

## Fungal Hyphal Growth – Spitzenkörper versus Apical Vesicle Crescent

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### Short Communication

The primary characteristic of filamentous fungi is hyphae – tube-like microscopic cells that exhibit polarized growth via apical extension [1,2]. Hyphal growth allows the fungus to interact with its environment through colonization of substrates, secretion of enzymes, nutrient assimilation, and responding to environmental stimuli [3-8]. Hyphal growth and differentiation must be strictly coordinated with cell wall synthesis, plasma membrane growth, vesicle transport, and cytoplasmic dynamics [2,9,10]. The phenomenon of polarized growth via apical extension is not restricted to the fungi and examples can be found throughout eukaryotic (e.g., pollen tubes and root hairs of higher plants, rhizoids of algae [11-13], neurons of animals [14,15] and prokaryotic organisms [e.g., filamentous bacteria [16-18]).

Previous studies have demonstrated that hyphal growth occurs at the apex of the cell [19-21]. Given the specificity of this localized growth, much attention has been focused on the transport of materials from their sites of origin (i.e., subapical Golgi body equivalents and plasma membrane) to the growing tip and the coordination and synthesis of materials being assembled for the expanding cell wall. The on-going construction of the cell wall and plasma membrane represents a significant undertaking given the rates of growth of fungi such as *Neurospora crassa* and *Gilbertella persicaria* which have been calculated at 0.2  $\mu\text{m/s}$  and 0.25  $\mu\text{m/s}$  respectively [22].

A primary cytoplasmic manifestation of polarized hyphal growth is the aggregation of secretory vesicles at the apex of growing cells and the alignment of organelles (e.g., mitochondria, ER) and cytoskeletal elements (e.g., microtubules) along the axis of growth. In hyphae of the Dikarya (Ascomycota and Basidiomycota) secretory vesicles and associated proteins aggregate into the Spitzenkörper (Spk), a term coined by Brunswik [23] after observing a dense apical body in fixed and stained hyphae of *Coprinus* (Basidiomycota). The Spk is a complex structure that is not bound by a membrane and shows variability in size, shape, position, and behavior in response to endogenous or environmental signals and perturbations. When viewed in living cells using phase contrast (PC) LM optics, the Spk appears as a dark spherical structure, with often a bright central core [24-26]. Its presence and location influences the rate and direction of hyphal growth [24,26,27]. Transmission electron microscopy (TEM) revealed that the Spk is composed of a dense accumulation of macrovesicles (70-100 nm in diameter), a core of smaller microvesicles (25-40 nm in diameter) embedded in a dense meshwork of actin microfilaments [25,28-31].

In contrast, a typical Spk has not been observed in the hyphae of most zygomycetous fungi. Instead, secretory vesicles accumulate in a crescent-shaped band subtending the hyphal tip. This apical vesicle crescent (AVC) exhibits a looser organization of vesicles than the Spk. Vesicles observed in the AVC also demonstrated a higher degree of variability in average size and are larger than the vesicles observed in

the Spk. For example, in surveyed members of the order Kickxellales, Mortierellales, and Mucorales; microvesicle averages ranged from approximately 30-80 nm in diameter and macrovesicles averaged 80-180 nm in diameter [32]. It has long been debated whether the AVC represents an alternative form of the Spk. While Grove and Bracker [25] suggested that the AVC observed in *Gilbertella persicaria* did not represent a Spk, Girbardt [19] concluded that the AVC observed in *Phycomyces blakesleeianus* and *Micromucor ramannianus* was a Spk. Like the Spk, the AVC appears to be involved in polarized growth – hyphae with an AVC grow more rapidly than those without an AVC, but the degree to which it is correlated to growth direction is unclear (Fisher and Roberson [32]). While the Spk has been documented primarily in the Dikarya, two exceptions outside this group of fungi have been reported: in hyphae of *Allomyces macrogynus* [33] and *Basidiobolus* (Entomophthoromycotina; Roberson et al. [34]).

Is the AVC an alternate form of a Spk? Or is it a unique vesicle aggregation that behaves similarly to a Spk? The relationship and evolutionary history between the Spk and AVC remains unclear. The presence of an AVC in the zygomycetous fungi corresponds with hyphal growth rates, but further research is needed to explore the role and mechanics of the AVC, such as vesicle origin and trafficking. Molecular studies examining the proteins responsible for cell polarity in the Dikarya should be conducted in the zygomycetous fungi to determine if homologous sequences exist, and, if so, do they encode similar proteins. The presence of a recognizable Spk in two (and possibly more) fungi outside of the Dikarya suggest multiple evolutionary origins of the Spk, particularly since the Spk observed in *Basidiobolus* and *A. macrogynus* each possess unique characteristics not seen in Spk of the Dikarya. The Spk, or similar vesicle aggregations may have evolved as a superior way to maintain cytoplasmic polarity, efficiently target material needed for cell wall and plasma membrane construction, and promote rapid growth.

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