

## NOTES AND BRIEF ARTICLES

## THE FORMATION OF AGARIC GILLS

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The spore-bearing gills of agaric fungi are plates of differentiated tissue suspended from the fruit-body cap. Intuitively, it would seem likely that such plates would develop and extend by 'downward' growth of the distal edge of the gill; but this is not the case. Rather, the roots of the gills extend into the steadily replenished undifferentiated tissue of the cap context. The formative element appears to be a gill organizer in the tissue at the extreme end of the gill cavity.

The direction of gill development has been a matter of controversy since the turn of this century. It has been touched upon before as it refers to *Coprinus* species (Rosin, Horner & Moore, 1985; Rosin &

Moore, 1985) but the matter is dealt with in detail by Reijnders (1948, 1963). The crucial question is whether gill differentiation proceeds radially away from the stipe or radially towards the stipe in the

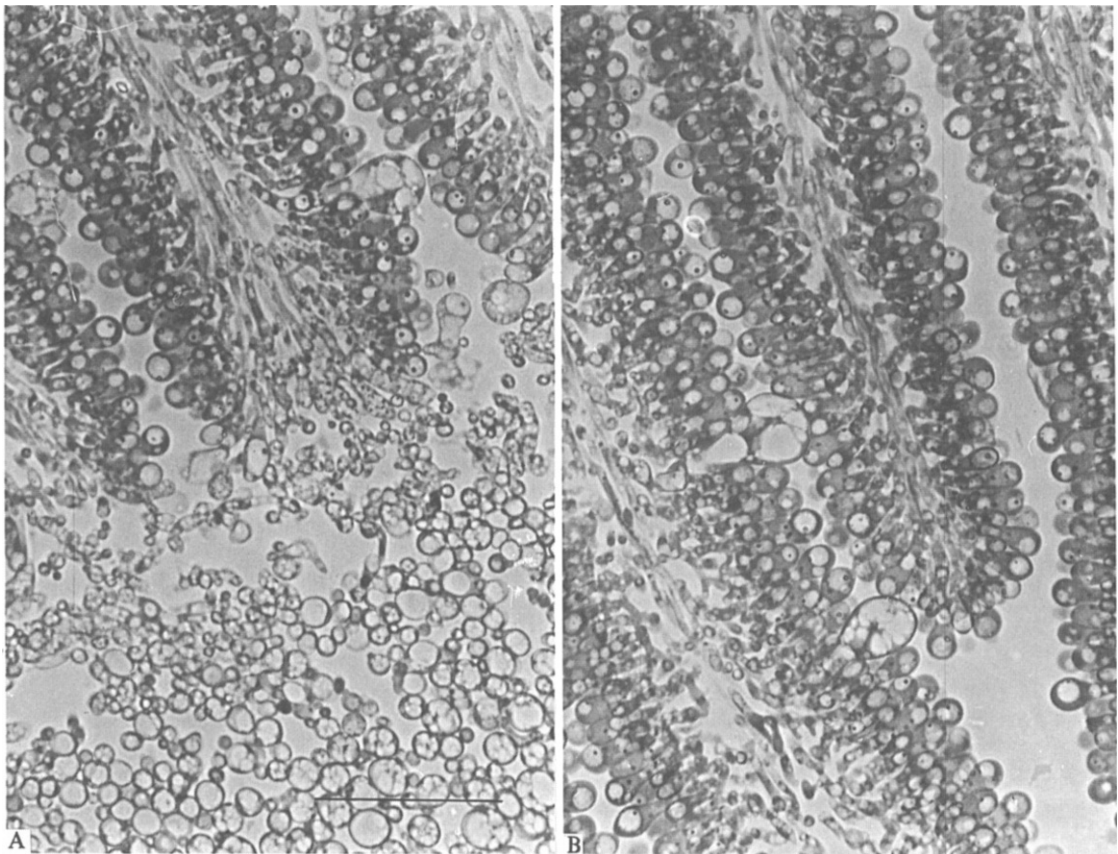


Fig. 1. Comparison of the edges of primary (A) and secondary (B) gills. Note the intimate connexion between the inner gill layer (the trama) and the outer layers of the stipe (which occupies the lower segment of A). In contrast, the hymenium of the secondary gill (in B) is continuous around the edge. Scale bar, 40  $\mu\text{m}$ .

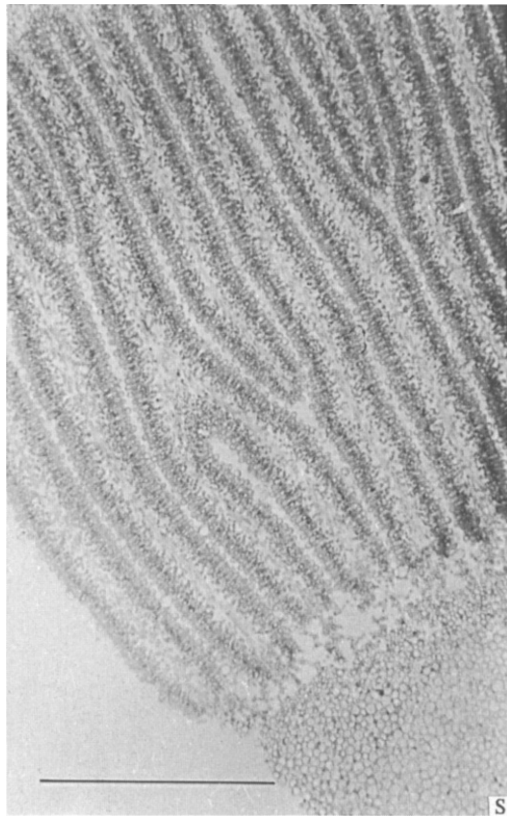


Fig. 2. Showing Y-shaped gill figures. S, stipe; scale bar, 250  $\mu$ m.

rather tubular-campanulate coprinoid primordial cap, or, irrespective of orientation, whether gills generally extend by growth at their edge or at their root (or both, or neither). This is no idle pursuit of some fine mystical point but a fundamental question of fruit-body construction. Control of morphogenesis must be exercised in the growing region; so it is necessary to know which region is growing before anything can be said about developmental regulation in the mushroom fruit body. Unfortunately, it is not possible to make continuous, non-destructive, observations of developing gills in very young primordia. The question has thus far been decided by discussion of the effects of cytological fixatives, by argument about the origin of gaps, spaces and cavities and by claims for detection, in fixed and sectioned material, of the presence or absence of impact or compression forces within and between fruit-body tissues. In the author's opinion two recent observations, coupled with appreciation of the geometry of the tissues involved, establish quite categorically the direction of differentiation in *Coprinus cinereus*

(Schaeff. :Fr.) S. F. Gray, and that the conclusions drawn can be applied with advantage to other gilled fungi.

The primordial coprinoid cap encloses the top of the stipe. Since gills are formed as essentially vertical plates arranged radially around the stipe, their mode of formation can be followed in transverse sections of the whole fruit body. Such a section presents the cap as an annulus surrounding, and concentric with, the stipe, the inner circumference of the annulus being represented by the surface of the stipe and the outer by the surface of the cap tissue. These circumferences increase enormously as the fruit body grows: the former by a factor of 9 and the latter by a factor of 15 as typical fruit-body primordia grow from one to 34 mm in height. This simple fact has some decisive geometrical consequences. There are two types of gill in even the youngest primordia: primary gills which, from formation, have their tramal tissue in continuity with the outer layers of the stipe, and secondary (and lesser ranked) gills in which the hymenium is continuous over the gill-edge (Fig. 1; and see illustrations of other *Coprinus* species by Reijnders, 1979). Considering first the primary gills, one would expect their intimate tramal connexion with the stipe interiorly and cap tissue exteriorly to be prone to widening as both cap and stipe circumferences (topologically, the surfaces to which the hymenia of primary gills are anchored) increase during maturation. But since mature *Coprinus* gills are narrow this cannot proceed to the full extent of the circumferential increase, so such a model would require that the widening be compensated by gill replication, i.e. formation of a new gill cavity and its bounding pair of hymenia within the trama of a previously formed primary gill. This would result in a Y-shaped 'replication fork' pointing in the direction of morphogenetic development of the new hymenia. Of course, an alternative model would be that increase in the circumference of cap and stipe is accommodated by growth between the preformed gills, to open-up space in which secondary gills might arise; but in this case no Y-shaped figures would be seen in transverse sections of the *Coprinus* cap. Such figures are seen, however (Fig. 2), and they are always oriented with the replication fork pointing away from the stipe. Given both the bifurcation of the gill and the trama-stipe connexion of both parts, there is no geometrically satisfactory alternative to the conclusion that primary gills extend morphogenetically away from the stipe; their roots growing into the cap tissue as the undifferentiated plectenchyma is continually renewed in the outer cap layers.

Consideration of secondary gills hinges on

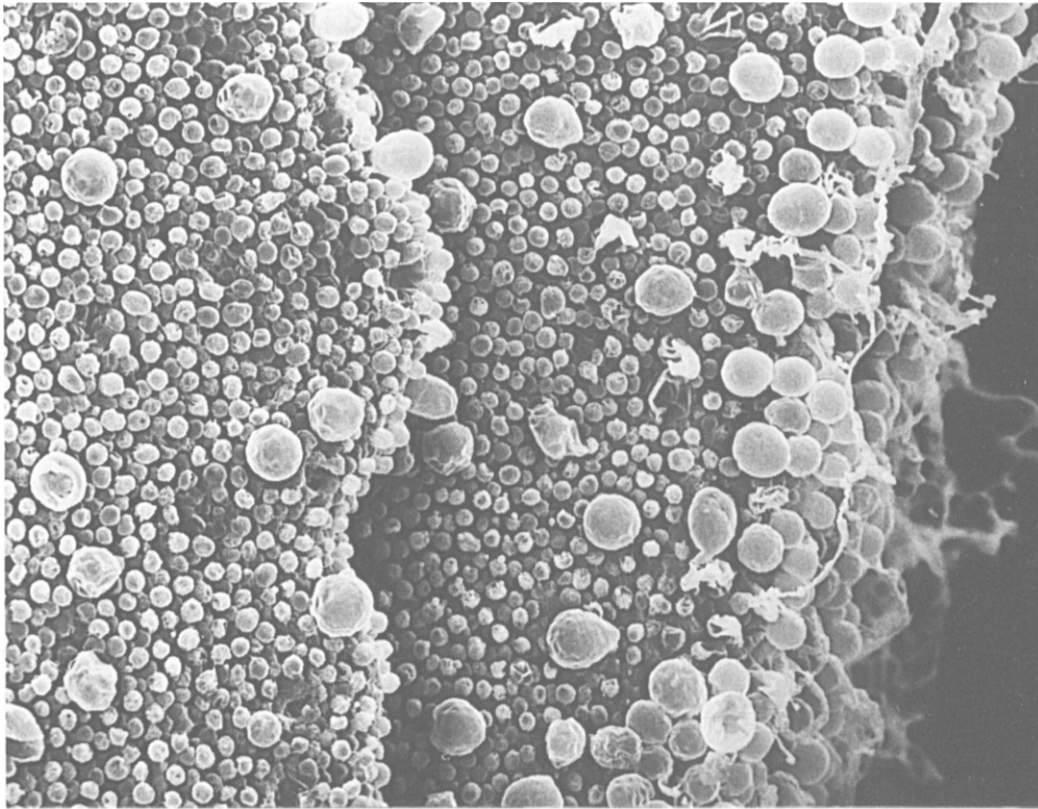


Fig. 3. Scanning electron micrograph showing cystidia (the inflated cells) gathered in increased frequency at the gill edge. Scale bar, 100  $\mu\text{m}$ .

observation of the distribution of cystidia over the hymenial surface (Fig. 3). There is an increased number of cystidia at the edge of secondary gills which is quite logically accountable to the need for additional buttressing at the free edge. Importantly, many of those 'additional' cystidia emerge from the hymenia of the primary gills on either side of the secondary gill which is being buttressed. But the very fact that there is a higher density of cystidia at the edge shows categorically that the edge remains stationary in space at its point of formation, i.e. it does not grow towards the stipe. The reason for this conclusion is that if the edge was responsible for growth of the gill and grew towards the stipe, then the zone behind the edge (and the zone behind that, etc.) would once have been the location of the edge and would therefore exhibit at least the cystidial density characteristic of edges. There is no evidence for cystidial death or removal at this formative stage and the cystidia are contributed by the two hymenia either side of the secondary gill, so if the edge extends then the body of the gill, being made up of every previous edge,

can have more cystidia than the edge but cannot have fewer. Since observation shows that the general body of the hymenial surface does have a lower density of cystidia than that which characterizes the edge, it follows that the edge does not extend and the secondary gills (and gills of lesser rank) grow at their roots.

Gills of all ranks in the *C. cinereus* fruit body, therefore, grow radially outwards, their roots extending into the steadily replenished undifferentiated tissue of the pileal context. The formative element appears to be in the tissue at the extreme end of the gill cavity where the change in structure occurs from the randomly intertwined hyphal context with large intercellular spaces to the highly compacted hymenial plates separated by the space of the gill cavity. In many respects this change can be interpreted as a re-organization of available space; many discrete but scattered intercellular spaces becoming combined, crystallizing almost, into the gill cavity. Clearly this must be done through the particular arrangement of hyphal branches, but how it is achieved is unknown.

The characteristic general arrangement of the stipe, hymenophore and cap which is the mushroom, constitutes the basic body plan of agaric fungi. The basic mammalian body plan can provide for animals as diverse as the giraffe and the blue whale, yet it is arrived at by essentially identical morphogenetic processes in those animals, such that the embryonic stages are virtually indistinguishable. In the face of this commonality it is inconceivable that agaric fungi would use a multitude of morphogenetic processes to arrive at the same basic mushroom body plan. Thus, the view that coprinoid gills grow by extension at the root and not by growth at the edge is extended to all agarics. The apparent contradiction, that in the coprinoid cap the margin forms first and is the developmentally oldest region, while in other agarics the cap grows outwards at the margin which must, therefore, be the developmentally youngest region, is only an apparent contradiction if it is accepted that in coprinoid forms it is not the case that the cap has 'collapsed' to envelope the stipe but that the cap has become radially reduced and vertically exaggerated. Thus, the homologous structure to the coprinoid cap is not the whole of the agaric cap, but only that part which encompasses the insertion of the gills. The margin of the coprinoid cap is analogous but not homologous to the margin of the non-coprinoid cap. Compared in this way the two mushroom structures have the

same morphogenetic ontogenies. Subsequently, of course, the coprinoid type undergoes autolysis and umbrella-like expansion – additional features developed to achieve effective spore dispersal from an essentially tubular fruiting structure.

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RUDIMENTARY FLAGELLA IN SPORANGIOSPORES OF *ACHLYA*

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TEM demonstrated that sporangiospores of *Achlya* spp. have the potential to produce rudimentary flagella. Sporangiospores with flagella of varying lengths were identified in sporangia of *A. flagellata* and *A. intricata*, ranging from short stubs, less than 0.5  $\mu\text{m}$  in length, to organelles 1–2  $\mu\text{m}$  in length with an extended axoneme. Though the sporangiospores did not produce heterokont flagella characteristic of the Oomycetes, this study confirms the zoosporic nature of these spores and supports the popular assumption of homology between the sporangiospores of *Achlya* and the primary zoospores of the diplanetic representatives of the Saprolegniaceae.

In Johnson's monograph of the genus *Achlya* Nees (Johnson, 1956), he referred to the '... still unsolved question of primary zoospore flagellation...'. This comment reflects the dichotomy of opinion which

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developed in the nineteenth century concerning whether or not the sporangiospores of *Achlya* were equipped with flagella, as is the case in genera such as *Saprolegnia* Nees and *Leptolegnia* de Bary with a clearly diplanetic asexual life cycle. Cornu (1872) described sporangiospores with a pair of anteriorly attached flagella as characteristic of the genus *Achlya*. Subsequently, flagellate sporangiospores were described in *A. polyandra* Hildebrand and