On carpophore-development in the genera *Cortinarius,* *Dermocybe* and *Leucocortinarius*

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Introduction

The shape of the very young primordia of the Agaricales varies from a thin stem to a bulb-shaped body; all intermediate forms are present. It is undeniable that this form of the primordia has some systematic significance: we come across the long, stretched-out shape predominantly at one side of the system (Hygrophoraceae, Tricholo-mataceae); the short, ellipsoid or round one at the other side (Vol-variaceae, Agaricaceae, Coprinaceae, Amanitaceae, etc., REIJNDERS 1963: 138—213).

Defined internal structures are correlative with these external shapes. So we meet with stipitocarpous primordia where the stem develops first, mainly in the long and thin form and hymenocarpous or pileocarpous ones with primary development of the hymenophore or the pileus in the short form.

This correlation, however, is not 100%. It has to be noticed that the external shape is probably influenced more strongly by factors of the environment. Thus primordia of fruit-bodies growing in bundles apparently have already a long shape as a result of the way they grow: the stem lengthens at an early stage. One has to look for still younger primordia to determine the sequence of the origine of the parts: stem, cap and hymenophore. Artificial culture-circumstances also can influence the external shape (MOSER 1960: 61).

Already ATKINSON and his school ascertained, as opposed to the opinion of SCHMITZ, that in various species the sequence of development during the primordial condition is not the same (REIJNDERS 1963; 4, 10, 11), but these research-workers could not yet establish a regularity in the appearance of these characteristics when the species were compared.

In our analysis of many primordia we have tried, in the first place, to define more fully what could be considered as a first indication of the shaping of a hymenophore, a cap and a stem (REIJNDERS, l. c. 235—245). The initial phase of a primordium is generally characterized by the appearance of a ball of intricate hyphae; we have called this the

primary protenchyma. This primary protenchyma therefore shows itself before the hyphae start growing into a certain direction. Part of this primary protenchyma soon differentiates into the basal plectenchyma which appears to be present universally at the lower part of the stem of Agaricales-carpophores. Sometimes a bulb originates from the primary protochyma first. The structure of these bulbs corresponds with that of the basal plectenchyma. In such a bulb we come across hyphae of which the cells soon get inflated, but protochymatic hyphae remain in between, out of which, later on, the other parts of the toadstool may develop. Sometimes the top of a bulb remains completely protenchymatic: a densely intricate tissue of thin generative hyphae.

Now we might talk of a hymenocarpous species if the down-growing hyphae in a ring around the axis of the primordium which will develop into the hymenophore, are the first to appear in this intricate protenchyma. We call the species pileocarpous when there are first the downward and centrally directed parallel hyphae of the pileus-margin. But the trama of the cap can also be the first in appearance before these parallel hyphae of the pileus-margin are visible. In that case the whole of the primordium of the pileus presents itself in coloured microscopic slides as a dark dome, consisting of a very dense tissue. Usually we notice these two characteristics of the rudimentary cap appearing simultaneously so that a strongly marked pileocarpy is not difficult to determine. It is much more difficult to find a satisfying criterion for the determination that the stem is under construction. In almost all Agaricales the stem of the mature carpophores is composed of parallel running hyphae (the Asterosporales and some other species are an exception to this, e. g. *Gyroporus cyanescens*). Thus it is obvious to take the appearance of these parallel hyphae as a starting-point for the determination that the stem is beginning to show, even more so because it is difficult to find another criterion. But the hyphae of the primordial bulbs, too, sometimes are in a slightly longitudinal direction or those of the primary protochyma above, without our being able to speak already truly of the development of a stem. If we should say that a stipitocarpous species has primordia in which (apart from the basal plectenchyma) the parallel hyphae of the stem show up first, even before there is any question of some other differentiation in the top, we have to take into account this complication. We still have to distinguish pileostipitocarpous primordia as well. In these primordia part of the primary protochyma remains interwoven at the top; this part is present from the beginning and thus it does not originate from the parallel running hyphae. For the hyphae of the pileus-trama are practically always interwoven, in stipitocarpous species as well, and then this pileus trama has originated from the interweaving of the first parallel hyphae. But in pileostipitocarpous species the parallel stem hyphae develop more in the centre of the

primordium and above that the interwoven primary protochyma remains. In connection with the upward growing hyphae of the bulb it sometimes is difficult to draw the line between stipitocarpous and pileostipitocarpous.

Nevertheless we thought we had to uphold this distinction since, in many cases, it is clear that the beginning of the pileus trama is formed from primary protenchyma separated from the basal plectenchyma by the longitudinal hyphae which originated under that primary protenchyma. We consider, in this connection, the pileostipitocarpous primordium as an intermediate form between the stipitocarpous primordium and the pileocarpous one. Thus the presence of a plectenchyma of protenchymatic hyphae at the top-end of the primordium since the very beginning is the criterion that matters here. It stands to reason that these structures can only be followed in the very early stages of their development. When in the publications of the school of ATKINSON, notably those by DOUGLAS (1916), it is mentioned that the stem is formed first, we shall have to be careful because here our histological criteria are not handled and because sometimes one relies more on rather vague contours.

Apart from these two publications from the school of ATKINSON (DOUGLAS 1916, SAWYER 1917) there has been done little research about the development of the fruit-bodies of the extensive genus *Cortinarius*. We were very much surprised at the research of two species of the Cortinariaceae (*Cortinarius calochrous, Inocybe asterospora*: REIJNDERS 1974) to find very pronounced pileocarpous forms. These are species with a marginated bulb. Now, within the genus *Cortinarius* there are species with very slender primordia and with bulbous ones. This has also struck MOSER (1960: 30—32), the authority on Cortinarii. As we are particularly curious about the morphogenetic relations between the types of development and their significance to the systematics (see also REIJNDERS 1975) we have tried, during a number of years, to collect primordia of *Cortinarius* and allied genera with the result that now about 15 species have been examined. It seems useful to us to compare the results. The best way to do this is by composing a conveniently arranged table with the most important characteristics of the development, by which, next to the succession, attention will be paid to the structure of the veil. We are pleased that the species to be compared are spread over the most important subgenera and moreover that they also belong to different groups. Even if the material is far from sufficient to obtain an accurate outline of the relations of the development inside these genera, it nevertheless allows, to our opinion, some conclusions which we shall draw in an observation at the end of this article. First, however, we shall describe some (not all) of the examined species somewhat more accurately in the course of which only the most important characteristics of the

development will be dealt with since it seems superfluous to describe the same structures again and again. The material has been treated according to the usual method (REIJNDERS 1963: 17): the fixative used was Bouin's liquid, the stains were: Mayer's haemalum and saffranin—gentian—violet.
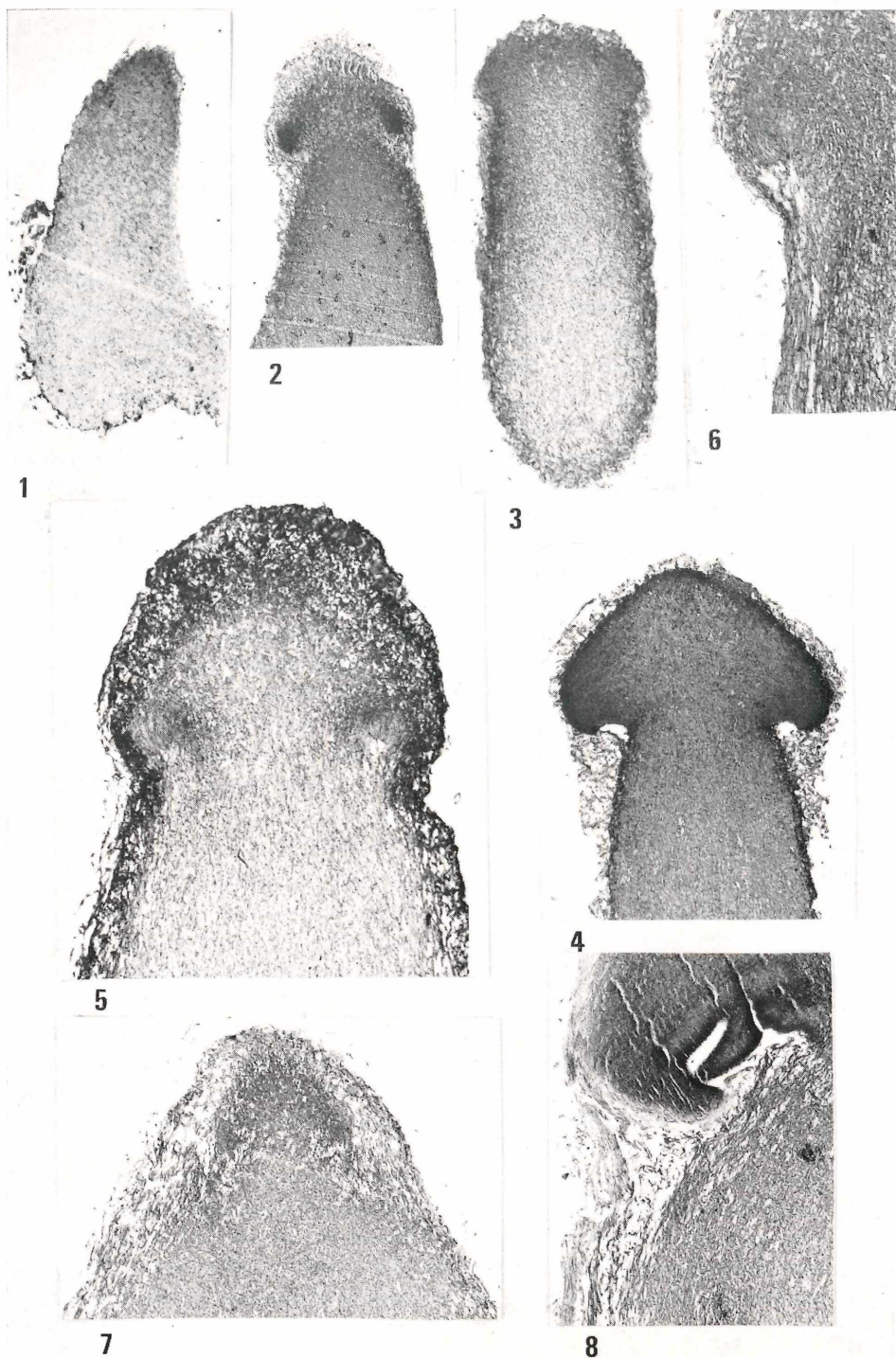
Dermocybe uliginosa (BERK.) MOSER

1. The earliest stage we examined consists of a tiny stem, bent at the bottom, about 2.3 mm long, at the foot about 1 mm wide and at the top below the conical point 567 μ (Pl. 1, fig. 1). It is composed of a basal plectenchyma stretching over 1/3 of the total length. Above that we come across almost parallel hyphae as far as the top. This one is surrounded by more loose protenchymatic hyphae, also longitudinally directed and at the surface slightly interwoven. Since in this slender primordium there is neither pileus nor plectenchyma above the parallel hyphae this species has a stipitocarpous development.

2. Soon, however, there is indeed a cap. This is already the case in a primordium of 2.5 mm length (bent at the base), width at the hymenophore 510 μ (Pl. 1, fig. 2). Here the pileus-margin is formed by a bundle of hyphae curving downward and inward, visible in the median section as two dark spots. The pileus-trama consists of inter-woven protenchyma. The universal veil goes along the stem for a short distance but covers it only at the top, the outer hyphae of the veil are wider (diam. 5—6 μ). So a lipsanenchyma, consisting of proten-chyma, can be distinguished underneath the pileus margin. The hyphae of the lipsanenchyma pass gradually into those of the universal veil.

3. Older stages show that the gills originate by folding, that the trama of the lamellae is divergent and that a cortex of the pileus under the universal veil does not develop until much later.

Cortinarius acutus (FR.) FR.

1. In the earliest stage of this species, examined by us, the pileus-margin has hardly developed, the primordium is slightly conical or a column (width at the pileus-margin about 240 μ, Pl. 1, fig. 3). The largest part of this primordium consists of hyphae mainly in a longi-tudinal direction although they are also rather strongly interwined, especially in the upper part. In the upper part of the basal plectenchyma too, where the hyphae are already inflated, we meet with a predo-minantly longitudinal direction. The universal veil is still narrow and borders only the upper part of the primordium. It consists of adjoining hyphae, directed upward only over the cap, but having there at the outside a periclinal direction as well (width of the veil hyphae 3—6 μ).

1. *Dermocybe uliginosa*. Youngest stage before the pileus shows up. ×20;
2. *Dermocybe uliginosa*. Somewhat more advanced stage. Beginning of pileus-formation. ×32; 3. *Cortinarius acutus*. Young stage. Beginning of pileus-formation. ×50; 4. *Cortinarius hemitrichus*. Somewhat more advanced stage. The cap and the homogeneous veil. ×32; 5. *Cortinarius delibutus*. Somewhat more advanced stage with cap-rudiment. ×50; 6. *Cortinarius camphoratus*. Somewhat more advanced stage. Pileus-margin and veil. ×50; 7. *Cortinarius limonius*. Young stage. Upper part of the primordium with pileus-rudiment. ×32; 8. *Cortinarius limonius*. More advanced stage. Pileus-margin with duplex veil and lipsanenchyma. ×32

2. Later on the hyphae of the veil form more tufts e. g. along the stem. Remarkable are the balls of short cells in highly intertwined parts. There is a thin line of lipsanenchyma consisting of thin protenchymatic hyphae.

3. Later stages (width of the cap about 1.9 mm) make it clear that the lamellae originate from folding, that the lamellae trama is divergent and that the pileïpellis can be best described as a cortex with short cells so that this looks like a pseudoparenchyma in the sections. This is covered by the universal veil of which the hyphae on the cap have a periclinal direction; from the pileus-margin to the stem the veil also consists of a bundle of parallel narrow hyphae but on the stem itself the veil develops flocks. Of the lipsanenchyma nothing much can be seen anymore. We should rather like to call this species pileostipitocarpous (because the strictly parallel hyphae of the stem present themselves only later on); thus it is just like the previous species bivelangiocarpous but the lipsanenchyma has been scantily developed and also it is neither strengthened by hyphae of the surroundings nor by intercalary growth.

Although the veil of *Cort. hemitrichus* (FR.) FR. is wider, more flocky and looser in earlier stages (Pl. 1, fig. 4), the development of this species looks so much like that of *Cort. acutus* that we think we should omit a description and restrict ourselves to giving the most important data in the table.

Cortinarius delibutus FR.

1. The development of this *Myxacium*, the only one that has been examined so far, is somewhat more complicated than that of the two previous species because of the appearance of a chromophil stratum of intensely intertwined thin hyphae at the upper side. This stratum belongs for the greater part to the cap trama but is, at the same time, the matrix of the universal veil. The stratum is already present in the earliest stages when no differentiation of cap and stem has taken place so far. Under and inside this stratum the hyphae of the future cap trama are also interwoven while underneath there are the parallel hyphae of the stem. A few of these examined early stages were respectively 1.2 mm long and about 200 μ to 378 μ wide. At the very bottom there is the basal plectenchyma with already widened hyphae. The universal veil shows up already as a narrow zone of more or less parallel hyphae at the exterior. On account of the plectenchyma in the upper part which is already present so early, we may call this species pileostipitocarpous.

2. When the pileus margin and hymenophore start developing by forming a ring of parallel protenchymatic hyphae at a right angle to the axis of the primordium, part of the above mentioned darker

coloured stratum remains at the outside of this ring and continues towards the stem; the matrix of the universal veil (Pl. 1, fig. 5, diam. of the primordium at the future hymenophore 770 μ). The dark stratum at the periphery of the cap trama is about 250 μ wide, the part going on towards the stem at the level of the hymenophore about 80 μ. The universal veil is at this stage already rather strongly mucous on the cap, less so on the stem where it is visible as a thin stratum of highly coloured hyphae.

3. In the further course of development very few fundamentally new structures appear. Noteworthy is that the universal veil, consisting at the outside mostly of periclinal hyphae, will also show loose, dispersed hyphae locally, possibly because of the developing mucus. There is only little lipsanenchyma. At later stages the veil, consisting of a bundle of parallel hyphae, joins the pileus margin and the stem until the veil breaks. The peripherical stratum of the cap trama now becomes a dense cortical structure. Clamps are numerous in the veil.

Cortinarius camphoratus FR.

1. The early stages examined by us consisted of a rather wide column or an oval-conical body e. g. 6.4 mm long and 1.8 mm wide. Everywhere the hyphae are intertwined, longitudinally directed hyphae do not yet exist, the cells can be wide already (diam 16 μ), which is especially the case in the upper section. The primordium is surrounded by a stratum of narrow hyphae (protenchyma) either in longitudinal direction or more or less intertwined.

2. The pileus-margin is formed by hyphae bending outward and downward. This happens inside the surface so that there is a veil outside the pileus margin. This veil is only slightly more than a thin line of protenchyma which runs along the pileus margin to the stem (Pl. 1, fig. 6). There is hardly lipsanenchyma, some hyphae underneath the evolving pileus-margin are being pulled apart. At this stage part of the hyphae in the stem section is longitudinal but some distance below the hyphae of the pileus margin one can still find intertwined tissue.

3. Nothing much alters anymore, the primordia become wide (e. g. diam. 5 mm) but the lateral part of the cap is still only a slightly projecting edge, surrounded by a thin veil mainly consisting of parallel hyphae. The hyphae in the stem now become more and more longitudinally orientated, the veil is, especially on the cap and along the stem little differentiated and hardly distiguishable from the cortex underneath.

This species is therefore very distinctly pileostipitocarpous because of the intricate tissue which in the upper part of the primordium is present from the beginning and is moreover monovelangiocarpous.
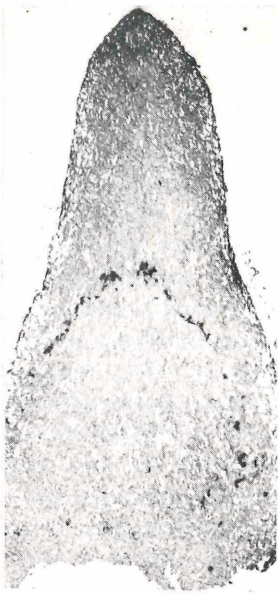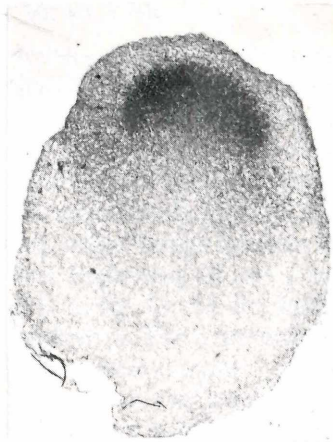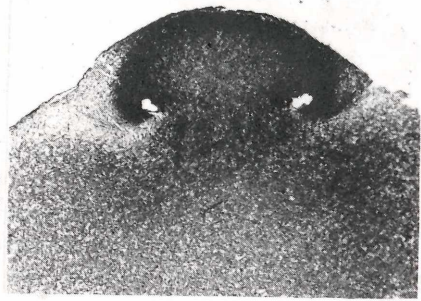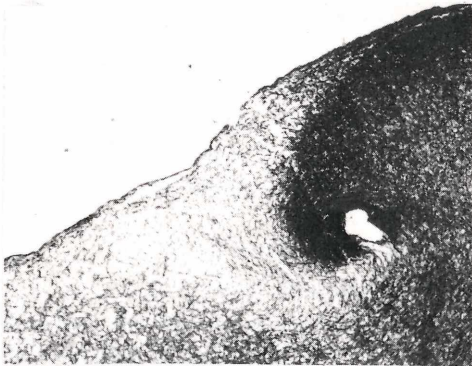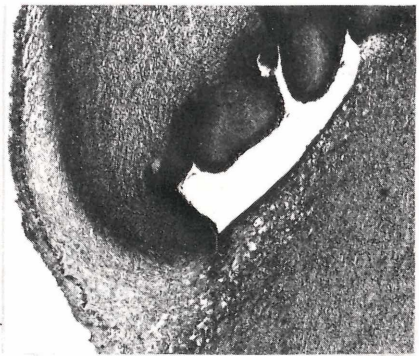
9. *Cortinarius subtortus*. Young stage before the pileus shows up. ×20; 10. *Cortinarius varius*. Advanced stage. Pileus-margin, duplex veil and the rest of the lipsanenchyma. ×32; 11. *Leucocortinarius bulbiger*. Young stage with cap-rudiment. ×20; *Leucocortinarius bulbiger*. Somewhat more advanced stage. The pileus-margin is showing up. ×20; 13. *Leucocortinarius bulbiger*. Rather advanced stage. Cap, lipsanenchyma and universal veil are differentiated. ×9; 14. *Leucocortinarius bulbiger*. Detail of preceding stage. Pileus-margin and lipsanenchyma. ×20

Cortinarius limonius (FR. ex FR.) FR.

1. In this species the sequence of the development has moved more to the pileocarpous structure. It is true that in the earliest primordia which are oval-conical (length e. g. 2.6 mm, largest width just under the middle 1.28 mm) parallel hyphae present themselves in the centre, but above this we meet with a closely interwoven plectenchyma in which, at a somewhat later stage (length 2.9 mm, widest part 1.6 mm), the shape of the cap becomes visible, among other things because two dark spots show up in the section: the first beginning of the pileus-margin with downward pointing hyphae (Pl. 1, fig. 7). At the bottom of the primordium there is the basal plectenchyma. The universal veil, being rather wide at this stage (under the pileus-margin ± 250 μ) surrounds the cap-primordium; it still consists, for the greater part, of periclinal or longitudinal hyphae as far as about half the height of the bulb, but now the characteristic balls of intertwined hyphae, divided into short cells, are already present in several places.

2. A somewhat further developed stage, when the width underneath the hymenophore (parallel palisade-hyphae), already present, is ± 2 mm, shows that the lipsanenchyma consists only of few hyphae passing into those of the universal veil towards the outside, of which the hyphae are up to 10 μ wide (Pl. 1, fig. 8). The lipsanenchyma does not grow anymore. Here the hyphae of the stem underneath the cap are intricate as well.

3. At a still further developed stage (young toadstool, width ± 4.5 mm) the veil between pileus-margin and stem consists of a narrow bundle of parallel hyphae at the outside (the periclinal and longitudinal hyphae). This bundle however breaks. More to the side and along the stem the veil is composed of intricate hyphae forming loose flocks with the above mentioned cell-groups. On the cap the hyphae of the veil are chiefly periclinal. A wide cap-cortex with, for the greater part, highly inflated elements (-16 μ) develops underneath.

The universal veil, slightly more developed in this species, thus has a duplex structure but the lipsanenchyma (accessory of the partial veil) is poorly developed.

Cortinarius subtortus (FR.) FR.

1. DOUGLAS (1916) described the development of *C. infractus* and called the species stipitocarpous. We examined the earliest stages of the related *C. subtortus* (Pl. 2, fig. 9). These are conical and consist for the greater part of plectenchyma, although the hyphae in the centre (diam. ± 5 μ) show a more longitudinal direction and consequently are indeed almost parallel. In the top of the primordium, however, the hyphae are again more intricate. The small body is surrounded by a zone of narrower (diam. $1.5-3$ μ) and looser hyphae with large

Name	Author	Shape of the primordium, succession	Lipsanenchyma	Universal veil
subgenus *Phlegmacium* Calochroi: *C. calochrous* (FR.) FR.	REIJNDERS 1974	globular pleocarpous	a loose tissue under and beside the pileus-margin	Periclinal hyphae at the outside and a looser tissue at the inside. Duplex structure. Not over the stem.
Coerulescentes: *C. caesiocanescens* MOSER	MOSER 1960	globular, probably pileocarpous		Probably as in the preceding species
Coerulescentes: *C. varius* (FR.) FR.	REIJNDERS 1976	unknown	present bivelangiocarpous	Well developed, also over the stem. Duplex structure.
Amarescentes: *C. infractus* (FR.) FR.	DOUGLAS 1916	conical-ellipsoidal stipitocarpous or somewhat pileo-stipitocarpous	bivelangiocarpous	Nearly as in the preceding species
Amarescentes: *C. subtortus* (FR.) FR.	REIJNDERS 1976	conical-ellipsoidal somewhat pileo-stipitocarpous	scanty	Duplex structure
subgenus *Sericeocybe* Anomali: *C. pholideus* (FR.) FR.	SAWYER 1917	a slender column stipitocarpous	rather scanty bivelangiocarpous	The universal veil has duplex structure, but the outer layer consists of radiating or upward growing hyphae, the inner layer of periclinal hyphae
Sericeocybe: *C. camphoratus* FR.	REIJNDERS 1976	a broad column pileo-stipitocarpous	scanty	The veil is thin with duplex structure
Sericeocybe: *C. traganus* (FR.) FR.	KÜHNER 1926	a globular body pileo-stipitocarpous	?	The author does not mention a duplex structure

Taxon	Reference	Shape	Veil	Structure
subgenus *Myxacium* Delibuti: *C. delibutus* Fʀ.	Rᴇɪᴊɴᴅᴇʀs 1976	a rather slender column rather pileo-stipitocarpous	scanty bivelangiocarpous	Well developed with an under-lying matrix-layer and duplex structure, gelatinizing
subgenus *Telamonia* Tenuiores: *C. acutus* (Fʀ.) Fʀ.	Rᴇɪᴊɴᴅᴇʀs 1976	a rather slender column or somewhat conical; rather pileo-stipitocarpous	scanty	At first made up of periclinal or longitudinal parallel hyphae and at the pileus-margin remaining so, floccose over the stem
Iliopodii: *C. hemitrichus* (Fʀ.) Fʀ.	Rᴇɪᴊɴᴅᴇʀs 1976	a rather slender column, rather pileo-stipitocarpous	scanty bivelangiocarpous	Consisting of loose and entangled hyphae from the beginning. No duplex structure
Armillati: *C. armillatus* (Fʀ.) Fʀ.	Dᴏᴜɢʟᴀs 1916	a column pileo-stipitocarpous	bivelangiocarpous	With characteristic duplex structure
subgenus *Leprocybe* Limonii: *C. limonius* (Fʀ.) Fʀ.	Rᴇɪᴊɴᴅᴇʀs 1976	ellipsoidal or nearly globular almost pileocarpous	bivelangiocarpous	Duplex structure; parallel hyphae at the outside and a looser texture with clusters of short cells more inside
Limonii: *C. distans* Pᴇᴄᴋ	Dᴏᴜɢʟᴀs 1916	unknown		Description incomplete but parallel hyphae probably present in the veil
genus *Dermocybe* subgenus Dermocybe: *D. cinnamomea* (Fʀ.) Wüɴsᴄʜᴇ	Dᴏᴜɢʟᴀs 1916	probably a slender column, probably stipitocarpous	scanty	No distinct duplex structure as in the following species
subgenus Dermocybe: *D. uliginosa* (Bᴇʀᴋ.) Mᴏsᴇʀ	Rᴇɪᴊɴᴅᴇʀs 1976	a slender stalk stipitocarpous	scanty	Floccose, no distinct duplex structure but parallel hyphae present at the outside of the veil near the pileus-margin
genus *Leucocortinarius* *L. bulbiger* (A. & S. ex Fʀ.) Sɪɴɢ.	Rᴇɪᴊɴᴅᴇʀs 1976	globular, pileo-carpous	large, a loose tissue under and beside the pileus-margin	Duplex structure as in *C, calochrous*

spaces in between (width of this zone at the top 80—110 μ, lower down it becomes narrower) with on the outside a narrow layer of periclinal or longitudinal hyphae. The loose part together with this narrow layer is the universal veil.

2. The twofold character of the universal veil continues at later stages as well. The lipsanenchyma is small in size. At later stages remaining parts of the veil are as a thin layer of periclinal hyphae on the cap; the partial veil also consists of these periclinal hyphae on the outside and of looser tissue on the inside.

Although this species belongs to the Elastici FR. with a slender stem it is after all amazing that this *Phlegmacium*, the sub-genus in which the strongly concentrated primordia appear as well, is at most pileostipitocarpous. Thus no strong concentration is noticeable here.

Leucocortinarius bulbiger (ALB. et SCHW. ex FR.) SING.

1. The development of this species is characterized by a strongly marked pileocarpy like we have come across in the Phlegmacia with a marginated bulb (REIJNDERS 1974). The earliest stage we have examined still has a homogeneous plectenchyma (width at the base 1083 μ), which is, however, in the upper part more chromophil. There is no clearly differentiated universal veil, the cortex of the bulb is somewhat metachromatic (width ±30 μ). At a slightly later stage (Pl. 2, fig. 11; height ±2 mm, greatest width 1613 μ) a darker coloured dome consisting of densely intricate protenchyma shows up clearly in the upper half: this is the beginning of the pileus.

2. The next differentiation is that of the pileus-margin, showing up by a bundle downward and inward growing hyphae (Pl. 2, fig. 12, diam. ±3 mm). The whole primordium consists of interwoven tissue; neither externally nor by parallel hyphae the stem is perceptible and there also is still no universal veil.

3. At a further stage first the cap becomes more extended (Pl. 2, fig. 13, width of the bulb 7.5 mm). Now there is a narrow zone inside the curled pileus-margin where the hyphae run parallel: this is the very beginning of the stem. Underneath and outside the pileus-margin there is a very loose tissue: the lipsanenchyma which, however, is not yet sharply circumscribed in regard of the bulb tissue (Pl. 2, fig. 14). The forming of a dense pileus cortex results in the remaining of the universal veil (80—100 μ thick) over the pileus. This veil consists of a thin layer of periclinal hyphae at the outside. These hyphae pass into the cutis of the bulb, underneath which, there is a thin layer of looser hyphae. In the pileus-cortex, therefore underneath the veil, there is some mucosity.

4. At a still later stage (width of the bulb at the top ±11 mm) the stem starts to develop more energetically. At the same time the lip-

sanenchyma is also separated from the bulb by the development of parallel hyphae on the surface of the bulb. This lipsanenchyma consists of a rather extended triangular zone of a very loose tissue. At first it remains covered on the outside by the universal veil attached to the edge of the bulb. Consequently the thin fibres of the cortina will run from the cap to the bulb when the stem extends more. Inside the stretched fibres there are looser ones of the lipsanenchyma. The stem itself is, just like in *Cortinarius calochrous* completely free of the veil, due to the delayed development and the more inward situation. *Leucocortinarius* has, at the early stages, a bulb with a rather sharp edge but it lacks the raised border as found in *Cortinarius calochrous* (compare REIJNDERS 1974; Pl. 2, fig. 4 and 6).

Discussion and Conclusions

Succession. The systematic importance of many characteristics of the Agaricales sometimes is rather contradictory. Can they be used perfectly in some groups for the distinction of the genera, sections etc., in other groups they are of considerably less importance (amyloïdity of membranes and tissues, clamp-connections, the presence of a ring in mature carpophores etc.). It looks as if the structures, appearing during the development, are no exception here. Do we find many genera where a strongly concentrated development with globular primordia and pileocarpy, hymenocarpy etc. seems to be the rule (*Amanita, Volvariella, Agaricus* etc.), while in others elongated primordia with a diffuse development appear exclusively (e. g. *Tricholoma, Clitocybe, Hygrophorus*), in the domain of the Cortinariaceae, in which this research is engaged, both types occur and at the same time a wide range of intermediate forms.

On account of the data in the table we establish that closely allied species also generally show the same type of development. We also, occasionally, meet with a deviation of this rule (*Psathyrella pyrotricha—Psath. velutina*; *Armillariella mellea—A. tabescens*), but in that case the deviation remains within certain limits.

We record: in the genus *Dermocybe*, now separated from *Cortinarius*, thin, stalky primordia appear to predominate (notice also the nature of the veil); *Cortinarius traganus* and *C. camphoratus* clearly are pileo-stipitocarpous; *C. acutus* and *C. hemitrichus* show primordia which much resemble each other; *C. calochrous* and *C. caesiocanescens* have the same development, while that of *Leucocortinarius bulbiger* joins in. In the subgenus *Leprocybe* a species appears with rather strongly concentrated development (*C. limonius*); still more remarkable is the diversity occuring in the subgenus *Phlegmacium*. Here *C. infractus* and *C. subtortus* definitely do not show the clear pileocarpous development of *C. calochrous* and *C. caesiocanescens*,

but they are almost stipitocarpous (slightly pileo-stipitocarpous). *C. varius* with a distinct but not marginated bulb and a universal veil over the stem, could be an intermediate form here. We did not have the disposal of the earlier stages of this species and consequently we had to confine ourselves to entering the data about the veil into the table. Now, the relatively small amount of species that has been examined of such a large genus as *Cortinarius* or *Phlegmacium* naturally is not sufficient to determine the relations of these structures accurately. Still, the conclusion seems justified that in the course of evolution concentrated development (at least towards pileocarpy) can originate faster than, at first, we had presumed. Likewise the origin of concentrated forms in very different groups points to that. This phenomenon, as well, could be considered from the adaptation point of view. Probably the concentrated form has something to do with the advantage of the garantee of a longer subterranean development (delayed forming of the stem). About the profits of this for the species we already made some suggestions (REIJNDERS 1974).

As to the phylogeny, we still consider it most probable that in cases like in *Cortinarius* the concentrated form has developed from the slender, diffuse type, in other words, we agree with MOSER and HORAK (1975) that the different forms of *Thaxterogaster* have developed from *Cortinarius*. We should like to add, to the motives of these authors (l. c.: 32—33), our argument, based on the ontogeny. It seems to us much more probable that a cap and a stem, being functional, are subject to regression due to certain circumstances, e. g. drought, than that these organs, first in imperfect condition, therefore non-functional, should have originated from subterranean forms, where they do not have any importance. This does not mean that we do not consider it possible that, in some cases, a subterranean bulb evolves into a fruit-body having an Agaricus-like appearance and emerging from the soil.

We hope to devote further considerations to the histogenetic implications of these problems before long.

The veils in *Cortinarius*. When we compare with other genera of the Cortinariaceae it appears that the veil of *Cortinarius* often has been composed in a rather more complex way. The development of one or more species of *Galerina*, *Gymnopilus*, *Rozites*, *Alnicola*, *Hebeloma*, *Inocybe* is known, beside the development of the species we are dealing with here. An innate universal veil is characteristic for most of these genera. Nowhere the lipsanenchyma shows a strong development, except in *Rozites* and in certain South-American species of *Cortinarius* (MOSER and HORAK 1975), probably also in some species of *Inocybe* and *Hebeloma*, so that, by far, most of the species of this family are monovelangiocarpous. In its most simple form the veil consists of a

rest of protenchyma that remains at the periphery after differentiation of the cap and stem-cortex and which soon is torn apart into flocks. Similar structures, like those we meet in the present-day genera *Galerina* and *Alnicola*, may be called primitive, moreover all these species are stipitocarpous. We gather that *Cortinarius* and *Inocybe* are genera in full development and that they include forms (besides *Rozites* and possibly *Hebeloma*), which are the highest evolved ones in this family.

The complication in the veil of *Cortinarius* consists in the fact that it often has a duplex structure: an exterior layer of periclinal and longitudinal hyphae (along the stem) and an interior of a looser texture. Exceptions to this are only *Cortinarius acutus, C. hemitrichus, Dermocybe cinnamomea* and *D. uliginosa*. In *C. pholideus* the layer of parallel, tightly packed hyphae is more to the inside and the outer layer consists of radiating hyphae. Between pileus-margin and stem there are almost always parallel hyphae, sometimes also coming from the narrow lipsanenchyma. These parallel hyphae of the veil, which hardly grows anymore, explains the structure of the cortina in mature specimens with the cobweb-like longitudinal fibres.

It is remarkable that the lipsanenchyma does not show a secondary growth and confines itself to a narrow zone of protenchyma between the cap and stem. Owing to this the cortina is mainly part of the universal veil; therefore it is more correct not to speak of a partial veil. If a partial veil should really develop (in mature specimens) the lipsanenchyma grows considerably. This could happen through intercalary growth, but it could also be reinforced by hyphae originating from the pileus-margin, the stipe and even from the edge of the lamellae (see e. g. REIJNDERS 1971).

MOSER and HORAK (1975: 20—22) emphasize that in South-American species the lipsanenchyma can develop into a membraneous ring and that there the universal veil also can show a denser texture up to the forming of a volva.

In *Cortinarius delibutus* a mucosity presents itself in the universal veil and that generally will, no doubt, be the case in *Myxacium*. In *Cortinarius calochrous*, too, the universal veil, lying exclusively over the cap, becomes mucous, but in *Leucocortinarius bulbiger* we saw a probably passing mucosity in the pileïpellis. It seems as if in *Cortinarius varius* the veil becomes mucous rather than the cortex.

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