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Aethalium cortex formation in the myxomycete Lycogala terrestre
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very painstaking, although sometimes a little confusing. The plasmodium, he informs us 'first rises from the wood as a group of small coral-red papillae which soon extend to form a cushion-like mass of closely convoluted veins or sporangia; these are more or less separated from each other by narrow tubular air-passages'. The airpassages give rise to the pseudocapillitium. Lister's account is somewhat curtailed in his third edition [3] but substantially identical, despite his restriction there of the term 'pseudocapillitium' to the innermost airpassages.

The following is an attempt to improve on Lister's account.

**Materials and Methods**

Developing aethalia were obtained by first locating recently matured ones on *Picea* logs and slicing them away together.

**Introduction**

*Lycogala terrestre* Fries is a common and conspicuous myxomycete. Indeed, T.H. Macbride [4] claimed that it was 'no doubt the most common slime-mould in the world' (this of course was prior to the discovery of bark culture species). By this date several accounts of fruiting in *Lycogala* had appeared. Rostafinski's brief treatment in Cooke [1] had been expanded by Massee [5], who based his taxonomy on the 'capillitium', as both authors termed the mass of branching tubes in the cortex. Eventually Lister [2] discovered that these tubes were filled with air, and therefore quite unlike the capillitium of other myxomycetes. He referred to them as a 'pseudocapillitium'. For a view of the pseudocapillitium under SEM see the paper by Schoknecht & Small [6].

Lister's description of the fruiting process appears...
with the underlying bark. This was kept wet and scanned at intervals of 2-3 hours with a lowpower stereoscope. As more aethalium emerged from the wood and developed samples were removed and fixed in 2.5% v/v glutaraldehyde in 0.1 M sodium cacodylate buffer prior to postfixation in 1% osmic acid and subsequent examination with SEM and TEM.

Results

The stages in aethalium formation characterized by Lister as 'papillae' form bunches of bladders, resembling diminutive pink blackberries. Still earlier stages are not at all papillate but rather form simple blobs of protoplasm bounded by a thin peridium. Figure 1a shows an example after critical point drying. If such a specimen is split with a razor blade, recoated with gold-palladium alloy and replaced in the SEM, the peridium is seen to have curled back, revealing a smooth inside surface as no trace of pseudocapillitium has yet developed. The outer surface however exhibits a scattering of shallow punctures. In aethalium a few hours older these will deepen and an arrangement of sulci appears, sometimes connecting and sometimes surrounding them, and giving the fructification a lobate appearance (Figure 1b). Views into the punctures at this stage show some entrances to deeper passages (Figure 1c) but the inside surface of the peridium still appears smooth when separated.

Figure 1d shows a section across a sulcus with TEM. Nuclei and storage material in the protoplast may be identified. A surface membrane covers a superficial water layer but folds in to meet the peridium along the floor of the sulcus. From this line of contact a narrow partition of medium electron-density projects vertically into the protoplast. More of this material appears to the right of the sulcus: it will become the principal substance of the cortex, which term replaces 'peridium' from this point.

Figure 1e corresponds to Lister's 'group of papillae' and occurs some hours later. Essentially, papillae are extruded from the regions between sulci. Lister's characterization of them as 'sporangia' appears dubious. Figure 1e also shows the beginning of the subsequent process of collapse of the papillae, giving rise to folds. At the same stage, sections across sulci exhibit a proliferation and extension of the partitions running into them, as in Figure 1f. Lister observes that 'tubular air-passages are enclosed between the folds, which together with the deeper air-passages and the surface of the aethalium are bounded by a delicate membrane'. The membrane, enclosing water, is visible, and the partition running into the protoplast is now bisected by a central electron-dense lamina. The same feature appears in another partition from a slightly later preparation, in Figure 2a. Note here the alignment of numerous mitochondria at the sides of the lamina, and the many water vacuoles in the entire region. Such alignments have been seen in several other sections.

After perhaps 12 hours the aethalium resembles Figure 2b. The inner surface of the cortex is no longer smooth but instead incorporates a tangle of air tubes (Figure 2c). Collapsed matter around the mouths of some tubes may form a pleated rim (Figure 2d). Such material is the remains of what were folds. Protoplasm trapped within it becomes separated from the main protoplast and forms the multinucleate warts found on the surfaces of mature aethalium. Rostafinski and Massee referred to these as 'cells', the latter author considering that the pseudocapillitium originated in them. Lister called them 'vesicles' and noted that their nuclei remained sharply defined until spore cleavage was completed.

As the aethalium matures, the pseudocapillititial tubes continue to thicken, and in fractured TEM preparations a concentrically layered structure is visible (Figure 2e).

The layers appear more closely adpressed when viewed with TEM (Figure 2f).
partitions as vacuoles which would have emptied at the edge of the cortex causing the bulging-out of the papillae as in Figure 1e. In living material some of these papillae appear almost colourless and seem to be little more than water-sacs. Once the pseudocapillitium has formed they gradually collapse, the water being presumably returned to the center of the aethalium.

Processes similar to these probably occur in the other Lycogala species. The remaining Reticulariaceae, Reticularia, Tubulifera and Dictydiaethalium all produce a sporocarp in which distinct sporangia are compacted. The extrusion of papillae in Lycogala is an element of pseudocapillitium formation and there is no certainty that it evolved from a partial cleavage of sporangia. It may however have done so, and the distinction would not thereby justify the removal of Lycogala to a separate family.

Finally, what function has this web of airpassages? Lycogala often appears on the exposed upper surfaces of logs and stumps, and the insulating cortex may help to reduce overheating in direct sunlight, which would impair spore

Figure 2. a. VS aethalium at papillate stage showing mitochondria (mi), central lamina (l) with splits (sp) and nodules (no), and water vacuoles (w), TEM. Scale bar = 10 ìm. b. Aethalium appx 12 hours after emergence, SEM. Scale bar = 100 ìm. c. Fractured aethalium at same stage as b, showing pseudocapillitium (pc) on inner cortical surface, SEM. Scale bar = 100 ìm. d. Portion of exterior surface of same preparation, SEM. Scale bar = 25 ìm. e. Detail of e, SEM. Scale bar = 25 ìm. Righthand portion is enlargement of window, showing fractured pseudocapillitium (pc). f. TS pseudocapillitium, TEM. Scale bar = 10ìm.