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# THE DEVELOPMENT OF THREE SPECIES OF THE AGARICACEAE AND THE ONTOGENETIC PATTERN OF THIS FAMILY AS A WHOLE

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(With Plates 48–50 and one Table)

The developmental types within the family Agaricaceae vary considerably but it looks as if the ontogenetic pattern is not without regularity. About 20 species have been examined. On one side the stipitocarpous genera *Cystoderma*, *Phaeolepiota*, and *Chamaemyces*, on the other side genera with highly concentrated primordia like *Macrolepiota* and *Agaricus* (isocarpous, pileocarpous or hymenocarpous). *Lepiota*, *Leucocoprinus* and *Leucoagaricus* with a more concentrated development may occupy an intermediate position. Some remarks are made on developmental problems in *Squamanita*.

In *Chamaemyces fracidus* the radiating elements on the cap are not a palisadodermium sensu stricto but they belong to the universal veil. However this structure is limited to the pileus-surface, so we have to suppose that an ontogenetic factor affects in some way the formation of the pileus and that of these radiating elements. In other species a layer of tightly packed, erect elements forming part of the universal veil envelops also the pileus-margin and the upper part of the stem (with *Lepiota clypeolaria* at the outside and with *Lepiota ignipes* as an emanating veil at the inside of the universal veil). A trichodermium which is afterwards changed into a paradermium is to be found in *Leucocoprinus* whereas a true palisadodermium occurs in *Macrolepiota*.

## INTRODUCTION

It was Monsieur V. Fayod (1889) who, under influence of the evolution theory, divided the Agaricales into a number of series (tribes, genera) with independent and convergent development. As an example of such convergent lines Fayod (l.c.: 399) advanced *Amanita* and *Volvaria* according to their external appearances but put them into very different series. At present, however, when we want to visualize the phylogenetic relations within this order we certainly shall not divide it into a number of independent series but we prefer to use the idea of the top of a tree of which the trunk and most of the larger branches have disappeared. Then we can admit that series with a convergent development remain and that, here and there, they are very clear amongst the tangle of tiny twigs.

Since we know that the Aphyllophorales and the Gasteromycetes are involved in the phylogenetic development of the Agaricales in a peculiar way we do not take it for granted that the latter should have originated from one main stock. Long ago there must have been common lines of descent for certain groups of the three large divisions of higher Basidiomycetes.

Because we have examined the development of many species of Agaricales (at the moment more than 150) we have been able to affirm the experience of Fayod and to determine certain convergent lines of development, this time not concerning the appearance or habitus of the fungus but specified organs and their origin.

In our analysis of the veils we frequently came across the same structures. Thus the innate veil (i. e. the veil primarely originating from protenchyma which remains at the periphery of the primordium when the surface of the pileus and the stipe differentiate in the deeper layers) can develop, among other things, into a spherocysts-veil or it can become mucose. We have met with these developments in very different genera (Reijnders, 1963: 352). But the secundary angiocarpies, caused by emanating veils, appear in very different groups as well. Here it is especially remarkable that within one genus such veils sometimes may occur in a few species.

We shall leave out of further consideration the analysis of the veils in so far as it does not have reference to the species to be described below. However, we only want to remark that the appearance of innate veils (and therefore the primary angiocarpies as well) clearly show correlations with the sequence of development, in this sense, that few primary angiocarpies present themselves in stipitocarpous primordia. Yet a good many occur in pileo-, iso-, pileohymeno-, and hymenocarpous species (in the last ones no gymnocarpy). It is namely this sequence of development of the parts of the primordium we have come to consider the most important datum the study of the ontogeny of this group of plants has produced so far. The structure of the primordia varies considerably. Sometimes the pileus, sometimes the hymenophore differentiates first. Such development we have called concentrated.

The history of this discovery has been dealt with in our monograph (Reijnders, 1963). Singer (1975), who considers the ontogenetic structures important enough to devote ample attention to this subject, has, in the third edition of his 'Agaricales in modern Taxonomy', however not emphasized the significance of this phenomenon because: (1) so far too few species have been examined, (2) 'some well-studied genera, though undoubtedly homogenous, show a large number of different types of succession and even *Psathyrella velutina* and *P. pyrotrycha* have different succession types'. So 'one is reconciled with the idea that this character has diagnostic value only when one notices that all volvate Amanitaceae and Volvariaceae are pileocarpous and that all Polyporaceae studied are stipitocarpous.'

This is true to be sure, but we distinguish different gradations concerning this sequence: pileostipitocarpous, isocarpous, and hymenopileocarpous. Besides, there is a difference whether a certain species represents a pronounced type and is e. g. pileocarpous in that sense that the pileus differentiates first very clearly and that it takes rather a long time before we can see the parallel hyphae of the stem. If, for instance, *Lacrymaria velutina* is pileostipitocarpous and *Lacrymaria pyrotricha* pileocarpous then the pileus-margin of the latter should show itself according to the definition only somewhat earlier than the parallel stem-hyphae. But this is something completely different from the pronounced pileocarpy of, for instance, *Amanita* or *Volvaria* of which the complete pileus is clearly shaped long before differentiation of the stipe or before the hymenophore is visible. The difference between the two *Lacrymaria* or *Psathyrella* species is, in this respect, only slight and a certain latitude of variation has to be taken into consideration. Even when we distinguish many types unfortunately not all gradations can be expressed in that way. Nor do we believe that the exterior of the primordium determines the type of sequence completely. Although there is a correlation between shape and sequence one has to know the direction and differentiation of the hyphae to determine the sequence (Reijnders, 1963: 244; Moser, 1960: 32; Singer, 1975: 29).

We have to admit that, writing our publication in 1963, we still thought that there was mainly one general bifurcated line of stipitocarpous development towards pileocarpy and hymenocarpy. The first one should chiefly appear in a definite form in genera like *Amanita*, *Volvaria*, and also *Pluteus*, the latter in many chromosporous genera like *Coprinus*, *Psathyrella*, *Panaeolus*, *Conocybe*, *Bolbitius* etc. The remaining genera should show a smaller concentration and, for that matter, should group themselves between the stipitocarpy of the, in our opinion, lower Agaricales and the strong concentration as has been found in above-mentioned genera. As for this, new experiences have changed our mind. The very pronounced pileocarpy found in *Cortinarius* sect. *Scauri*, the isocarpy met in *Inocybe asterospora* (Reijnders, 1974) and the fact that pileocarpy as well as hymenocarpy is manifest in *Coprinus*, together with other reflections like the isocarpy of *Squamanita* (see the discussion under this heading) and the fair concentration of, for instance, *Deliculata* etc. have convinced us that we are dealing with parallel series in Agaricales as to the concentration of the development. However, we still consider the strongly concentrated forms as specialized because there are so many transitions from stipitocarpy to these concentrated forms occuring in different places (often coupled with innate-veil formation) and, moreover, because the concentrated primordia are to be found in genera which are considered specialized for the reason of other characteristics. Thus we are inclined to attribute phylogenetic importance to these phenomena and to speak of convergent series. We think we could demonstrate these, for instance, in the family of the Cortinariaceae, Strophariaceae, Coprinaceae and, in this case, the Agaricaceae. Of course there also are other similar series, whereas it is quite possible that concentrated forms sometimes are more or less isolated because only the top of an evolution branch remained.

In this publication we hope to demonstrate such a series in fungi which have been considered, in the course of time, as belonging to the family of Agaricaceae.

## DESCRIPTIONS

### CHAMAEMYCES FRACIDUS (Fr.) Donk

1. The first stage represented (Pl. 48A) consists of a slender column (length 2.5 mm, width 720 μm) which is somewhat broader towards the base. The hyphae in this

basal part are strongly interwoven (diameter 3–6.5 μm). In the higher portion of the little stalk the orientation of the hyphae is more longitudinal though always fairly intertwined (diameter 2–4 μm). The primordium is surrounded by a universal veil (width along the stem 400–550 μm) of a loose texture of somewhat wider hyphae (diameter 3–4 μm). At the tip we can see tufts of hyphae growing upwards. The universal veil, though not clearly delimited, may be somewhat broader here and its short-celled hyphae are already radiating in this stage (diameter 3 μm). This uppermost portion of the column has been photographed separately (Pl. 48B).

2. The second primordium of which we represent a median section (Pls. 48C; 49A) shows the origin of the cap (diameter at the level of the pileus 2.25 mm, diameter of the stem 1.5 mm). The pileus has arisen through the formation of a border of protenchyma (the generative tissue) at the periphery of the primordium just below the top and through the growth of these hyphae in a centrifugal and downward direction. The hyphae in the stipe run preponderantly in a longitudinal direction. A differentiation into a cortex zone and a marrow zone is perceptible, the tissue in the latter being somewhat looser, but the difference is not striking. The cells in the lower part of the stem are already inflated (diameter up to 20 μm). The stipe is surrounded by a universal veil (width 120–180 μm) consisting of loosely interlaced hyphae (diameter 2–3 μm), which are metachromatic at the periphery where the direction often is longitudinal.

Though the structure of the pileus trama is quite different from that of the stipe tissue we do not observe an abrupt demarcation between stipe and pileus, the longitudinal hyphae of the stem merging gradually into the completely intertwined tissue of the cap trama. The hyphae of the latter are more swollen in the centre (diameter 3–8 μm) but at the periphery they conserve their protenchymatic character (diameter 2–4 μm, with clamp-connections). Outwards we pass through a zone of very thin loose hyphae running in centrifugal direction and giving rise to a layer of palisades which are closely pressed together (width 30–35 μm; Pl. 48D). Although the palisades at the tip of slender hyphae are relatively short over the centre of the cap as well, they are lacking in the lateral part where the radiating hyphae still are entirely short-celled. Here and there at the outside of the palisade layer we observe fragments of the adjacent metachromatic hyphae of the outermost part of the veil. It is interesting to study the transition of the veil covering the cap into the one at the outside of the stem. This connection is to be found at the outside of the pileus margin. There we notice that the character of the veil is modified rather suddenly. The hyphae of the palisade layer lose their centrifugal direction immediately below the pileus margin and change into the interwoven hyphae of the covering of the stem (Pl. 49B). It is obvious that the palisade is limited to the cap and the question arises whether the palisade layer has to be called a trichodermium or whether it actually constitutes part of the universal veil. In the general discussion we intend to deal with this question in detail.

3. We insert a photomicrograph of a somewhat more advanced stage (diameter of the pileus *c.* 2.6 mm, length 6.4 mm; Pl. 48E) to show that here the plectenchyma at

the base has swollen into a bulb. We could call this inflated portion a primordial bulb, but this structure often is significant of the formation of the primordium as a whole since the first protenchyma arises in its interior (Reijnders, 1974). While *Chamaemyces* is clearly stipitocarpous this is not the case here and the bulb chiefly broadens later on, its cells being very inflated in this stage (diameter up to 45 μm). The demarcation between longitudinal stipe hyphae and interwoven pileus trama has become more clearly defined.

### LEUCOCOPRINUS DENUDATUS (Rab.) Sing.

1. The youngest stage represented shows a slender column (Pl. 49C; width *c.* 360 μm, length *c.* 760 μm), which consists of rather intricate narrow hyphae (diameter 2–3 μm). Though these hyphae in the centre do not run strictly parallel to each other a preponderant longitudinal direction is observable. A basal plectenchyma is not yet sharply outlined. A short distance underneath the summit the hyphae are more densely interwoven and therefore this spot stands out somewhat darker. This is the rudiment of the centre of the pileus. At the outside of this dark-coloured zone the hyphae are loosely intertwined and this is also the case at the side of what will be the stem part later on. Although the universal veil is therefore not sharply outlined we meet with adjacent metachromatic hyphae at the periphery.

2. Before long there will be more differentiation in the upper part of the primordium. We photographed only the head of the column (Pl. 49D; width *c.* 610 μm, length 1.3 mm). Characteristic is a ring of chromophilous hyphae which has arisen in the upper part of the primordium perpendicular to the axis of the primordium. In the median section we observe two dark spots where the parallel hyphae are running down obliquely. These hyphae represent the rudiment of the cap margin and, more inward, of the hymenophore. The universal veil consists of two zones, the inner zone of loosely interwoven, somewhat enlarged hyphae (diameter *c.* 5 μm) and the outer zone of circumjacent periclinal hyphae. The basal plectenchyma is now obvious and composed of inflated cells (diameter up to 10 μm). There is not yet a distinct cap covering; this will differentiate later on. By short radiating hyphae with short cells crowded between the passing hyphae of the veil a chromophilous layer is formed. Afterwards this layer gives rise to a derm composed of a pseudoparenchyma (width of that layer *c.* 50 μm) of irregular isodiametric cells; consequently there is no hymeniderm. The scanty remnants of the universal veil are at the outside of the derm. At this stage the margin of the cap is still attached to the stem by the veil (width at the margin of the downward curved pileus 1.4 mm. We did not photograph this stage).

3. The only picture we insert is that of the pileus margin in a somewhat more advanced stage (diameter of the cap 1.3 mm; Pl. 49E) to show that the veil is of some more importance in this species. The lipsanenchyma is well developed and differs from the inner part of the universal veil by a denser texture of the hyphae.

The lamellae originate by folding. In this stage the derm of the pileus begins to differentiate as we described above. It is obvious that the lipsanenchyma has increased by intercalary growth and perhaps also by the hyphae coming from the stem and the pileus margin. When we compare this part of the primordium with that of similar stages of species like *Leucoagaricus naucinus* (Pl. 50F) or *Leucocoprinus cepaestipes* (Reijnders, 1948: pl. 7 fig. 30) or *Agaricus arvensis* (Atkinson, 1914: pl. 1, fig. 5, 6) we observe a striking conformation.

## LEUCOAGARICUS NAUCINUS (Fr.) Sing.

This species looks much like a cultivated mushroom. We tried to obtain primordia of wild mycelia several times but it seems that even when the carpophores are still young and just coming out of the soil the superfluous primordia have disappeared already. When it turned out that they are very easily grown on about the same compost which is the substratum of the cultivated mushroom (Manz, 1971) I asked Miss G. Fritsche (Mushroom-breeding Station at Meterik, Limburg) to grow them for me; the mycelium was original from a stock present at the 'Centraalbureau voor Schimmelcultures' (Baarn).

1. The very young primordium (Pl. 50A; diameter somewhat beneath the rounded top 755 μm, length *c.* 1.4 mm) consists of a short rather bulbous or conical body with a rounded upper end. The tissue is dense, the protenchyma is composed of interwoven hyphae (diameter 2–3 μm). At the base they have the same character but, here and there, they are slightly more inflated (diameter up to 7 μm). Towards the upper end the hyphae are narrow, densely intricated and they are richer in protoplasmic content. This portion is surrounded by a universal veil (width of this layer 70–100 μm, photographed in detail on Pl. 50B). The veil has not developed at the periphery of the bulbous part, nevertheless it must be called universal veil because it will envelop, in later stages, the part where the hymenophore arises as well. The protenchymatic hyphae of the veil (diameter 1.5–2 μm) are radiating slightly but they also are intricate. At the periphery however, they are periclinal, parallel to the rounded surface of the primordium. We meet here with about the same structure as in the preceding species.

2. When the primordium is somewhat older the shape is more oblong (Pl. 50C; width beneath the tip 680 μm, length *c.* 1.6 mm). The texture is as described above, the basal part with the more inflated hyphae (diameter up to 7 μm) now taking up about one third of the primordium. Then a rather darker central portion follows towards the summit and finally we come to a chromophilous dome surrounded by the universal veil which is even less clearly outlined against the inner tissue than in the preceding stage. The chromophilous portion is, of course, the rudiment of the pileus.

3. The third stage represented (Pl. 50D; width at the level of the hymenophore 770 μm) shows the beginning of the hymenophore in two peripheral tufts of downward and outward growing hyphae under the dome. This is exactly the way in which

this structure arises in *Leucocoprinus cepaestipes* (see Reijnders, 1948: pl. 7 fig. 28). On the left side of the photograph we observe a lighter area due to the fact that some parts of these sections absorb less dye. The cause of this phenomenon is unknown; it concerns only this particular material. We did not meet with it before.

4. It is a characteristic of the material bred this way that twins are often found in it, i. e. there are two primordia united on one bulb. Leaving out of consideration the lighter spots with reduced coloration the twins develop normally and both often reach maturity (Pl. 50E; diameter of the largest specimen *c.* 1.25 mm, of the smallest one 1.15 mm). The bulb consists of rather homogenous and intricate hyphae which are much more inflated in the lower part (diameter up to 10 μm) than in the centre under the stipe (diameter up to 6.5 μm, usually 3–5 μm). The stem is rather highly coloured and still short. It consists of slender, parallel hyphae but the trama of the pileus is again composed of interwoven tissue (diameter of the hyphae *c.* 5 μm). The transition from stipe to pileus trama is not yet abrupt. Under the pileus we observe, at the sides, the downward growing protenchymatic hyphae which will form the hymenophore. The veil which, in the former stages, was very much like that of *Leucocoprinus* has undergone some changes; it now consists of more densely intricate short-celled hyphae and the difference between the radiating part and the outer part of periclinal hyphae is less striking.

Finally, over the pileus, it is almost entirely absorbed into the pileopellis but there will remain at the pileus margin a well-developed veil composed, to a large extent, of the lipsanenchyma and moreover of the universal veil at the outside. We have photographed the pileus margin and the veil of a more advanced stage (Pl. 50F; diameter of the cap 1.65 mm) to compare the structure of this part with that of *Leucocoprinus* and *Agaricus* (see there). The lamellae present themselves as folds and, at the origin, their trama is clearly divergent (Pl. 50G).

Consequently there is in this species a tendency towards pileocarpy and moreover it is bivelangiocarpous.

## DISCUSSION

THE VEIL OF CHAMAEMYCES.— It appears that in the covering tissue of the Lepiotaceae often a layer of erected, radiating elements is to be found. The difficulty however is to decide whether this layer belongs to the universal veil or to the pileopellis. The universal veil is, according to the definition, a separately differentiated part on the outside of the primordium which also covers the spot where the hymenophore originates or will originate and which often covers, at least partly, the stipe (Reijnders, 1963: 27). The pileopellis is a covering layer restricted only to the pileus. The name 'pileopellis' has been proposed by C. Bas to indicate this layer in a general sense because one has attached all kinds of particular meanings to the name 'cuticula'.

Atkinson (1914) has described, in *Lepiota clypeolaria*, a universal veil already existing in a very early stage consisting of an inner zone of more or less pseudoparenchymatic tissue and an outer layer of tightly packed, radiating hyphae. Later on it becomes concrete with the pileus because this one extends through the protenchyma. Anyway this is a universal veil for it is also present at the side of the stem. Less clear is the situation in *Lepiota cristata* (Atkinson, 1916). Here there is also a cap of radiating hyphae in the veil over the pileus but these hyphae will not extend far below the pileus-margin, even in later stages. The photographs show that they are non-existent just under the pileus-margin. The pileus becomes concrete with this layer. The veil along the stipe, actually present, has another structure. One would be inclined to consider the radiating elements here as a trichodermium, but Atkinson regards them as a universal veil, possibly in comparison with *L. clypeolaria.* Now veils with radiating hyphae developing into spherocysts-veils afterwards do really appear in Lepiotaceae: *Lepiota acutesquamosa* (Greis 1937) is a well-known example. Less distinct was the radiating development of the hyphae in the spherocysts-veils of *L. sistrata* and *Melanophyllum* (Reijnders, 1963: 106–107). But also a tricho- or palisadodermium frequently occurs in this family. *Leucocoprinus* has a similar structure dividing into many cells later on while *Macrolepiota* (*rhacodes*) has a distinct palisadodermium with slender, tightly packed palisades.

In *Chamaemyces* we found a peculiar structure which possibly throws some light on the controversy between *Lepiota clypeolaria* and *L. cristata.* Here the young primordium is unmistakably enveloped by a universal veil with a somewhat deviating, looser structure of partly broadened hyphae. Only at the top we already find radiating hyphae at the outset. Afterwards when the pileusmargin has differentiated the entire cap portion is enveloped by a veil consisting of two layers, an outer layer of erect hyphae and an inner one of interwoven hyphae with wider interspaces. The radiating hyphae however end just under the pileus-margin, so that the stem-portion of the veil exists exclusively of intricate hyphae. It is as if an organizing or determinating factor, confining itself to the pileus, asserts itself in the universal veil as well. For because of the continuation of the layer of loose hyphae of that universal veil along the stipe we have to go on calling this structure a universal veil. However, in nature no allowance is made for our classifications. This is also apparent from a structure found by Hugueney (1966) in *Lepiota ignipes* Locquin. This species from the section with spurred spores has, according to Singer (1975: 474) a 'cuticle of the pileus with a palisade'. To the opinion of Hugueney this layer however consists of part of the universal veil which here indeed continues a certain distance under the pileus-margin (but for the greater part not along the stem). At the outside of this layer there is a thin veil with periclinal protenchymatic hyphae. This was not the case in *Lepiota clypeolaria* with which Hugueney otherwise compares the veil. Here it is becoming rather difficult to tell what exactly is the veil and what the pileopellis.

LEUCOCOPRINUS.— We made researches into the development of *Leucocoprinus cepaestipes* before (Reijnders, 1948: pl. 6 figs. 25–27, pl. 7 figs. 28–33). Since it became evident that the development of the very closely related *L. luteus* (Bolt. ex Fr.) Locquin [=*L. Birnbaumii* (Corda) Sing., is homologous to that of *L. cepaestipes*, we do not consider it necessary to photograph and to describe the development of this species once more. In this species again a structure of the young primordium which we could call pileostipitocarpous (in the earliest stages approaching stipitocarpy), again the same way of origin of the hymenophore and pileus-margin, the same structure of the veil and later on of the pileopellis. *Lepiota denudatus* (Rab.) Sing. deviates little from this type. Possibly the pileostipitocarpy is slightly more pronounced or there is even a tendency towards pileocarpy. In a very early stage which here too consists of a slender column, there is a dark spot in the upper part, being composed of interwoven tissue. Only the structure of the 'pileopellis' is slightly different in *L. denudatus.* While *L. cepaestipes* and *L. luteus* both have a pileopellis consisting of closely packed, erect elements which, in earlier stages, we could call a palisadodermium (although the palisades are divided into chains of short cells and the arrangement gets lost later on), *L. denudatus* has, afterwards, a paradermium consisting of several layers of pseudoparenchymatic cells. In both cases the adjacent hyphae of the universal veil are found at the outside.

LEUCOAGARICUS.—Singer (1975: 452) writes: 'This genus is intermediate between *Macrolepiota* and *Leucocoprinus.* The absence of clamp-connections in the trama of the pileus and the stipe makes it possible to distinguish it from *Macrolepiota.*' There should be a number of other characteristics which are more or less correlated with it. Others (Heinemann) consider this genus difficult to define since it includes a number of species not classifiable elsewhere. Be it as it may, the development does support the intermediate position between *Leucocoprinus* and *Macrolepiota.* The concentration (disposition to pileocarpy) is higher in *Leucoagaricus naucinus* than in *Leucocoprinus* but less high than in the pileocarpous *Macrolepiota rhacodes.* And how much does a section like the one in Pl. 50E resemble an analogous section of *Macrolepiota* (Reijnders, 1963: pl. 45 fig. 1). One should, for instance, pay attention to the oblique position of the tardy hymenophore. Singer gives in *Leucoagaricus* the existence of a trichodermium which however can be scattered. In *L. naucinus* the pileus is concrete with the universal veil; there are some broader elements protruding out of the veil but there is no question of a trichodermium.

THE DEVELOPMENT OF THE AGARICACEAE.—We would like to bring together, once again, the most important features of the development of the tested species (*Squamanita* excepted) in a scheme. Most of them are taken from our research of 1963. Thus we can see the *Cystoderma* species with little concentrated development on one side. The monovelagiocarpy and the lack of a differentiated pileipellis also underline the primitive character of these species among which we reckon *Phaeolepiota* as well. But there is indeed a special universal veil consisting of spherocysts originated from a matrix-layer. On the other side there are the genera with a highly concentrated development: *Macrolepiota* and *Agaricus.* The species of these genera also are often provided with a distinct bulb. In the beginning the primordia are bulbous or, at the most, oval. The pronounced bivelangiocarpy with a lipsanenchyma which, later on, develops intensively (so that the mature fungi often have a luxuriant ring) belongs herewith.

We already presumed earlier (Reijnders, 1974) that the long development under ground enabled by the inversion of the succession leads to the origin of large specimen. These indeed are numerous in the genera *Agaricus* and *Macrolepiota*. A second reason for a prolonged subterranean development might be, we suppose, that thus we obtain species which, by inflation of cells, can rise above the soil in a short time which could be an advantage when e. g. the substratum should dry up fast or when the fungi have to make use of a shower of rain to sporulate quickly. Although *Leucocoprinus* does not show a strong concentration of development (pileostipitocarpy) the total structure of the carpophore seems to be related to a rapid unfolding; the thin sulcate pileus, the slender stipe. Possibly one thing and another are also connected with the fact that *Leucocoprinus* is to be found in warm regions or in hothouses.

In the scheme we have given once more the details of the structure of the veil and of the pileopellis accurately. Just the less concentrated forms of Agaricaceae are really specialized as to the covering layers. This is also true when the species are monovelangiocarpous or when the lipsanenchyma is underdeveloped. The difficulties in interpretation what has to be regarded as a veil and what as the pileopellis have been talked about in this discussion before. Apparently factors of development, limited to the pileus, sometimes work in the veil as well. We have to remark however that when the veil consists of a layer of closely packed elements there is no trichodermium or palisadodermium and vice versa. It is remarkable that neither the universal veil nor the pileopellis are particularly organized in the specialized genus *Agaricus*.

As to the ontogeny of the carpophores some other large taxa within Agaricales show about the same picture as the Agaricaceae. We hope to deal with the pattern of development in the Cortinariaceae and the Coprinaceae later on.

SQUAMANITA.—Finally we have to make some remarks on the genus *Squamanita* Imbach (=*Coolia* Huijsman) which we left out of consideration so far. We have examined the development of *Squamanita odorata* (Reijnders, 1952; 1963: 166–169). The ontogeny of this genus is very interesting because of the presence of 'protocarpic tubers'. Unfortunately our material was in a rather defective state and we did not have the disposal of sufficiently young stages to determine exactly the developmental succession. We stated that this succession might be at least isocarpous for the in youngest primordium available hymenophore and cap were present and the stipe was short (Reijnders, 1952: pl. 4 fig. 2). This relatively high degree of concentration is undoubtedly connected with the origin of the primordia in the protocarpic tubers which are presumably specialized primordial bulbs (Reijnders, 1974).

If *Squamanita* should belong to the Tricholomataceae, as has been suggested several times, we might consider this high concentration as a continuation of the developmental trend, met with in some sections of the Tricholomataceae with a somewhat bulbous stem.

Now Bas (1965) and Singer (1975: 481) emphasize the affinity of *Squamanita* with *Cystoderma* and their arguments are very convincing. The existence of an intermediate form, *Squamanita paradoxa* (Smith and Sing.) Bas [=*Dissoderma paradoxum* (Smith and Sing.) Sing.] is especially important in this respect. In one way the close affinity of

*Cystoderma* and *Squamanita* is somewhat astonishing for the species of the first genus, which have been examined, show stipitocarpous primordia.

Up to the present we believed that forms with a highly concentrated development are to be found in several sections of the system of the Agaricales and that at least in some of these genera this phenomenon presents itself without exceptions. We mentioned some of these genera before (see Introduction). There should be a gradual transformation towards the extremely concentrated models, which might prove that the latter did not arise readily in the course of evolution. As yet the instance of *Squamanita* and *Cystoderma*, where the forms with more concentrated development of the former genus are closely related to the stipitocarpous species of the latter, is still a rather exceptional case, which seems to support Singer's idea that different developmental types can occur in the same taxon. The distribution of the froms with concentrated development over the system certainly needs further study. The distribution of the forms with concentrated development over the system certainly needs further study.

Once more, we do not know exactly the degree of concentration of the primordia of *Squamanita*. However, we are inclined to think that this taxon represents the end of a short lateral branch in the pattern of evolution, which has arisen from species with non-concentrated primordia (diffuse development).

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## Résumé

Les types du développement des carpophores dans la famille des Agaricaceae varient considérablement mais son patron ontogénétique n'est pas sans ordre. Environ 20 espèces ont été examinées. D'un côté les genres *Cystoderma*, *Phaeolepiota* et *Chamaemyces* dont les espèces paraissent être stipitocarpes, de l'autre côté les primordiums très concentrés de *Macrolepiota* et d'*Agaricus* (isocarpes, piléocarpes ou hyménocarpes). Les genres *Lepiota* et *Leucocoprinus* occupent évidemment une position intermédiaire comme *Leucoagaricus* dont le développement est plus concentré. Les problèmes concernant le développement chez *Squamanita* ont été traité séparément.

Les éléments rayonnants sur le pileus de *Chamaemyces fracidus* ne représentent pas un palissadoderme dans un sens stricte, mais ils font partie du voile universel. Cependant cette structure se restreint à la surface du chapeau et c'est pourquoi qu'il faut admettre qu'un facteur ontogénétique influe sur la formation du chapeau aussi bien que sur celle de cette couche vélaire. Il y a d'autres espèces où une couche a éléments dressés et serrés enveloppe

TABLE I

| Species | Order of succession | Veils | Pileopellis |
|---|---|---|---|
| *Cystoderma amianthinum* | stipitocarpous | monovelangiocarpous a spherocysts veil, no radiating hyphae | a simple cortex |
| *Cystoderma carcharias* | stipitocarpous | monovelangiocarpous, a spherocysts veil, no radiating hyphae | a simple cortex |
| *Phaeolepiota aurea* | stipitocarpous or pileostipitocarpous | monovelangiocarpous a spherocysts veil, no radiating hyphae | a simple cortex |
| *Chamaemyces fracidus* | stipitocarpous | monovelangiocarpous, no universal veil with radiating hyphae at the outside, only over the pileus | none |
| *Cystolepiota sistrata* | pileostipitocarpous | bivelangiocarpous lipsanenchyma scanty | a cortex |
| *Cystolepiota hetieri* | probably pileostipitocarpous | bivelangiocarpous lipsanenchyma scanty | a cortex |
| *Melanophyllum echinatum* | probably pileostipitocarpous | bivelangiocarpous lipsanenchyma scanty | a cortex |
| *Lepiota cristata* | stipitocarpous | bivelangiocarpous lipsanenchyma scanty | a trichodermium? |
| *Lepiota clypeolaria* | pileostipitocarpous | bivelangiocarpous universal veil with radiating hyphae at the outside | none |
| *Lepiota acutesquamosa* | pileostipitocarpous | bivelangiocarpous, universal veil with radiating hyphae at the outside | none |
| *Lepiota ignipes* | ? | bivelangiocarpous, universal veil with radiating hyphae at the inside | none |
| *Leucocoprinus cepaestipes* | pileostipitocarpous | bivelangiocarpous | at first a palisadodermium |
| *Leucocoprinus luteus* | pileostipitocarpous | bivelangiocarpous | at first a palisadodermium |
| *Leucocoprinus denudatus* | pileostipitocarpous | bivelangiocarpous | a paradermium |
| *Leucoagaricus naucinus* | somewhat pileocarpous | bivelangiocarpous lipsanenchyma luxuriant | none |
| *Macrolepiota rhacodes* | pileocarpous | bivelangiocarpous lipsanenchyma luxuriant | a palisadodermium |
| *Agaricus comtulus* | isocarpous | bivelangiocarpous lipsanenchyma luxuriant | a cortex |
| *Agaricus arvensis* | isocarpous | bivelangiocarpous lipsanenchyma luxuriant | a cortex |
| *Agaricus bitorquis* | hymenocarpous | bivelangiocarpous lipsanenchyma luxuriant | a cortex |
| *Agaricus bisporus* | hymenocarpous | bivelangiocarpous lipsanenchyma luxuriant | a cortex |

aussi la marge pilérique et la partie supérieure du stipe (chez *Lepiota clypeolaria* a la périphérie et chez *Lepiota ignipes* au côté interne du voile universel comme une structure secondaire). Nous trouvons chez *Leucocoprinus* un trichoderme qui se transforme après en un paraderme; un vrai palissadoderme se présente chez *Macrolepiota.*

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## EXPLANATION OF PLATES 48–50

### PLATE 48

Figs. A-E. *Chamaemyces fracidus*: Fig. A. young stage × 17.5; Fig. B. top of A × 94; Fig. C. intermediate stage × 10.5; Fig. D. detail of veil on the pileus of Fig. C × 224; Fig. E. intermediate stage with bulb × 14.

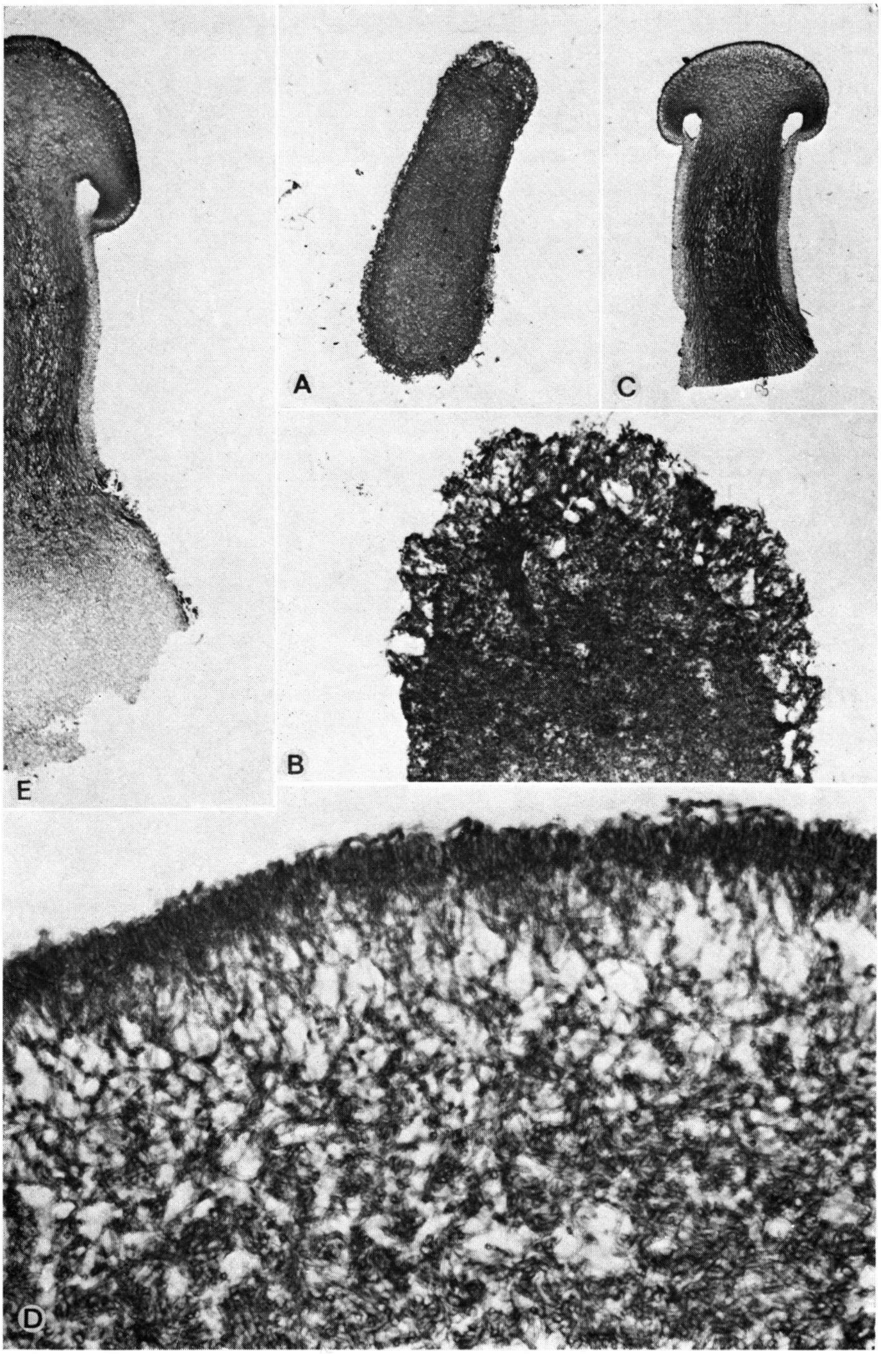
### PLATE 49

Figs. A-B. *Chamaemyces fracidus*: Fig. A. detail of Pl. 48C × 44.8; Fig. B. detail of pileus margin of the same stage × 179.

Figs. C-E. *Leucocoprinus denudatus*: Fig. C. young stage × 82; Fig. D. intermediate stage, upper part × 83; Fig. E. more advanced stage, pileus margin, slightly tangential × 82.

### PLATE 50

Figs. A-G. *Leucoagaricus naucinus*: Fig. A. young stage × 20; Fig. B. veil on pileus of stage in Fig. A × 200; Fig. C. slightly more advanced stage × 32; Fig. D. intermediate stage, origin of the hymenophore × 80; Fig. E. twins, somewhat more advanced as in Fig. D × 20; Fig. F. pileus margin, same stage as in Pl. 49E × 94; Fig. G. the origin of the lamellae in a similar stage × 200.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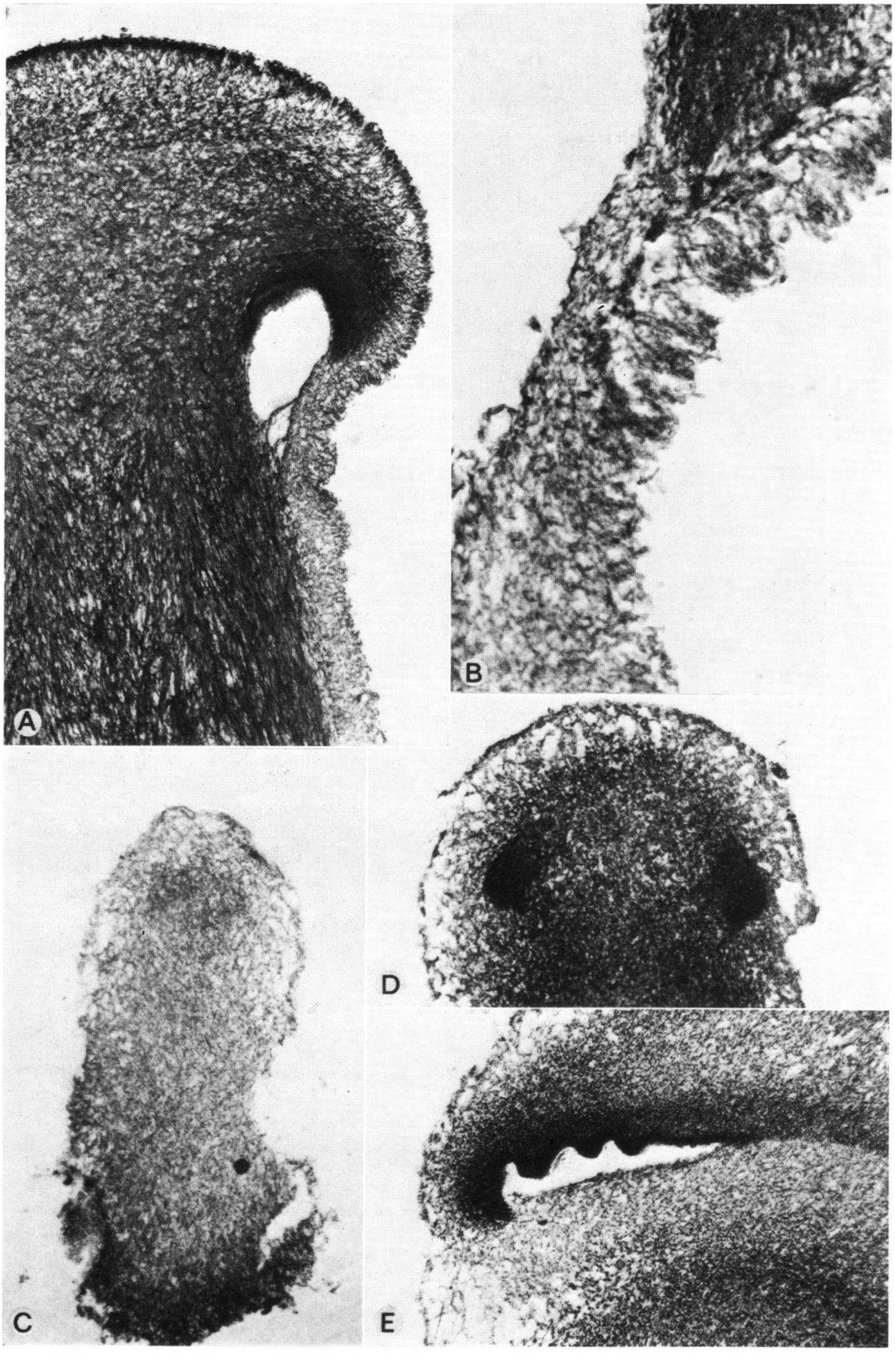
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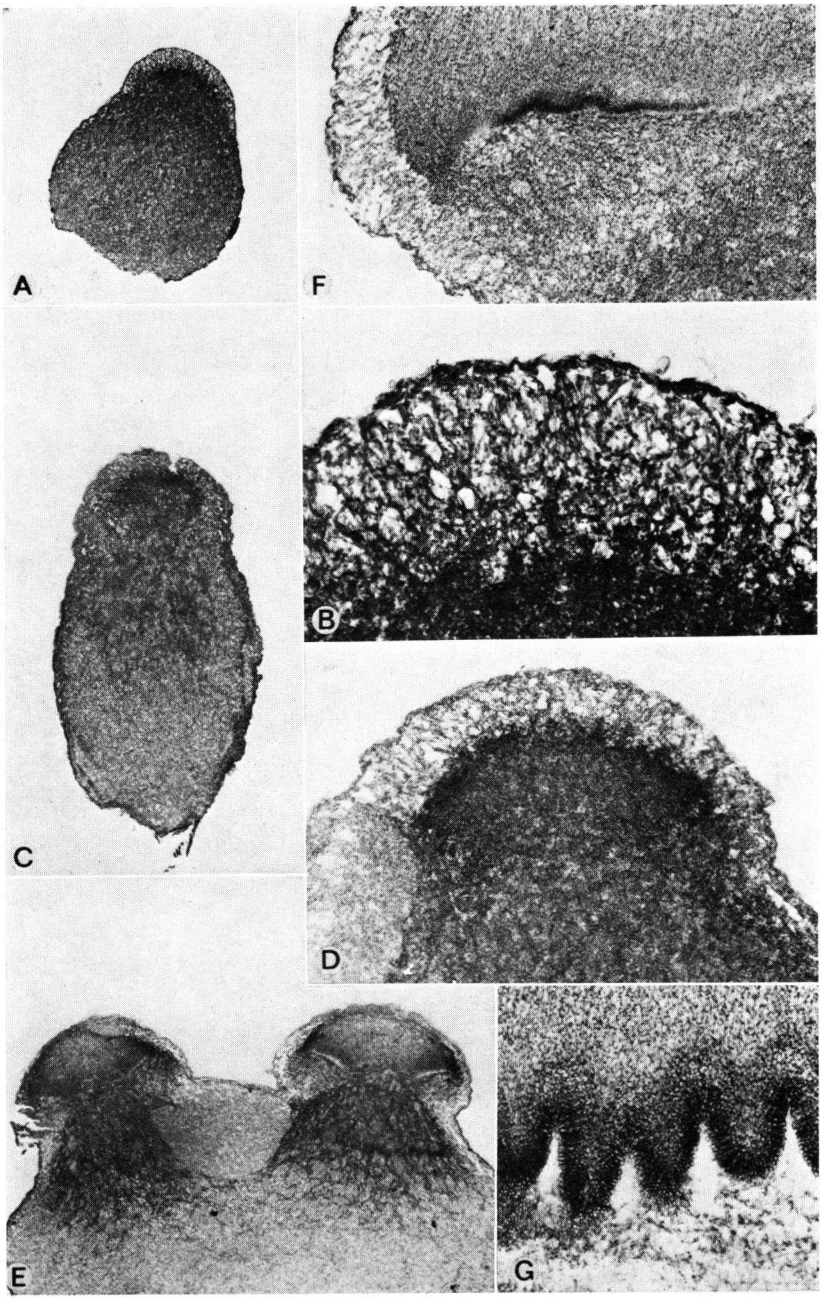
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