form of germination occasionally observed in cultures of *S. pylaisaei*.

Aberrant spore germination patterns have previously been reported for members of the Ceramiaceae: in *Callithamnion tetricum* (Boney, 1963) and in *C. roseum* (Konrad-Hawkins, 1972).

L'Hardy-Halos (1970) figured *in situ* germination of carpospores of *Antithamnion plumula* resembling the early stages of the unipolar

pattern. Carpospores undergoing *in situ* germination in *Scagelia pylaisaei* however, showed a typical bipolar pattern and atypical germinations were not observed in *Callithamnion roseum* in this study.

The high incidence of loosely attached spores showing unipolar germination suggest that enlargement and nuclear division take place without spore settlement. Bipolar germination may thus be inhibited by either the spore becoming multinucleate, or may be dependent on substrate contact; this problem requires further investigation.

Polarity of germination is independent of culture conditions, and *in situ* germination of carpospores appears as a continuation of the apical growth of the gonimoblast initial. L'Hardy-Halos (1970) has observed similar *in situ* germination in *Antithamnion plumula*, which is in agreement with the observations of Weber (1960) for several species of the Ceramiales.

There are numerous reports of *in situ* germination in nature, of carpospores, tetraspores and monospores of members of the Rhodophyta, they are reviewed by L'Hardy-Halos (1970).

In this study the only *in situ* germination observed in field material was in the paraspores of *Plumaria elegans* as previously reported by Drew (1939). The *in situ* germination shown by developing paraspores at St. Bernard appears to be a temperature dependent phenomenon. The culture experiments have shown that developing parasporangia continue growth and ultimately release paraspores at 10°C, but at 2°C further production of paraspores is inhibited and those formed germinate *in situ* to produce vegetative filaments.

The significance of *in situ* germination of tetraspores has

been recognised (Dixon and West, 1967; Scott and Dixon, 1971) as potentially leading to the development of a haploid axis on a diploid thallus. It has been suggested (Scott and Dixon, 1971) that such germination could ultimately lead to the elimination of the tetrasporangium and its replacement as the site of meiosis by a morphologically somatic apical cell. This phenomenon is reported to occur in the life history of *Lemanea mamillosa* (Siridot) Silva (Magne, 1967).

Paraspores of *P. elegans* are produced mitotically and are thus analogous with the monospores of *Erythrotrichia carnea* (Dillw.) J. Ag. which occasionally germinate *in situ* (Dixon and West, 1967). Such germination in *E. carnea* gives the appearance of branching in an otherwise simple filament, and may lead to errors in identification. The *in situ* germination of *P. elegans* causes minor morphological changes, but does not create any taxonomic confusion and appears to have little biological significance.

Life Histories in Field and Culture

The assumption that all members of the Ceramiaceae display a *Polysiphonia*-type of life history is only partially supported by this study. The life histories described can be placed in four categories

(i) *Polysiphonia*-type with no apparent deviations; *Callithamnion roseum*, *Antithamnionella floccosa* (assuming that the monospores' observed in some specimens of *A. floccosa* are functionless, or are merely abortive tetrasporangia).

(ii) *Polysiphonia*-type, but with accessory reproduction of the gametophyte generation by apomeiotic tetrasporangia;

Scagelia pylaisaei.

(iii) *Polysiphonia*-type, but with monoecious gametophytes and the occurrence of procarps and spermatangia on the tetrasporophytes, suggesting the potential existence of triploid and tetraploid generations; *Callithamnion tetragonum*.

(iv) Apparent absence of alternation of generations; reproduction by mitotic spores (paraspores) *Plumaria elegans* or by vegetative fragmentation *Callithamnion corymbosum*.

Cytological observations have demonstrated that *Antithamnionella floccosa* has a *Polysiphonia*-type of life history and no deviations were observed in field material. The life history in culture remains unconfirmed, as plants derived from both carpospores and tetraspores failed to become fertile. The nature of the monospore-like bodies, also observed by Jaasund (1965), remains unknown. The occasional observation of cruciate divisions suggests they may be immature or abortive tetrasporangia.

Callithamnion roseum shows a *Polysiphonia*-type of life history with no observed deviations in either field or culture.

From observations of field material and from cytological studies, both varieties of *Scagelia pylaisaei* were presumed to have a *Polysiphonia*-type of life history. Culture experiments, however, showed that the majority of gametophytes were capable of producing apomeiotic tetrasporangia in addition to either spermatangia or procarps.

Apomeiotic tetrasporangia do not appear to be common in natural populations of *S. pylaisaei* in Newfoundland. Such sporangia have been

detected on only three occasions and then the plants also bore gametophytic reproductive organs. This is in direct contrast to the Scandinavian material (Sundene, 1962) which appears to be obligately apomeiotic. The formation of apomeiotic tetrasporangia on the gametophyte phase suggests that the strains of *S. pylaisaei* reported from Scandinavia may be gametophytes, which have partially, or totally, lost the ability to undergo normal gametophytic reproduction. The reports of spermatangial plants (Rosenvinge, 1923-1924; Lund, 1959a; Sundene, 1962) often also bearing tetrasporangia can be explained in this way.

It is, however, possible that the Scandinavian material is diploid, but produces apomeiotic tetrasporangia. The occasional reports of spermatangia could be explained if the plants were of a strain similar to that derived on a single occasion from carpospores of *S. pylaisaei* var. *pylaisaei*. The carpospores produced diploid plants which bore spermatangia in addition to meiotic tetrasporangia. No evidence for the production of apomeiotic tetrasporangia on diploid plants has been obtained in this study. The problem of whether the apomeiotic Scandinavian plants are haploid or diploid can only be finally resolved by cytological study.

Attempts to fertilize a haploid female gametophyte with spermatangia from a diploid plant, with the potential for the production of a triploid generation, were unsuccessful. It is conceivable, however, that procarps could be formed on diploid plants in the same manner as spermatangia, which could be fertilized by diploid spermatia to produce tetraploid carpospores. This situation

would be similar to that shown by Drew (1934, 1943) for *Spermothamnion repens*.

The life history of *C. tetragonum* differs from the *Polysiphonia*-type in having monoecious gametophytes and by the development of procarps and spermatangia on tetrasporangial plants. Spermatia are capable of fertilizing procarps produced on the same plant. *C. tetragonum* (as *C. baileyi*) in North America is reportedly either monoecious or dioecious (Taylor, 1957), but all material examined in this study in both field and culture was monoecious.

There are two previous culture studies of members of the Ceramiaceae supposedly involving monoecious gametophytes. Rueness (1971) obtained the life history of *Spermothamnion repens*, a reportedly monoecious species (Rosenvinge, 1923-1924; Drew, 1934, 1943) and found it to be dioecious. Hassinger-Huizinga (1952) occasionally found monoecious plants in cultures of *Callithamnion corymbosum*, but the majority were dioecious. This study is the first report of the culture of a member of the Ceramiaceae with obligately monoecious gametophytes in its life history.

Two other species of the Rhodophyta, *Pseudogloiophloea confusa* (Ramus, 1969) and *Rhodochorton purpureum* (West, 1969, 1970) were shown in culture to possess both monoecious and dioecious gametophyte strains. A similar situation could exist in *C. tetragonum*, and cultures of material from other localities are needed to solve this problem.

The culture experiments show that spermatangia and procarps develop on the tetrasporangial phase of *C. tetragonum* rather than the converse, as occurs in *S. pylaisaei*. Though no chromosome counts were

obtained the situation is similar to that shown cytologically (Drew, 1934, 1943) for *Spermothamnion repens*. The presence of a carposporophyte on the tetrasporangial phase cultured in the absence of gametophytes suggests the potential occurrence of a tetraploid generation. Cytological data needed to confirm this suggestion are, however, lacking. Whilst the spermatangia and procarps are functional it is not known whether the potentially tetraploid carpospores are viable. In contrast to *Spermothamnion repens* (Drew, 1934) tetrasporangia and other reproductive organs of *C. tetragonum* were not observed to occur on the same plants in nature.

Plumaria elegans shows a direct life history with the triploid paraspores reproducing the parasporangial plants in both field and culture. This confirms the observations of Drew (1939) and Rueness (1968) on northern European populations of *P. elegans*. The only possible deviation from this life cycle is the occurrence of tetrasporangia on some plants; they have been shown to be cytologically aberrant and there is no evidence that they are functional.

The life history of *Callithamnion corymbosum* in both field and culture appears to be fundamentally dependent on vegetative propagation by fragmentation. This is at variance with the previous reported life history in culture (Hassinger-Huizinga, 1952), which although showing some anomalies, was of the *Polysiphonia*-type. Tetraspores are produced in Newfoundland material of *C. corymbosum* in both field and culture, but appear to have only limited viability in culture and their function in nature remains unknown. The apparent lack of gametophytes suggests that they are either nonfunctional or apomeiotic. It may be, however,

that environmental conditions in the field will not support the growth of gametophytes, though there is no evidence to support this suggestion.

Growth and Reproduction in Culture

As has already been discussed, vegetative growth of all species studied in this work is greatest at high temperatures. Only the rates of cell division of *S. pylaisaei* and *A. floccosa* appear significantly affected by daylength, being reduced under short day conditions.

Comparable growth rate data for gametophytes and tetrasporophytes have only been obtained for *C. tetragonum* and *S. pylaisaei*. The two phases show no significant differences in the rate of cell division under any culture conditions. The findings are in agreement with the results previously obtained for other species of the Rhodophyta, both in culture (Edwards, 1971; Rueness, 1971) and the field (Lewis, 1912).

Light intensities do not show the same marked effects on the rate of cell division as either temperature or daylength. A notable exception is that the combination of high light intensities (1200 x 500 lx) and low temperature (2°C) is lethal to cultures of *C. corymbosum*.

Only two species, *S. pylaisaei* and *A. floccosa*, showed a constant reproductive response under all culture conditions. The former eventually always becomes fertile, while the latter was never induced to form any reproductive organs. The other species showed differing responses under different culture conditions. As with growth rates the most important factors were temperature and daylength, with light intensity having the least effect. Under conditions which allowed plants to eventually become fertile the time required for the

production of reproductive structures is related to vegetative growth rate.

The time required to reach reproductive maturity for gametophytes and tetrasporophytes is similar in *C. tetragonum*. In *S. pylaisaei* gametophytes usually require a slightly shorter culture period than tetrasporophytes, whilst in *C. roseum* the converse occurs. In gametophyte cultures of all species spermatangia were usually observed before procarps. The requirement of similar maturation periods has previously been reported for tetrasporophytes and gametophytes of *C. byssoides* (Edwards, 1969a). Rueness (1971), however, found that development of tetrasporangia in *Spermothamnion repens* took two to six times as long as the development of spermatangia and procarps.

Within a species different types of reproductive bodies apparently require similar stimuli for their production. A contrasting situation has been reported for *Achrochaetium pectinatum* (Kylin) Hamel (West, 1968) where tetrasporangial plants formed monospores under all conditions tested, but required short daylengths to form tetrasporangia. In the present study an analogous situation exists in the formation of apomeiotic tetrasporangia of *S. pylaisaei*, which in culture only occurs at 10°C and above. The conditions which lead to the formation of apomeiotic tetrasporangia have not been conclusively determined; some strains examined did not appear to produce them under any conditions, but it is impossible to tell whether this failure was due to a genetic or an environmental factor. In some instances, gametophytes produced tetrasporangia while others in the same culture did not. Apomeiotic tetrasporangia only formed under the conditions which promoted the

most vigorous growth. Their formation in dense cultures, and their inhibition by subculture into fresh medium suggests that the formation is dependent on crowded conditions. Whether this is due to physical contact, extracellular products, nutrient depletion or other factors has not been established.

Temperature also controls reproductive maturity in *C. corymbosum* and *P. elegans*, which become fertile at 10°C and above, irrespective of daylength. *C. corymbosum* however, remains sterile at high intensities (2300 lx) at 15°C, the only light intensity mediated response observed in this study.

No parasporangia were formed on plants grown from spores of *P. elegans* at 10°C under short daylength, but did form on plants derived from detached apices. No explanation for this phenomenon can be given; it is possible that although the sporelings had achieved sufficient vegetative size a further period in culture was required to induce parasporogenesis. It is also possible that induction has already occurred in the field, but required the transfer to higher temperatures before it was manifested.

Irrespective of other physical factors, *C. roseum* never became fertile under short daylength conditions. However, fertile cultures transferred to short daylengths continued to produce reproductive bodies. In this respect *C. roseum* satisfies one of the definitions of a true photoperiodic response (Terborgh and Thimann, 1964). Further cultures, involving light breaks in the dark period, must be undertaken before this can be confirmed. Reproduction in *C. roseum* is also affected by temperature; sporelings derived from tetraspores became

fertile at 5°C, but remained sterile at 2°C, even though sufficient vegetative growth had apparently occurred.

C. tetragonium became fertile under all conditions at 10°C and above, but only at long daylengths at 5°C. No further data were obtained on the nature of this response, but it would appear to be mediated by a photosynthetic (Dixon, 1970a) rather than a photoperiodic mechanism.

Reproductive Periodicity

The data obtained in culture on life history, growth rates and reproductive maturation can be used to interpret reproductive periodicity shown in the field.

The quantitative measurement of reproductive periodicity allows the observation of seasonal trends, in species such as *S. pylaisaei*, where the majority of plants are fertile throughout the year. Such trends would be obscured in simple presence or absence data, which are usually presented in phenological studies.

From the data obtained the species in this study can be divided into three groups

(i) Gametophytes and sporophytes of *S. pylaisaei* are present or fertile throughout all or most of the year, though not necessarily in equal abundance. *P. elegans* can also be included in this group as parasporangia can be found throughout the year.

(ii) Gametophytes and sporophytes of *C. roseum* and *C. tetragonum* are fertile at the same time, but only for a limited period.

C. corymbosum shows a similar seasonal behaviour and can be included in this group although only tetrasporophytes are known in Newfoundland.

(iii) Gametophytes and sporophytes show a seasonal disjunction. There are two fertile periods, only sporophytes occur in one while in the other both sporophytes and gametophytes are found; this group includes only *A. floccosa*.

Both varieties of *S. pylaisaei* show the same trends, which are more marked in *S. pylaisaei* var. *boreale* than in *S. pylaisaei* var. *pylaïsaei*. Tetrasporophytes are the commonest fertile plants throughout the year, but in the colder months sterile plants predominate and the gametophytes are least evident. The trends cannot be explained by the culture data, as both gametophytes and tetrasporophytes became fertile under all conditions tested. The culture of apical fragments and the cytological examinations show that both gametophytes and tetrasporophytes are present in the sterile population, but do not indicate why they are sterile in nature. Cytological examination of specimens from a collection (St. 104.19) obtained during the winter months show that tetrasporogenesis was occurring.

Parasporangial plants of *P. elegans* are present throughout the year at St. Bernard. Paraspores in culture, however, were formed at 10°C and above, but did not form at 5°C or 2°C, even though vegetative growth occurred. The distribution of the parasporangia on the plants in nature, suggests that they are only being formed when found in the immediate subapical regions. The parasporangia are thus formed in late summer and fall when water temperature is at a maximum. The

water temperature falls in winter, vegetative growth continues, but no further spores are produced. This would account for the parasporangia being absent in the apical regions. In early summer, as previously discussed, the paraspores formed on the lower parts germinate *in situ*. Later the first new parasporangia are also found in this region presumably formed from initials produced during the previous season. New parasporangial initials then develop in the subapical region. It would appear that temperature in both culture and field plays a major role in the induction of parasporangia, and that while parasporangia are present throughout the year they remain dormant when the water temperature is low. In this manner *P. elegans* shows greater affinities with the second phenological group, comprised of the *Callithamnion* species, than with *S. pylaisaei*.

Callithamnion roseum is only found to be fertile in the field between July and October. In culture reproductive maturation is controlled by daylength and temperature, but the daylength phenomenon is the most striking. In the field in Newfoundland water temperature rather than daylength is probably more important in controlling reproductive periodicity. If daylength alone were the controlling factor plants would presumably become fertile in the late spring, but they do not until July and August, when higher water temperatures also occur. In the field the tetrasporophytes become fertile before the gametophytes; this observation based on data for a single season, may not be significant. However, in culture tetrasporophytes have shorter maturation periods than gametophytes, and this is most pronounced at

lower temperatures. Cultures of sterile fragments show that both tetrasporophytes and gametophytes overwinter.

No detailed phenological observations were made in *C. tetragonum*, which is sterile at Grand le Pierre between January and July, suggesting that either water temperature or daylength may be factors controlling reproductive periodicity. Reproduction in culture is principally controlled by temperature, as at 10°C and above plants matured under all conditions. At lower temperatures plants only become fertile at long daylength, but this is probably a photosynthetic rather than a directly photoperiodic response.

Callithamnion corymbosum, in addition to showing a distinct reproductive periodicity also shows marked seasonal changes in local abundance. It reaches its maximum vegetative development in late summer and becomes fertile shortly afterwards. Culture studies indicate that temperature is the major factor controlling both growth and reproduction and that daylength has little or no effect. The fate of the tetraspores produced remains unknown, but the species has been shown to spread through fragmentation. As the water temperature falls the exposed plants die, but viable vegetative fragments remain in the detritus layer. It is significant, that at low temperatures in culture high light intensities were lethal, but at low intensities plant fragments remained alive, though no apparent growth occurred. The fragments can be found throughout the winter suggesting that the species perennates in this manner, with growth recommencing in late summer when water temperatures become favorable.

A. floccosa is found throughout the year and shows two periods

of fertility. One occurs from October to February, when both gametophytes and sporophytes are found, the other in June and July when nearly all plants are fertile tetrasporophytes. As *A. floccosa* could not be induced to become fertile in culture, the culture studies cannot be used to interpret phenological observations. On the basis of field and cytological investigations the following interpretation is suggested.

Tetrasporophytes persist as sterile plants during August and September when water conditions inhibit tetrasporogenesis, they become fertile in October. Tetraspores released in June and July germinate and the resulting gametophytes also become fertile in October and November. Fertile gametophytes and sporophytes persist until February. Carpospores released during this period germinate to produce tetrasporophytes. No detailed examination was made of juvenile plants, but young sporelings of *A. floccosa* have been reported during this period in Nova Scotia (Edelstein and McLachlan, 1966). From March until June the majority of plants are sterile, and these are diploid. The cytological data and the almost exclusive occurrence of fertile tetrasporophytes in June and July indicate that the tetrasporophytes overwinter, but that the gametophytes do not. However, the occurrence of a few carposporophytes in April and June suggests that female gametophytes also occasionally persist.

It has been suggested (Dixon, 1965) that as a species approaches its northern limits it successively loses its gametophyte and sporophyte stages, and that at extreme stations it becomes sterile, persisting either by immigration or by vegetative reproduction. Of the species

examined in this study, *C. roseum*, *C. tetragonum*, *C. corymbosum* and *P. elegans* reach their known North American limits in Newfoundland. Gametophytes and tetrasporophytes of *C. roseum* and *C. tetragonum* occur, but gametophytes are absent in *C. corymbosum*. *Plumaria elegans* lacks both gametophytes and tetrasporophytes, and occurs only as the triploid parasporophyte as it does at its northern limits in Europe (Rueness, 1968).

The reasons for the different distributions of the gametophyte and tetrasporophyte generations or for the greater abundance of sporophytes, as found in *S. pylaisaei* and *A. floccosa*, are unclear. Perennation or vegetative reproduction could modify the distribution, but for one generation to predominate would suggest that it is more fitted to the prevailing environmental conditions. In this study, cultures of both gametophytes and sporophytes show similar growth responses and their reproductive maturation is induced by the same factors. There is thus no evidence to support such a suggestion.

Edwards (1969b, 1970, 1971) showed that the growth rates of the gametophytic and tetrasporic generations of several species of the Ceramiales were similar under a wide range of culture conditions. This has also been shown in the field (Lewis, 1912). It would thus seem more likely that the factors controlling the distribution of the gametophyte and sporophyte generations are linked to reproduction rather than to vegetative growth.

Geographic Distribution

Using the phenological and culture observations it is possible to comment on the factors controlling the geographic distribution of the species studied.

S. pylaisaei is apparently circumboreal, occurring in the north-east Pacific, and is widespread in the North Atlantic. Field observations suggest that at the southern limits growth might be controlled by water temperatures. Bleaching and death of *S. pylaisaei* var. *boreale* occurred during a period of high water temperature (St. 104.15), and it is reported that at its southern limits (Farlow, 1881, as *A. americanum*) it breaks down in summer. *S. pylaisaei* from southern Scandinavia (Printz, 1926; Sundene, 1953 as *A. boreale*) also disappears in late summer. There appear to be no northern limits for the species, and its distribution is dependent on suitable substrate, as at the depths to which it occurs in the Arctic regions it would be unaffected by ice scouring. The plants must have the ability, however, to resist long periods of darkness or reduced insolation due to the low solar angle and ice cover in high latitudes.

Because of the overlap in morphologies of the two varieties it is impossible to map their geographic ranges in detail solely on the basis of herbarium records. It would, however, appear that entities resembling the two varieties described here exist together over a considerable portion of the total geographic range.

In Europe the Oslofjord strain (*A. boreale* var. *boreale*) cultured by Sundene (1962) shows obvious morphological similarities

with *S. pylaisaei* var. *boreale*. The material illustrated by Børgesen (1902) as *A. plumula* var. *boreale* f. *corallina* from the Faeroes resembles field material of *S. pylaisaei* var. *pylaisaei* found in late summer in Newfoundland. Harvey's material (*A. americanum*) from southern Massachusetts held in TCD, and other material examined in this study (St. 4.1; St. 18.5, etc.) indicates that both varieties occur at the southern limits in North America.

No Pacific Ocean specimens of *S. pylaisaei* were personally examined, but Kjellman (1883) quite clearly distinguished Ruprecht's (1851) *Callithamnion corallina* and *Callithamnion lapponicum* from the Okhotsk Sea. The two taxa would now be referable to *S. pylaisaei* var. *pylaisaei* and *S. pylaisaei* var. *boreale* respectively.

Both varieties also appear to occur at the northern extremes of the range, *S. pylaisaei* var. *pylaisaei* is found in Spitzbergen (Sundene, 1962 as *A. boreale* var. *corallina*) and *S. pylaisaei* var. *boreale* has a type locality in the White Sea (Gobi, 1878 as *A. plumula* var. *boreale*).

In Newfoundland, culture and comparative morphological studies of herbarium material show that *S. pylaisaei* var. *pylaisaei* occurs on all coasts, but *S. pylaisaei* var. *boreale* appears to be confined to the southern and western coasts of the island. The restriction in local distribution is difficult to explain in view of the wide geographic range apparently shown by the two varieties.

The south coast area is exemplified in this study by St. Bernard. The only environmental parameter monitored was water temperature and the measurements, taken as single surface temperatures

at each visit, have only limited value. Higher summer water temperatures were recorded at St. Bernard than at Bay Bulls. It is more significant, however, that at St. Bernard the low winter temperatures persist for a shorter period than at Bay Bulls, and conversely the period of higher water temperatures is also extended.

The three *Callithamnion* species and *P. elegans* reach their northern limit, in North America, in Newfoundland. They are confined to the south and west coasts, the reproductive periodicity and their behaviour in culture suggest that their northern distribution is controlled by water temperature. No evidence has been obtained in this study to suggest factors which may limit the southern distribution of the species.

A. floccosa has the most restricted geographic distribution, and it is not as widespread in the north as *S. pylaisaei*. It does not extend as far south as the other species examined in this study. The two periods at Bay Bulls when sterile plants predominate coincide with the periods of lowest and highest water temperatures. The apparently restricted temperature range required for reproduction may limit the geographic distribution. *A. floccosa*, much more than *S. pylaisaei*, is limited in its vertical occurrence to the immediate sublittoral and it is possible that at its northern limits ice action also controls its distribution.

The present study supports the generally accepted contention that temperature is of primary importance in controlling the reproductive periodicity and the geographic distribution of marine algae. Daylength either alone or in conjunction with water temperature also

appears to influence the seasonal periodicity of algal floras. The conclusions agree with those of a field and culture study, made by Edwards (1969b) in the Gulf of Mexico, a region of significantly higher seawater temperatures. They are, however, at variance with the suggestion of Conover (1958, 1964) for algal floras from Cape Cod and Texas, that light intensity is a major factor controlling seasonal periodicity.

Conclusions

Two major conclusions have emerged from this study:

(i) it is possible to use cultures under defined conditions to delimit genotypic variation in the Ceramiaceae. Such studies in combination with measurements of seasonal changes in morphology can be used to solve taxonomic problems.

(ii) culture techniques in combination with field observations can be used to determine the factors affecting growth and reproductive periodicity in nature.

Previous taxonomic studies in the Ceramiaceae, e.g. L'Hardy-Halos' (1968) treatment of *Antithamnion* are of a static nature. The approach is acceptable when specific delimitation depends on the presence or absence of a readily definable character. An example is the separation of *Antithamnion tenuissimum* from other members of the genus in the English Channel (L'Hardy-Halos, 1968), by its lack of gland cells. L'Hardy-Halos (1968) separates other species e.g. *A. spirographidis* and *A. carniense* by characters based on cell size and numbers of whorl branchlets per axial cell. The two species have also

been regarded as conspecific (Sundene, 1964a; Parke and Dixon, 1968). The situation is thus similar to that occurring in *S. pylaisaei*, and it is suggested that the morphogenetic approach utilized in this study could be used to resolve this and other similar taxonomic problems in the Rhodophyta.

A number of taxonomic problems concerning *S. pylaisaei* still remain. It is important to the correct typification of *S. pylaisaei* var. *boreale* that Gobi's material of *A. plumula* var. *boreale* be examined. It may include both varieties, recognised in this study, or it may be entirely of var. *pylaisaei*. In either instance the epithet *boreale* would be incorrectly applied in this study, and an alternative would have to be sought.

The culture of specimens of *S. pylaisaei* from areas throughout its range is of primary importance to confirm the geographic distribution of the two varieties, to determine the range of the obligately apomeiotic strains, and to distinguish other morphological varieties or reproductive strains that may exist in nature.

Further culture studies of a more intensive nature should be undertaken on morphogenetic problems and especially directed at determining specific factors controlling cell division and enlargement.

The biology of the species in the field, apart from reproductive periodicity, and in *S. pylaisaei* seasonal changes in morphology, remains largely unknown. Considerably more work could be carried out on population dynamics and especially on the factors limiting vertical distribution, which have not been considered in this study. The physical factors, temperature, light intensity and daylength while

undoubtedly important are only three of the many factors acting in the marine environment. Biological factors of competition and predation, as well as chemical factors, such as nutrient limitation, have long been recognised as control agents of phytoplankton dynamics. There is no reason to suppose that they are less important in relation to benthic marine algae.

Many of the chemical and biological problems could be examined in axenic culture in a controlled physical environment. This study, however, emphasizes that neither field nor culture studies should be used alone. Only through careful integration of observations made with both techniques will an understanding of the biology of marine algae be achieved.

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APPENDIX I

PREPARATION OF CULTURE MEDIA

I. ER medium

Erd-Schreiber medium (Føyn, 1934) as modified by Burrows (1958) by the addition of tris-hydroxymethyl aminomethane buffer (TRIS), disodium ethylene diamine tetracetate as a chelating agent, vitamin mix S_3, vitamin B_{12} and the range of trace elements, in the concentrations given for the ASP_2 medium of Provasoli *et al.*, (1957). The final concentrations of these additives to 1000 ml of seawater is:-

1	Sodium nitrate	100	mg
	Disodium hydrogen phosphate $.12H_2O$	20	mg
2	Soil extract	50	ml
	TRIS	1	g
	Na_2EDTA	30	mg
3	Iron	0.8	mg
	Zinc	0.15	mg
	Manganese	1.2	mg
	Cobalt	0.003	mg
	Copper	0.0012	mg
	Boron	6	mg
4	Vitamin B_{12}	0.002	mg
5	Thiamine hydrochloride	0.5	mg
	Nicotinic acid	0.1	mg
	Calcium pantothenate	0.1	mg

5	p-aminobenzoic acid	0.01 mg
	Biotin	0.001 mg
	Inositol	5 mg
	Folic acid	0.002 mg
	Thymine	3 mg

1. Nutrient Salt Solution

Made up as a stock solution

Sodium nitrate		20 g
Disodium hydrogen phosphate	$12H_2O$	4 g
Distilled water		1000 ml

5 ml of this solution is added to each litre of heat treated seawater.

2. Soil Solution

100 gm of soil was autoclaved with 1000 ml of distilled water for 1 h at 15 lb/sq in, it was then filtered through Whatman #1 filter paper. Storage was at 2°C and the solution was periodically re-autoclaved to reduce fungal and bacterial contaminants.

3. Trace Elements

All metals with the exception of boron were added as their chlorides. Boron was added as boric acid. 1000 ml of stock solution was made up of elements at 100 times the concentration given for the final medium. 10 ml of this stock solution was added to each litre of heat treated seawater.

4. Vitamin B_{12}

A stock solution of 1 mg of vitamin B_{12} in 500 ml distilled water was utilized. 1 ml of this solution was added to each litre of seawater.

5. Vitamin Mix

The vitamins given in the medium are those of the vitamin mix S_3 of Provasoli *et al.*, (1957). A stock solution of 200 times the amounts given in the final medium was made up in 1000 ml of distilled water. 1 ml of this solution was added to each litre of seawater.

II. ES Medium

ES medium was made up according to the schedule given by Provasoli (1968) by the addition of 20 ml of ES enrichment to each litre of heat treated seawater.

ES enrichment

Distilled water	1000	ml
Sodium nitrate	3.5	g
Sodium glycerophosphate	500	mg
Iron EDTA solution[1]	250	ml
P_{II} metal solution[2]	250	ml
Vitamin solution[3]	1	ml
TRIS	5	g

The enrichment was placed in screw top vials in 20 ml aliquots, the solution was then sterilized by autoclaving at 15 lb/sq in for 20 minutes.

1. Iron EDTA solution

Ferrous ammonium sulphate	700	mg
Disodium ethylene diamine tetracetate	760	mg
Distilled water	1000	ml

2. P_{II} metal solution

Boric acid	1.14	g
Ferric chloride $.6H_2O$	50	mg
Manganese sulphate $.4H_2O$	165	mg
Zinc sulphate $.7H_2O$	22	mg
Cobalt sulphate $.7H_2O$	5	mg
Disodium ethylene diamine tetracetate	1	g
Distilled water	1000	ml

3. Vitamin solution

Vitamin B_{12}	10	mg
Thiamine	500	mg
Biotin	5	mg
Distilled water	100	ml

III. Germanium dioxide

1 g of germanium dioxide was fused with 2 g of potassium hydroxide in a porcelain crucible and then dissolved in approximately 100 ml distilled water. The solution was neutralized with concentrated hydrochloric acid and diluted to 1000 ml. 3 ml of the stock solution were added to each litre of culture medium.

APPENDIX II

LIST OF LOCATIONS FROM WHICH SPECIMENS WERE EXAMINED, INCLUDING HERBARIUM MATERIAL AND PERSONAL COLLECTIONS

Each location and collection date is designated by a station/date number.

The species examined for each station/date number are designated A to G

A - *Scagelia pylaisaei*

B - *Antithamnionella floccosa*

C - *Antithamnion cruciatum*

D - *Callithamnion tetragonum*

E - *Callithamnion corymbosum*

F - *Callithamnion roseum*

G - *Plumaria elegans*

Station/Date Number	Location	Co-ordinates of Location	Date of Collection	Water Temp. °C	Species present						
					A	B	C	D	E	F	G
1.1	Highlands, N.J.	40°24'N 73°59'W	2-8-1874			+					
2.1	New York Bay							+			
3.1	Staten Is., N.Y.	40°35'N 74°02'W	1850					+			
3.2	Fort Hamilton, N.Y.	40°37'N 74°02'W	16-8-1892					+			
4.1	Orient, Long Is.	41°09'N 72°18'W	5-4-1914		+						
4.2	Peconic Bay, Long Is.	41°00'N 72°25'W	7-1880		+						
5.1	Bridgeport, Conn.	41°12'N 73°12'W			+			+			
6.1	Woodmont, Conn.	41°14'N 73°00'W	19-4-1903		+						
7.1	Faulkners Is., Conn.	41°12'N 72°38'W	11-1880					+			
8.1	Conanicut Is., R.I.	41°30'N 71°20'W	3-1898					+			
9.1	Brenton Pt., R.I.	41°27'N 71°21'W	28-6-1965								+
10.1	Newport, R.I.	41°30'N 71°19'W	1-1898								+
10.2			12-1900					+			
10.3			7-1905			+					
11.1	Martha's Vineyard, Mass.	41°21'N 70°50'W	21-7-1927								+
11.2			13-8-1952								+
12.1	Woods Hole, Mass.	41°31'N 70°39'W	12-4-1922		+						
12.2			23-7-1925						+		
13.1	Falmouth, Mass.	41°33'N 70°39'W	18-8-1882					+			
13.2			19-11-1969					+			

Station/Date Number	Location	Co-ordinates of Location	Date of Collection	Water Temp. °C	Species present						
					A	B	C	D	E	F	G
14.1	Penikese Is., Mass.	41°27'N 70°56'W	11-7-1927								+
15.1	Black Rock, Buzzards Bay, Mass.	41°35'N 70°51'W	26-7-1926					+			
15.2	Angelica Pt., Buzzards Bay, Mass.	41°38'N 70°46'W	26-8-1961					+			
16.1	Cape Cod, Mass.	41°41'N 70°40'W	9-5-1971	11	+			+			
17.1	Onset, Mass.	41°45'N 70°37'W	7-1890					+			
18.1	Revere Beach, Mass.	42°21'N 70°59'W	8-9-1879		+						
18.2			16-5-1882		+						
18.3			5-1889		+						
18.4			4-1890		+						
18.5			25-5-1890		+						
18.6			5-1893			+					
18.7			29-9-1895					+			
19.1	Nahant Bay, Mass.	42°55'N 70°55'W	17-2-1891								+
20.1	Marblehead, Mass.	42°30'N 70°50'W	7-4-1891		+						
21.1	Magnolia Beach, Mass.	42°34'N 70°43'W	6-1882		+	+					
21.2			10-5-1971	8.5		+					
22.1	Gloucester, Mass.	42°37'N 70°41'W				+					
23.1	Cape Ann, Mass.	42°39'N 70°37'W			+	+					
23.2			5-1874			+					
24.1	Salisbury Beach, Mass.	42°50'N 70°50'W	31-5-1890			+					

Station/Date Number	Location	Co-ordinates of Location	Date of Collection	Water Temp. °C	Species present						
					A	B	C	D	E	F	G
28.1	York Is., Me.	43°07'N 70°36'W	7-1894		+						
29.1	Cape Neddick, Me.	43°10'N 70°36'W				+					
30.1	Portland Hrb., Me.	43°41'N 70°18'W			+	+		+			
31.1	Inner Mach Is., Me.	43°45'N 70°10'W	29-8-1903					+			
32.1	Harpswell, Me.	43°46'N 70°00'W	16-7-1902		+						
32.2			7-1903		+						
32.3			6-7-1904		+						
32.4			7-1906		+						
33.1	Popham Beach, Me.	43°44'N 69°50'W	8-1900					+			
34.1	Griffith Head, Me.	43°47'N 69°43'W	2-5-1971	7		+					
35.1	Grey Camp, Me.	43°48'N 69°39'W	8-5-1971	9	+						
36.1	Eagle Is., Me.	44°12'N 68°47'W	7-1896		+						
37.1	Mt. Desert Is., Me.	44°21'N 68°10'W	1-5-1971	9	+	+					+
38.1	Culter, Me.	44°41'N 67°12'W	6-7-1902			+					
41.1	Drews Head, N.B.	45°04'N 66°44'W	28-4-1971	2	+	+					+
42.1	Pea Pt., N.B.	45°09'N 66°30'W	28-4-1971		+	+					
43.1	Point Lepreau, N.B.	45°04'N 66°28'W	5-6-1965			+					
43.2			5-7-1969								+
43.3			27-4-1971		+	+					+
44.1	Shippegan Is., N.B.	47°45'N 64°44'W	27-6-1965		+						

Station/Date Number	Location	Co-ordinates of Location	Date of Collection	Water Temp. °C	Species present						
					A	B	C	D	E	F	G
45.1	Sandy Cove, N.S.	44°30'N 66°12'W	8-6-1964			+					
45.2			1-4-1965			+					
45.3			27-7-1965			+					
46.1	Tommy's Beach, N.S.	44°27'N 66°10'W	30-12-1967			+					
46.2			12-7-1968								+
47.1	Horseshoe Cove, N.S.	44°18'N 64°23'W	4-5-1966		+						
48.1	Lunenberg, N.S.	44°23'N 64°21'W	22-4-1965		+						
49.1	Peggy's Cove, N.S.	44°38'N 63°45'W	17-5-1965			+					
49.2			27-5-1965			+					
49.3			8-2-1966			+					
49.4			23-3-1966			+					
49.5			18-4-1966			+					
50.1	Ketch Hrb., N.S.	44°30'N 63°35'W	4-3-1966								+
50.2			9-6-1966		+						
51.1	Herring Cove, N.S.	44°36'N 63°35'W	9-6-1964			+					
52.1	Halifax, N.S.	44°38'N 63°35'W			+						
52.2			1882						+		
53.1	Lawrencetown, N.S.	44°38'N 63°21'W	6-6-1966			+					
54.1	Louisburg, N.S.	45°56'N 59°58'W	2-9-1971	15		+					
55.1	Boularderie, N.S.	46°04'N 60°45'W	16-5-1971	10	+						

Station/Date Number	Location	Co-ordinates of Location	Date of Collection	Water Temp. °C	Species present						
					A	B	C	D	E	F	G
56.1	Middle Cape, N.S.	46°05'N 60°50'W	4-1971	9	+						
57.1	Monk Head, N.S.	45°41'N 61°50'W	4-10-1968				+				
58.1	Campbell Pt., P.E.I.	46°28'N 62°08'W	9-7-1968		+						
59.1	Iles de la Madeleine	ca. 47°30'N 61°45'W	9-7-1966		+						
59.2			12-8-1966		+						
61.1	Grande Rivière, Que.	48°23'N 64°50'W	17-9-1965		+						
62.1	Gaspé Pen., Que.				+						
62.2			1882		+						
63.1	Cap d'Espoir, Que.	48°26'N 64°20'W	19-10-1964		+						
64.1	Ile de Bonaventure, Que.	48°31'N 64°11'W	17-8-1965		+						
65.1	Percé, Que.	48°32'N 64°14'W	17-8-1965		+						
66.1	St. Pierre, Que.	48°31'N 64°14'W	28-8-1965		+						
67.1	Baie de Gaspé, Que.	ca. 48°-50°N 64°30'W	15-7-1965		+						
68.1	Gaspé, Que.	48°50'N 64°30'W	14-8-1959		+						
68.2			15-8-1968		+						
69.1	ChapChat, Que.	49°06'N 66°42'W	7-11-1917		+						
70.1	Matane, Que.	48°50'N 67°31'W	9-9-1966		+						
71.1	Pt-au-Père, Que.	48°32'N 68°25'W			+						

Station/Date Number	Location	Co-ordinates of Location	Date of Collection	Water Temp. °C	Species present						
					A	B	C	D	E	F	G
71.2			10-7-1968		+						
71.3			5-6-1969		+						
72.1	Rocher Blanc, Que.	48°27'N 68°33'W	30-5-1969		+						
72.2			21-8-1970		+						
73.1	Anse-au-Sable, Que.	48°26'N 68°32'W	13-6-1969		+						
73.2			27-8-1969		+						
73.3			18-7-1970		+						
74.1	Rivière Hatée, Que.	48°24'N 68°42'W	1-6-1969		+						
74.2			17-6-1969		+						
75.1	Bic, Que.	48°23'N 68°43'W	4-9-1967		+						
75.2			31-5-1969		+						
75.3			4-9-1969		+						
76.1	Cap-à-l'Original, Que.	48°20'N 68°48'W	8-1970		+						
77.1	St. Fabien-sur-Mer, Que.	48°19'N 68°51'W	8-9-1966			+					
77.2			5-9-1967		+	+					
77.3			15-7-1969		+						
77.4			19-7-1970		+						
78.1	St. Simon-sur-Mer, Que.	48°12'N 69°20'W	2-9-1969		+						
79.1	Trois Pistoles, Que.	48°10'N 69°09'W	17-9-1966		+						
80.1	Ile Verte, Que.	48°10'N 69°25'W	27-8-1969		+						
81.1	Cacouna, Que.	47°55'N 69°32'W	11-7-1968		+						

Station/Date Number	Location	Co-ordinates of Location	Date of Collection	Water Temp. °C	Species present						
					A	B	C	D	E	F	G
81.2			20-8-1969		+						
82.1	Cap-aux-Oies, Que.	47°30'N 70°15'W	1-8-1969		+						
83.1	Cap-à-l'Aigle, Que.	47°45'N 70°00'W	16-7-1905		+						
84.1	Port-aux-Saumon, Que.	47°44'N 69°59'W	30-7-1969		+						
85.1	Port-au-Persil, Que.	47°47'N 69°57'W	2-7-1969		+						
91.1	Diamond Cove, Nfld.	47°36'N 58°44'W	10-7-1971	7	+						
92.1	Rose Blanche, Nfld.	47°35'N 58°40'W	21-4-1971	3.5	+						
93.1	Burgeo, Nfld.	47°36'N 57°37'W	16-10-1970	11.5	+						
94.1	Ramea, Nfld.	47°31'N 57°25'W	19-10-1970	11		+					+
95.1	Hermitage, Nfld.	47°34'N 55°55'W	20-10-1970	10.5	+				+		
96.1	Pass Island Tickle, Nfld.	47°30'N 56°11'W	4-9-1971	13	+						
97.1	Seal Cove, Nfld.	47°28'N 56°05'W	21-10-1970	10.5	+						
98.1	Belleoram, Nfld.	47°31'N 55°24'W	12-10-1970	11					+		
98.2			3-12-1970	8	+						
99.1	Pool's Cove, Nfld.	47°41'N 55°25'W	11-10-1970	11					+		
99.2			3-12-1970	6	+						
100.1	English Hrb. East, Nfld.	47°38'N 54°55'W	20-5-1972	3							+
101.1	Grand le Pierre, Nfld.	47°41'N 54°47'W	28-6-1971	11	+	+			+		+
101.2			22-8-1971	15	+				+		+
101.3			6-11-1971	7.5	+			+	+		+
101.4			12-12-1971	5	+			+	+		+

Station/Date Number	Location	Co-ordinates of Location	Date of Collection	Water Temp. °C	Species present						
					A	B	C	D	E	F	G
101.5			9-1-1972	1.5	+			+	+		+
101.6			5-4-1972	1.5	+			+			+
101.7			21-5-1972		+			+			+
101.8			1-7-1972		+			+	+		+
102.1	Terrenceville, Nfld.	47°39'N 54°43'W	28-6-1971	10	+						
103.1	Harbour Mille, Nfld.	47°35'N 54°53'W	15-3-1971	0	+						+
103.2			13-4-1971	3	+	+					+
104.1	St. Bernard, Nfld.	47°31'N 54°47'W	30-5-1969	6	+						+
104.2			4-1-1970	2.5	+						+
104.3			26-5-1970	2	+						+
104.4			12-9-1970	12	+				+		+
104.5			23-9-1970	12	+				+		+
104.6			24-10-1970	12	+				+		+
104.7			5-11-1970	8	+				+		+
104.8			7-12-1970	7	+				+		+
104.9			2-1-1971	4	+	+			+		+
104.10			15-2-1971	1.5	+	+			+		+
104.11			15-3-1971	-1	+	+			+	+	+
104.12			13-4-1971	3	+				+	+	+
104.13			6-6-1971	4	+					+	+
104.14			4-7-1971	6	+				+	+	+

Station/Date Number	Location	Co-ordinates of Location	Date of Collection	Water Temp. °C	Species present						
					A	B	C	D	E	F	G
104.15	St. Bernard, Nfld. (Cont.)	47°31'N 54°47'W	1-8-1971	19	+				+	+	+
104.16			18-9-1971	16	+	+			+	+	+
104.17			17-10-1971	0	+				+	+	+
104.18			28-12-1971	3.5	+	+			+	+	+
104.19			15-1-1972	1.5	+				+	+	+
104.20			18-2-1972	0.5	+				+	+	+
104.21			10-3-1972	0	+	+		+	+	+	+
105.1	Frenchman's Cove, Nfld.	47°15'N 55°25'W	25-5-1970	4							+
106.1	Grand Beach, Nfld.	47°07'N 55°30'W	28-6-1971	9							+
107.1	Allan's Lighthouse, Nfld.	46°51'N 55°48'W	27-6-1971	8		+					+
110.1	Lannon Pt., Nfld.	46°54'N 55°58'W	27-6-1971	8		+					
112.1	Brookside, Nfld.	47°26'N 54°49'W	27-11-1971	6	+						
113.1	Saint Pierre, Fr.	ca. 47°N 56°20'W	17-9-1944			+					
116.1	North Hrb., Nfld.	47°08'N 53°37'W	8-4-1969		+						
121.1	La Manche, Nfld.	47°10'N 52°51'W	26-5-1970	4	+						
122.1	Gull Is., Nfld.	47°15'N 52°46'W	19-6-1970	3	+						
124.1	Bay Bulls, Nfld.	47°17'N 52°47'W	9-8-1968			+					
124.2			26-10-1968		+						
124.3			30-3-1970	0.5	+						
124.4			6-4-1970	1	+						
124.5			19-6-1970	3	+						

Station/Date Number	Location	Co-ordinates of Location	Date of Collection	Water Temp. °C	Species present						
					A	B	C	D	E	F	G
124.6	Bay Bulls, Nfld. (Cont.)	47°17'N 52°47'W	30-7-1970	10	+						
124.7			24-9-1970	12	+						
124.8			7-10-1970	10	+	+					
124.9			5-11-1970	8.2	+	+					
124.10			19-11-1970	7	+						
124.11			9-12-1970	2	+	+					
124.12			26-1-1971	0	+						
124.13			30-1-1971	-1	+	+					
124.14			11-2-1971	-0.5	+	+					
124.15			6-3-1971	-1.5	+						
124.16			30-3-1971	0	+	+					
124.17			31-3-1971	0	+	+					
124.18			15-4-1971	0.5	+	+					
124.19			22-5-1971	1.5	+	+					
124.20			16-6-1971	2	+	+					
124.21			21-6-1971	2	+	+					
124.22			16-7-1971	8	+	+					
124.23			17-8-1971	15	+	+					
124.24			8-9-1971	11	+	+					
124.25			24-10-1971	6.5	+	+					
124.26			22-11-1971	4.5	+	+					

Station/Date Number	Location	Co-ordinates of Location	Date of Collection	Water Temp. °C	Species present						
					A	B	C	D	E	F	G
124.27	Bay Bulls, Nfld. (Cont.)	47°17'N 52°47'W	15-12-1971	1.5	+	+					
124.28			15-1-1972	-0.5	+	+					
124.29			31-1-1972	-1	+	+					
124.30			29-3-1972	-1.5	+	+					
124.31			9-4-1972	0	+	+					
124.32			17-5-1972	2.5	+	+					
126.1	Cape Spear, Nfld.	47°31'N 52°31'W	11-9-1969	13		+					
127.1	St. John's Hrb., Nfld.	47°33'N 52°41'W	31-3-1969			+					
128.1	Logy Bay, Nfld.	47°37'N 52°39'W	4-6-1968		+	+					
128.2			13-6-1968		+						
128.3			26-6-1968		+						
128.4			28-11-1969			+					
128.5			2-2-1970	0	+						
128.6			29-4-1970	1	+						
128.7			13-2-1971		+	+					
128.8			26-3-1971	-1.5	+						
128.9			20-6-1971		+						
128.10			18-8-1971	10	+						
128.11			24-8-1971	15	+						
128.12			28-10-1971	5.8	+						
128.13			18-1-1972	0	+	+					

Station/Date Number	Location	Co-ordinates of Location	Date of Collection	Water Temp. °C	Species present						
					A	B	C	D	E	F	G
131.1	Flat Rock, Nfld.	47°42'N 52°42'W	18-12-1970	4	+	+					
131.2			7-3-1972	-2	+						
133.1	Cape St. Francis, Nfld.	47°48'N 52°47'W	1-9-1969	13	+						
133.2			2-4-1971	0	+	+					
134.1	Bauline, Nfld.	47°43'N 52°50'W	17-12-1968	3	+						
134.2			28-11-1971		+	+					
135.1	Portugal Cove, Nfld.	47°37'N 52°52'W	8-1968		+						
135.2			9-1968		+						
135.3			27-1-1969	1		+					
135.4			16-2-1969			+					
135.6			14-4-1969	2.5		+					
135.7			27-1-1970	0		+					
135.8			4-3-1970	0		+					
135.9			14-7-1970	9.8	+	+					
135.10			28-7-1970	16.5	+	+					
135.11			17-11-1970	8	+	+					
135.12			30-12-1970	0	+	+					
136.1	Kelly's Is., Nfld.	47°34'N 52°56'W	10-10-1965		+						
137.1	Foxtrap, Nfld.	47°32'N 52°58'W	27-9-1968			+					
139.1	Chapel Cove, Nfld.	47°26'N 53°08'W	12-6-1970	12	+	+					
139.2			22-6-1971	6	+						

Station/Date Number	Location	Co-ordinates of Location	Date of Collection	Water Temp. °C	Species present						
					A	B	C	D	E	F	G
143.1	Bay de Verde, Nfld.	48°04'N 52°54'W	16-4-1969			+					
143.2			7-4-1970	1	+	+					
145.1	New Chelsea, Nfld.	48°02'N 53°13'W	11-7-1971	8	+	+					
148.1	Southwest Arm, Nfld.	48°03'N 53°29'W	19-3-1972	-1		+					
149.1	Hogs Nose, Nfld.	48°21'N 53°21'W	19-6-1971	6	+						
150.1	Random Sound, Nfld.	48°00'N 53°48'W	21-2-1969	1.5		+					
152.1	Seal Is. Tickle, Nfld.	48°35'N 53°45'W	22-12-1971	2	+						
153.1	Swale Is., Nfld.	48°36'N 53°46'W	9-6-1970	11.3	+						
154.1	Newman Sound, Nfld.	48°35'N 53°47'W	10-12-1969	2	+						
156.1	Lumdsen North, Nfld.	49°18'N 53°37'W	13-7-1968		+						
158.1	Twillingate, Nfld.	49°41'N 54°48'W	12-7-1968		+	+					
158.2			26-7-1971	6	+	+					
159.1	Brent Cove, Nfld.	49°51'N 55°45'W	9-7-1968		+						
160.1	Wild Bight, Nfld.	49°38'N 55°56'W	10-7-1968		+						
161.1	Groais Is., Nfld.	50°57'N 55°38'W	23-9-1971	8	+						
162.1	Goose Cove, Nfld.	51°18'N 55°38'W	16-7-1971	10	+						
163.1	St. Anthony, Nfld.	51°22'N 55°33'W	16-7-1971	7	+						
163.2			29-9-1971	6	+						
164.1	Cape Onion, Nfld.	51°37'N 55°36'W	17-7-1971	9	+						
166.1	Eddies Cove, Nfld.	51°25'N 56°27'W	15-7-1971	11		+					

Station/Date Number	Location	Co-ordinates of Location	Date of Collection	Water Temp. °C	Species present						
					A	B	C	D	E	F	G
170.1	Three Mile Rock, Nfld.	50°00'N 57°45'W	14-7-1971	12	+	+					
171.1	Bonne Bay, Nfld.	49°36'N 57°56'W	31-10-1970	9					+		
171.2		TO	16-1-1971	-1	+				+		
171.3		49°30'N 57°50'W	6-2-1971	-2					+		
171.4			25-5-1971	8.5		+					
171.5			26-7-1971	16	+	+			+	+	+
171.6			31-10-1971	9.5				+	+		
171.7			26-4-1972	1	+	+		+			+
171.8			30-5-1972	7		+					
172.1	Trout River, Nfld.	49°29'N 58°08'W	7-7-1968		+	+					
173.1	Bay of Islands, Nfld.	49°07'N 58°26'W	23-8-1967		+						
173.2			2-7-1968		+						
173.3			15-5-1971	4	+	+					
174.1	Port au Port Bay, Nfld.	48°44'N 58°50'W	6-6-1969	11	+						
174.2			1-8-1969	15.5	+						
176.1	Pinware Bay, Lab.	51°37'N 56°43'W	18-7-1971	2.5	+						
178.1	Fisherman's Pt., Lab.	52°21'N 55°45'W	20-10-1971	2.7	+						
179.1	Cape North, Lab.	53°46'N 56°30'W	7-10-1971	5	+						
181.1	East Sister Is., Lab.	54°16'N 58°03'W	13-10-1971	4.5	+						
182.1	North Green Is., Lab.	54°25'N 57°19'W	15-10-1971	4.5	+	+					

Station/Date Number	Location	Coordinates of Location	Date of Collection	Water Temp. °C	Species present						
					A	B	C	D	E	F	G
184.1	Alliak Bight, Lab.	54°30'N 57°23'W	15-10-1971	4.5	+						
202.1	Wakeham Bay, N.W.T.	61°39'N 72°00'W	5-8-1967		+						
204.1	S. Baffin Is., N.W.T.	62°49'N 69°50'W	24-7-1967		+						
205.1	S. Baffin Is., N.W.T.	64°17'N 72°22'W	30-7-1967		+						
206.1	Richmond Gulf	56°15'N 76°20'W	24-8-1920		+						
207.1	Hudson's Bay	ca. 55°N	28-8-1920		+						
208.1	Grey Goose Is., Que.	53°55'N 79°54'W	31-7-1920		+						
209.1	Long Pt., Hudson's Bay	52°45'N 78°52'W	2-9-1920		+						
210.1	Murray Bay	71°45'N 93°55'W	8-1-1941		+						
211.1	Dolphin and Union Strait	68°-70°N113°-118°W	14-9-1915		+						
212.1	Wollaston Land	69°-70°N115°W	14-9-1915		+						
212.2			27-7-1916		+						
213.1	Alaska	69°35'N 163°27'W			+						
214.1	Nome, Alas.	64°30'N 165°30'W	20-9-1919		+						
215.1	Uyak Bay, Alas.	57°30'N 154°00'W	23-8-1899		+						
216.1	Chignik Lagoon, Alas.	56°18'N 158°27'W	23-7-1911		+						
232.1	Upernavik, Grnld	72°50'N 56°00'W	18-7-1886		+						

Station/Date Number	Location	Co-ordinates of Location	Date of Collection	Water Temp. °C	Species present						
					A	B	C	D	E	F	G
240.1	Eastern Greenland		24-7-1889		+						
241.1	Kangertitvatskig Fj., Grnld	66°17'N 35°37'W	6-8-1971		+						
242.1	Ikerssuaq Fj., Grnld	66°40'N 34°36'W	22-8-1971		+						
247.1	Vestmannaeygar, Ice.	63°25'N 20°15'W	14-5-1897			+					
248.1	Reykavik, Ice.	64°09'N 21°58'W	31-3-1897			+					
248.2			14-4-1897							+	
248.3			7-8-1897								+
249.1	Vidhey, Ice.	64°10'N 21°51'W	17-4-1897			+					
250.1	Dyrafjördur, Ice.	65°55'N 23°35'W	30-9-1896		+						
251.1	Grjótnes, Ice.	66°28'N 16°31'W	26-7-1896		+						
252.1	Seydisfjördur, Ice.	65°16'N 14°02'W	15-5-1896			+					
256.1	Fuglefjord, Faer.	62°14'N 6°49'W	19-5-1885			+					
257.1	Vágo, Faer.	62°05'N 7°15'W	4-6-1896								+
258.1	Peterhead, Scot.	57°30'N 1°46'W				+					
259.1	Aberdeen, Scot.	57°10'N 2°04'W	4-1847			+					
260.1	Firth of Forth, Scot.	ca. 56°10'N 3°00'W	8-5-1885			+					
262.1	Kiel, Ger.	54°20'N 10°08'E	8-1890		+						
263.1	Langelands Belt, Den.	54°50'N 11°00'E	20-5-1895		+						
264.1	Gilleleje, Kattegat, Den.	56°08'N 12°19'E	6-8-1913					+			

Station/Date Number	Location	Co-ordinates of Location	Date of Collection	Water Temp. °C	Species present						
					A	B	C	D	E	F	G
265.1	Berlevåg, Nor.	70°50'N 29°09'E	18-7-1887			+					
265.2			22-8-1891		+						
267.1	Syltefjord, Nor.	70°32'N 30°10'E	23-7-1881			+					
269.1	Mussel Bay, Spitz.	79°50'N 15°30'E	1872		+						
269.2			7-12-1872		+						

Voucher specimens for records of *S. pylaisaei* are located in the herbaria listed in Appendix III.

For the other species:

All Newfoundland and Labrador (St 91 - 184) material is located in NFLD.

All Quebec material (St.59 - 85) is in QAC.

New Brunswick material (St.41 - 44) prior to 1971 in ARL, post 1971 in NFLD.

U.S.A. material (St.1-38) prior to 1971 in NY, post 1971 in NFLD.

Scottish material (St.258 - 260) in BM.

Scandinavian (St.263 - 269) and Icelandic (St.247 - 257) material in C.

APPENDIX III

MORPHOLOGICAL MEASUREMENTS OBTAINED FROM HERBARIUM MATERIAL OF *SCAGELIA PYLAISAEI*

Herbarium: Abbreviations are given as in Materials and Methods. The numbers, where present, are Herbarium Accession numbers.

Four specimens from two exsiccatae were examined:

NY[1] Phycotheca-boreale Americana #42

NY[2] Phycotheca-boreale Americana #1110

NY[3] Phykotheca Universalis #501

NY[4] Phycotheca-boreale Americana #1661

A.W. Annot. No.: Personal annotation number.

Measurements: All measurements of cell size, distribution of whorl branchlets and gland cells were obtained by the methods described in the *S. pylaisaei* section: Morphological variation in herbarium material.

P.D.W.B.A.C.: Percentage distribution of whorl branchlets per axial cell.

Gland Cell: + = present but less than 1%

Reproductive Structures: T = tetrasporangia

long axis x short axis. µm

Dev. = developing.

C = carposporophyte with mature carpospores

M = spermatangia

S = sterile

Original identification appearing on the herbarium sheet:

a = *americanum*

b = *boreale*

b.c. = *boreale* f. *corallina*

c = *cruciatum*

f = *floccosum*

p = *pylaisaei*

pab = *pylaisaei americanum boreale* complex

pl = *plumula boreale*

sp. = no epithet

Station/ Date Number	Herbarium	A.W. Annot. No.	P.D.W.B.A.C. 2 3 4	Axial Cell µm	Whorl Branchlet Basal Cell µm	Whorl Branchlet Longest Cell µm	Gland Cell %	Reproductive Structures	Original Identification
4.1	NY	516	78 22	1350 x 100	40 x 20	30 x 8	9	T 60 x 40	p
4.2	NY	508	86 14	930 x 110	40 x 20	60 x 30	10	C	p
5.1	NY[1]	547	100	500 x 48	60 x 10	100 x 8	+	T 40 x 28	a
6.1	NY[2]	545	100	1150 x 130	110 x 40	160 x 36	+	T 68 x 52	a
6.1	NY[2]	546	100	700 x 80	50 x 24	120 x 28	+	S	a
12.1	NY	543	100	900 x 100	110 x 12	160 x 16	+	T 60 x 40	a
16.1	NFLD 6401	716	100	900 x 70	100 x 10	120 x 8	+	T 60 x 30	a
16.1	NFLD 6400	807	100	950 x 80	90 x 15	160 x 15	+	T 60 x 40	a
18.1	NY	544	100	1250 x 110	110 x 30	120 x 20	+	T 62 x 42	a
18.3	NY	520	100	800 x 150	70 x 35	120 x 40	+	S	f
18.4	NY	511	100	1000 x 70	150 x 50	110 x 30	+	T 50 x 45	a
18.5	NY[3]	542	100	1000 x 150	90 x 25	150 x 25	2	S	a
18.5	NY	501	25 75	1000 x 150	70 x 30	100 x 25	6	T 62 x 43	p
18.5	NY[4]	515	78 22	950 x 150	100 x 30	120 x 30	7	T 56 x 44	p
20.2	NY	509	70 30	700 x 110	70 x 40	100 x 35	+	S	p
21.1	NY	500	14 86	700 x 150	60 x 30	120 x 50	25	C	p
21.1	NY	502	20 80	900 x 150	25 x 20	60 x 25	3	S	p
23.1	NY	505	92 8	900 x 140	40 x 30	80 x 30	8	T 40 x 30	p
23.2	NY	506	100	1000 x 110	85 x 20	120 x 20	+	S	f

Station/ Date Number	Herbarium	A.W. Annot. No.	P.D.W.B.A.C. 2	3	4	Axial Cell µm	Whorl Branchlet Basal Cell µm	Whorl Branchlet Longest Cell µm	Gland Cell %	Reproductive Structures	Original Identification
28.1	NY	512	60	40		350 x 100	60 x 20	60 x 20	7	S	p
30.1	NY	311	100			1000 x 110	60 x 36	100 x 60	8	T 40 x 32	b
32.1	NY	309	92	8		700 x 110	80 x 20	100 x 25	14	T 32 x 20	b
32.2	NY	519	100			900 x 70	50 x 30	80 x 30	7	S	f
32.3	NY	513	56	44		750 x 100	90 x 40	70 x 40	8	S	p
32.4	NY	312	100			550 x 80	80 x 15	150 x 12	16	T 40 x 32	b
35.1	NFLD 6392	730	100			810 x 110	80 x 32	120 x 40	9	S	sp.
36.1	NY	310	100			450 x 110	40 x 20	100 x 30	7	S	b
37.1	NFLD 5951	781	46	54		550 x 120	40 x 20	70 x 25	5	T 60 x 40	b
39.1	NFLD 6039	812	100			700 x 120	40 x 20	100 x 20	8	T 58 x 32	b
41.1	NFLD 5823	779	22	78		800 x 150	50 x 20	100 x 20	1	T 48 x 32	p
41.1	NFLD 5735	718	25	75		1300 x 160	80 x 60	150 x 70	5	T 60 x 40	b
42.1	NFLD 5884	780	36	64		800 x 110	50 x 20	140 x 40	2	T 40 x 30	b
43.3	NFLD 5874	776	95	5		500 x 100	50 x 25	80 x 30	8	S	b
44.1	ARL 2028	372									a
44.1	ARL 2028	371									sp.
47.1	ARL 3550										sp.
48.1	ARL 1242										c
50.2	ARL 2662										p

Station/ Date Number	Herbarium	A.W. Annot. No.	P.D.W.B.A.C. 2 3	Axial Cell µm	Whorl Branchlet Basal Cell µm	Whorl Branchlet Longest Cell µm	Gland Cell %	Reproductive Structures	Original Identification
52.1	NY	504	100	650 x 110	80 x 40	125 x 18	+	T 45 x 25	c
55.1	NFLD 6408	728	100	1200 x 120	120 x 40	200 x 60	+	T 50 x 40	sp.
56.1	NFLD 6473	729	100	800 x 100	50 x 15	100 x 15	4	T 60 x 48	sp.
58.1	CANA 7417								sp.
59.1	QAC 4231	347	100	580 x 120	60 x 30	90 x 25	8	T 60 x 50	sp.
59.2	QAC 4227	415	43 57	1020 x 100	60 x 20	80 x 32	+	T 55 x 40	sp.
61.1	QAC 4034	341	91 9	800 x 100	80 x 40	200 x 50	11	S	sp.
61.1	QAC 2662	378	61 39	700 x 50	50 x 25	60 x 25	23	C	sp.
62.1	NY	316	80 20	1000 x 80	80 x 20	120 x 20	12	S	b
62.2	CANA 5517								p
63.1	QAC 829	374	50 50	350 x 40	25 x 10	50 x 15	+	T 40 x 30	sp.
64.1	QAC	366	50 50	750 x 80	110 x 30	200 x 35	+	T 40 x 35	sp.
65.1	QAC 3616	365	42 58	450 x 210	40 x 30	110 x 40	6	C	sp.
66.1	QAC 3609	382	17 83	800 x 120	70 x 40	160 x 30	16	S	sp.
67.1	QAC 2172	369	88 12	800 x 100	50 x 15	120 x 30	2	T 35 x 25	sp.
67.1	QAC 753	363	62 38	600 x 100	55 x 35	40 x 30	12	S	sp.
69.1	NY	503	70 30	850 x 150	60 x 40	100 x 50	+	S	sp.
70.1	QAC 4261	342	90 10	650 x 80	70 x 30	100 x 30	5	S	sp.
71.1	QAC 5852	423	36 54	110 x 28	80 x 35	95 x 40	12	S	sp.

Station/ Date Number	Herbarium	A.W. Annot. No.	P.D.W.B.A.C. 2 3 4	Axial Cell µm	Whorl Branchlet Basal Cell µm	Whorl Branchlet Longest Cell µm	Gland Cell %	Reproductive Structures	Original Identification
71.1	QAC 3610	364	29 71	600 x 80	60 x 35	85 x 30	2	C	sp.
71.2	QAC 5850	395	33 67	990 x 110	150 x 28	150 x 28	3	T Dev.	sp.
71.3	QAC 197A	400a	41 59	935 x 118	56 x 40	110 x 45	4	S	sp.
72.1	QAC 15A	401	82 18	1120 x 105	80 x 45	100 x 35	4	S	sp.
72.1	QAC 74A	402	52 48	940 x 120	65 x 30	100 x 35	5	S	sp.
72.2	QAC 1944A	381	68 32	300 x 80	40 x 25	87 x 20	7	S	b
73.1	QAC 382	412	67 33	1450 x 100	90 x 20	110 x 50	+	S	sp.
73.2	QAC 1512	413	100	800 x 50	60 x 25	75 x 35	abs.	S	sp.
73.3	QAC 2196A	391	100	500 x 100	60 x 25	100 x 25	+	T 60 x 30	a
74.1	QAC 126A	419	67 33	810 x 128	50 x 30	80 x 38	12	S	sp.
74.1	QAC 37A	348	62 38	1500 x 130	110 x 40	90 x 20	+	S	sp.
74.2	QAC 392A	416	86 14	772 x 122	60 x 20	70 x 30	4	S	sp.
74.2	QAC 394	417	86 14	772 x 122	60 x 20	70 x 30	1	S	sp.
74.2	QAC 391	336	58 42	1200 x 100	50 x 25	50 x 20	2	S	sp.
75.1	QAC 5241	353	48 52	950 x 100	70 x 35	70 x 30	+	S	sp.
75.2	QAC 107A	400b	84 16	1020 x 128	70 x 48	100 x 30	4	S	sp.
75.3	QAC 5243	360	94 6	350 x 60	60 x 25	100 x 35	7	S	sp.
76.1	QAC 2031A	377	69 31	1200 x 60	50 x 15	50 x 20	3	S	b
76.1	QAC 6299	355	75 25	400 x 100	65 x 20	66 x 25	6	T 45 x 35	sp.

Station/ Date Number	Herbarium	A.W. Annot. No.	P.D.W.B.A.C. 2 3 4	Axial Cell µm	Whorl Branchlet Basal Cell µm	Whorl Branchlet Longest Cell µm	Gland Cell %	Reproductive Structures	Original Identification
76.1	QAC 6268	354	66 34	500 x 70	25 x 20	30 x 15	5	T 50 x 30	b
76.1	QAC 2040A	388	92 8	700 x 90	60 x 25	100 x 30	8	T 40 x 30	b
76.1	QAC 2417A	392	100	650 x 100	50 x 20	150 x 15	+	T 55 x 30	sp.
77.2	QAC 5296	394	100	650 x 120	70 x 25	100 x 25	8	S	sp.
77.2	QAC 5304	362	100	400 x 80	70 x 20	100 x 30	+	S	sp.
77.2	QAC 5293	361	100	700 x 80	60 x 25	60 x 25	5	S	sp.
77.2	QAC 4338	356	100	750 x 60	70 x 40	80 x 40	6	T 60 x 40	sp.
77.2	QAC 5302	350	94 6	350 x 50	80 x 30	120 x 30	+	S	sp.
77.2	QAC 5295	351	57 43	400 x 70	50 x 30	80 x 35	2	S	sp.
77.2	QAC 5297	352	64 36	1200 x 100	80 x 40	120 x 30	10	T 50 x 35	sp.
77.3	QAC 733A	340	83 17	850 x 90	70 x 25	100 x 30	5	S	sp.
77.4	QAC 2217	393	88 12	650 x 70	60 x 20	80 x 15	+	T 42 x 18	sp.
78.1	QAC 153A	398	100	740 x 96	60 x 26	116 x 31	+	S	sp.
79.1	QAC 4308	343	84 16	350 x 70	75 x 20	100 x 25	6	T 35 x 28	sp.
79.1	QAC 4295	359	92 8	850 x 100	60 x 15	100 x 12	4	T 40 x 25	sp.
79.1	QAC 4312	357	91 9	400 x 100	70 x 25	100 x 25	5	S	sp.
79.1	QAC 4318	418	82 18	955 x 95	90 x 20	140 x 18	11	S	sp.
79.1	QAC	338	100	650 x 70	15 x 5	30 x 8	4	S	sp.
79.1	QAC 4310	344	31 69	500 x 80	70 x 30	110 x 15	4	M	sp.

Station/ Date Number	Herbarium	A.W. Annot. No.	P.D.W.B.A.C. 2	3	4	Axial Cell µm	Whorl Branchlet Basal Cell µm	Whorl Branchlet Longest Cell µm	Gland Cell %	Reproductive Structures	Original Identification
79.1	QAC 4320	345	100			700 x 70	40 x 25	90 x 15	5	S	sp.
80.1	QAC 1494A	346	40	60		600 x 100	80 x 30	110 x 50	10	S	sp.
81.1	QAC 5956	396	100			840 x 118	76 x 27	85 x 20	7	S	sp.
81.1	QAC 5904	403	100			1090 x 118	100 x 20	180 x 20	2	T 50 x 35	sp.
81.2	QAC 2374A	387	88	12		950 x 140	70 x 20	100 x 25	27	S	b
81.2	QAC	337	100			650 x 40	20 x 5	30 x 5	18	S	p
81.2	QAC 2380A	390	100			1000 x 70	60 x 20	100 x 20	3	S	a
82.1	QAC 1216A	408	88	12		630 x 98	35 x 28	60 x 40	13	C	sp.
83.1	QAC	414	100			990 x 120	50 x 30	100 x 34	+	S	b
84.1	QAC 926A	411	85	15		980 x 85	70 x 25	140 x 22	16	S	sp.
84.1	QAC 928A	410	100			920 x 98	60 x 12	120 x 20	9	S	sp.
85.1	QAC 1042A	409	94	6		780 x 100	60 x 20	90 x 20	14	S	sp.
91.1	NFLD 6787	845	68	32		1000 x 120	60 x 20	120 x 20	+	T Dev.	sp.
92.1	NFLD 5766	777	100			600 x 140	40 x 15	80 x 20	10	T Dev.	b
93.1	NFLD 4686	768	94	6		420 x 60	50 x 10	100 x 12	+	C	b
95.1	NFLD 4691	772	100			600 x 75	80 x 8	70 x 7	2	S	f
96.1	NFLD 7254	704	83	17		250 x 70	50 x 20	70 x 15	3	S	pab
97.1	NFLD 4723	766	82	18		380 x 40	50 x 20	80 x 20	7	S	b
98.2	NFLD 5499	809	100			400 x 70	40 x 16	80 x 25	32	S	b

Station/ Date Number	Herbarium	A.W. Annot. No.	P.D.W.B.A.C. 2 3 4	Axial Cell µm	Whorl Branchlet Basal Cell µm	Whorl Branchlet Longest Cell µm	Gland Cell %	Reproductive Structures	Original Identification
99.2	NFLD 5498	806	100	1000 x 100	100 x 30	250 x 20	abs.	S	b
101.2	NFLD 7018	856	100	350 x 70	62 x 25	100 x 20	5	S	sp.
101.3	NFLD 7255	705	100	800 x 110	85 x 40	120 x 25	4	T 80 x 48	sp.
101.4	NFLD 7316	733	100	1200 x 110	80 x 20	120 x 20	12	S	sp.
101.5	NFLD 7242	734	100	500 x 50	70 x 28	80 x 30	13	S	sp.
102.1	NFLD 6448	850	100	480 x 100	37 x 15	100 x 15	6	T 22 x 15	sp.
103.1	NFLD 5397	786	80 20	700 x 180	70 x 50	70 x 40	+	T 50 x 40	b
103.2	NFLD 6397	783	13 87	700 x 150	80 x 80	100 x 70	+	T 50 x 30	b
104.4	NFLD 4324	763	100	300 x 60	30 x 16	78 x 8	+	T 48 x 36	b
104.5	NFLD 4325	764	100	500 x 100	80 x 15	180 x 25	7	S	b
104.9	NFLD 5198	774	100	350 x 80	70 x 20	80 x 15	6	S	b
104.10	NFLD 5332	796	93 7	1100 x 150	140 x100	150 x 90	7	T 60 x 40	b
104.11	NFLD 5404	790	100	500 x 160	70 x 40	100 x 25	2	S	b
104.13	NFLD 8842	810	100	900 x 150	100 x 40	100 x 50	2	T 50 x 30	sp.
104.15	NFLD 7024	844	100	900 x 150	75 x 20	120 x 30	11	T 40 x 30	sp.
104.21	NFLD 8089	722	100	650 x 150	80 x 60	150 x 70	21	S	sp.
112.1	NFLD 7321	723	100	700 x 80	50 x 15	150 x 15	2	S	sp.
116.1	NFLD 2728	757	100	600 x 150	50 x 25	100 x 25	3	C	b
121.1	NFLD 4159	745	100	700 x 200	80 x 40	120 x 16	9	S	p

Station/ Date Number	Herbarium	A.W. Annot. No.	P.D.W.B.A.C. 2	3	4	Axial Cell µm	Whorl Branchlet Basal Cell µm	Whorl Branchlet Longest Cell µm	Gland Cell %	Reproductive Structures	Original Identification
122.1	NFLD 4158	744		100		300 x 100	50 x 15	100 x 40	8	T 48 x 25	p
124.3	NFLD 4008	814	9	91		800 x 150	80 x 60	120 x 60	abs.	T Dev.	a
124.4	NFLD 4164	743		70	30	800 x 200	80 x 30	130 x 30	12	T 50 x 30	p
124.4	NFLD 4164	747	87	13		100 x 40	50 x 15	70 x 30	+	S	b
124.5	NFLD 4157	528		89	11	650 x 200	80 x 40	120 x 50	+	T 44 x 20	p
124.6	NFLD 4154	537		100		500 x 150	40 x 20	100 x 50	16	T 40 x 20	p
124.7	NFLD 5672	784	72	28		350 x 100	50 x 20	80 x 20	9	T 48 x 40	b
124.7	NFLD 5682	785	44	56		150 x 60	40 x 16	64 x 16	13	S	b
124.9	NFLD 4735	767	60	40		400 x 100	86 x 35	100 x 40	6	T 50 x 30	b
124.10	NFLD 4658	770	60	40		650 x 120	80 x 40	150 x 40	+	T 64 x 48	b
124.14	NFLD 5323	797	9	91		350 x 110	24 x 24	80 x 20	6	S	b
124.14	NFLD 5345	793		100		650 x 150	60 x 45	84 x 36	8	T 40 x 32	b
124.18	NFLD 6396	782	21	79		600 x 150	80 x 50	80 x 40	9	T 50 x 40	b
124.20	NFLD 6390	749	32	68		700 x 150	48 x 32	88 x 48	14	T 50 x 30	p
124.20	NFLD 6390	749	40	60		600 x 100	80 x 60	100 x 60	10	T 44 x 32	p
124.21	NFLD 6477	852		100		700 x 140	75 x 30	100 x 40	14	T 50 x 37	sp.
124.23	NFLD 7019	855	60	30		500 x 100	70 x 30	100 x 35	21	S	sp.
124.26	NFLD 7266	717		100		300 x 100	50 x 24	80 x 28	5	T 80 x 56	sp.
124.27	NFLD 7332	752	50	50		400 x 90	50 x 15	70 x 10	2	T 40 x 24	p

Station/ Date Number	Herbarium	A.W. Annot. No.	P.D.W.B.A.C. 2 3 4	Axial Cell µm	Whorl Branchlet Basal Cell µm	Whorl Branchlet Longest Cell µm	Gland Cell %	Reproductive Structures	Original Identification
124.28	NFLD 7237	753	21 79	550 x 140	70 x 35	120 x 40	+	T 60 x 40	p
128.1	NFLD 914	804	100	800 x 120	100 x 20	60 x 20	15	S	a
128.2	NFLD 938	803	67 33	420 x 110	50 x 25	80 x 20	2	T 50 x 40	sp.
128.3	NFLD 981	700	90 10	1000 x 50	70 x 20	100 x 20	3	T 40 x 24	b
128.5	NFLD 4006	811	22 78	550 x 120	80 x 55	120 x 70	6	C	a
128.6	NFLD 4160	746	30 70	700 x 100	80 x 30	150 x 60	17	T 50 x 30	p
128.7	NFLD 5337	795	38 62	500 x 120	90 x 40	90 x 30	11	T Dev.	b
128.8	NFLD 5703	789	75 25	550 x 200	35 x 20	60 x 20	11	S	b
128.8	NFLD 5725	792	50 50	900 x 150	60 x 40	90 x 50	10	S	b
128.9	NFLD 6391	751	100	950 x 200	50 x 40	70 x 40	8	T 48 x 40	p
128.12	NFLD 7252	702	90 10	320 x 110	80 x 25	120 x 28	9	T 60 x 40	sp.
128.13	NFLD 7235	754	20 80	500 x 180	60 x 36	100 x 24	17	C	p
131.1	NFLD 5374	791	71 29	500 x 120	100 x 50	150 x 40	7	S	b
131.2	NFLD 8083	721	39 61	380 x 120	50 x 40	100 x 40	7	S	sp.
133.2	NFLD 5711	788	8 84 8	1200 x 140	50 x 50	100 x 40	4	T 60 x 40	b
134.2	NFLD 7265	715	61 39	900 x 150	60 x 30	100 x 30	3	T 60 x 40	sp.
135.1	NFLD 2727	759	58 42	800 x 150	80 x 24	140 x 28	4	T 60 x 44	b
135.2	NFLD 3133	758	88 12	420 x 100	60 x 20	50 x 25	5	C	b
135.2	NFLD 4009	813	93 7	700 x 120	60 x 20	100 x 20	abs.	abs.	a

Station/ Date Number	Herbarium	A.W. Annot. No.	P.D.W.B.A.C. 2	3	4	Axial Cell µm	Whorl Branchlet Basal Cell µm	Whorl Branchlet Longest Cell µm	Gland Cell %	Reproductive Structures	Original Identification
135.10	NFLD 4156	761	92	8		170 x 70	40 x 10	50 x 12	6	M	b
135.11	NFLD 4662	769	100			800 x 90	60 x 10	110 x 10	2	T 60 x 40	b
135.11	NFLD 4663	771	50	50		600 x 50	80 x 16	80 x 24	+	S	f
135.12	NFLD 5213	773	77	23		550 x 80	50 x 20	100 x 30	+	T 60 x 40	b
139.1	NFLD 3978	756	50	50		300 x 90	32 x 12	50 x 20	4	T 40 x 32	b
139.1	NFLD 3977	765	90	10		550 x 150	50 x 20	80 x 25	3	T 50 x 40	b
139.2	NFLD 6482	853	62	38		650 x 150	62 x 25	75 x 40	20	T 40 x 30	sp.
143.2	NFLD 4161	339		70	30	700 x 200	60 x 40	80 x 48	15	T 40 x 32	p
145.1	NFLD 6849	846	50	50		1300 x 120	90 x 50	150 x 40	2	S	sp.
149.1	NFLD 6393	731	56	44		700 x 120	80 x 40	150 x 30	3	T 48 x 24	sp.
152.1	NFLD 7048	857	100			700 x 100	70 x 20	150 x 20	4	T 52 x 30	sp.
153.1	NFLD 5664	787	38	62		500 x 80	60 x 30	150 x 30	9	T 60 x 35	b
154.1	NFLD 3704	755	77	33		800 x 80	80 x 25	160 x 30	3	T 40 x 28	b
156.1	NFLD 1293	800	10	90		550 x 120	70 x 30	100 x 30	7	T 50 x 30	a
158.1	NFLD 1386	805	74	26		1200 x 100	80 x 40	120 x 40	15	T 60 x 40	a
158.2	NFLD 6467	851	80	20		350 x 120	50 x 20	90 x 15	+	T 50 x 40	sp.
159.1	NFLD 1355	802		100		700 x 100	70 x 50	70 x 40	8	T 48 x 40	a
160.1	NFLD 1315	798	70	30		650 x 90	60 x 30	90 x 30	13	T 50 x 30	a
161.1	NFLD 7257	707	56	44		900 x 160	50 x 20	50 x 15	8	T 60 x 40	sp.

Station/ Date Number	Herbarium	A.W. Annot. No.	P.D.W.B.A.C. 2	3	4	Axial Cell µm	Whorl Branchlet Basal Cell µm	Whorl Branchlet Longest Cell µm	Gland Cell %	Reproductive Structures	Original Identification
162.1	NFLD 7263	713	65	35		400 x 120	90 x 20	100 x 20	8	T 64 x 36	sp.
163.1	NFLD 7264	714	100			250 x 80	48 x 20	88 x 24	4	S	sp.
163.2	NFLD 7261	711	79	21		650 x 120	60 x 15	100 x 15	4	T 60 x 32	sp.
164.1	NFLD 6695	848	38	62		300 x 120	50 x 20	90 x 30	5	S	sp.
170.1	NFLD 6866	847	60	40		400 x 110	62 x 25	110 x 35	2	S	sp.
171.2	NFLD 5196	775	100			500 x 120	60 x 15	100 x 10	8	S	b
171.5	NFLD 7262	712	100			600 x 110	40 x 20	110 x 24	6	T Dev.	sp.
171.5	NFLD 7249	719	100			760 x 80	64 x 12	100 x 24	3	T 70 x 40	sp.
171.5	NFLD 8841	701	100			700 x 200	80 x 40	120 x 40	+	S	sp.
171.5	NFLD 7250	718	100			600 x 30	40 x 8	120 x 8	+	S	sp.
171.5	NFLD 7253	703	100			600 x 70	80 x 6	300 x 20	4	T 80 x 32	sp.
171.5	NFLD 7023	843	100			650 x 70	85 x 25	130 x 20	4	S	sp.
171.5	NFLD 7022	842	100			1000 x 100	50 x 25	165 x 12	+	S	sp.
171.5	NFLD 7020	854	100			500 x 120	80 x 25	130 x 25	abs.	S	sp.
171.7	NFLD 8105	724	82	18		300 x 100	50 x 25	60 x 30	8	T 60 x 40	sp.
171.7	NFLD 8113	725	100			730 x 130	70 x 20	130 x 20	+	S	sp.
171.7	NFLD 8048	720	100			600 x 120	70 x 30	100 x 20	29	S	sp.
172.1	NFLD 1176	816	50	50		1200 x 100	80 x 40	150 x 40	+	T 50 x 35	a
173.2	NFLD 968	799	92	8		1000 x 100	90 x 20	120 x 20	15	T 65 x 30	a

Station/ Date Number	Herbarium	A.W. Annot. No.	P.D.W.B.A.C. 2	3	4	Axial Cell µm	Whorl Branchlet Basal Cell µm	Whorl Branchlet Longest Cell µm	Gland Cell %	Reproductive Structures	Original Identification
173.2	NFLD 1198	801	50	50		900 x 80	100 x 30	180 x 30	+	T 60 x 40	a
173.3	NFLD 6496	727	57	43		850 x 120	120 x 50	150 x 60	+	C	sp.
174.2	NFLD 4168	762	100			200 x 35	80 x 10	100 x 10	3	S	b
176.1	NFLD 6721	849	48	52		500 x 100	60 x 30	100 x 25	+	S	sp.
178.1	NFLD 7258	708		100		800 x 100	80 x 40	100 x 40	+	T 50 x 35	sp.
179.1	NFLD 7256	706		50	50	300 x 90	65 x 20	75 x 15	4	S	sp.
181.1	NFLD 7015	808	8	92		250 x 100	60 x 20	90 x 20	10	T 64 x 45	a
182.1	NFLD 7260	709		50	50	950 x 120	100 x 40	140 x 40	5	T 80 x 40	sp.
184.1	NFLD 7259	710	100			420 x 40	50 x 15	100 x 12	+	T 48 x 40	sp.
202.1	CANA 9174	903	100						+		f
202.1	CANA 9175	904	100						+		f
204.2	CANA 8769	905	100								a
205.1	CANA 9172	906									a
206.1	CANA 4163	907									b
207.1	NY	307	100			300 x 50	20 x 10	60 x 6	+	S	b
208.1	NY	308	50	50		350 x 90	60 x 20	80 x 20	8	S	b
208.1	CANA 4165	908									b
209.1	CANA 4164	909	92	8							b
210.1	NY	306	57	43		600 x 40	60 x 20	100 x 30	18	S	b

Station/ Date Number	Herbarium	A.W. Annot. No.	P.D.W.B.A.C. 2 3 4	Axial Cell µm	Whorl Branchlet Basal Cell µm	Whorl Branchlet Longest Cell µm	Gland Cell %	Reproductive Structures	Original Identification
211.1	CANA 4053	910	100	400 x 100	60 x 18	80 x 20	2	S	b
212.1	NY	303	100	400 x 80	45 x 12	90 x 18	4	S	b
212.2	CANA 4047	911	100	450 x 120	80 x 25	120 x 30	6	S	b
213.1	NY	302							b
214.1	NY	317	92 8	500 x 80	60 x 24	100 x 24	6	S	b
215.1	NY	305	100	240 x 60	28 x 12	50 x 16	8	C	bc
216.1	NY	318	77 23	700 x 80	50 x 20	72 x 12	10	T 70 x 48	b
241.1	NFLD	900	40 60	400 x 70	50 x 15	120 x 15	7	S	sp.
241.1	NFLD	901	62 38	230 x 70	80 x 20	110 x 25	4	T Dev.	sp.
242.1	NFLD	902	39 61	600 x 80	55 x 30	130 x 22	5	S	sp.
250.2	C	819	15 85	600 x 100	40 x 24	100 x 40	3	T 60 x 40	pl
251.1	C	818	34 66	500 x 110	40 x 16	80 x 25	19	T 60 x 40	pl
262.1	NY	314	100	350 x 50	40 x 12	104 x 14	3	S	b
263.1	NY	304	100	400 x 80	40 x 8	120 x 16	+	T 60 x 32	b
265.2	NY	313	100	800 x 90	90 x 20	160 x 20	+	T Dev.	b
269.1	C	817b	82 18	1000 x 90	150 x 60	200 x 50	5	S	bc
269.3	C	817a	55 45	1000 x 150	100 x 50	210 x 50	7	S	bc

APPENDIX IV

MORPHOLOGICAL CHANGES IN CULTURE OF VEGETATIVE APICES OF *SCAGELIA PYLAISAEI*

The tables are in two sections, the first of Form A and the second of Form B.

i = The data prior to culture.

ii = The data obtained from the plants after 30 - 40 days in culture (ER or ES 10:16-8:500)

All dimensions are in µm

Axial cell number 30 --30th axial cell from the apical cell.

Max.W.B.Cell Ax.Cell 30 --longest cell borne on axial cell number 30.

Max.Ax.Cell --longest axial cell found in the plant.

Max.W.B.Cell Max.Ax.Cell--longest cell in the largest whorl branchlet borne on the largest axial cell.

Axial Branchlet Pattern --number of whorl branchlets: two, three or four borne on each axial cell expressed as a percentage of the total number of axial cells examined.

SECTION I

FORM A

Source of Material & Culture Medium	i = Pre-culture ii = Post-culture	Ax.Cell 30	Max.W.B.Cell Ax.Cell 30	Max.Ax.Cell	Max.W.B.Cell Max.Ax.Cell	Axial Branchlet Pattern			Form of Whorl Branchlet
						2	3	4	
St.128.12	i	180 x 35	65 x 6	1100 x 150	150 x 18	63	37		irregular
ES	ii	350 x 45	65 x 10			45	55		secund-irregular
St.158.2	i	110 x 40	40 x 12	350 x 120	130 x 30	60	40		irregular
ES	ii	250 x 32	65 x 15			26	74		secund-irregular
St.121.1	i	100 x 60	100 x 20	600 x 150	100 x 30		100		secund-irregular
ER	ii	250 x 30	50 x 12.5			33	67		secund-irregular
St.135.10	i	260 x 35	60 x 15	1200 x 100	140 x 25	46	54		pinnate
ER	ii	300 x 30	65 x 15			53	47		secund-irregular
St.133.2	i	300 x 70	120 x 40	500 x 100	150 x 30	15	85		pinnate
ER	ii	300 x 30	62 x 10			25	75		secund-irregular
St.124.14	i	160 x 60	40 x 25	400 x 100	100 x 20		72	28	pinnate--bipinnate
ER	ii	380 x 35	65 x 10			39	61		secund-irregular
St.124.12	i	170 x 70	90 x 20	680 x 130	110 x 40		92	8	pinnate
ER	ii	270 x 30	65 x 12.5			47	53		secund-irregular

SECTION I. FORM A. (CONTINUED)

Source of Material & Culture Medium	i = Pre-culture ii = Post-culture	Ax.Cell 30	Max.W.B.Cell Ax.Cell 30	Max.Ax.Cell	Max.W.B.Cell Max.Ax.Cell	Axial Branchlet Pattern			Form of Whorl Branchlet
						2	3	4	
St.122.1	i	400 x 80	90 x 20	750 x 140	100 x 35	46	54		irregular-pinnate
ER	ii	360 x 50	77 x 11			17	83		secund-irregular
St.135.8	i	150 x 40	60 x 20	400 x 100	90 x 25	42	58		irregular-pinnate
ER	ii	250 x 30	70 x 15			42	58		secund-irregular
St.124,19	i	160 x 80	70 x 25	450 x 100	80 x 20	64	36		pinnate-bipinnate
ER	ii	250 x 25	62 x 8.7			36	64		secund-irregular
St.124.8	i	620 x 90	100 x 20	700 x 100	120 x 20	56	44		irregular-pinnate
ER	ii	260 x 40	50 x 7.5			28	72		secund-irregular
St.128.7	i	400 x 100	120 x 50	1250 x 150	150 x 70		68	32	pinnate-bipinnate
ER	ii	190 x 30	50 x 12.5			34	66		secund-irregular
St.124.7	i	140 x 50	120 x 20	320 x 70	120 x 20	58	42		irregular-pinnate
ER	ii	210 x 32	86 x 12.5			27	73		secund-irregular
St.133.2	i	500 x 100	100 x 60	1100 x 120	100 x 60		58	48	pinnate-bipinnate
ER	ii	250 x 35	75 x 10			15	85		secund-irregular

SECTION I. FORM A. (CONT.)

Source of Material & Culture Medium	i = Pre-culture ii = Post-culture	Ax.Cell 30	Max.W.B.Cell Ax.Cell 30	Max.Ax.Cell	Max.W.B.Cell Max.Ax.Cell	Axial Branchlet Pattern			Form of Whorl Branchlet
						2	3	4	
St.124.25	i	400 x 100	90 x 15	850 x 100	150 x 20	76	24		irregular
ES	ii	190 x 25	65 x 15			19	81		secund-irregular
St.124.4	i	110 x 50	20 x 10	580 x 160	80 x 50		100		pinnate
ER	ii	235 x 40	55 x 10			28	72		secund-irregular
St.124.24	i	150 x 60	60 x 20	680 x 160	80 x 50	16	84		pinnate
ES	ii	360 x 35	50 x 2.5			51	49		secund-irregular
St.124.24	i	350 x 50	100 x 8	800 x 100	180 x 10	93	7		irregular
ES	ii	225 x 25	55 x 10			15	80		secund-irregular
St.124.24	i	120 x 40	30 x 20	720 x 80	160 x 40	28	72		pinnate
ES	ii	266 x 32	62 x 12.5			35	63		secund-irregular

SECTION II

FORM B

Source of Material & Culture Medium	i = Pre-culture ii = Post-culture	Ax.Cell 30	Max.W.B.Cell Ax.Cell 30	Max.Ax.Cell	Max.W.B.Cell Max.Ax.Cell	Axial Branchlet Pattern			Form of Whorl Branchlet
						2	3	4	
St.104.13	i	150 x 40	80 x 25	450 x 80	100 x 25	90	10		secund-irregular
ES	ii	350 x 40	75 x 7.5			100			simple-secund
St.102.1	i	180 x 35	80 x 20	350 x 60	90 x 18	94	6		secund-irregular
ES	ii	260 x 35	87 x 7.5			100			simple-secund
St.104.15	i	220 x 18	80 x 10	750 x 50	120 x 10	100			secund-irregular
ES	ii	180 x 30	82 x 7.5			100			simple-secund
St.104.10	i	160 x 85	80 x 50	780 x 150	160 x 80	94	6		pinnate
ES	ii	300 x 20	112 x 8.2			100			simple-secund
St.104.10	i	100 x 65	50 x 25	1200 x 150	150 x 70	88	12		pinnate-bipinnate
ES	ii	270 x 30	112 x 10			100			simple-secund
St.171.4	i	70 x 30	50 x 18	500 x 110	80 x 28	100			pinnate
ER	ii	260 x 35	95 x 10			100			simple-secund
St.104.5	i	160 x 40	140 x 20	860 x 160	140 x 20	100			irregular
ER	ii	300 x 40	87 x 10			100			simple-secund

SECTION II. FORM B. (CONTINUED)

Source of Material & Culture Medium	i = Pre-culture ii = Post-culture	Ax.Cell 30	Max.W.B.Cell Ax.Cell 30	Max.Ax.Cell	Max.W.B.Cell Max.Ax.Cell	Axial Branchlet Pattern			Form of Whorl Branchlet
						2	3	4	
St.112.1	i	120 x 25	100 x 10	500 x 80	110 x 10	100			irregular
ES	ii	300 x 40	105 x 10			100			simple-secund
St.101.2	i	70 x 50	70 x 20	550 x 90	120 x 20	95	5		pinnate
ES	ii	270 x 30	100 x 7.5			100			simple-secund
St.101.2	i	80 x 30	50 x 20	650 x 80	100 x 15	100			irregular
ES	ii	260 x 30	85 x 10			100			simple-secund
St.101.2	i	300 x 45	120 x 20	900 x 150	120 x 18	100			pinnate
ES	ii	350 x 35	112 x 10			100			simple-secund
St.104.11	i	140 x 60	80 x 50	850 x 160	140 x 70	84	16		pinnate
ER	ii	300 x 35	100 x 7.5			100			simple-secund