

## NEW OBSERVATIONS ON THE BASIDIOME ONTOGENY OF CHAMONIXIA CAESPITOSA (SEQUESTRATE BOLETACEAE)

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The description of basidiome development of *Chamonixia caespitosa* made by Eduard Fischer during the first quarter of the last century is extended, based on a new investigation of the original permanent mounts. This puffball-like fungus is exocarpic, claustropileate and amphicleistoblemate. A hymeniform palisade on the primordial stipe becomes partly covered and obliterated by the pileus margin and an amphicleistoblemma. The morphological data confirm the molecular-taxonomic position of *Chamonixia* in the Boletaceae.

*Chamonixia caespitosa* Rolland is a puffball-like Basidiomycete with a finely tomentose peridium turning blue when bruised. Molecular analyses showed that the genus *Chamonixia* has phylogenetic affinities with the boletes (Bruns et al., 1998; Kretzer & Bruns, 1999).

In 1925 the Swiss mycologist Eduard Fischer published a description of the fruit-body development of *C. caespitosa* based on thick sections that he made from material collected by E. Soehner (1922, as *Hymenogaster caerulescens* Soehner). He strongly emphasised the resemblance of the early stages of *Chamonixia caespitosa* with early stages of gymnocarpic agarics with a free pileus margin, such as *Gymnopus dryophilus* (*Collybia dryophila*), and he explained the puffball-like appearance of the mature basidiome with the fact that the pileus margin grows towards the primordial stipe and fuses with it, while the hymenophore, instead of being regular as in agarics, becomes sponge-like (Fig. 1). Therefore, Fischer (1925) called the development of *C. caespitosa* gymnocarpic, whereas Reijnders (1963), who based his judgement exclusively on the description made by Fischer, called it pilangiocarpic. Fischer described and made drawings of numerous hyphae growing out of the pileus surface and pileus margin, but neither he nor Reijnders (1963) took this fact into consideration when assigning this fungus to a developmental type.

In this paper, the presence of a pileoblema, a cauloblema, a hymeniform palisade on the primordial stipe, and an irregular context in the primordial stipe base are described, using the sections made by Fischer.

### MATERIAL AND METHODS

Eduard Fischer left a legacy of 12 unstained permanent mounts that are conserved at the Institute of Plant Sciences (formerly Botanical Institute) of the University of Bern, Switzerland. The slides were examined with bright field microscopy and photographed with an Olympus D11 digital camera mounted on a Zeiss Orthoplan microscope.



Fig. 1. Early development of *Chamonixia caespitosa*. Drawings by Fischer (1925) and photographs by Cléménçon (2004) of the permanent mounts that served to make the drawings. At first the pileus margin is free, but later it fuses with the primordial stipe. Gleba chambers develop instead of gills. The hyphae growing out from the pileus surface and margin are clearly drawn.

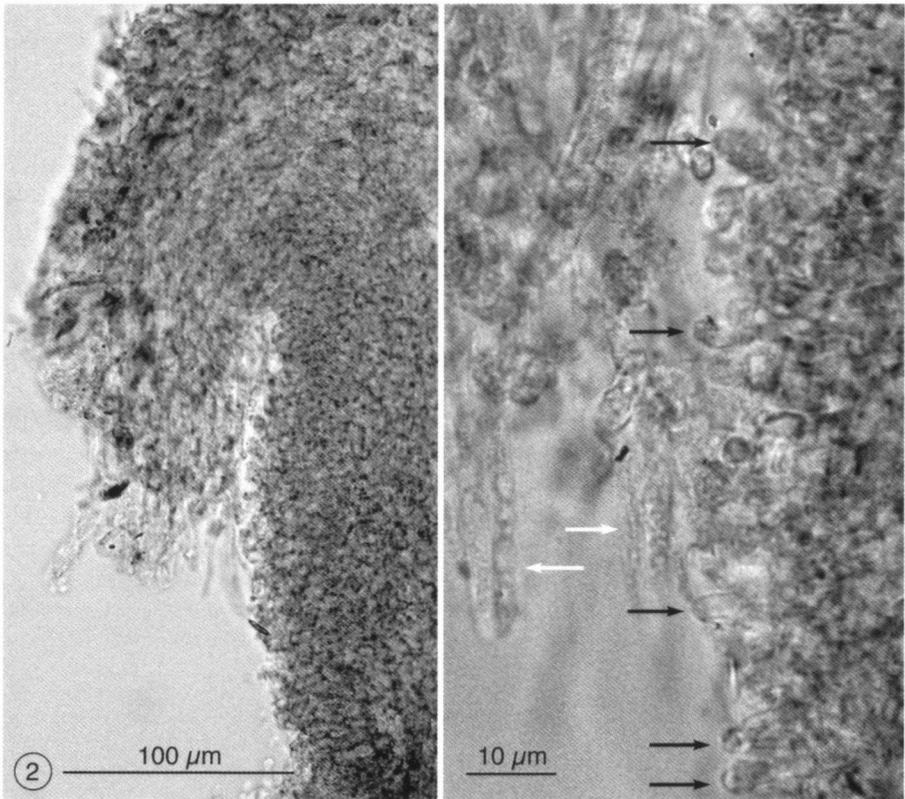


Fig. 2. Hyphae growing out from the pileus margin (white arrows) and palisade layer on the primordial stipe (black arrows) of the small primordium in Fig. 1.

The photographs were adjusted for printing with Adobe Photoshop on a Macintosh G4 computer. Since Fischer's sections are thick, it was difficult to make useful photographs, but the details necessary for a reappraisal are still visible, albeit not in optimal quality.

## RESULTS

The hyphae growing out from the pileus margin and pileus surface are readily visible (Figs. 2, 4). In older primordia, hyphae are also growing out from the stipe surface, but Fischer (1925) did not mention them. The hyphae on the upper part of the stipe grow obliquely upward to meet the hyphae growing down from the pileus margin (Fig. 4), but the hyphae of the lower part of the stipe grow more or less horizontally and intertwine frequently. At maturity, a tomentose layer originating on the pileus and on the stipe covers the entire basidiome.

Inspection of Fischer's slides reveals the presence of a hymeniform layer on the stipe (Figs. 2, 3). It extends from within the narrow fold formed by the pileus margin to almost down to the base and becomes buried under the involute pileus margin and the tomentose layer of outgrowing hyphae. Fischer (1925) does not mention this hymeniform layer.

The context in the base of the stipe is composed of slightly inflated and irregularly arranged hyphae (Fig. 3). This context contrasts with the subregular, vertical hyphae of the stipe, as indicated in the drawings by Fischer (1925), but this author did not pay any attention to it.

## DISCUSSION

Fischer's drawings of the hyphae growing out of the pileus and stipe strongly suggest an emanated veil (Reijnders, 1948, 1963). It is therefore surprising that Reijnders (1963) did not pay any attention to it. Moreover, Reijnders (1963) specifically affirmed that there is no marginal veil in *C. caespitosa*.

In 1997 Cléménçon introduced the concept of metablemas formed by hyphae growing out of almost any part of a basidiome. Metablemas are not synonymous with emanated veils, since the final organs formed by them may become not only veils, but also surface layers such as pileipelles and stipitipelles. The hyphae growing out of the pileus and stipe of *C. caespitosa* are a pileoblema and a cauloblema, respectively. Since the hyphae of the two blemas intermingle at the level of the pileus margin and form a continuous, veil-like layer, *Chamonixia caespitosa* is covered by an amphicleistoblema.

One year after Fischer's publication, Kühner (1926a, b) published his studies on the basidiome development of two boletes, *Suillus grevillei* (as *Suillus flavus*) and *Boletinus cavipes* (Fig. 5). The pilei of both boletes curve down toward the stipe to form a secondary prehyemial cavity. In *Boletinus cavipes* the pileus margin does not quite touch the stipe, but the small distance left is bridged by an amphicleistoblema. In *Suillus grevillei* the pileus margin touches the stipe, and a pileocleistoblema grows down from the pileus onto the stipe. The secondary cavity of both species is lined with a hymeniform layer that also covers the surface of the stipe, extending down well beyond the level of the pileus margin. Part of the hymeniform layer becomes buried under the pileus margin and the cleistoblema.

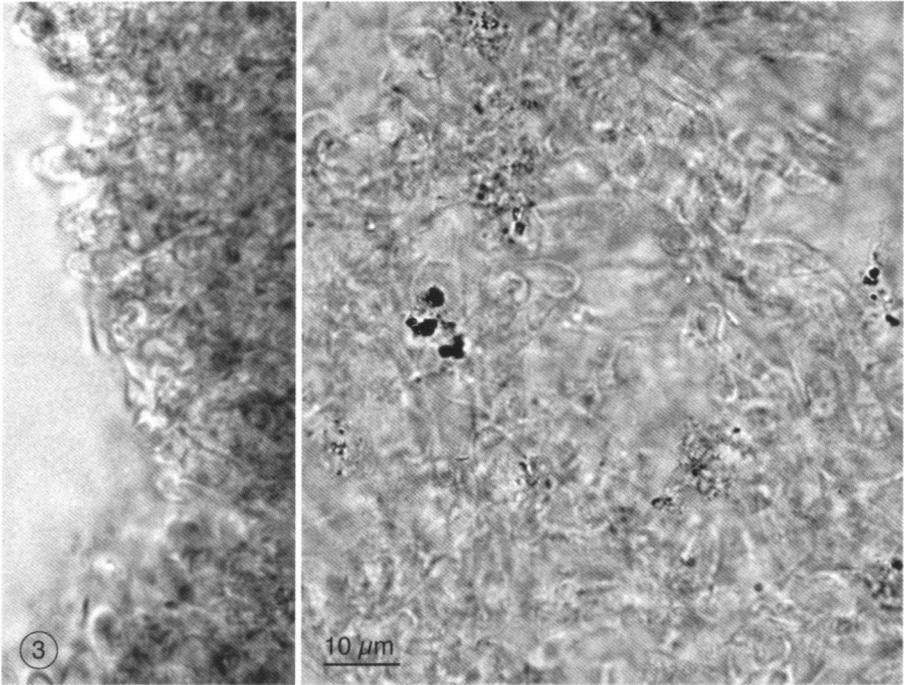


Fig. 3. Palisade layer on the lower part of the primordial stipe (left) and irregular context in the stipe base, indicating the presence of a nodulus. From the small primordium in Fig. 1.

Comparing the carpogenesis of *Chamonixia* with that of the two boletes, we find four developmental steps in *Chamonixia* identical with those described from *Suillus* and *Boletinus*: An involute pileus margin forming a secondary cavity; a cleistoblemma; a hymeniform layer extending from the cavity onto the stipe; and an overgrowth of part of this layer by the pileus margin and the cleistoblemma.

There is still another developmental similarity between *Chamonixia* and the two boletes. The irregularly arranged, inflated hyphae in the stipe base of *Chamonixia* indicate the presence of a nodulus from which a shaft of subregularly arranged hyphae grows up and forms the primordial stipe. Thus, in the terminology of Cléménçon (1997, 2004) *Chamonixia* is epinodular and exocarpic like *Suillus grevillei* and *Boletinus cavipes*.

Conclusion: The development of *C. caespitosa* is remarkably similar to that of the two boletes, confirming the taxonomic conclusion based on the molecular studies mentioned above.

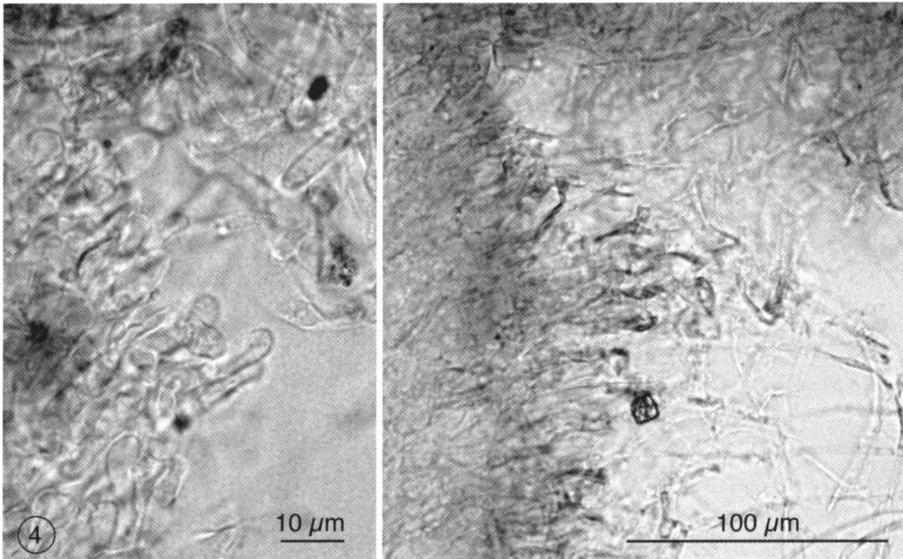


Fig. 4. Development of the cauloblema and the pileoblema. The left photograph is from the right primordium in Fig. 1, the right photograph is from an older primordium not discussed by Fischer (1925). Both blemas form a loose weft of long, thin hyphae and intermingle under the pileus margin, forming an amphicleistoblema. This is the tomentose peridium described by Fischer.

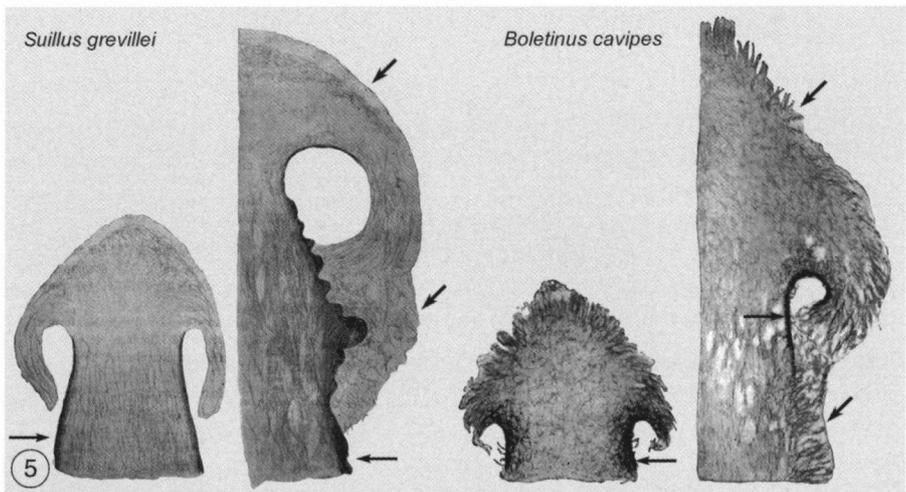


Fig. 5. Carpogenesis of *Suillus grevillei* and *Boletinus cavipes* showing the same developmental details as *Chamonixia caespitosa*: involute margin, cleistoblemas (slanted arrows), and a partly covered hymeniform layer extending from the secondary cavity down over the stipe (horizontal arrows; from Kühner, 1926a, b).

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