THE VEIL OF AGROCYBE AEGERITA (AGARICALES)

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SUMMARY

An investigation of young primordia of *Agrocybe aegerita* (Brig.) Singer shows that the veil of mature carpophores is of secondary origin. Nevertheless there is also a primary angiocarpy: the species is bivelangiocarpous and pileo-stipitocarpous. Some observations on systematic relationships in the genus *Agrocybe* are made in connexion with these ontogenetic facts.

1. INTRODUCTION

The dark primordia of *Agrocybe aegerita* (Brig.) Singer, a species which is common only in the southern regions of Europe and which occurs in the Netherlands chiefly in some coastal provinces, arise in numerous tufts on the bark of poplars and willows, developing mostly into large groups of light-coloured mushrooms. When we cut young specimens longitudinally we observe a luxuriant veil which is inserted very high under the gills, the edges of the latter being in contact with the partial veil which presents itself as a thick lump of cotton-wool between the underside of the pileus and the stipe. Later on, when the pileus expands, the margin of the cap soon becomes detached from the veil which becomes a thick but narrow ring round the upper part of the stem. The aim of this investigation was to determine the origin of this veil; we examined for that purpose a series of primordia including the youngest stages: they were fixed in Bouin's solution, embedded in paraffin and the sections were stained with Mayer's haem-alum solution.

2. DEVELOPMENT

2.1. The first stage photographed (*fig. 1*) represents a section of a primordium which has a width of 470 μ and a length of 830 μ (the width has always been measured at the level of the hymenophore). At the base where the strongly stained particles of the substratum are visible there is a kind of stroma consisting of intricately interwoven hyphae (3–5 μ wide) with short cells. In the center of the primordium the hyphae show preponderantly a longitudinal direction, nevertheless they are somewhat interwoven (diam. 3–5.5 μ). At the top of the primordium we find somewhat wider (–6.5 μ) radiating hyphae with thicker walls; at the periphery there are more loosely entangled hyphae (–8 μ) with chains of short rounded cells at the end.

2.2. Diameter of the primordium 710 μ. A clear separation of the stipe (with parallel longitudinal hyphae 2–5 μ broad, mostly 3μ) and the trama of the pi-

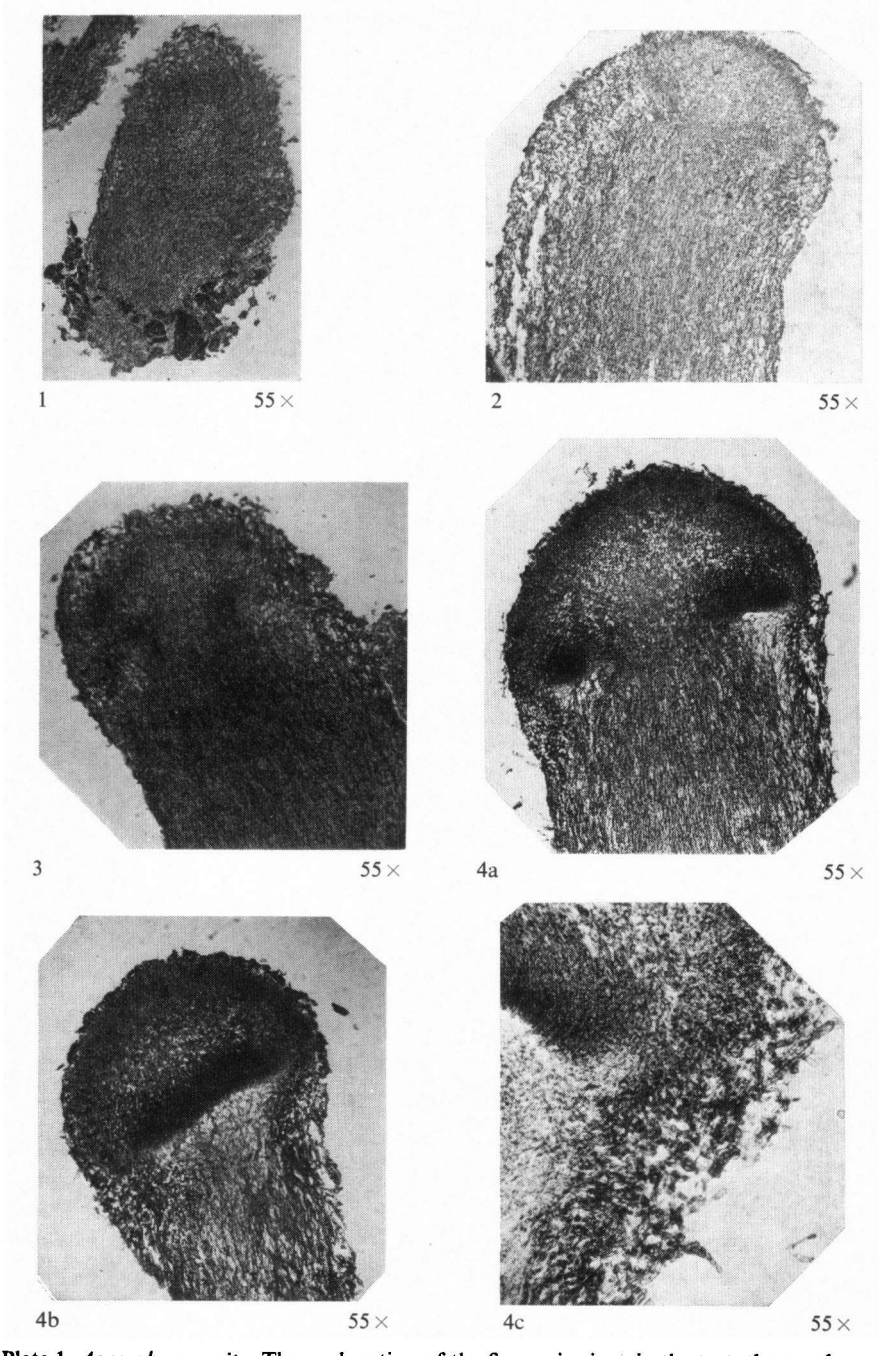


Plate 1. *Agrocybe aegerita.* The explanation of the figures is given in the text, the numbers of the described sections correspond with the numbers of the figures.

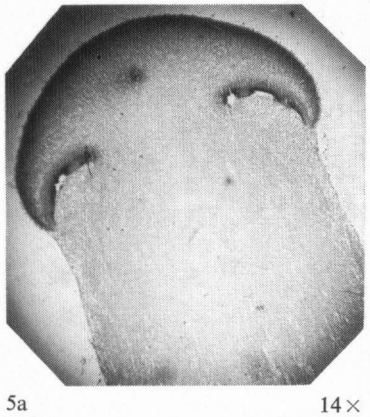
leus with interwoven hyphae of the same diameter has become obvious: the transition is rather abrupt (*fig. 2*). The universal veil enveloping the stipe is only 15–30 μ wide, but at the site of the rudiment of the hymenophore it measures 100 μ. On the pileus there are desintegrating tufts of the universal veil, the radiating hyphae underneath these form a sort palissade: the future derma. Below it there are formed new radiating hyphae which penetrate continuously into this region. The very early beginning of the hymenophore becomes outlined by a somewhat darker staining ring in which the hyphae are directed already outwards.

2.3. The primordium of *fig. 3* (width 670 μ) has the same structure but the universal veil on the pileus is broader (80μ) and still coherent. At the level of the hymenophore it measures 100–120 μ and at its inside the lipsanenchyma is recognizable (as a lighter area).

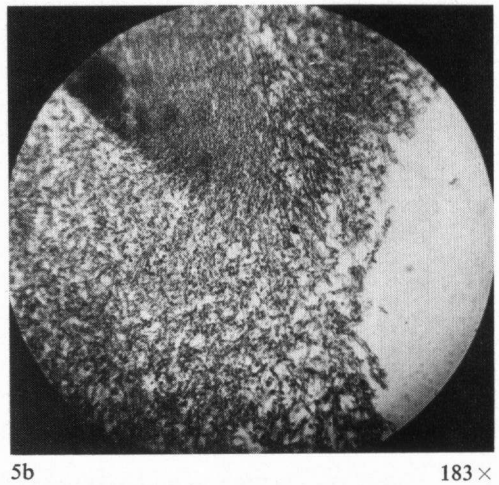
2.4.1. This median section only the apical portion of which has been photographed and which has a width of 790 μ reveals no new details, but the structure of the preceding stages becomes more and more distinct (*fig. 4a*). The hyphae in the stipe are not yet much swollen (diam. up to 6.5 μ). The palissade hyphae of the hymenophore are conspicuous, so is the lipsanenchyma underneath them. The hyphae of this primordial tissue, which is left in the corner between hymenophore and stipe at the inside of the universal veil, are in this case already shrunken, showing that they do not participate in the further development of the partial veil which in this species is a secondary structure. The hyphae of the pileus margin merge already into the veil. The trama of the pileus is still made up of slender hyphae (diam. 2–3 μ). The pileipellis (term introduced by Bas to replace the word cuticle: see there p. 327) consists of a layer of crowded palissades which are in reality chains of short cells. The new palissade-like hyphae arise from a lower region of intricately interwoven hyphae (width of the two layers 100–130 μ).

2.4.2. A tangential section of this stage (diam. 670 μ) shows that the hymenophore-palissades constitute a continuous layer, the downward directed tips arrange themselves at the same level; the surface remains at first somewhat fringed (*fig. 4b*). The lipsanenchyma with degenerating hyphae may be conspicuous. The pileus-margin of a similar stage is shown at a higher magnification in *fig. 4c*.

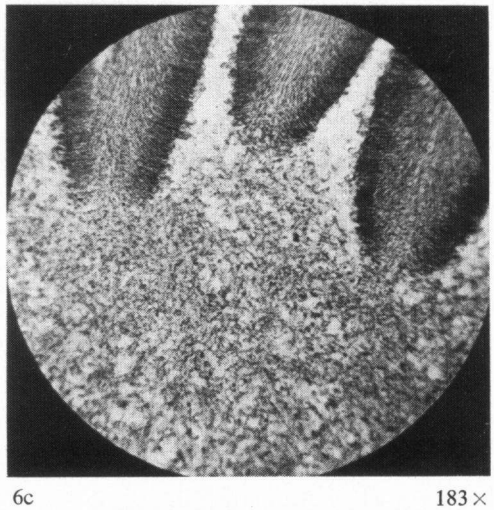
2.5. Now we proceed to a stage of intermediate development. The stipe has already reached a considerable length (which is often the case in species which are growing caespitose) and therefore only the uppermost part has been photographed (diam. 1.64 mm) (*fig. 5a*). The hyphae in the stipe are not yet swollen (diam. –6.5 μ). There are only some sparse remainders of the veil on the pileus and along the stem but it is quite noteworthy that in this stage a new lipsanenchyma is filling up the gap under the lateral portions of the pileus: the whole primordium preserves therefore the shape of a column. This secondary tissue



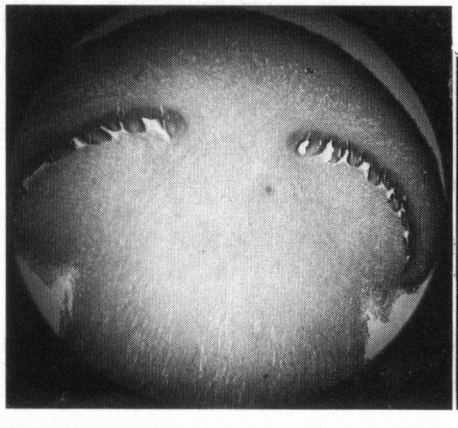
5a 14×



5b 183×



6c 183×



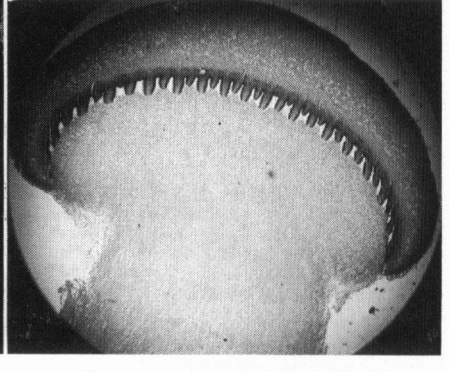


Plate 2. *Agrocybe aegerita* 6a 14× 6b 14×

arises from the upper portion of the stipe, from the pileus-margin (*fig. 5b*) and, as we shall see further, also from the edges of the lamellae which come into existence in the usual way as folds. The edges of these folds open immediately after their origin, allowing hyphae to merge into the veil.

2.6. The median section has a diam. of 5 mm (*fig. 6a*). Now the cells of the hyphae in the lower part of the stipe are mostly swollen (diam. upto 16 μ); at the level of the lipsanenchyma which acquired a great extension they are all still protenchymatic. The trama of the pileus is made up of interwoven hyphae some of which are wider (up to 10 μ). The arching of the pileus is due to the direction of the hyphae near the margin (outward and downward) and to the crowding of the palissades which give rise to the derma. The remnants of the veil on the pileus are scarce but there are many pileocystides which protrude sometimes as far as 30μ and have a slender neck. Under the pileus there is a strongly developed partial veil (lipsanenchyma). The passing of the trama-hyphae of the gills into the veil at this stage is shown in *fig. 6c*, a detail of the tangential section of *fig. 6b*, where the extension of the lipsanenchyma is particularly striking. In consequence of a light expansion of the pileus margin the veil tissue is torn apart from the stipe. The secondary lamellae do not reach the lipsanenchyma. The trama of the lamellae is simply divergent, the tips of the outward curved hyphae become the hymenial palissade, between which many cystides are already present.

3. DISCUSSION

It becomes evident from the study of the development that the veil which exists in nature specimens is a secondary structure. It has been formed by the growing out of hyphae, coming from the pileusmargin, the upper side of the stem, and the edges of the lamellae. A similar structure occurs frequently in various families of Agaricales, but only rarely it is composed of hyphae which emanate from three places: commonly it is restricted to hyphae emerging from stipe and pileus margin (secondary angiocarpy: REIJNDERS 1963: 226, 227, 232–235). We have not often found that the edges of the gills are involved in this process: nevertheless we have met with the striking instance of *Tricholomopsis rutilans* (REIJNDERS 1963: 59, Pl. 17, *fig. 6*) where the hyphae of the gill trama curve outward and have been mistaken for cystides (l.c.: 354).

The youngest stage which we have examined shows that the universal veil constitutes the very first differentiation in the protenchymatic primordium. In this very young specimen the hyphae in the centre are mainly parallel and have a longitudinal orientation, but near the top there is an area where the hyphae are more interwoven. In the second stage the demarcation between the three principal parts: stem, pileus, and hymenophore, is obvious. The trama of the pileus is already made up of interlaced hyphae and the very early beginning of the hymenophore is perceptible. In such cases we prefer the designation pileostipitocarpic as to the order of succession of the parts, although it is near the isocarpic mode of development.

It is remarkable that *Agrocybe aegerita* shows besides the luxuriant development of the secondary veil also an undeniable primary angiocarpy. In very young stages there is an universal veil and a lipsanenchyma. The latter tissue degenerates and is replaced by the secondary veil. *It is therefore of no use and appears to be an inherited remnant expressing the development of the group.* SINGER (1962) devided the genus *Agrocybe* into two subgenera: *Eu-Agrocybe* with truncate spores which are provided with a distinct germ-pore, and *Aporus*. The latter comprises two subsections: *Velatae* and *Evelatae*. *Agrocybe aegerita* belongs to the first section. We examined previously the development of some species of *Eu-Agrocybe: A. praecox* and *semiorbicularis* (REIJNDERS 1952: 35–39). It is a striking fact that in these paravelangiocarpic species the universal veil is completely lacking. The presence of a ring in *Agrocybe praecox* is only due to the lipsanenchyma. There is some evidence that the universal veil is also present in other species of the section *Velatae* of *Aporus* since RICKEN (1915: 460) and MOSER (1967: 232) recorded white flakes on the pileus (near the margin) of *Agrocybe ombrophila* (Cf. COOKE: Pl. 377, 358). *In case the development of Agrocybe ombrophila and erebia would be characterized likewise by the presence of a vanishing universal veil, the contrast between Eu-Agrocybe and Aporus would be accentuated,* left out of consideration the position of *Agrocybe firma* (*Evelatae*).

Obviously the luxuriant secondary lipsanenchyma must be of some significance. We look upon it as a xerophytic adaptation. In this connexion we call attention to the fact that wood-inhabiting fungi with carpophores growing rather high on the trunks of trees frequently show xerophytic structures, such as slimy coatings: *Oudemansiella mucida*, *Pholiota aurivella* and *adiposa* or thick veils: *Pholiota squarrosa*, *flammans* and *destruens*. One should also take into consideration that *Agrocybe aegerita* is a southern species; the summers are dry in its area.

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