# THE LIFE-HISTORY OF PORPHYRA ATROPURPUREA *(OLIVI) DE TONI. I.*

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## 1. INTRODUCTION.

It is already known since the discovery made by DREW (1949) and later confirmed by numerous experiments DREW (1954), YAMASAKI (1954), GRAVES (1955), HOLLENBERG (1958), KORNMANN (1960), that *Porphyra* has an alternation of two dissimilar generations. The plant bearing the name *Porphyra* being the leafy, macroscopic sexual phase of a much branched uniseriate filament growing inside dead shells, the other phase; this one being very similar in appearance to an alga described as early as 1892 by BATTERS as *Conchocelis rosea*. This discovery led to the conclusion that the so-called *Conchocelis rosea* is nothing else than one phase on the life-cycle of *Porphyra*. Recently it was shown by IWASAKI (1961) that the production of sexual organs by the leafy *Porphyra* or the spores by the filamentous *Conchocelis* and the vegetative growth of both phases are controlled by the duration of the day-length. This finding explains the yearly disappearance of *Porphyra* during the summer-months and its resettlement at the end of autumn. It is interesting to note that for at least one species, *Porphyra perforata* J. G. Agardh, whose development was described by HOLLENBERG (1958), has not the filament pattern of the typical *Conchocelis* of other species since this species does not grow naturally inside shells. On the other hand we know that at least for one species of *Porphyra* whose *Conchocelis* filaments naturally occur inside shells, can, in

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culture, develop without shells, as was shown recently by IWASAKI (1961).

## 2. MATERIAL AND METHODS.

The cultures were carried in natural sea-water previously filtered and, or boiled. This water after returning to the temperature of the laboratory was well aerated before starting the experiments. We used two types of containers: glass cylinders of ca. 3 1 capacity and Petri dishes of ca. 80 $cm^3$ capacity. The bottom of the containers were covered with sterilized sand. This sand was collected in three different beaches near Santos. Slender pieces of mollusk shells (flakes) collected at a "sambaquí" (Indian mound) and belonging to the genera *Ostrea* and *Atrina* and another mollusk from the freshwater genus *Diplodon* (3) were dispersed over the sandy layer. The cultures were maintained near a north-facing window. To prevent undue evaporation, the Petri-dishes were maintained closed and the glass-cylinders were covered with transparent glass. The temperature of the water in the cultures was controlled daily. It showed a variation from 14°C to 25°C (from late winter to summer). The cultures started at the end of the winter of 1961 and are still going on. Small fertile portions of the thallus margin either containing monospores or carpospores were selected under a microscope and placed in the containers. Two days later these portions were removed. All the following descriptions are based in cultures obtained with this method.

Observations began three days after the removal of the blade portions from the cultures. During the first month, each 3 days, a fragment of shell infested with spores was selected and examined under the microscope. Afterwards weekly observations were made.

## 3. THE LEAFY THALLUS.

The vegetative thallus of *Porphyra atropurpurea* is a monostromatic, irregularly shaped blade attached by an inconspicuous holdfast to the rocks located above the usual high-tide line, on well

(3) Kindly identified by Prof. J. C. Mendes.

exposed situations. This leafy thallus starts to attract attention on the shore by the end of the autumn-season (late May in the southern hemisphere). From there on the plant is very common and can be found at the proper stations till the beginning of the summer (December). During the summer the plants almost completely disappear. Isolated and apparently protected individuals, sometimes reaching unusual dimensions, can be occasionally found after this time. The mature thallus reproduces by the usual formation of monospores (Figs. 1-3) at the margins of the blades during the winter season and the beginning of spring. At the end of the winter season (August), during the springtime and with increasing intensity at the beginning of the summer, the blades produce also sexual organs. These, carpogonia and spermatangia, are formed on the same plant, since this species is a homothallic one. These organs are produced, like the monosporangia, at the well thorn margin by then. The first indication of the production of carpogonia in our species is that the blade becomes distromatic, near the fertile margins (Figs. 4-5), as seen in transsections. The two layers of carpogonia are not continuous, since many cells remain vegetative and others produce spermatia. Each carpogonium has a small protuberance towards the free surface. This is usually referred to as a primitive tricogyne. As can be seen from Fig. 6, several carpogonia are in the process of fertilization or on post fertilization stages. The remains of spermatia are seen in the drawing. After fertilization takes place, the zygote still surrounded by the wall of the carpogonium undergoes two successive divisions leading to the production of four capospores. These are arranged in two tiers of twos. The carpospores are liberated by the progressive desintegration of the blade.

## 4. DEVELOPMENT OF MONOSPORES.

Monospores produced by the leafy thallus are liberated by desintegration of the margin of the blade. They are able to escape from the gelatinized margins by slow ameboid movements (Figs. 3, 7-9). The rounded monospore, when still in place, gradually assumes an elongated form, apparently squeezing itself out of the muscillaginous margin. After liberation the rounded form is reassumed. Some mo-

nospores, by an unknown reason, failing to escape, are able to germinate "in situ". Others having successfully escaped from inside the frond remained attached to its surface and there germinated (Fig. 10). Both kinds were found in freshly collected material from which the Figs. 8, 11 and 12 were made. The monospores have the same size as carpospores. They have a diameter of about 18μ. The striking difference between monospores and carpospores, besides the way they are produced, is the behavior during germination. The monospores through successive divisions of its contents and accompanying enlargement, become a leafy structure. Very soon rhizoids start to grow from the lower cells. As one can see from Figs. 8 and 11, the monospore does not produce a germination tube like the carpospore. In culture the monospores started to develop a leafy structure clearly seen in Figs. 13-15. No further development was followed. Apparently after one month the development was proceeding at a very slow rate, if one compares the Fig. 15 (3 months old thallus) with the preceding Figs. 13 and 14 (near one month and a little over one month old thallus).

## 5. DEVELOPMENT OF CARPOSPORES.

The carpospores liberated by the desintegration of the frond are a roundish structure (Fig. 16) about the same size as the monospores. They have a diameter ranging from 14μ to 20μ, being 18μ the more frequent size. The carpospores after escaping the frond, sometimes germinated when still immersed in the gelatinous vicinity of the blade margins (Fig. 17). They can produce 1, 2 and sometimes up to 3 germination tubes. The carpospores allowed to germinate upon slender pieces of shells did develop very rapidly. The beginning of the germination (Fig. 18) showed the same pattern as above described. One or two, sometimes more, germination tubes started to grow on the surface of the shell and afterwards penetrated inside. The development inside the shell was surprisingly rapid, confirming the previous findings of DREW (1954) for *Porphyra umbilicalis*. Our Figs. 19 and 20 were obtained 8 and 9 days, respectively, after the beginning of the experiments. Fig. 21 shows another filament 14 days old. It can be seen from this figure that some carpospores have

started to develop at a considerably slow rate. (Note the spore with a short germination tube at the lower left). It can also be seen from Figs. 19 and 20 the beginning of the irregular branching pattern characteristic of the *Conchocelis-like* phase. Note also that apparently no transverse septa have develloped. Figs. 22 and 23 are from a filament 11 and 15 days old, respectively. It is possible to see at the center of the last-mentioned figure the membrane of the spore that did originate the filament (rounded structure with a broken line at the surface of the shell). Fig. 24 shows a one month old plant. Further development was at a very rapid rate and after 4 months (by the middle of December), the shells were completely infested by the filamentous "*Conchocelis*". The development of this phase was very similar to that obtained by DREW (1954). As described by her, the *Conchocelis* filament inside the shell does not have a regular formation of septa. Another feature very characteristic is the fusion that takes place between neighbouring filaments. In old plants, this fusion can assume the aspect shown in Figs. 25 and 26. DREW (1954) also reports such unusual feature of the *Conchocelis* filaments. By the end of the summer season, seven months after the beginning of the cultures, a different pattern of the filament appeared in the shells. These started first as a localized swelling of a lateral branch (Figs. 27-32). This swelling has a denser content than the usual *Conchocelis* filaments. As development proceeds, a certain number of cells, organized as a uniseriate ramified filament, are clearly seen from above (Figs. 33-34). These filaments show very little branching and are composed of few cells. They appear everywhere in the shell. They are of the same kind referred to by DREW (1954) as the "fertile cell rows". Indeed, in our material, shortly after the appearance of these "fertile cell rows", it was possible to find a few isolated rounded cells upon the shell surface. Trying to clarify the origin of these cells, it was found that they were liberated from inside the shell by special pores develloped at the free end of the "fertile cell rows" (Figs. 35-36). These were growing from below directly to the surface in a somewhat upright fashion. At the surface a clear pore is seen ending such filaments (Figs. 35 and 36). This is in agreement with the findings of YAMASAKI (1954) and TSENG and CHANG (1955) for *Porphyra tenera*. The spores are liberated one by one,

apparently by active sliding movements through this aperture. This is accomplished through the dissolution of the transverse septa separating the cell row at the end of such filaments (Fig. 35). This breaking--down of the transverse septa were already reported by DREW (1954) as well as by YAMASAKI (1954) and TSENG and CHANG (1955). At the end of this process, an emptied tube, with a definite pore is seen from above.

Experiments are being carried on in order to elucidate the behaviour and the fate of this kind of spore, called by some authors, "conchospores".

## 6. DISCUSSION.

The facts observed are in agreement with the findings of previous authors regarding the production of the *Conchocelis-like* phase by the germinating carpospore of different species of *Porphyra*.

From the observations above described it is now possible to explain how the conchospores, produced from cells of the "fertile cell rows" inside the shell, are liberated.

If the development of monospores produced by the leafy thalli of other species of *Porphyra* is similar to the above described process of germination, they cannot be confounded with the behaviour of the carpospores. Perhaps the previous references of the behaviour of "neutral" spores by other authors (usually with the origin of this kind of spore not well defined) can possibly be a mistake with carpospores, since it is difficult, not knowing its origin, to separate them, because, as we have seen, they have the same size.

## 7. ABSTRACT.

*Porphyra atropurpurea* is a common rock-weed in Southern Brazil. A *Conchocelis*-like phase, unknown for this species has been obtained by cultures of carpospores. A detailed description of the methods employed, as well as the results obtained, are given.

Direct observation showed the way conchospores produced by the filamentous phase, are liberated from inside the shell through a well-develloped pore. Cultures started from monospores liberated

by the leafy thallus resulted in the production of the leafy phase. Detailed description of this process shows remarkable difference in behaviour of this kind of spore regarding its germination. Experiments are still in progress.

## 8. SUMÁRIO.

*Porphyra atropurpurea* é uma alga vermelha comum nas costas rochosas do Sul do Brasil. Através da cultura de carpósporos obteve-se o desenvolvimento da fase filamentosa, conhecida pelo nome de *Conchocelis*. Culturas de monósporos produzidas pelo talo adulto, mostraram que estas estruturas dão origem ao talo foliáceo por um processo de germinação inteiramente diferente da germinação dos carpósporos. Uma detalhada discussão dos métodos empregados e dos resultados obtidos é apresentada. As experiências continuam.

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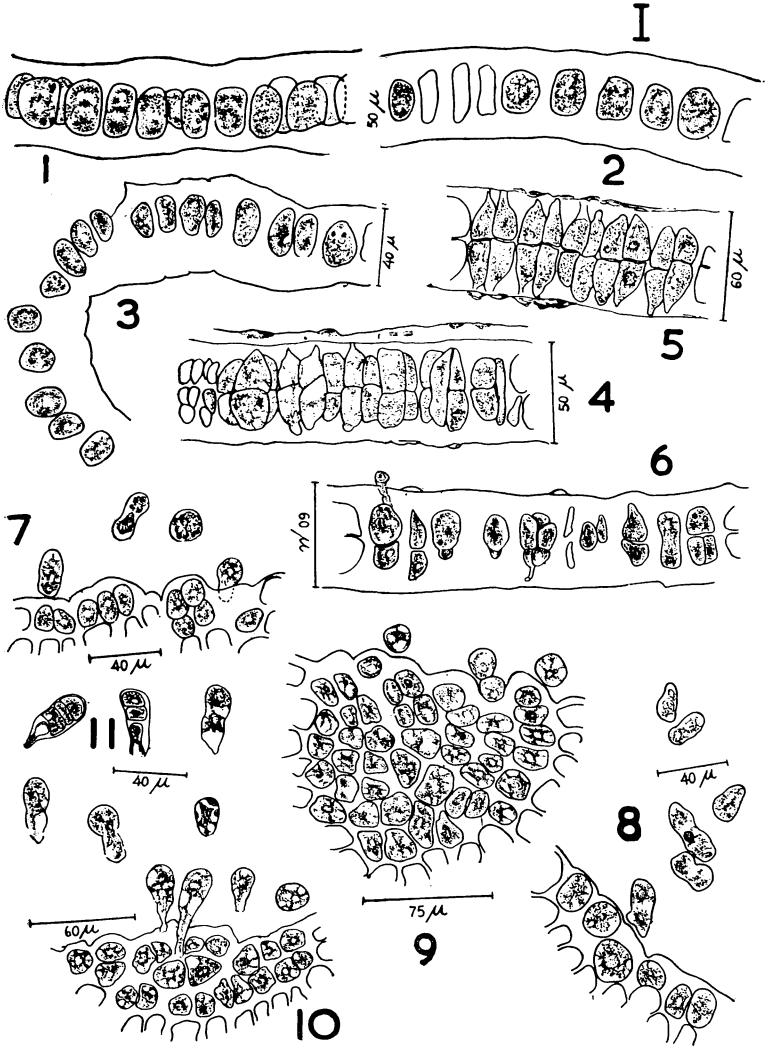
## PLATE I

Figs. 1, 2, 3. Transections of blade. Note several monosporangia; in the last figure several spores are escaping the frond (living material).

Figs. 4, 5, 6. Transections of the blade. Note double layer of cells, several carpogonia with trichogyne, espermatangia; in the last figure, the fertilization process (living material).

Figs. 7, 8, 9, 10, 11. Margin of monosporic blades (seen from above). Note several monospores in the process of liberation and the begining of the germination. Note how the monospore give rise to new plants without producing germination tubes (living material).


I
50 μ
1
2
40 μ
60 μ
3
5
50 μ
4
6
60 μ
7
40 μ
11
40 μ
9
75 μ
8
40 μ
60 μ
10

## PLATE II

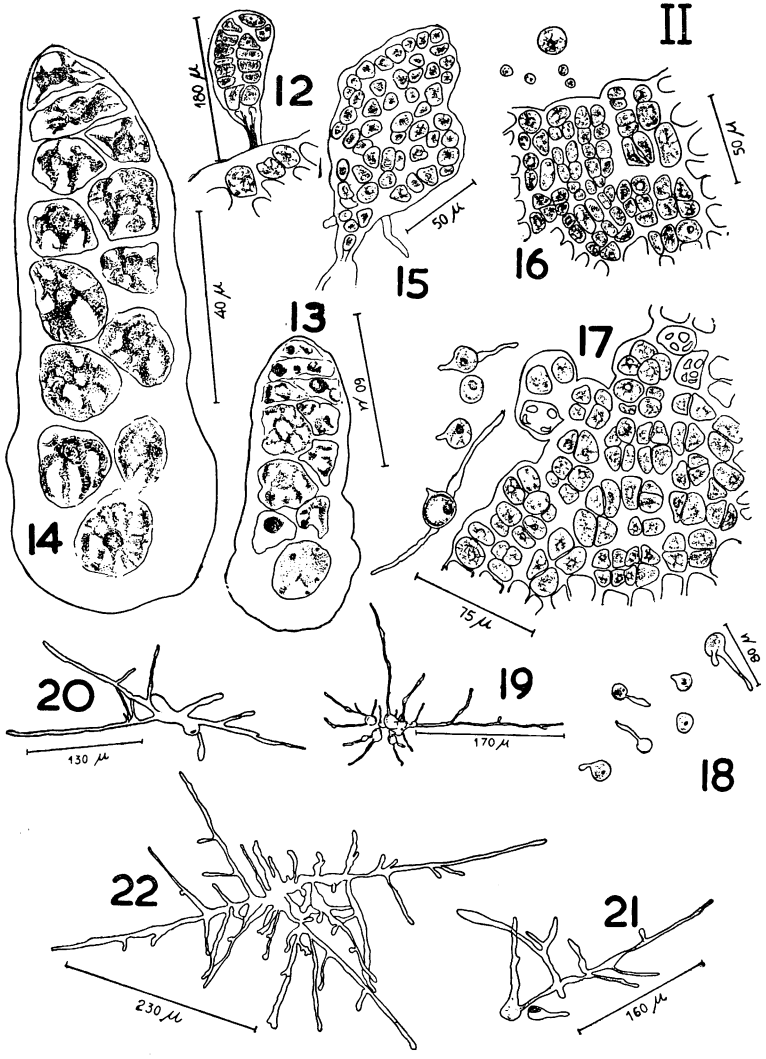
Fig. 12. Plantled originated by monospore, growing attached to the margin of the blade (living material).

Figs. 13, 14, 15. Plantlets obtained in culture from monospores, 30, 34 and 84 days old respectivily (living material).

Figs. 16, 17. Margin of carposporic blade (seen from above). Note at fig. 16 one carpospore and 4 spermatia in the neighboorhood of the blade, and several carpospores in place. Note at fig. 17, 4 germinating carpospores and several spores in place (living material).

Fig. 18. Culture material. Germinating carpospores (living material).

Figs. 19, 20, 21, 22. Culture material. "Conchocelis" filaments, 8, 9, 14 and 11 days old plants respectively, growing inside *"Ostrea"* flakes (living material).

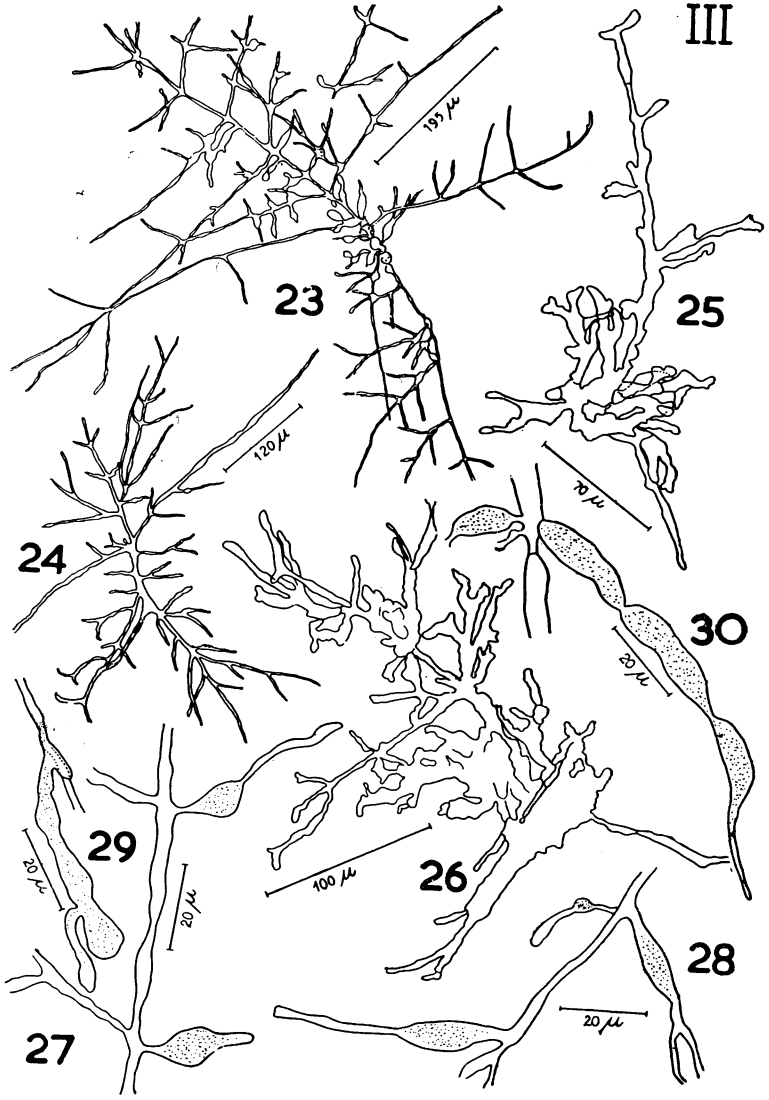

II
12
180 μ
15
50 μ
16
50 μ
40 μ
13
90 μ
14
17
75 μ
20
130 μ
19
170 μ
18
80 μ
22
230 μ
21
160 μ

## PLATE III

Figs. 23, 24. "Conchocelis" filaments. Note at fig. 23 the inicial carpospore still visible at the surface of the shell. Note also the characteristic branching pattern and the absence of septa (living material).

Figs. 25, 26. "Conchocelis" filaments. The last fig. 32 days old plant. Note the fusion between neighboors filaments (living material).

Figs. 27, 28, 29, 30. Localized swellings of "Conchocelis" filaments in 9 months old cultures (living material).


III
23
195 μ
25
120 μ
24
20 μ
30
20 μ
29
20 μ
20 μ
100 μ
26
28
20 μ
27

## PLATE IV

Figs. 31, 32. Normal "Conchocelis" filaments, showing the beginning of the swellings (living material).

Figs. 33, 34. The formation of the "fertile cell rows" (living material).

Figs. 35, 36, 37. Fertile cell rows, showing several pores at the surface of the shell (living material).

IV