LIFE-HISTORY STUDIES ON RHODOPHYCEAE I. ACROSYMPHYTON PURPURIFERUM (J. AG.) KYL.

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SUMMARY

The life-history of *Acrosymphyton purpuriferum* from the Mediterranean is heteromorphic diplohaplontic. Carpospores grew into creeping plants much resembling the species *Hymenoclonium serpens* (Crn.) Batt. The *Hymenoclonium* phase produced tetrahedral tetrasporangia the tetraspores of which grew into *Acrosymphyton* gametophytes. Short day conditions induced the formation of the tetrasporangia. The *Hymenoclonium* phase could reproduce itself vegetatively by 4-celled structures resembling seriate tetrasporangia. The induction of these structures did not show any relationship to temperature or daylength.

1. INTRODUCTION

MAGNE's (1964) critical studies on the caryology of a number of *Florideophycidae*, in which studies he profoundly shattered the general belief in the existence of haplobiontic *Rhodophyceae*, considerably stimulated the interest in life-history studies in this group of algae. A number of authors have succeeded in demonstrating, by culture studies, the existence of diminutive tetrasporophytes in the life-histories of *Florideophycidae* until recently considered haplobiontic (VON STOSCH 1965, for *Liagora farinosa*; UMEZAKI 1967, for *Nemalion vermiculare*; FRIES 1967, for *Nemalion multifidum*; RAMUS 1968, for *Pseudogloiophloea conferta*; BOILLOT 1968, 1969, for *Scinaia furcellata*; DIXON & RICHARDSON 1969, for *Thuretellopsis peggiana*). However, the existence of strongly heteromorphic diplohaplontic *Florideophycidae* had already been demonstrated several decades ago with the discovery, in cultures, of small tetrasporophytes in the life-histories of *Halarachnion ligulatum* (DAMMANN 1930, later confirmed by BOILLOT 1965), and *Bonnemaisonia asparagoides* and *Asparagopsis armata* (J. & G. FELDMANN 1942).

MAGNE (1967) demonstrated for six *Lemanea* species, that meiosis takes place in the apical cell of the young *Lemanea* plant budding from a creeping basal system. According to BOILLOT (1968) the carpospores of *Naccaria wiggii* and *Atractophora hypnoides* grow into filamentous germlings, from which new gametophytes arise directly, and she suspects that meiosis takes place in the same site as in *Lemanea*.

There still remain a number of *Florideophycidae* for which only gametophyte phases are known, and which might be expected to have tetrasporophytic phases in their life-histories.

The recent discovery of (KUROGI *et al.* 1962) and critical investigations on (DRING 1967; RENTSCHLER 1967) the short day induction of the formation of

conchospores in the *Conchocelis* phase of *Porphyra tenera*, has stimulated research on the possible existence of short day and long day effects in other *Rhodophyceae*. EEST (1967, 1968, 1969) described the induction of the development of tetrasporangia under short day conditions in *Rhodochorton purpureum*. *Rhodochorton tenue* and *Acrochaetium pectinatum*.

For a recent review, see MARTIN (1969).

At the Department of Systematic Botany of the University of Groningen we are investigating at present a number of Rhodophycean life-histories and the effect of daylength and temperature on some of these life-histories.

One of the species under investigation is *Acrosymphyton purpuriferum* (J. Ag.) Kyl. (*Cryptonemiales, Dumontiaceae*) of which previously only gametophytic plants were known.

2. MATERIAL AND METHODS

Acrosymphyton purpuriferum plants, bearing carpospores, were collected by an aqualung diver from a depth of 20–25 m near Cap-Béar (Banyuls, Pyrénées Orientales, France) on 12 September 1967. Unialgal cultures were started from vegetative fragments of gametophytes as well as from carpospores.

To obtain vegetative isolates ten small fragments, consisting of determinate laterals, were drawn through the surface of a sterilised 3% seawater-agar plate to remove contaminating algae. Each fragment was cultured separately in a slanted culture tube containing 10 ml of a modified Erdschreiber-medium. Vegetative isolates were cultured firstly to get an insight into the regenerative capacity of adult differentiated tissues; secondly, if it proved possible to obtain regenerated gametophytes from vegetative isolates, to have available culture-grown gametophytes for comparison with presumed gametophytes obtained from tetraspores in culture. For, as a rough generalisation, it can be stated that the more complicated an alga is, the more dificult it is to obtain normal growth in culture. Therefore it was our aim to be able to differentiate gametophytes from sporophytes, even if the former did not differentiate in precisely the same way in culture as in nature.

Carpospores or clumps of carpospores were isolated by dissecting the gonimocarp from the gametophyte. A dissected gonimocarp was put into a drop of sterilized seawater on a slide and gently pressed with a cover-glass. The cover-glass was removed and the loosened carpospores or clumps of carpospores were picked up with a micro-pipette and cultured, each separately, in one of a series of ten culture tubes each containing 10 ml of the modified Erdschreiber-medium. The process of isolation was observed with a binocular dissecting microscope.

The culture fluid was a modified Erdschreiber-medium in which the Na_2HPO_4 concentration was kept relatively low. The composition of the Erdschreiber-medium was as follows: to 950 ml filtered seawater was added: 0.278 mg $FeSO_4$; 0.269 mg Na_2HPO_4; 42.50 mg $NaNO_3$; 0.02 mg $MnCl_2$; 3.72 mg EDTA; 5.0 mg GeO_2 (to prevent the growth of diatoms) and 50 ml forest

soil-extract. The complete medium was sterilised at 100 °C for one hour and after that filtered. The medium was kept at 4 °C.

The isolated vegetative fragments and carpospores were kept in a 17° (±1°) C culture room and exposed to a light intensity of ca 1000–1500 lux for 16 hour photoperiods daily. The light was emitted by white fluorescent tubes (Philips TL 34 and TL 33).

For the experiments the cultures were kept in deep 40 ml petri dishes each containing 20 ml culture fluid; this permitted observation with the binocular dissecting microscope or a high power microscope (water immersion).

The isolates used for the investigation of the influence of daylength and temperature on their morphogenesis were subjected to the following experimental conditions which were intended to simulate the succession of the seasons. However, in our experiments "summer" (17 °C long day conditions) suddenly changed to "winter" (12 °C short day or 4 °C short day) and vice versa without intermediate "autumn" or "spring" conditions. "Short day" corresponds to 8 hour photoperiods daily, "long day" to 16 hour photoperiods daily.

Seven petri dishes were kept at 4 °C short day for twenty weeks after which 5 were transferred to 17 °C long day and 2 stayed at 4 °C short day. 2 petri dishes were kept continuously at 4 °C long day.

Seven petri dishes were kept at 12 °C short day. After 20 weeks 5 of these were transferred to 17 °C long day and 2 stayed at 12 °C short day. 2 petri dishes were kept continuously at 12 °C long day.

Twelve petri dishes were kept at 17 °C long day. After 20 weeks 5 of these were transferred to 12 °C short day, 5 to 4 °C short day and 2 stayed at 17 °C long day.

Different light intensities were obtained by varying the distance between the TL tube and the culture vessel or by covering the culture vessels with one or more layers of white filter-paper. The light intensities were measured with an AEG lux-meter. The values given are intensities of the light falling on the surfaces of the deep petri dishes or the culture tubes.

All cultures kept at 17 °C where given new medium once every 4 weeks. The 12 °C and 4 °C cultures were given new medium once every 8 weeks.

3. RESULTS

3.1. Hymenoclonium-like plants grown from carpospores

After about three months under 17 °C long day conditions the carpospores of *Acrosymphyton* had grown into creeping plants 3–4 mm in diameter. The morphology of this creeping stage appeared to closely resemble that of *Hymenoclonium serpens* (Crn.) Batt. (*figs. 1–5, 24*). It will be referred to in the next pages as the *Hymenoclonium* phase of *Acrosymphyton.*

3.2. The effects of different combinations of temperature and daylength on the Hymenoclonium phase

Because the *Hymenoclonium* phase grew firmly attached to the glass of the

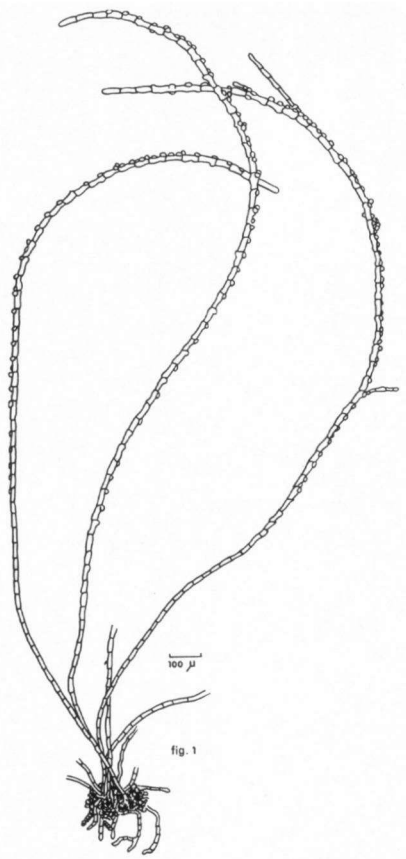


Fig. 1. *Hymenoclonium* phase grown from carpospores in about three months. The erect filaments arising from the creeping system are morphologically similar to the main filaments of the creeping system. The lenticular cells cut off from the cells of the erect filaments grow into lateral creeping branch-systems when they are in contact with the substrate (see *fig.* 2).

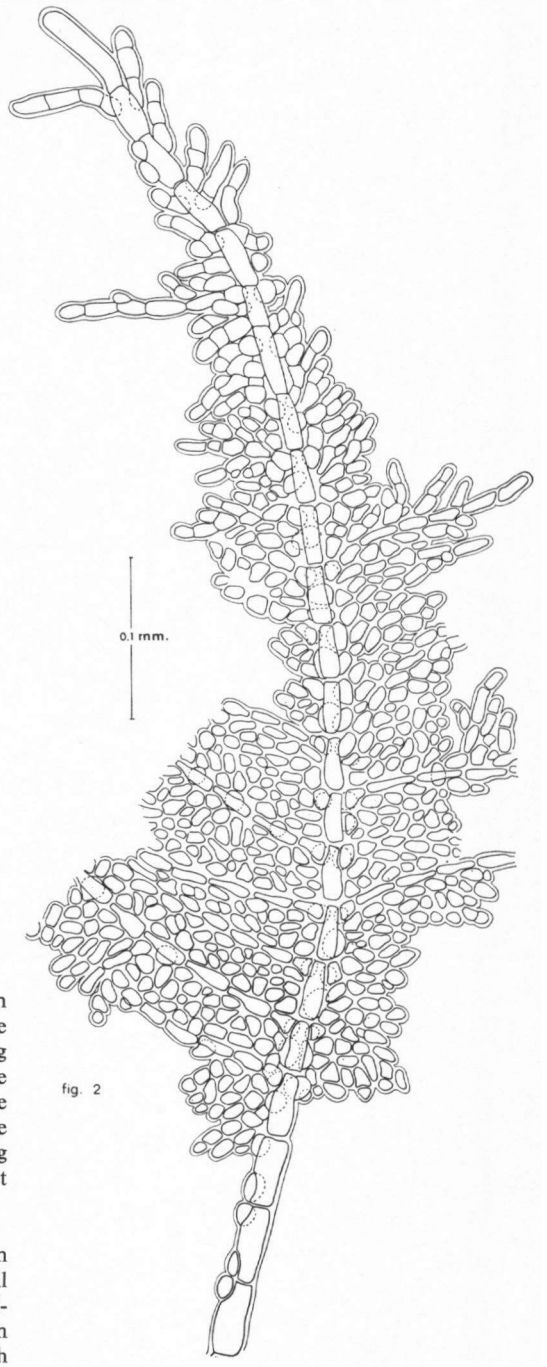
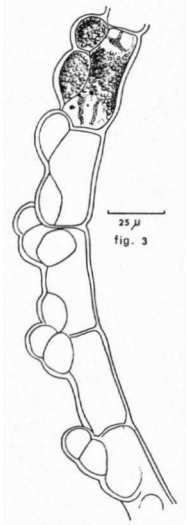
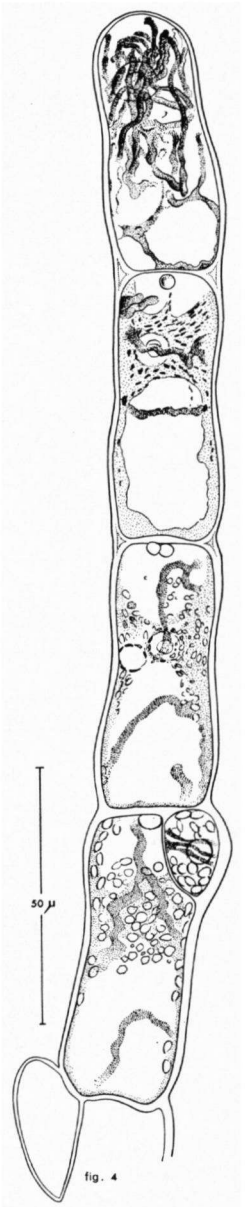


Fig. 2. *Hymenoclonium* phase grown from carpospores in about three months. Detail of the creeping sytem. Note that the lenticular cells cut off from the cells of the main filament grow into lateral creeping branch systems.





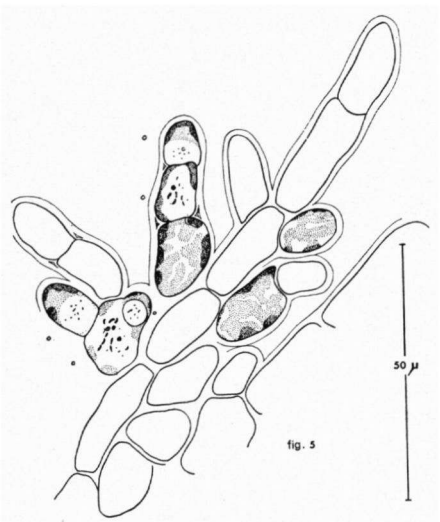


Fig. 3. *Hymenoclonium* phase. Detail of erect filament with lenticular cells. Note the parietal reticulate chromatophore and the numerous grains of floridean starch in one of the cells.

Fig. 4. *Hymenoclonium* phase. Detail of erect filament with apical cell, in which the nucleus is visible in vivo. Note the narrow strap-shaped and branched chromatophores.

Fig. 5. *Hymenoclonium* phase. Detail of creeping system. Note the parietal reticulate chromatophores.

culture tubes, the tubes were crushed and small fragments of glass with *Hymenoclonium* growing attached to them were used for testing the influence of daylength and temperature.

3.2.1. All *Hymenoclonium* plants cultured at 4 °C under short day as well as under long day conditions died after several weeks. This is in accordance with the southern distribution of *Acrosymphyton purpuriferum*. In relation to this observation it is interesting to note that isolates of *Nemalion helminthoides* from Banyuls grew very well at 4 °C.

3.2.2. Three months after the start of the experiment one of the seven petri dishes kept at 12 °C short day conditions contained a young 1.7 mm high *Acrosymphyton* plant. Apart from this plant it contained the original *Hymenoclonium* plant and about 40 young *Hymenoclonium* plants (about 0.5–1 mm in diameter). Evidently some sort of dissemination had taken place. It is curious that only one of the seven petri dishes kept at 12 °C short day conditions showed unmistakable evidence of dissemination, resulting in the formation of predominantly new *Hymenoclonium* plants and only one *Acrosymphyton* plant.

3.2.3. Three months after the start of the experiment the *Hymenoclonium* plants kept under 17 °C long day conditions showed only vegetative growth.

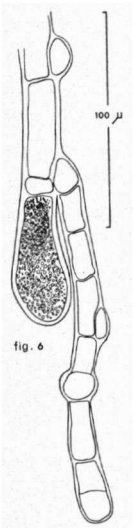
3.2.4. Twenty weeks after the experiment started a number of petri dishes were transferred to other combinations of temperature and daylength (see 2, material and methods).

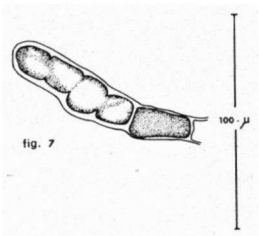
Three months after this transfer two of the five petri dishes coming from 17 °C long day conditions and now kept at 12 °C short day conditions contained young *Acrosymphyton* plants. One of these two contained the original *Hymenoclonium* plant plus four young *Acrosymphyton* plants 6, 6, 1 and 2.5 mm high respectively (*figs. 16–19*). The second of these two petri dishes contained only the original *Hymenoclonium* plant plus one young *Acrosymphyton* plant 3 mm high. Seven months after the transfer to 12 °C short day conditions *Acrosymphyton* plants appeared in two more of the five petri dishes together with young *Hymenoclonium* plants. *Acrosymphyton* plants never arose from *Hymenoclonium* plants but always had their own few-celled bases (*figs. 16, 19, 20*).

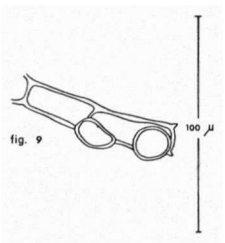
Neither the five petri dishes transferred from 12 °C short day to 17 °C long day nor the two petri dishes continuously kept at 12 °C long day showed any dissemination.

3.3. The influence of aeration on the Hymenoclonium phase

3.3.1. To test the possible effect of aeration on the *Hymenoclonium* phase five 500 ml erlenmeyers containing each one glass fragment with a *Hymenoclonium* plant growing attached to it were kept under 17 °C long day conditions while the culture fluid was aerated. During this experiment the light intensity was ca 400 lux. Three weeks after the onset of aeration young *Hymenoclonium*







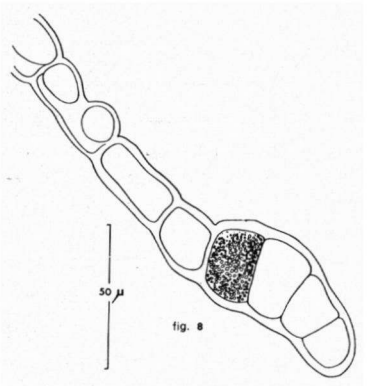


Fig. 6. *Hymenoclonium* phase. Initial of "seriate tetrasporangium".
Fig. 7. *Hymenoclonium* phase. Young "seriate tetrasporangium". Four "spores" not yet fully differentiated.
Fig. 8. *Hymenoclonium* phase. "Seriate tetrasporangium".
Fig. 9. *Hymenoclonium* phase. Collar-like structure terminating upright filament. Probably the remnant of a broken-off "seriate tetrasporangium".

germlings appeared. One of the five erlenmeyers, for instance, contained at that time ca 100 young *Hymenoclonium* plants (ca 0.5–3 mm in diameter); the other four erlenmeyers contained comparable numbers of *Hymenoclonium* offspring. Structures resembling seriate tetrasporangia were observed (*figs. 6–8, 25, 26*). However, no empty seriate tetrasporangium was ever seen. Frequently observed collar-like structures terminating upright filaments (*fig. 9*) suggested that these four-celled structures could break off and function as propagula. At this stage the original *Hymenoclonium* plant on the glass fragment was removed and the aeration was stopped. The new generation not only continued to grow vegetatively but also to produce increasing numbers of *Hymenoclonium* offspring so that the first mentioned erlenmeyer, five weeks after the start of the experiment, contained ca 300 young *Hymenoclonium* plants (1–3.5 mm in diameter). Among the numerous young *Hymenoclonium* plants not one single *Acrosymphyton* plant was observed. These observations made it plausible that the young *Hymenoclonium* generation arose from the above mentioned four-celled structures resembling seriate tetrasporangia. We did not succeed in observing whether each of the four cells or the undivided structure developed into a new *Hymenoclonium* plant.

3.3.2. Since aeration evidently stimulated growth and dissemination of *Hymenoclonium*, aeration of cultures kept at 12 °C short day conditons was

started in an attempt to obtain a more numerous *Acrosymphyton* offspring from the *Hymenoclonium* phase. The cultures were kept at a light intensity of 2000 lux. In five 30 ml deep petri dishes each containing a glass fragment with a *Hymenoclonium* plant growing attached to it the culture fluid was aerated. Two months after the start of the experiment a vigorous dissemination was observed. For instance in one of the culture vessels the young generation consisted of ca 35 young *Acrosymphyton* plants (2–10 mm high) and ca 20 young *Hymenoclonium* plants (1–5 mm in diam.).

3.4. The effect of "short day" conditions on the Hymenoclonium phase

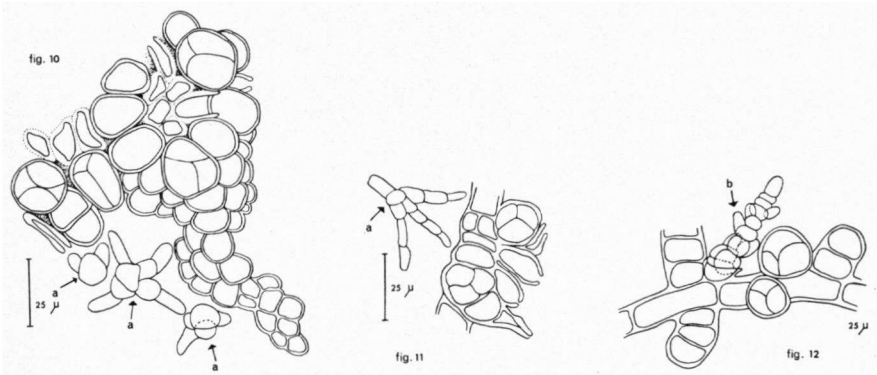
The next step was to investigate whether the relatively low temperature (12 °C) or the short day conditions, or both, induced the formation of spores, giving rise to new *Acrosymphyton* plants.

3.4.1. Into each of five 30 ml deep petri dishes with 20 ml medium a glass fragment with a *Hymenoclonium* plant was placed. The culture vessels were kept under 17 °C short day conditions while the light intensity was 3000 lux. After 6 weeks all cultures contained young *Acrosymphyton* plants (*fig. 21*) as well as young *Hymenoclonium* plants. One of the culture vessels contained ca 20 young *Acrosymphyton* plants (1–8 mm high) and ca 50 young *Hymenoclonium* plants (ca 1–3 mm in diam.). The other culture vessels contained comparable numbers of *Acrosymphyton* and *Hymenoclonium* offspring. A further examination of the young *Hymenoclonium* plants revealed tetrahedral tetrasporangia (*figs. 10–12*). These tetrahedral tetrasporangia were arranged in a cell layer on top of the creeping basal system or laterally inserted on upright filaments. Empty tetrasporangia were also seen. Dense swarms of few-celled *Acrosymphyton* germlings were regularly observed around *Hymenoclonium* discs bearing numerous empty tetrasporangia. In one case an *Acrosymphyton* germling was seen growing in an empty tetrasporangium (*fig. 12*). These results make it extremely likely that young *Acrosymphyton* plants grow from tetraspores formed in tetrahedral tetrasporangia; and that the formation of tetrahedral tetrasporangia is induced by short day conditions.

3.4.2. Five 30 ml deep petri dishes each containing 20 ml culture fluid and a *Hymenoclonium* plant on a glass fragment were kept at 12 °C long day conditions under a light intensity of 1700 lux. The culture fluid was aerated. After 4 months the young generation consisting of only *Hymenoclonium* plants (1–6 mm in diam.) was observed. This observation confirms the conclusion that the factor inducing the appearence of *Acrosymphyton* plants is the short daylength, and not the low temperature.

3.5. The influence of different light intensities on the Hymenoclonium phase

The influence of different light intensities on the *Hymenoclonium* plants was



Figs. 10–12. *Hymenoclonium* phase. Plants grown under 17 °C short day conditions. Details showing tetrahedral tetrasporangia, germlings of the *Acrosymphyton* phase (arrows a), and one young plant of the *Acrosymphyton* phase grown from a tetraspore in its tetrasporangium (arrow b).

tested under 12 °C short day and 17 °C long day conditions. Glass fragments with *Hymenoclonium* plants growing attached to them were kept in 20 ml culture tubes containing 10 ml culture fluid. Five culture tubes were exposed to each of the following light intensities:

12 °C short day	17 °C long day
4700 lux	4400 lux
1200 lux	1400 lux
600 lux	600 lux
65 lux	55 lux
15 lux	10 lux

Light intensities less than 100 lux inhibited growth and dissemination. In the range from 600–4700 lux increased light intensity stimulated growth and dissemination. Under 17 °C long day conditions only *Hymenoclonium* offspring was obtained. Under 12 °C short day conditions *Acrosymphyton* (*fig. 20*) as well as new *Hymenoclonium* plants developed in all culture tubes exposed to a light intensity higher than 600 lux. These results indicate that the inhibition of the formation of *Acrosymphyton* plants under 12 °C long day and 17 °C long day conditions cannot be ascribed to an excess of light given to the cultures.

3.6. Vegetative isolates

After about three months the vegetative isolates of *Acrosymphyton* had grown into pale red, almost colourless, pompons up to 1 cm in diameter. These pompons, which did not show any resemblance to normal *Acrosymphyton* plants, consisted of indeterminate systems of branched hypha-like filaments (*figs. 13–15*). The cells contained narrow and pale chromatophores. In the original isolates the hypha-like filaments appeared to arise from cells of the determinate

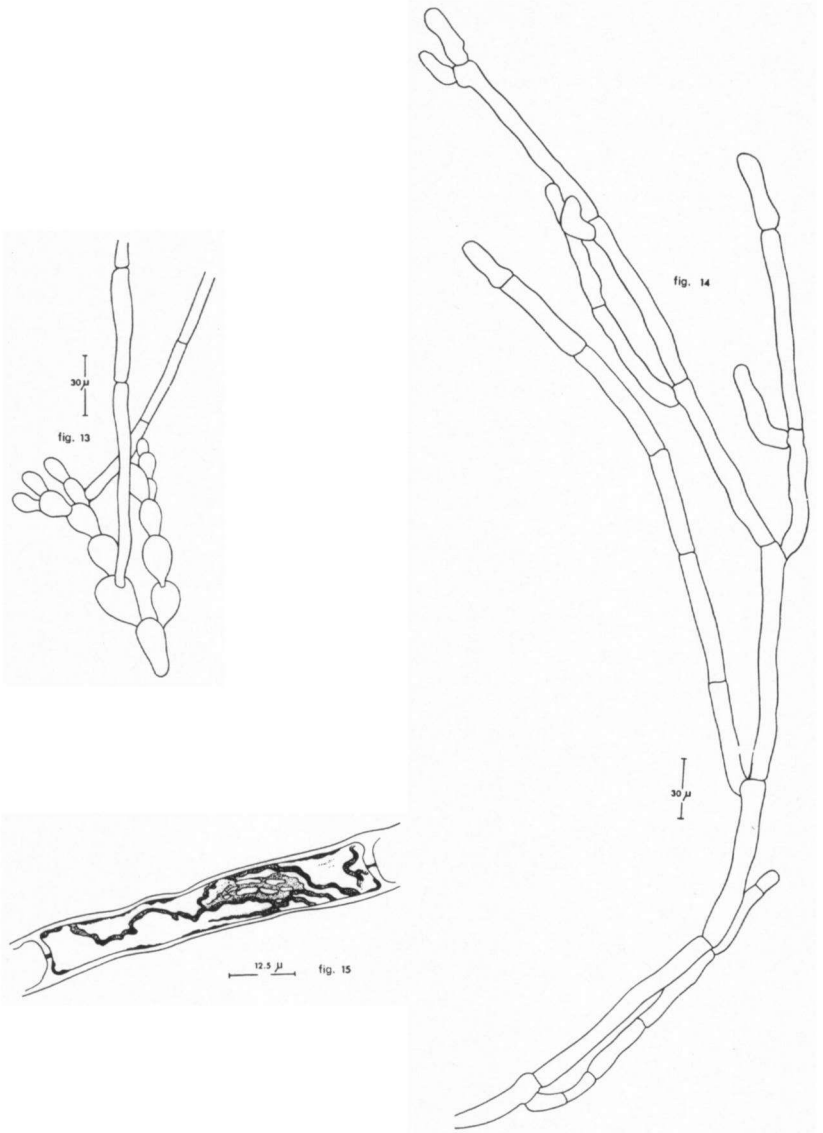
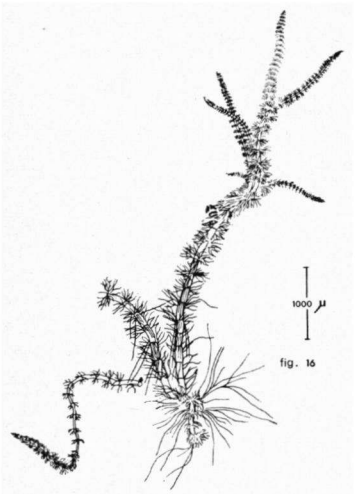
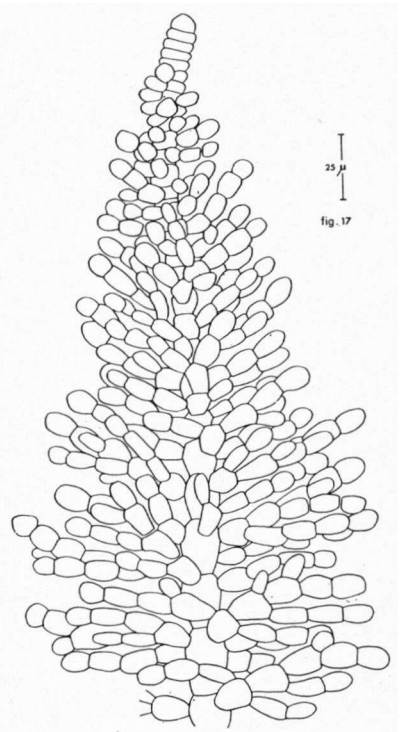


Fig. 13. Vegetative isolate from *Acrosymphyton* phase. Hypha-like filaments arising from cells of determinate laterals.
Fig. 14. Vegetative isolate from *Acrosymphyton* phase. Apical region of hypha-like filaments.
Fig. 15. Vegetative isolate from *Acrosymphyton* phase. Detail. Note narrow strap-shaped branched chromatophore (these chromatophores have a pale red colour).





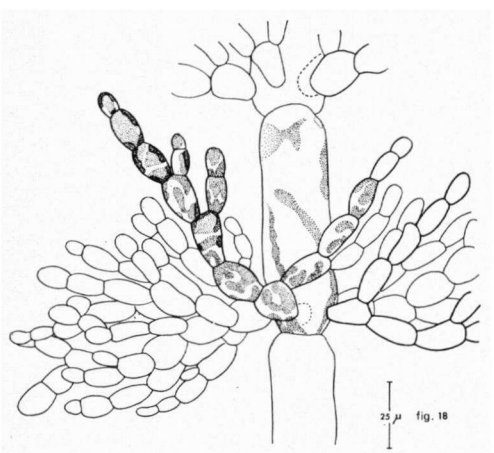


Fig. 16. Four young *Acrosymphyton* plants grown in a *Hymenoclonium* culture kept under 12 °C short day conditions during three months.
Fig. 17. Apical part of young *Acrosymphyton* plant pictured in *fig.* 16.
Fig. 18. Intercalary part of young *Acrosymphyton* plant pictured in *fig.* 16.

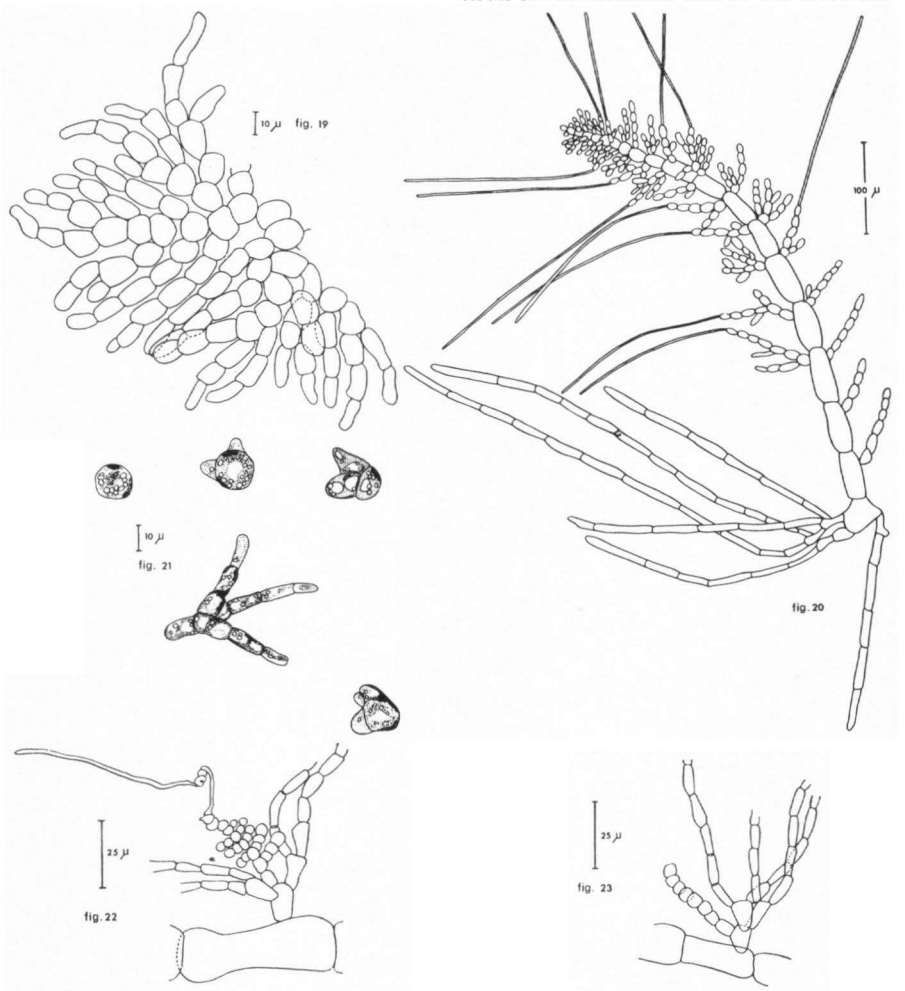


Fig. 19. Basal creeping system of *Acrosymphyton* plant. Note the differences with the *Hymenoclonium* phase (*figs.* 1–5): its loose structure (*Hymenoclonium* is very rigid and compact and strongly adheres to glass); its single ramifications (in *Hymenoclonium* several laterals can arise from the apical as well as the basal poles of the cells composing the main filaments); and the absence of lenticular cells (the characteristic initials of the lateral creeping branch-systems in *Hymenoclonium*). In fact the basal creeping system consists of one to several specialised determinate laterals.

Fig. 20. Young *Acrosymphyton* plant grown in a *Hymenoclonium* culture kept under 12 °C short day conditions and relatively high light intensity (ca 4700 lux) during three months. Note the loose structure of the basal creeping system consisting of three determinate laterals. The determinate laterals of the erect system are often terminated by long colourless hairs.

Fig. 21. Germlings of the *Acrosymphyton* phase obtained under 17 °C short day conditions.

Fig. 22. *Acrosymphyton* plant grown in culture. Carpogonial branch system (fertile *Acrosymphyton* plants were obtained under 17 °C long day conditions).

Fig. 23. *Acrosymphyton* plant grown in culture. Auxiliary cell branch.

laterals (*fig. 13*). In fact they are quite similar to the downward growing hyphae of *Acrosymphyton* plants. After a year no change in the morphology could be observed. However, in about two years old cultures of vegetative isolates several young *Acrosymphyton* plants were observed to arise from places where hyphae had contacted the wall of a culture tube. These *Acrosymphyton* plants were attached by small organized basal creeping systems. Since we succeeded in obtaining normal *Acrosymphyton* plants from tetraspores we did not subject the vegetative isolates to further experiments.

3.7. Acrosymphyton plants from tetraspores

In several experiments under short day conditions young *Acrosymphyton* plants arose from tetraspores. When the plants were young they were still fully organised, showing the typical *Acrosymphyton* morphology (*figs. 16–20, 24a, 27–29*) (for a description see KYLIN 1956). When a plant grew older the determinate laterals gave rise to downward-growing hyphae which formed a dense covering around the central axis. After being cultured several weeks under 17 °C long day conditions the excessive development of the hyphae dominated apical growth and this resulted in the formation of rather disorganized pale red pompon-like *Acrosymphyton* plants. These disorganized *Acrosymphyton* plants resembled the pompons grown from vegetative isolates of the original *Acrosymphyton* plants (*cf.* 3.6.).

After being cultured for two months under 17 °C long day conditions several *Acrosymphyton* plants bore carpogonial branches with carpogonia and trichogynes and auxiliary cell branches in the still fully organised apical regions of the plants (*figs. 22, 23*). For a description of the development of the gonimocarp see KYLIN (1956), OLTMANNS (1922), and FELDMANN (1942). A new *Hymenoclonium* generation could be isolated. So we succeeded in following the life-history of *Acrosymphyton purpuriferum* in culture from carpospore, via tetrasporophyte, tetraspores, and new gametophytes up to a second generation of tetrasporophytes.

4. CONCLUSIONS AND DISCUSSION

A carpospore of *Acrosymphyton purpuriferum* grows into a tetrasporophyte which differs morphologically very much from the gametophyte and which resembles the species *Hymenoclonium serpens* (Crn.) Batt. (*figs. 1–5, 24*). The tetrasporophyte is therefore very similar to the *Hymenoclonium* phase of *Bonnemaisonia asparagoides* (J. & G. FELDMANN 1942; G. FELDMANN 1965, 1966) and of *Ptilonia okadai* (CHIHARA 1962; *Bonnemaisoniaceae*). However, in *Bonnemaisonia asparagoides* and *Ptilonia okadai* the new gametophytes arise directly on the *Hymenoclonium* phase. Perhaps the life-histories of these two species are comparable to that of *Lemanea* (MAGNE 1967), in which species meiosis takes place in the apical cell of the young gametophyte budding from a filamentous diploid basal system. However, the *Hymenoclonium* phase of *Acrosymphyton purpuriferum* is undoubtedly a tetrasporophyte because it

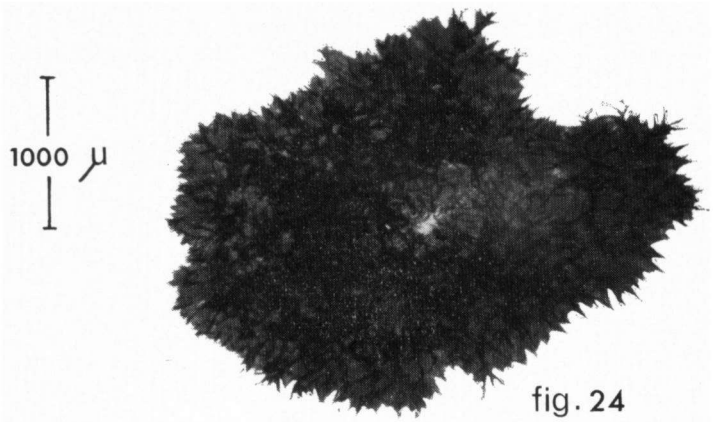
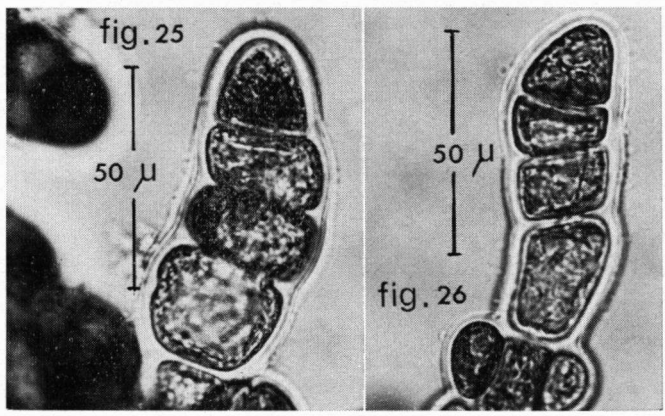


Fig. 24. *Hymenoclonium* phase. Habit of a more than one year old plant.

produces tetrahedral tetrasporangia, the tetraspores of which grow into gametophytes (*figs. 10–12*). Our experiments produced evidence for the induction of the tetrahedral tetrasporangia under short day conditions. In nature, in casu in the Mediterranean, the short day conditions would correspond to winter conditions. This means that young *Acrosymphyton* plants could be expected in nature in early spring, and that adult *Acrosymphyton* plants could be found in late spring and summer. According to FUNK (1927, 1955) and FELDMANN (1942) this is actually the case in the Mediterranean. *Hymenoclonium serpens* plants, on the other hand, could be expected the whole year round. This is also in accordance with literature data (FUNK 1927, 1955). *Hymenoclonium* plants have been collected growing epiphytically on other algae and on the sponge *Cliona* (FELDMANN 1942). It would of course be comparatively difficult to find epilithic *Hymenoclonium* plants. The Mediterranean *Hymenoclonium* plants could be part of the life-history of *Acrosymphyton purpuriferum* or that of *Bonnemaisonia asparagoides*. FUNK (1955), without comment, gives two very characteristic photographs of *Hymenoclonium*-like plants grown from *Acrosymphyton* carpospores (Tafel IX, fig. 5, 6 as "Jugendstadien" of *Acrosymphyton*). J. & G. FELDMANN (1942) give figures of tetrahedral tetrasporangia observed on *Hymenoclonium* plants collected in November.

For quite a few *Rhodophyceae* it is now known that tetrasporangia are formed in the winter half year, and gametangia in the summer half year (for a review see ETTL *et al.* 1967). WEST (1967, 1968) demonstrated for two *Rhodochorton* and one *Acrochaetium* species that the formation of the tetrasporangia was induced under short day conditions. The *Falkenbergia* phases of *Asparagopsis armata* and *Asparagopsis taxiformis* (FELDMANN, G. 1965; CHIHARA 1961; MCLACHLAN 1967) and the *Trailliella intricata* phase of *Bonnemaisonia hamifera* (KOCH 1950; CHIHARA 1961) form tetraspores in the winter half year, whereas the gametophytes are spring to summer annuals. At Helgoland the

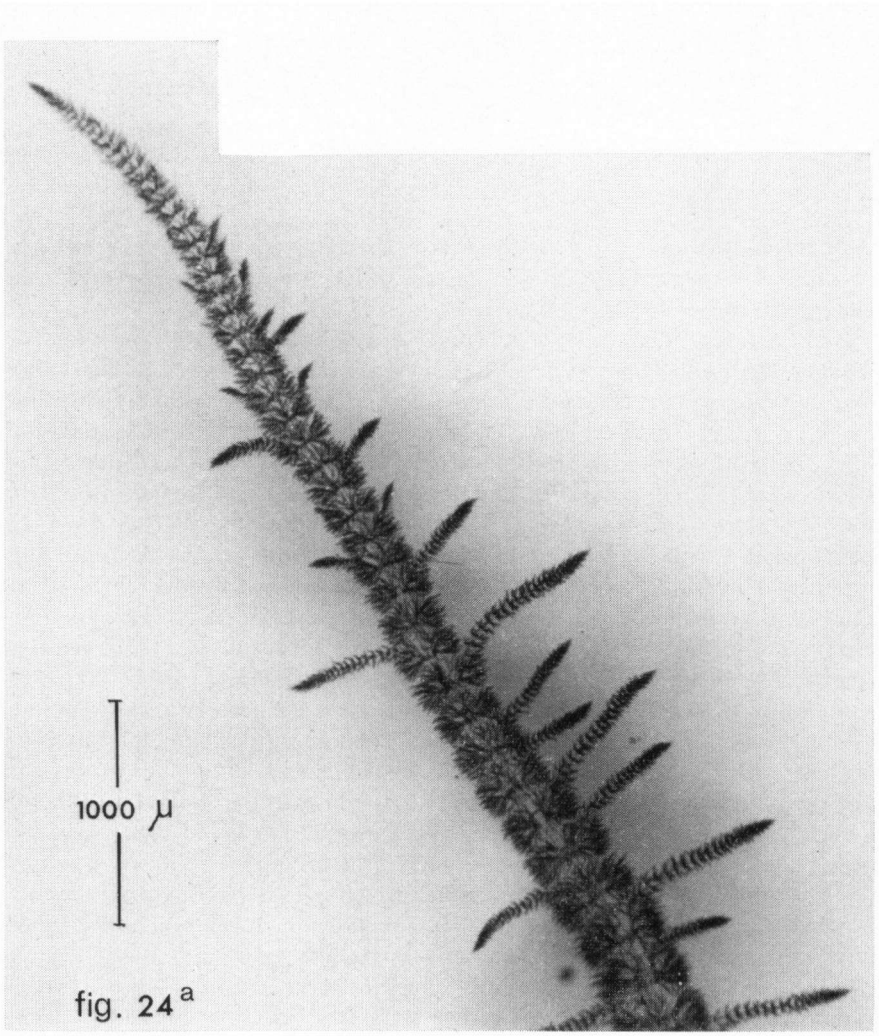


Figs. 25, 26. *Hymenoclonium* phase. "Seriate tetrasporangia".

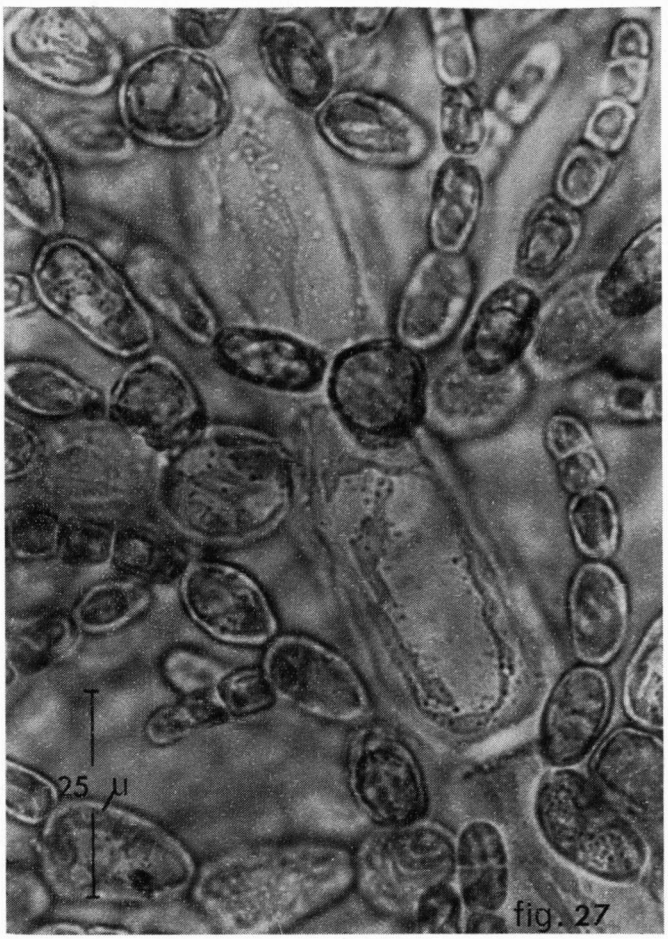
Halarachnion ligulatum gametophyte is a spring to summer annual whereas the discoid tetrasporophyte forms its seriate tetrasporangia in culture during winter (DAMMANN 1930).

The short day induction of tetrahedral tetrasporangia on the *Hymenoclonium* phase of *Acrosymphyton* does not depend on a relatively low total amount of light received by the *Hymenoclonium* plants. For, notwithstanding the fact that some *Hymenoclonium* plants grown under high light intensities and short day conditions received more illumination than some *Hymenoclonium* plants grown under low light intensities and long day conditions, the former invariably produced *Acrosymphyton* plants, and the latter not. Whether the short day induction is a true photoperiodic response analogous to the photoperiodic responses known in flowering plants remains to be investigated. WEST (1968) states that it is unlikely that typical phytochrome-mediated photoperiodic responses can function in marine algae, because in coastal waters far red light penetrates to less than 1 m and red light does not penetrate further than 10 m below the water surface. Perhaps blue light could mediate in a photoperiodic response. RENTSCHLER (1967) in testing conchospore formation in the *Conchocelis* phase of *Porphyra tenera* found that a light break of 60 minutes or less with blue light during the dark period of 16 hours inhibited the short day induction of conchospores. Here blue light was nearly as effective as red light when used for a light break. *Porphyra tenera*, a species of the upper sublittoral and the lower littoral zone, is the only red alga for which a perhaps truly photoperiodic response was found. The inhibition of conchospore formation after a light break with red light disappeared when, during the light break, red light was followed by far red light. These results suggest the mediation of a phytochrome system similar to that in flowering plants (DRING 1967). At present the short day induction of tetraspores on the *Hymenoclonium* phase of *Acrosymphyton* is the subject of further study.

Besides tetrahedral tetrasporangia the *Hymenoclonium* phase produces structures resembling seriate tetrasporangia (*figs. 6–9, 25, 26*). These structures cannot be considered real tetrasporangia because their function is the vegetative reproduction of the *Hymenoclonium* phase. The induction of these sporangia does not show any relation to the temperature or the daylength but aeration stimulates their formation. The "seriate tetrasporangia" enable the *Hymenoclonium* phase to be independent of the *Acrosymphyton* phase for its reproduction. Theoretically the *Hymenoclonium* phase could be expected to have a wider geographical distribution and to be more common than the *Acrosymphy-*



Figs. 24a, 27–29. Culture-grown *Acrosymphyton* phase; apical and intercalary parts at different magnifications.



ton phase. The tetrasporophyte of *Asparagopsis armata* (the *Falkenbergia* phase) and the tetrasporophyte of *Bonnemaisonia hamifera* (the *Trailliella* phase) do have wider geographic distributions and are more common than their corresponding gametophytes (FELDMANN 1957; DIXON 1965). But in these two cases the independent reproductive capacity of the tetrasporophytic phases has not been convincingly demonstrated.

The cytological evidence of the diploid nature of the *Hymenoclonium* phase still has to be produced and this is one of our aims for the future. It appeared to be possible to obtain normal *Acrosymphyton* plants (at least young plants) in culture (*figs. 16–23, 24a, 27–29*); this contrasts with *Nemastoma dichotoma* cultures grown from carpospores. In these cultures a normal morphology of the tetrasporophytes of *Nemastoma dichotoma* was not obtained (VAN DEN HOEK & CORTEL-BREEMAN, unpublished).

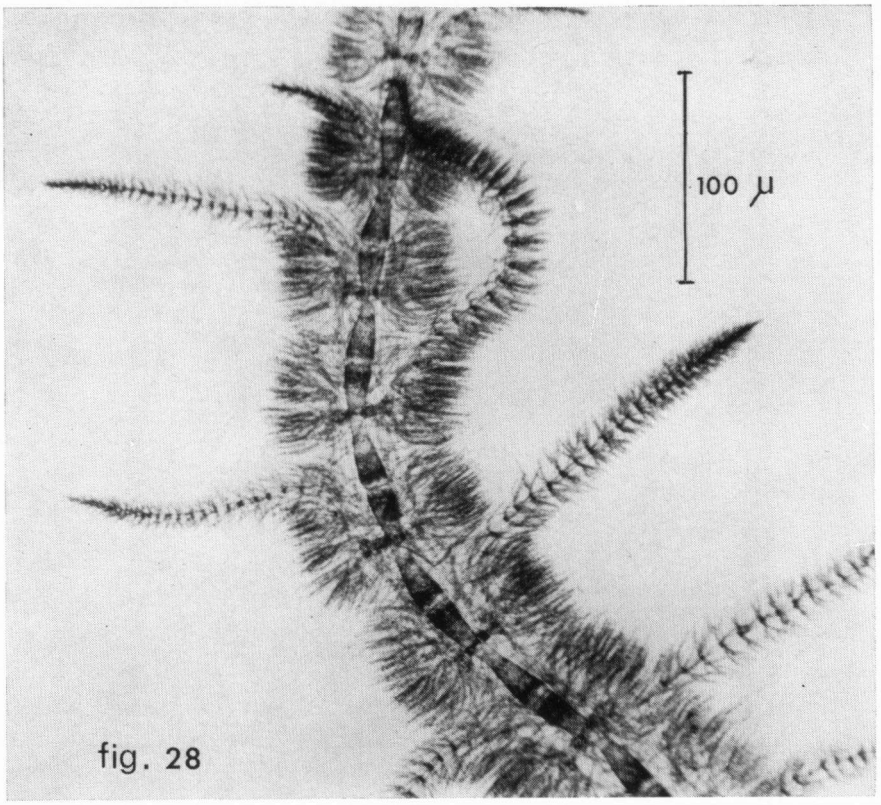


fig. 28

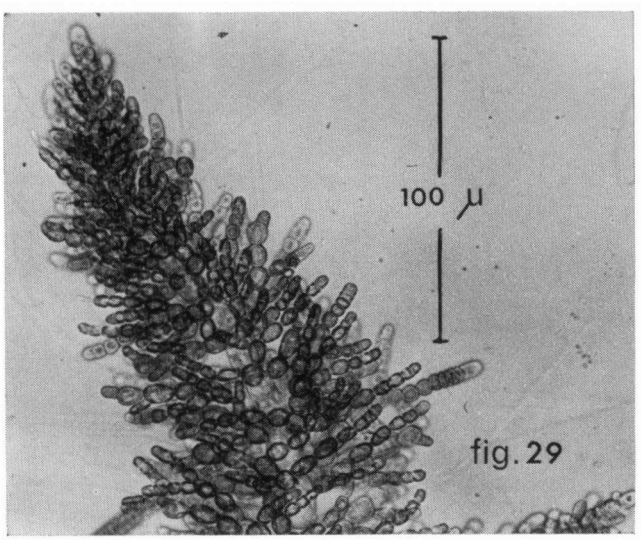


fig. 29

The vegetative isolates from *Acrosymphyton* plants had grown into pale red pompons of branched, indeterminate hyphae (*figs. 13–15*). After two years fully organized *Acrosymphyton* plants started to grow from such hyphae where these contacted the wall of a culture tube. Apparently the hyphae of the pompons had not completely lost their totipotency.

As a final conclusion we can characterise the gametophyte of *Acrosymphyton purpuriferum* as a summer annual, while the tetrasporophyte is a perennial. The tetrasporophyte is completely independent of the gametophyte for it can reproduce itself by "spores" formed during the whole year. The gametophyte completely depends for its existence on the tetrasporophyte, for it can only grow from tetraspores produced in tetrasporangia formed during the winter half year, and it lacks means of vegetative propagation.

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