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Interdependence of the actin and the microtubule cytoskeleton during fungal growth

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Cell polarization is a theme in biology conserved from bacteria to man. One of the most extremely polarized cells in nature is the hyphae of filamentous fungi. A continuous flow of secretion vesicles from the hyphal cell body to the tip is essential for cell wall and membrane extension. Microtubules (MTs) and actin, along with their corresponding motor proteins, are involved in the secretion process. Therefore, the arrangement of the cytoskeleton is a crucial step to establish and maintain polarity. Here we review recent findings unraveling the mechanism of polarized growth with special emphasis on the role of the actin and MT cytoskeletons and cell end markers linking the two cytoskeletons. We will mainly focus on *Neurospora crassa* and *Aspergillus nidulans* as model organisms.

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Introduction

Filamentous fungi are highly polarized eukaryotic cells, which continuously elongate their hyphae at the tips. In distal parts, hyphae can initiate new sites of polar growth in the process of branch formation. The establishment and maintenance of polar growth is a fascinating question in biology [1–3]. Some filamentous fungi are pathogen to animals and plants and often growth in the host is accompanied by a dimorphic switch from hyphal growth to yeast-like growth or *vice versa* [4]. Other fungi are useful in biotechnology, such as for enzyme production, and fermentation in food industry due to their high ability for enzyme secretion [5]. Thus, the analysis of polarized growth of filamentous fungi can contribute to medical, agricultural and biotechnological fields.

The actin cytoskeleton

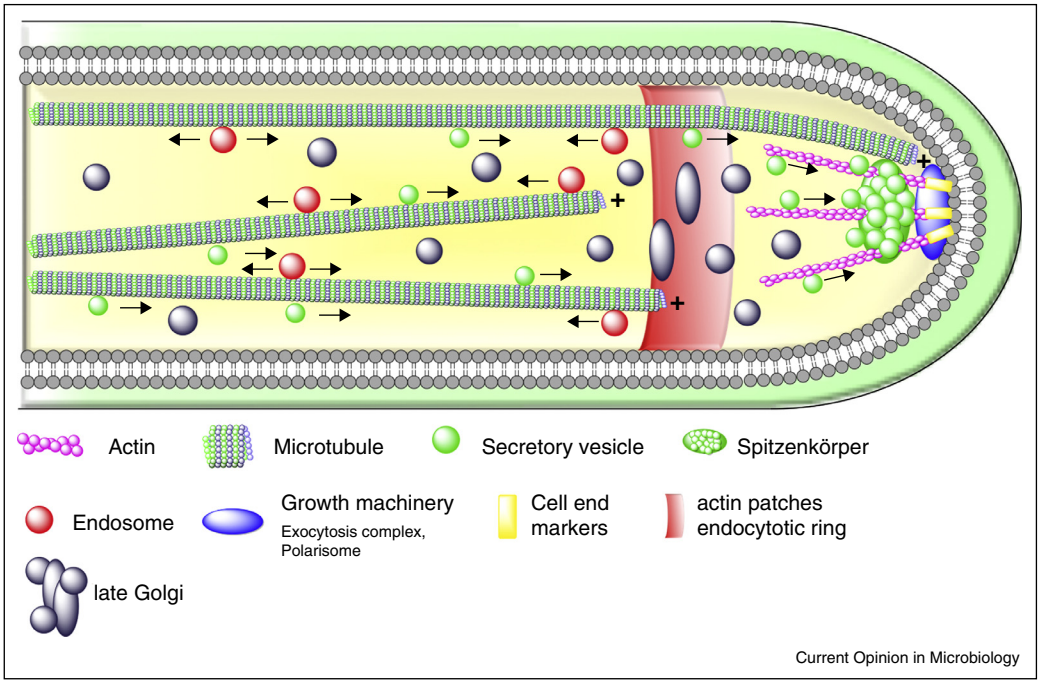
The actin cytoskeleton plays a central role in cell morphogenesis of filamentous fungi [6,7]. There are three high order F-actin structures with distinct functions: actin rings, patches, and cables. The actin rings in cooperation with myosin II function in septum formation [8••,9]. Actin patches are peripheral punctate structures, which localize to regions where also probably the endocytic machinery is located [10•]. The predominant localization of these patches at subapical regions suggests spatial coupling of apical exocytosis and subapical compensatory endocytosis (Figure 1) [11], in addition to endocytic recycling of polarized material at the hyphal tip [12].

The very dynamic actin cables are generally very difficult to visualize. However, recently specific markers, such as Lifeact and tropomyosin were developed [9,13••,14]. Actin cables are present at the apex of hyphae and are thought to serve as tracks for myosin V-dependent secretory vesicle transport to the tip (Figure 1) [6,8••,13••]. The 'basic' growth machinery involved in the formation of actin cables, vesicle transport and exocytosis, such as formin, the polarisome, myosin V and the exocyst complex are relatively conserved among eukaryotic cells and localize to the apex of hyphae (see references in [1,15]). Before fusion with the cell membrane, the secretion vesicles accumulate at the hyphal tip in a structure called 'Spitzenkörper' [16,17], a special structure in filamentous fungi, which determines growth direction of the hyphae [18] (Figure 1). The exact composition and organization is still not completely understood, although one model proposes that the Spitzenkörper acts as vesicle supply center for growing tips (see Riquelme *et al.* in this issue [19]).

The microtubule cytoskeleton

Microtubules (MTs) play a crucial role during mitosis, but also have additional functions in interphase in filamentous fungi. They are important for the distribution of nuclei or other organelles and serve as tracks for vesicles such as endosomes. Thus they are important for rapid hyphal growth [2,11,20••,21,22]. However, they are not

Figure 1

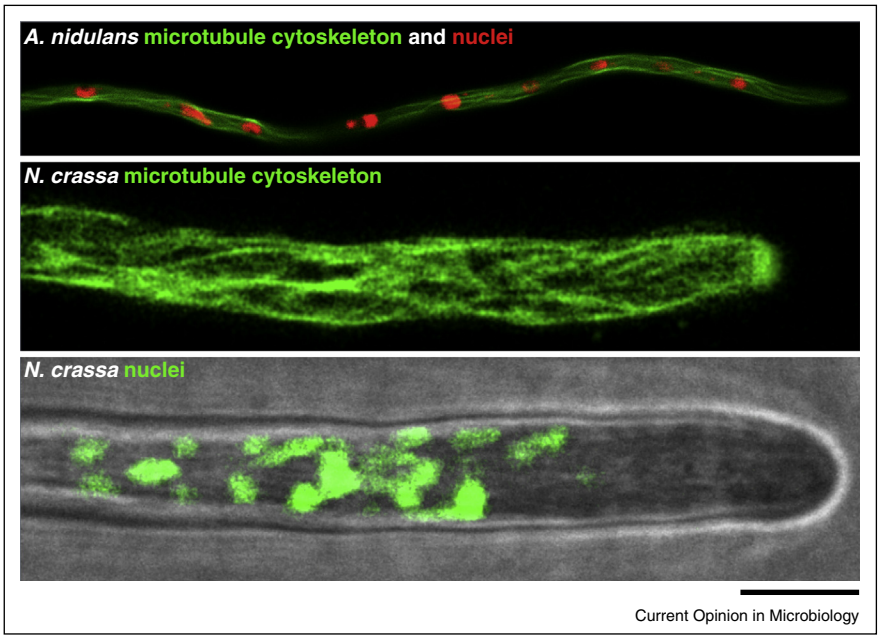


Scheme of an *A. nidulans* hyphal tip showing organelles, cytoskeletons and polarity factors, based on the localization of proteins tagged with fluorescent proteins.

essential for spore germination, but only for site selection of germination [23,24].

The rather stable minus end of MTs is located at the MT-organizing center (MTOC), whereas the plus end is

Figure 2



Microtubule and nuclear arrangement in *A. nidulans* and *N. crassa*. **(a)** The *A. nidulans* microtubule cytoskeleton was labeled with GFP::TubA (α-tubulin), and nuclei were labeled with DsRed::StuA(NLS). Scale bar equals 12 μm. **(b)** The microtubule cytoskeleton was labeled with Bml::sGFP (β-tubulin) in *N. crassa*. Scale bar equals 10 μm. **(c)** *N. crassa* nuclei were labeled with hH1::sGFP (Histone H1) merged with the corresponding bright field image. Scale bar equals 10 μm.