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STUDIES IN ASCOSTROMATIC LICHEN-FUNGI—II

Types of ascostromata [1]

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Attention is drawn to the fact that the development of ascostromatic fungi is so diverse that it is possible to recognize a number of differently organized groups. Some of these groups correspond to the developmental types recognized by Luttrell but it is also shown that his *Pleospora*-type is not homogeneous, comprising as it does a number of categories, each of which has its own type of development of the ascocarp.

To designate structures not indicated before, the new terms t i c h u s, c a t a p h y s i s, and t i n o p h y s i s are introduced.

The ascostromatic fungi were recognized by Nannfeldt (1932) as a group of 'higher Ascomycetes' characterized by the development and structure of their ascocarps. According to him the development of the ascocarps starts with the formation of a stromatic tissue. The ascogenous system initiates within this tissue. The asci produced by the ascogenous cells or hyphae push into the stromal tissue to form monascous or pluriacous loculi that remain separated. The remnants of the stromal tissue, which separate the loculi, are known as interthecial filaments or strands. Because of the formation of loculi in the ascocarp Nannfeldt named the group Ascoloculares. Luttrell wanting to give this group definite taxonomic rank therefore proposed to call it Loculoascomycetes, as a new subclass of the Ascomycetes.

More recent studies on ascostromatic ascocarps have revealed that the tissue separating the asci is not always formed by the original stromal tissue. Miller, followed by Luttrell (1951), pointed out that in certain ascostromata the hyphal elements separating the asci are produced before the latter start their development. Consequently, these hyphal elements cannot be regarded as compressed remnants of the original stromal tissue.

In a number of cases, according to Luttrell, after a locule has been formed in the centre of the stroma, it becomes filled with newly formed hyphal elements. The asci arising from the ascogenous tissue at the bottom of the locule push their way between these hyphal elements, which have been called pseudoparaphyses. There are ascostromata in which the pseudoparaphyses, instead of being formed in the centre, result from a differentiation of hyphae in the apical region of the stroma.

However, it has become clear in the meantime that in many ascostromata the

[1] The term ascomata is also in use. It was introduced by Wallroth (1833: 407) as follows: "... stromate ascophoro, i. e. *a s c o m a t e* fibroso-carnoso s. gelatinoso-lubrico ..."

pseudoparaphyses do not fill a pre-existing locule or, at any rate, the locules are somewhat illusory. In these types of ascostroma the pseudoparaphyses are the result of a differentiation of the stromal tissue into a central and a peripheral tissue. The central tissue turns into pseudoparaphyses, while the peripheral tissue forms the stromal wall. Thus the structure gives the impression of a locule filled with pseudoparaphyses and surrounded by a wall but at no time has there ever been a central cavity in the stroma.

On the basis of the characters mentioned above the ascostromatic Ascomycetes may be divided into two groups: (1) 'ascolocular', viz. non-pseudoparaphysate, Ascomycetes and (2) pseudoparaphysate Ascomycetes. The first group comprises (1a) ascolocular Ascomycetes with monascous loculi and (1b) ascolocular Ascomycetes with pluriascous loculi. Where the loculi are pluriascous, there is a bundle or palisade of aparaphysate asci. In the second group there are again two subdivisions, (2a) pseudoparaphysate Ascomycetes with 'internal' pseudoparaphyses, and (2b) pseudoparaphysate Ascomycetes with 'external' pseudoparaphyses.

Luttrell (1951, 1955) accepted the above variations in the structure of the centre of the ascocarp as the basis for a subdivision of the pyrenocarpous Ascomycetes into a number of "developmental types." As far as the ascostromatic Ascomycetes are concerned, he originally distinguished three types: (i) the *Dothiora*-type, (ii) the *Pleospora*-type, and (iii) the *Elsinoe*-type. Judging from the descriptions, the *Dothiora*- and the *Dothidea*-types comprise the ascolocular Ascomycetes with pluriascous loculi (group 1b), the *Pleospora*-type represents the pseudoparaphysate Ascomycetes (group 2a), while the *Elsinoe*-type might be called the 'true' ascolocular Ascomycetes with monascous loculi (group 1a).

From the term "developmental type" one would suppose that the ascocarps of the fungi of a certain type all develop similarly. On the contrary, the ascocarps of several of them develop very differently. An example of this is to be found in the following species which Luttrell regarded as belonging to the *Pleospora*-type.

PLEOSPORA HERBARUM (Fr.) Rabenh.—The first authors to describe details of development of this species are Cavara & Mollica (1907), but from their cursory description it is impossible to acquire an accurate picture of the development of the ascocarp. A better description has, however, been provided by Kerr (1961).

Kerr established that the young stage of the ascocarp consists of a spherical, pseudoparenchymatic body. She did not explain, however, how this body comes into being, so that the initial stage remains unknown. According to her the pseudoparenchymatic body becomes differentiated into a central part composed of vertically aligned hyphal elements and a pseudoparenchymatic stromal wall, to which the hyphal elements are attached by their tips and bases. She concluded that they were attached at both ends from the beginning. It is, therefore, very likely that they come into being by the stretching and intercalary growth of the central cells of the pseudoparenchyma. As the hyphal elements are derived from the original stromal tissue and precede the asci, they are pseudoparaphyses. Kerr's Fig. 4B

(p. 477) shows that in the mature ascocarps the tissue in the top of the stromal wall disintegrates. Hence the pseudoparaphyses, originally connected with that part of the stromal wall, develop free tips.

The peripheral cells of the stromal wall turn compact, hard, and dark-coloured, constituting a distinct protective wall; for this the term t i c h u s is proposed.

Of the development of the asci nothing was stated except that they arise from the bottom of the locule.

VENTURIA RUMICIS (Desm.) Wint.—The ascostroma of this species very probably initiates in the same way as the ascostroma of *Pleospora herbarum*. The initial stage of the stroma of *V. rumicis* is illustrated by Kerr in Fig. 2A (p. 471). It may easily be mistaken for a cell-fusion, which explains Cavara & Mollica's impression about the initiation of the ascostroma. The short bundle of crowded hyphae that sprout from the point of initiation soon constitutes a paraplectenchymatic body that is attached to a single hypha.

SPORORMIA LEPORINA Niessl. — The ascostroma of this fungus initiates as a single cell on a hypha (Arnold, 1928). Subsequent divisions in three directions cause the initial cell to grow out to become a true parenchymatic body. In the course of development the central cells of the body become detached from one another, resulting in the materialization of a central cavity. The original parenchyma continues its growth to constitute the stromal wall, while its peripheral cells turn brown, to form a tichus. In the top of the wall meristematic tissue is formed, from the cells of which pseudoparaphyses arise that grow down into the cavity. The apical cells of the pseudoparaphyses are swollen and are unusual in that on reaching the bottom of the cavity they form a placenta which produces the asci.

Comparison of the way the ascostromata of *Sporormia leporina* and *Pleospora herbarum* develop shows that they are basically different as to their origin and the formation of their structures. The ascostroma in *S. leporina* is parenchymatic, that in *P. herbarum* paraplectenchymatic. In the stroma of *S. leporina* a true cavity is formed, whereas in *P. herbarum* the locule is purely illusory, being only suggested by the different structures of the centre and the wall. The pseudoparaphyses of *S. leporina* grow downward from the roof of the cavity; the paraphyses of this type may be termed c a t a p h y s e s (κάτα = downward). The pseudoparaphyses in *Pleospora* are formed by the stretching and intercalary growth of the cells between the top and the bottom of the stromal wall. They remain connected with the top and bottom of the wall as long as possible. For this type of pseudoparaphyses the term t i n o p h y s e s (τείνω = to stretch) is proposed. As shown in the foregoing, the types of development of the two species under discussion have little in common.

OPHIOBOLUS GRAMINIS Sacc.—This species was discussed by the present author in the preceding paper (Groenhart, 1965). He came to the conclusion that the ascocarp is to be considered ascohymenial, so that its development is certainly not of the *Pleospora*-type.

MELANOMMA PULVIS-PYRIUS (Pers. ex Fr.) Fuck.—Chesters' description (1938) of the development of the ascocarp of this species is very incomplete. The young stage of the ascocarp is a more or less spherical, pseudoparenchymatic body with a core of thin-walled cells. This calls to mind the structure of a young ascocarp of *Ophiobolus*, as is also true of the way the branched and connected hyphal elements within the ascocarps are formed. However, nothing is said about the way the ascocarp initiates or about the origin of the cells of the core. Consequently, it is even impossible to decide whether the ascocarp is ascostromatic or ascohymenial.

PSEUDOTRICHIA AURATA (Rehm) Wehm.—Wehmeyer (1941) gave the following description of the development of *P. aurata*. The primordium of *P. aurata* consists of a mass of intertwined vegetative hyphae. Within the primordium a cavity is formed. The original stromal tissue constitutes the stromal wall which becomes differentiated into a hyphous inner layer and a tichus of brown-walled cells. From a meristematic tissue in the roof of the cavity cataphyses grow downward into the cavity. No written information is given about the tips of the cataphyses, but from Fig. 11 it may be seen that they are not swollen.

The ascocarps of *P. aurata* and of *S. leporina* agree in that in both a central cavity that becomes filled with cataphyses is formed. However, they differ considerably in the initiation and structure of the stromal tissue. The cataphyses are also different; those of *P. aurata* lack the swollen tips which constitute the placenta in *S. leporina*.

The examples discussed above show that what Luttrell thought of as belonging developmentally to his *Pleospora*-type actually comprises various fungi which differ widely in the mode of development of their ascostromata. The only feature they have in common is the formation of pseudoparaphyses in the centre of the ascostromata. These pseudoparaphyses, however, come into being in a number of very different ways that are not at all comparable. Moreover the ascostromata also initiate in quite different ways. Hence the pattern of development of the ascostroma of *Pleospora* is in no way typical of the entire group. The group would, therefore, have been better characterized by a name relating to the internal pseudoparaphyses.

By a "development type" the present author understands the entire sequence of changes during development, starting with the initiation of the ascostroma and ending with its maturity. As far as the ascostroma is concerned, the type of development is considered to be characterized by the mode of initiation, the kind of hyphal elements present in the ascostroma, the presence or absence of a stromal wall, and the way these are formed. In accordance with this view the author proposes to apply the term *Pleospora*-type only to the mode of development revealed by the ascostromata in *Pleospora*. This type is characterized by (i) the paraplectenchymatic initial stage of the stroma, composed of coalescent initial hyphae, (ii) the differentiation of the initial stage into a central and a peripheral tissue, (iii) the transformation of the central tissue into tinophyses, (iv) the formation of a distinct outer wall by the peripheral tissue.

The *Sporormia*-type is quite different, being characterized by (i) a true paren-

chymatic initial stage originating from a single initial cell, (ii) the formation of a central cavity within the initial body, (iii) the production of cataphyses growing downward from a meristematic tissue at the top of the cavity, (iv) the stromal wall which is formed by the undifferentiated tissue of the original body.

Types of development which would otherwise appear to be more or less related can thus be distinguished from one another. On the basis of these relationships it should be possible to establish taxa on which to build up a system in which at least the lichen-fungi may be arranged more naturally than in the current systems, both lichenological and mycological.

It may be pointed out here that in lichen-fungi the ascocarp is not always identical with the ascostroma. In several species the ascocarp is composed of the ascostroma clothed with one or two layers that are not produced by the ascostroma.

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