CLADONIA ECMOCYNA NYL. – INVESTIGATIONS ON THE ONTOGENY

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SUMMARY

1. The ontogeny of the podetium and the apothecium in *Cladonia ecmocyna* Nyl. is investigated morphologically and anatomically. The podetia are formed by generative tissue. Sexual organs and apothecia are only formed at the top of grown podetia. The development is the same as in *Cladonia chlorophaea*, described by JAHNS 1969.
2. The phyllocladia are formed by growth of the algal layer of the podetium. In the process a piece of the cortex is torn free at the basal side of the primordium of the phyllocladium and bent upwards.
3. Phyllocladia are also formed at the margin of old cups. The phyllocladia of old, rotten podetia can assume the function of the thallus horizontalis. New podetia emerge from them.
4. The tissue of the apothecium is not fundamentally determinant. It was observed that on the disc of an apothecium a phyllocladium had been formed by the subhymenial tissue. On this phyllocladium a pycnidium was found.

1. INTRODUCTION

In the history of lichenology investigations on the nature and development of podetia and apothecia in the genus *Cladonia* have always been of special interest. New investigations by JAHNS (1969) have shown that the species of *Cladonia* have real podetia when a podetium is defined as a thallus verticalis entirely constructed from generative tissue. Generative tissue in lichens is the name given to a complex of hyphae, forming a dense cluster or a bundle that occurs just once in the ontogeny of a fruiting body and can usually be seen quite distinctly. This tissue forms the paraphyses and in some genera the excipulum and the stalk of the fruiting bodies which is then called a podetium.

The investigations mentioned above have shown that apothecia in *Cladonia* can develop in two ways. In both cases ascogones and trichogynes are formed in the generative tissue. The ascogenous hyphae arise afterwards. In some species of *Cladonia* this occurs in the young primordium of the podetium before it has grown more than 100–150 μ above the thallus horizontalis. The ascogenous hyphae grow upwards with the primordium and participate in the formation of an apothecium at the top of a ripe podetium. An example of this kind of development, first described by KRABBE (1891), is *Cladonia turgida*.

In the second group of the genus *Cladonia* the ascogones only occur in the tips of full-grown podetia. Ascogenous hyphae are formed there immediately.

This kind of development, described by BAUR (1904), WOLF (1905), and LETROUIT-GALINOU (1966), occurs in *Cladonia chlorophaea*.

As said in the paper by JAHNS (1969) it is desirable that a greater number of

species of the genus *Cladonia* should be investigated to see whether their ontogeny belongs to the first or the second type. Only after a great number of species has been investigated can it be decided whether the differences between the two types of development are of taxonomic importance.

The work on *Cladonia ecmocyna* published here was intended as a contribution towards this end. Moreover the material showed numerous interesting deformities of apothecia and phyllocladia. These deformed organs will also be described with a special discussion of their relevance to the definitions of the terms "podetium" and "generative tissue" and of possible clues to the controversial question of the origin of the algae of the podetium.

The investigations were carried out during the course on systematic botany for third year students at the University of Groningen 1968.

2. MATERIAL AND METHODS

The material was gathered in Germany, Bayern, Bayerischer Wald, Lusen, on boulders covered with mosses under pine trees.

The material was cut with a freezing microtome into 10–20 μ thick sections. These were stained and mounted in lactophenol-cottonblue.

3. DEVELOPMENT OF PODETIA AND APOTHECIA

3.1. Habitus

The material consists of the thallus horizontalis and the thallus verticalis which reaches up to 5 cm in height. The young podetia are usually spear-shaped and become irregulary cup-shaped when old.

The margin of the cups has often given rise to new spear-shaped stalks. Quite striking are the large phyllocladia covering the podetia. They too give rise to small stalks. The habit of those protuberances emerging from the phyllocladia seems to be similar to the podetia developed on the thallus horizontalis. In the material examined the likeness is so great that it is not easy to distinguish the two organs. The difficulty is increased by the fact that old podetia begin to die and rot in their lower part or over their whole length. In this case they lie close to or in the substrate and the phyllocladia take on the function of the thallus horizontalis and give rise to new podetia.

The first stage of podetial development is a small brown spot on the thallus horizontalis or on a phyllocladium. These give rise to small warts which continue to grow upwards.

Apothecia are abundant and are always situated on the margin of the cups. Many single apothecia lie close together. Observations on apothecia which grow together will be described later. In one case apothecia seemed to be borne on the phyllocladia. But this proved to be a mistaken impression. An old podetium had lain close to the substrate and from the rim of its cup large phyllocladia had grown. The rim of the cup could hardly be seen by this stage and therefore the apothecia seemed to lie on the phyllocladia.

3.2. Anatomical observations

In sections of the thallus verticalis the above mentioned brown spots show the first stage of the development of the podetium (*fig. 8*). A dense bundle of hyphae coming from the algal layer has broken through the cortex. The hyphae of this tissue are packed more closely than in the other tissues of the thallus and the lumens of the cells show an intense colouring with cottonblue. This is certainly the generative tissue already discovered in the same form and at the same place in other species of *Cladonia*. Some single algae are carried upwards from the algal layer by the generative tissue.

The bundle of hyphae of the generative tissue grows upwards. Thus develops the young podetium in which, soon, a central hollow is formed. At the top of slightly older podetia the hyphae forming the margin of the primordium show a distinctly quicker growth than the central tissue. Thereby a cup is formed.

When the cup has developed the sexual organs appear in its rim. The ascogones consist of straight rows of rather short, thick cells and like all the other hyphae around them they lie parallel to the longitudinal axis of the podetium. The ascogones end in a long, hair-like trichogyne reaching far above the surface of the thallus (*fig. 4*). Trichogynes were abundant, one section contained as many as 36.

After the trichogynes have degenerated the ascogones give rise to the ascogenous hyphae. In the beginning the cells of the ascogenous hyphae are nearly square and strongly vacuolate. This distinguishet them from the ascogones. At this stage the paraphyses grow from the hyphae of the rim of the cup and form the hymenium. The ascogenous hyphae which are now becoming more irregular in shape, gather in the subhymenial layer. The ascogenous hyphae give rise to the asci which grow between the paraphyses.

The development of podetia and apothecia here described entirely corresponds with that of *Cladonia chlorophaea* (JAHNS 1969). The ascogenous hyphae do not grow upwards with the podetium; the reproductive organs develop only in the top of the full-grown thallus verticalis.

3.3. Growing together and separation of apothecia

Sometimes large ring-shaped apothecia can be observed with a central hollow. In sections it can be seen that this structure can develop in two ways. Either an old apothecium can continue to grow at the margin and at the same time fracture in the centre, or several small apothecia may grow together.

It is apparent that the tissue of *Cladonia ecmocyma* is inclined to grow out and to grow together. As was said when describing the habit phyllocladia develop everywhere on the podetium. Phyllocladia assume the rôle of the thallus horizontalis and give rise to new podetia. One must consider the effect of this observation on the definition of the podetium and the generative tissue. But before this is done it seems sensible first to investigate the normal development of the phyllocladia and to mention another anomaly that has been observed and that is also of great importance for the theoretical discussion.

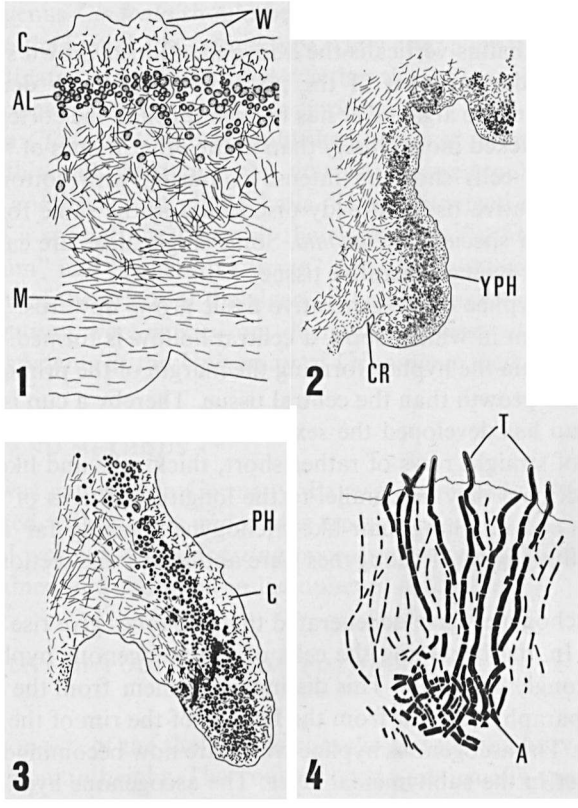

Fig. 1. *Cladonia ecmocyna;* longitudinal section through the podetium. AL-Alga, C-Cortex, M-Medulla, W-Warts of the cortex. (400 ×).
Fig. 2. *Cladonia ecmocyna;* longitudinal section through the podetium. CR-Cortex ruptured, YPH-young Phyllocladium. (100 ×).
Fig. 3. *Cladonia ecmocyna;* longitudinal section through the podetium. C-Cortex, PH-Phyllocladium. (200 ×).
Fig. 4. *Cladonia ecmocyna;* longitudinal section through the top of the podetium. A-Ascogon, T-Trichogyne. (220 ×).

3.4. Development of phyllocladia

Young podetia which do not yet bear phyllocladia often show little warts (*fig. 1*). In sections of the podetium it can be seen that they are the first stage of development of a phyllocladium. The hyphae of the algal layer multiply and push the cortex outwards. In older stages the cortex usually ruptures at the basal margin of the wart (*fig. 2*). Thus a scale is formed that begins to bend sideways. A young phyllocladium has originated, formed by the growth of the algal layer. The little scale continues to grow and a cortex is differentiated on its upper side while the lower side is bare (*fig. 3*). SAWYER (1931), showed that in *Cladonia ochrochlora* Flk. var. *ceratodes* Flk. the medulla of the podetium played a large part in the formation of phyllocladia. In *Cladonia ecmocyna* nothing of that sort could be seen.

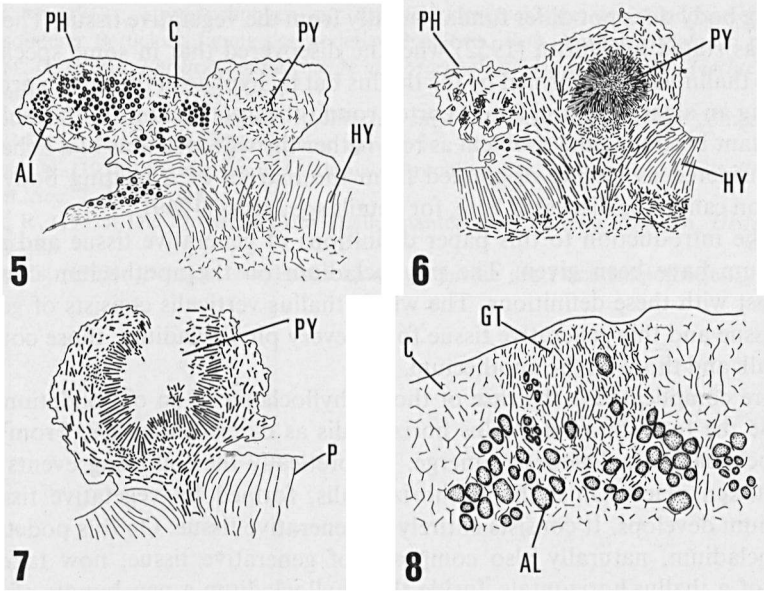

Fig. 5. *Cladonia ecmocyna;* longitudinal section through an apothecium bearing a phyllocladium. AL-Alga, C-Cortex, HY-Hymenium, PH-Phyllocladium, PY-Pycnidium. (200 ×).

Fig. 6. *Cladonia ecmocyna;* longitudinal section through an apothecium bearing a phyllocladium. HY-Hymenium, PH-Phyllocladium, PY-Pycnidium. (200 ×).

Fig. 7. *Cladonia ecmocyna;* longitudinal section through an apothecium bearing a phyllocladium. P-Paraphyses, PY-Pycnidium. (200 ×).

Fig. 8. *Cladonia ecmocyna;* section through a scale of the thallus horizontalis. AL-Alga, C-Cortex, GT-generative tissue. (260 ×).

Phyllocladia not only grow on the podetia themselves but also on the margin of the cups. In our material a phyllocladium together with a pycnidium was discovered in quite an unusual place.

3.5. Phyllocladium and pycnidium growing on an apothecium

On the disc of an apothecium a little phyllocladium was observed. Sections showed the following anatomical details. From the subhymenial layer a bundle of hyphae had grown through the hymenium. On the upper side of the apothecium this bundle had developed into a normal phyllocladium with normal upper cortex algal layer and medulla. On the phyllocladium near its base a normal pycnidium was found. *Figs. 5–7* show a series of sections through this phyllocladium and pycnidium.

4. DISCUSSION

The existence of a phyllocladium and a pycnidium on the disc of an apothecium shows clearly that there is no fundamental difference between the tissue forming reproductive organs and organs with photosynthetic activities. The tissue of the

fruiting body does not differ fundamentally from the vegetative tissue. The same fact was stated by DUGHI (1952) when he discovered that in some species the margo thallinus is not formed by the thallus but by hyphae of the margo proprius forming an algal layer and a new cortex round the apothecium. Both results are important in solving the problem as to whether the whole thallus of a lichen can be considered as having originated from the margin of a fruiting body. The question cannot be discussed here, for details see JAHNS (1969).

In the introduction to this paper definitions of generative tissue and a true podetium have been given. The phyllocladium on the apothecium does not contrast with these definitions. The whole thallus verticalis consists of generative tissue and this generative tissue forms every phyllocladium, those covering the stalk and those on the apothecium.

More complicated is the case of those phyllocladia of an old podetium that assume the function of a thallus horizontalis as described earlier. From these phyllocladia normal podetia emerge. Theoretically the following events must have taken place. On a thallus horizontalis, formed by vegetative tissue, a podetium develops. It consists entirely of generative tissue. On this podetium a phyllocladium, naturally also composed of generative tissue, now takes the place of a thallus horizontals. Inside the phyllocladium a new bundle of generative tissue is formed growing upwards to become a podetium. Generative tissue is newly formed in generative tissue, which is absurd.

Therefore it must be emphasized that the term "generative tissue" can only describe the presence of a certain stage of differentiation. As already said elsewhere (JAHNS 1969) the hyphae of the generative tissue do not differ fundamentally from those of the vegetative tissue. The term "generative tissue" is important as a good characteristic to distinguish the ontogeny of different lichens. Only in this context should it be used. A too formal application, as shown above, makes no sense.

Another question of interest is the origin of the algae in the phyllocladium borne on the apothecium. The algae of the podetium may come from the thallus horizontalis. The first primordium of the podetium distinctly shows the algae carried upwards from the algal layer by the bundle of generative tissue.

This observation contradicts the ideas of WEISE (1937) who assumes that the algae of the podetium come from outside the lichen and are newly acquired. But the phyllocladium on the apothecium has grown from the subhymenial layer where normally no algae can be found. Here in fact the algae may have come from outside the lichen but a final decision can only be reached by culture experiments.

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