LIFE-HISTORY STUDIES ON RHODOPHYCEAE III SCINAIA COMPLANATA (COLLINS) COTTON

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SUMMARY

The carpospores of *Scinaia complanata* grow into a filamentous tetrasporophytic phase, which is capable of self-reproduction. The tetraspores grow into a morphologically recognizable filamentous gametophytic stage, which is also capable of self-reproduction, and which can give rise to adult *Scinaia* thalli. Growth and reproduction of the tetrasporophyte and the gametophytic filamentous stage, as well as the development of adult *Scinaia* thalli, are furthered by 17 °C long day conditions, which roughly correspond to summer conditions in the Mediterranean.

1. INTRODUCTION

MAGNE's (1964) recent critical caryological investigations on a large number of *Rhodophyceae* shattered the widely accepted concept of haplobiontic *Rhodophyceae*, of which *Scinaia furcellata* was considered the prototype. SVEDELIUS (1915) gave evidence for the occurrence of reduction division in the zygote directly following fertilization. MAGNE (1964, pp. 600, 626), however, drew attention to the inadequacy of Svedelius's evidence, and was able to show that gonimoblast and carpospores are diploid.

Cultural investigations were still required to get a complete picture of the life-history of *Scinaia*. With this aim in mind we started, in September 1967, our investigations of the life-history of *Scinaia complanata*. In the mean time BOILLOT (1968) discovered that carpospores of *Scinaia furcellata* grew into filamentous tetrasporophytes. The tetrasporophytes produced tetraspores which developed into a filamentous protonema from which young *Scinaia* plants could arise (BOILLOT 1969). *Scinaia furcellata* belongs therefore to the group of *Rhodophyceae* with a strongly heteromorphic diplohaplontic life-history (for a more complete review, see CORTEL-BREEMAN & VAN DEN HOEK 1970).

2. MATERIAL AND METHODS

A *Scinaia complanata* plant bearing mature gonimocarps was dredged from a depth of 12 m near Cap Oullestreil, Banyuls (Pyrénées Orientales, France) in September 1967.

Unialgal cultures were started from ten vegetative cortex-fragments as well as from ten isolated carpospores.

The cultures were grown in a modified Erdschreiber-medium. They 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 cultures were kept in culture tubes containing 10 ml culture fluid, or in 300 ml Erlenmeyer flasks containing 150 ml culture fluid.

Thirty cultures grown from carpospores and kept in culture tubes were used to test the combined influence of daylength and temperature on morphogenesis and reproduction, according to the standard methods described in an earlier paper of this series (see CORTEL-BREEMAN & VAN DEN HOEK 1970).

3. RESULTS

3.1. Filamentous pompons and poorly organised plants grown from vegetative fragments

After 3½ months vegetative cortex-fragments had grown into small filamentous pale-red pompons 1–1½ mm in diameter (*fig. 1*), which had reached a diameter of 1½–4 mm after 5 months, and 2–8 mm after 9 months. After 9 months two of the pompons showed some tendency towards adult organization: the structure of the pompons was very compact, and the large, inflated, hyaline outer cortex-cells that are characteristic for *Scinaia* were developing (*figs. 2–5*). However, the "*Scinaia* plants" thus obtained were far from normal and had a very disorderly internal organization (*figs. 2, 3*). Up to this moment no unmistakable evidence was found that vegetative isolates could disseminate. Only rarely had the number of pompons in the same culture tube slightly increased. However, in 21 months old cultures the walls of the culture tubes were densely covered by filamentous plants, which showed that vegetative isolates were capable of dissemination. Unfortunately no observations were made on the structures producing this vegetative dissemination. Furthermore numerous *Scinaia* plants (ca 100 to 500 per culture tube; up to 10 mm long) were sprouting from the filamentous plants. One filamentous pompon mostly gave rise to several *Scinaia* plants (*cf. fig. 12*). The filamentous pompons often proliferated by creeping filaments.

In 40 culture tubes containing subcultures of the vegetative isolates the filamentous plants had also clearly disseminated, and in some of them young *Scinaia* plants were sprouting from the filamentous plants.

Four subcultures kept at 12 °C short day conditions during the last 5 months, however, only showed some dissemination, but had not produced *Scinaia* plants.

The filaments composing the pompons and the poorly organized "*Scinaia* plants" were characterized by thick mucilaginous walls. Furthermore the laterals of the generally indeterminate branch-systems in older cultures often terminated in spherical, swollen cells (*figs. 1, 4, 5*). These cells are probably homologous with the large inflated cortex-cells of a normal *Scinaia* plant.

3.2. Filamentous pompons grown from carpospores

After 3½ months the carpospores had grown into small filamentous pale-red pompons, 2–4 mm in diameter. The filaments in the centre of the pompons, where these were attached to the glass wall of the culture tube, were irregularly inflated and often short-celled (*fig. 6*). The peripheral filaments consisted of more elongate cells, though often the basal cells of the laterals were relatively short (*fig. 7*). A distinct difference from the filamentous pompons grown from cortex-fragments was the absence of thick mucilaginous walls.

Thirty pompons grown from carpospores and aged $3\frac{1}{2}$ months were used to test the combined influence of daylength and temperature on their morphogenesis and reproduction.

Fig. 1. Filamentous pompon grown from vegetative isolate; detail of filaments. Note the thick mucilaginous walls.

Fig. 2. Filamentous pompon grown from vegetative isolate and showing some tendency towards organization of the adult *Scinaia* plant; surface view on the pompon. Note the large, inflated cells characteristic for the outer cortex of *Scinaia* and their irregular distribution.

Fig. 3. Transverse section of the pompon pictured in *fig.* 2. Note the irregular distribution of the large inflated cells (which form a monostromatic outer cortex in normal *Scinaia* plants, *cf. fig.* 13).

Figs. 4, 5. Filamentous pompon grown from vegetative isolate; details showing young inflated cells. Note the thick mucilaginous walls, and, in *fig.* 5, the reticulate chromatophores (ill developed in the inflated cells).

Fig. 6. Filamentous pompon (tetrasporophyte) grown from carpospore in $3\frac{1}{2}$ months. Detail of filaments in centre of pompon; these filaments attach the pompon to the glass of the culture tube. Note the absence of thick mucilaginous walls.

Fig. 7. The same pompon as pictured in *fig.* 6. Detail of the peripheral filaments. Note the absence of thick mucilaginous walls and large inflated cells.

Fig. 8. Detail of the pompon pictured in *figs.* 6 and 7, showing the strap-shaped to reticulate chromatophores.

Fig. 9. Filamentous pompon (tetrasporophyte) grown from carpospore in $5\frac{1}{2}$ months. Detail of peripheral filaments. Note the absence of thick, mucilaginous walls.

Fig. 10. Detail of the same tetrasporophyte as pictured in *fig.* 9. Short-celled densely ramified branch-systems that give rise to tetrasporangia (one emptied tetrasporangium is pictured). Note the absence of thick, mucilaginous walls.

Fig. 11. Detail of the same tetrasporophyte as pictured in *fig.* 9. Short-celled densely ramified branch-system bearing tetrahedral tetrasporangia. New tetrasporangia can arise from the stalks of emptied tetrasporangia (arrow).

Fig. 12. New generation of *Scinaia* plants. Several *Scinaia* plants can arise from one filamentous gametophytic stage.

Fig. 13. Longitudinal section of a culture grown *Scinaia* plant. Note the monostromatic outer cortex of large hyaline cells and the multiaxial medulla.

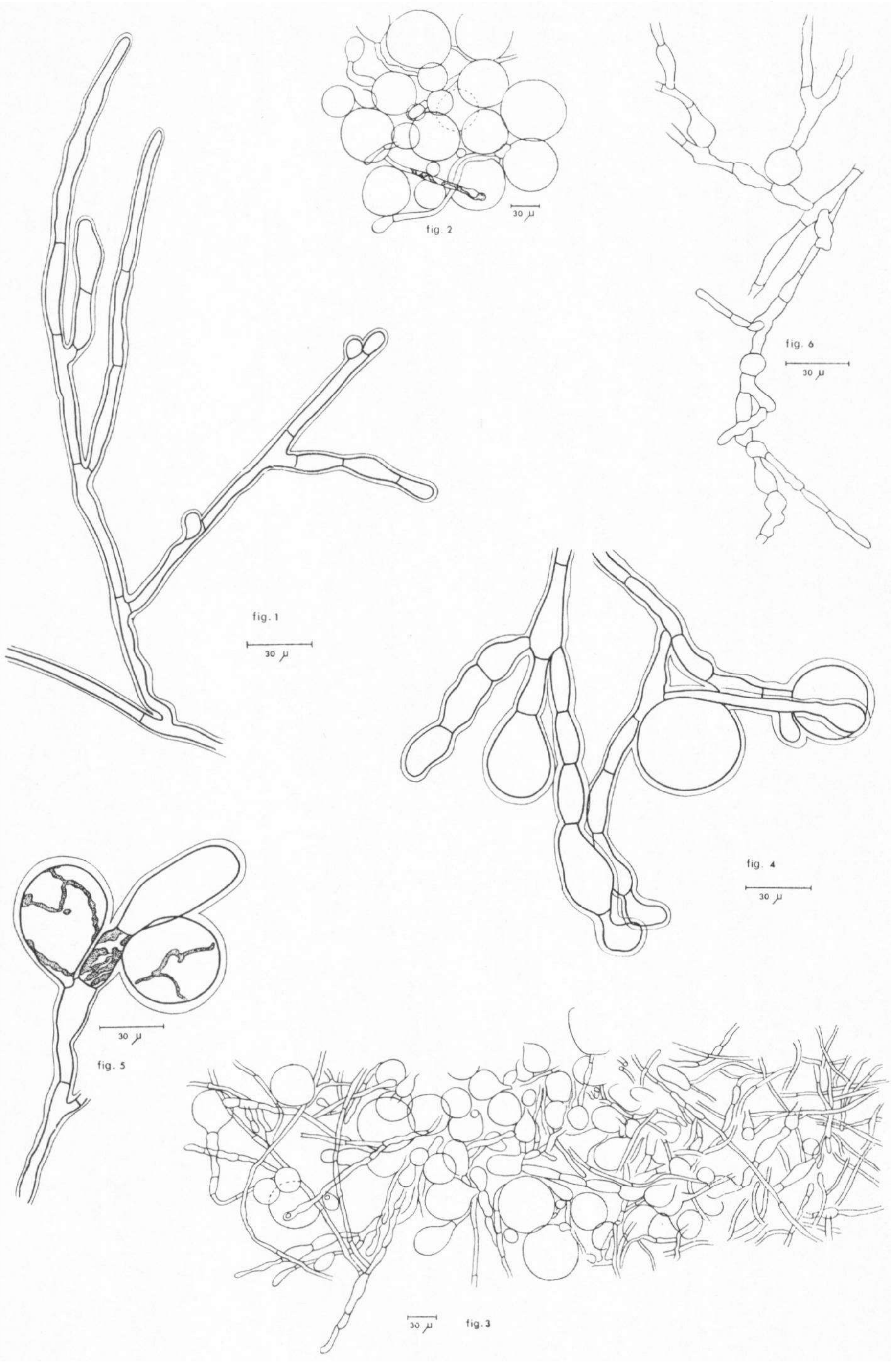
Fig. 14. Germling grown from a tetraspore.

Figs. 15, 16. Second tetrasporophyte generation grown from spores produced by the first tetrasporophyte generation. Short-celled branch-systems bearing tetrasporangia. Note the absence of thick mucilaginous walls.

Figs. 17, 18. New filamentous gametophytic generation grown from spores produced by the tetrasporophyte. Note the thick mucilaginous walls and the spherical apical cells.

Fig. 19. Initial of *Scinaia* plant arising from filamentous gametophytic stage. Uniaxial ontogeny.

Fig. 20. Initial of *Scinaia* plant arising from filamentous gametophytic stage. Multiaxial ontogeny.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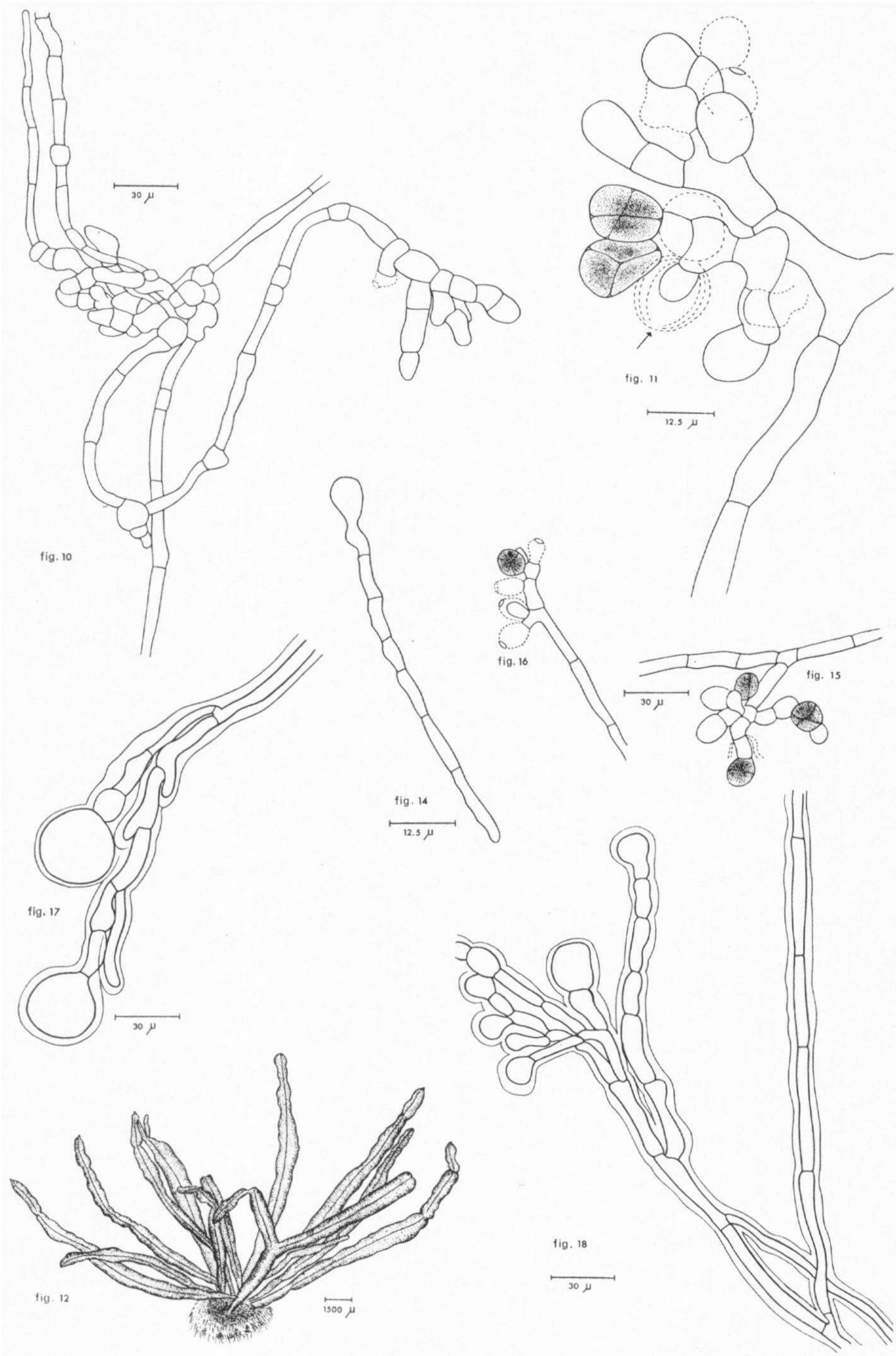
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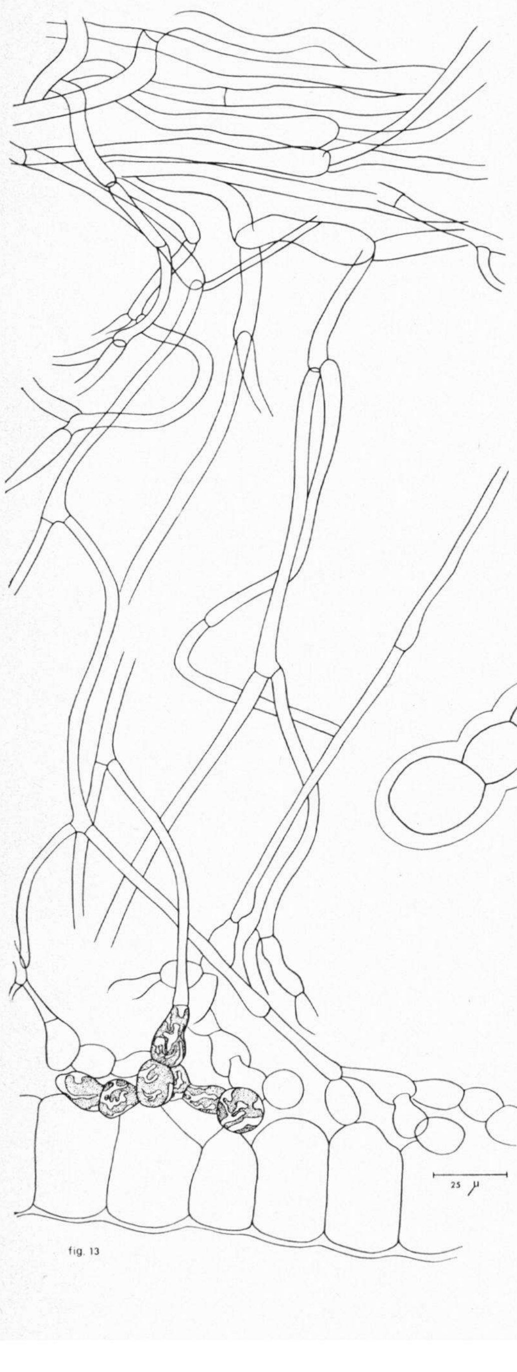

fig. 13

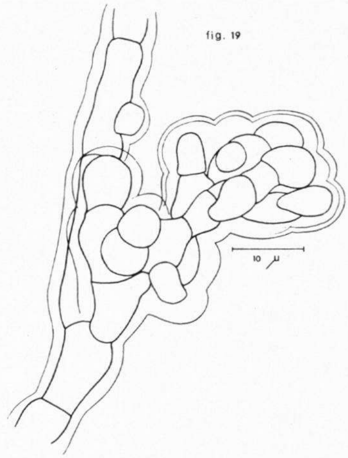

fig. 19

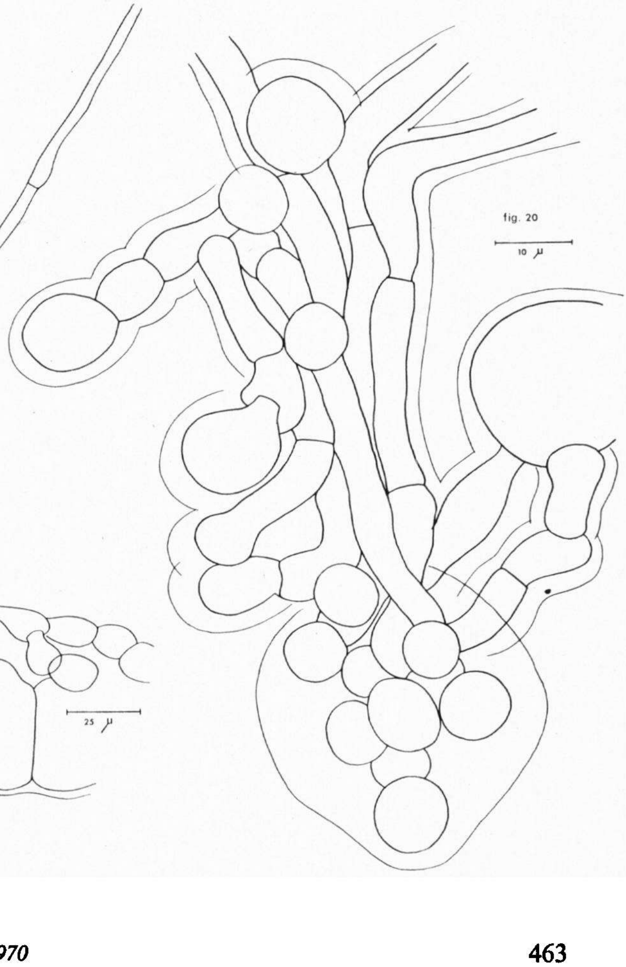

fig. 20

3.2.1. The combined influence of daylength and temperature on the formation of tetrasporangia and on morphogenesis

The filamentous stage grown from carpospores was suspected to be the tetrasporophyte. Thirty pompons grown from carpospores and aged 3½ months were transferred each into one of thirthy culture tubes and subjected to different combinations of daylength and temperature and changes of such conditions (4°C "long day" and "short day" conditions; 12°C "long day" and "short day" conditions; 17°C "long day" conditions). The applied standard method has been fully treated in CORTEL-BREEMAN & VAN DEN HOEK (1970).

The 4°C cultures did not show any growth and died within 3 months. This is in accordance with the tropical to subtropical distribution of *Scinaia complanata.*

The 12°C short day as well as the 17°C long day cultures after 2 months contained young offspring. This offspring had most probably developed from tetraspores produced by the tetrasporangia, which had developed on the original pompons. These tetrasporangia were characteristically grouped on short-celled densely ramified branch-systems (*figs. 9–11*).

In 17°C long day cultures the dissemination was much more vigorous than in 12°C short day conditions. The 12°C long day cultures, however, did not show any dissemination.

Twenty weeks after onset of the experiment 5 of the 7 cultures grown at 12°C short day cultures were transferred to 17°C long day conditions; and 5 of the 7 cultures grown at 17°C long day conditions were transferred to 12°C short day conditions. One month later the cultures transferred to 17°C long day conditions contained thousands of new germlings, whereas the cultures transferred to 12°C short day conditions did not contain any new offspring. One year later the cultures transferred to 17°C long day conditions and those kept continuously (ca 16 months) under 17°C long day conditions were completely filled with filamentous stages from which sprouted numerous young *Scinaia* plants (20–200 per culture tube; 1–10 mm high) (*fig. 12*). One year later the cultures transferred to 12°C short day conditions, however, and those kept continuously (ca 16 months) under 12°C short day as well as 12°C long day conditions did not contain young *Scinaia* plants. Therefore, reproduction of the tetrasporophyte of *Scinaia complanata* and the growth of *Scinaia* plants from filamentous gametophytic stages seem to be favoured by 17°C long day conditions.

3.2.2. Self-reproduction of the tetrasporophyte

Then young germlings grown from tetraspores were cultured, each separately, in culture tubes and kept in 17°C long day conditions, and seven such germlings in 12°C short day conditions. About 1½ months later six of the ten 17°C long day cultures had vigourously disseminated and contained numerous few-celled germlings. These germlings most probably had developed from tetraspores produced in tetrasporangia that had developed on the filamentous plants grown from tetraspores. The 12°C short day cultures, however, had not disseminated and did not contain tetrasporangia. Five months after the onset of this experiment all 17 °C long day cultures contained numerous filamentous offspring (sporophytic as well as gametophytic, see below) whereas in the 12 °C short day cultures still no dissemination had taken place and only very few tetrasporangia were found. Fifteen months after the onset of this experiment all ten 17 °C long day cultures contained numerous filamentous offspring and seven of them numerous young *Scinaia* plants (10 to 50 per tube; 1–8 mm long). The 12 °C short day cultures, however, showed almost entirely vegetative growth of the filamentous stage and hardly any dissemination; no *Scinaia* plants had developed.

It appeared that older tetrasporophytic cultures contained two types of filamentous offspring. One type showed characteristics of the tetrasporophyte (no thick mucilaginous walls; often clustered ramifications; thin and tapering filaments; often with clusters of tetrasporangia) (*figs. 14–16*), the other type showed characteristics of the filamentous gametophytic phase (thick mucilaginous walls; ramification hardly densely clustered; filaments often thicker towards the apices and often bearing spherical cells; without tetrasporangia) (*figs. 17, 18*). The cultures obtained from isolated cortical fragments of the gametophyte provided material for comparison (*figs. 1, 4, 5*).

These observations indicated that the tetrasporophyte is capable of reproducing itself as well as producing a new gametophytic phase. No special reproductive structures serving the purpose of self-reproduction were observed, but their existence should not be excluded. Possibly part of the tetraspores serve the purpose of self-reproduction. Seven secondary tetrasporophytes and eight young gametophytes were cultured each separately under 17 °C long day conditions. In a period of 10 months further distinctive dissemination had taken place in the sporophyte as well as in the gametophyte cultures. Two sporophyte cultures contained a few young *Scinaia* plants (1–2 mm high).

4. CONCLUSIONS AND DISCUSSION

The carpospores of *Scinaia complanata* give rise to filamentous, self-reproducing tetrasporophytes. Tetraspores can develop into a filamentous, self-reproducing gametophyte stage from which sprout adult *Scinaia* thalli.

The life-history of *Scinaia complanata* is strictly similar to that of *Scinaia furcellata* (BOILLOT 1968, 1969) and is not haplobiontic. *Scinaia complanata* belongs to the ever increasing category of *Rhodophyceae* for which strongly heteromorphic life-histories have been discovered (for a review see CORTEL-BREEMAN & VAN DEN HOEK 1970). The morphological details of the filamentous gametophytic phase make it possible to differentiate this phase from the tetrasporophytic phase. The gametophytic filamentous phase is characterized by thick mucilaginous walls and the tendency of the filaments to have swollen apical cells. BOILLOT (1969) mentions the same morphological particulars for the gametophytic filamentous stage of *Scinaia furcellata*.

BOILLOT (1969) obtained the initials of *Scinaia furcellata* plants in culture.

Such initials consisted of an axial filament bearing a botryoid cluster of laterals, so that, ontogenetically, *Scinaia furcellata* is uniaxial and not multiaxial. In our cultures adult *Scinaia complanata* plants could arise in the same way (*fig. 19*). In other cases, however, filaments originating far from one another united into one single *Scinaia* initial (*fig. 20*). Therefore, adult *Scinaia complanata* plants can be ontogenetically uniaxial as well as multiaxial. There is no sharp distinction between both possibilities.

The formation of the tetrasporangia was not induced by short day conditions, as in *Acrosymphyton purpuriferum* (CORTEL-BREEMAN & VAN DEN HOEK 1970), but seemed to be encouraged by 17°C long day conditions, which roughly correspond to summer conditions. However, under 12°C short day conditions (roughly corresponding to winter conditions in the Mediterranean) some reproduction by the tetrasporophytes can take place. Development of adult *Scinaia* thalli from the filamentous gametophytic stage only took place under 17°C long day conditions, and not under 12°C long day and 12°C short day conditions. These observations strongly suggest that, in the Mediterranean, reproduction of the tetrasporophyte and the gametophytic filamentous stage as well as development of the adult *Scinaia* thalli can only take place during the summer half-year.

As in *Acrosymphyton*, the strongly heteromorphic tetrasporophyte is capable of leading a life independent of the gametophyte as a result of its ability for self-reproduction. Possibly a part of the tetraspores is used for this self-reproduction, for other types of reproductive structures were not observed on the tetrasporophyte. The filamentous gametophytic stage is also able to live independently of the adult gametophytic stage, since it also is capable of self-reproduction (by unknown reproductive bodies). *Acrosymphyton*, on the other hand, lacks a gametophytic filamentous stage in its life-history.

The few records of the gametophyte of *Scinaia complanata* in the Mediterranean suggest that it is there a summer-annual (FELDMANN 1942). It is likely that the tetrasporophyte and the filamentous stage of the gametophyte ensure hibernation in the Mediterranean. Like *Halymenia floresia*, *Scinaia complanata* is a tropical to subtropical species, known from the Caribbean and the Mediterranean. In the Caribbean the adult gametophyte stage has been collected at different seasons of the year (TAYLOR 1928, p. 141; BØRGESEN 1915–1920). The data available suggest that the macroscopic stage of this tropical to subtropical species is perennial in the tropics, but that it retreats during winter into its filamentous stages at its northern subtropical boundaries. The same possibly holds true for *Halymenia floresia*.

REFERENCES

BOILLOT, A. (1968): Sur l'existence d'un tétrasporophyte dans le cycle de Scinaia furcellata (Turner) Bivona, Némalionales. *C. R. Acad. Sci. Paris* **266**: 1831–1832.

— (1969): Sur le développement des tétraspores et l'édification du gamétophyte chez Scinaia furcellata (Turner) Bivona, Rhodophycées (Némalionales). *C. R. Acad. Sci. Paris* **268**: 272–275.

BØRGESEN, F. (1915–1920): The marine algae of the Danish West Indies III. Rhodophyceae. *Dansk Bot. Ark.* **3**: 504 pp.

CORTEL-BREEMAN, A. M. & C. VAN DEN HOEK (1970): Life-history studies on Rhodophyceae I. Acrosymphyton purpuriferum (J. Ag.) Kyl. *Acta Bot. Neerl.* **19**: 265-284.

FELDMANN, J. (1942): *Les algues marines de la côte des Albères IV. Rhodophycées.* Paris.

HOEK, C. VAN DEN & A. M. CORTEL-BREEMAN (1970): Life-history studies on Rhodophyceae II. Halymenia floresia (Clem.) Ag. *Acta Bot. Neerl.* **19**: 341-362.

KYLIN, H. (1956): *Die Gattungen der Rhodophyceen.* Lund.

MAGNE, F. (1964): Recherches caryologiques chez les Floridées (Rhodophycées). *Cah. Biol. Mar.* **5**(5): 461–671.

SVEDELIUS, N. (1915): Zytologisch-entwicklungsgeschichtliche Studien über Scinaia furcellata. *Nov. Act. Reg. Soc. Sci. Upsaliensis, ser.* 4, **4**: 1–55.

TAYLOR, W. R. (1928): The marine algae of Florida with special reference to the Dry Tortugas. *Pap. Tortugas Lab.* **25**: 219 pp.

— (1960): *Marine algae of the eastern tropical and subtropical coasts of the Americas.* Ann Arbor, Univ. Michigan Press.