

Hierarchical Transition Via Individuation, Not Integration:  
How the Filamentous Fungi Challenge the Standard Model

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Thesis submitted in partial fulfillment of  
the requirements for the degree  
of Master of Science in the Department of  
Biology in the Graduate School  
of Duke University

2012

ABSTRACT

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## Abstract

In this project I expand the current model of hierarchical transition to include transition by individuation in addition to transition by integration and I apply my model of transition by individuation to the evolution and development of the filamentous fungi. I accomplish this in two parts. In the first section, I defend a general *Hierarchy Thesis*: A differentiated hierarchical whole can arise not only through the integration of individuated parts but also by the individuation of parts within an integrated whole. I elaborate an expanded model of hierarchical transition and discuss the relevance of part-level selection and part-hood regulation for different modes of transition.

In the second section, I defend a *Mycology Thesis*: The filamentous fungi have evolved a developmental cellularization process to meet ecological and reproductive demands for coenocytic growth in early development and cellularization in later development. I elaborate the origins and evolution of the filamentous fungi and argue that this history provides cases of hierarchical transition via individuation in both phylogeny and ontogeny.

The project provides an expanded evolutionary-developmental framework for hierarchical transition and a framing narrative for the evolutionary development of filamentous fungi, an evolutionarily significant and ecologically ubiquitous group, and has implications for the study of similar organisms outside *Fungi* and of hierarchical transition in general.

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# 1. Introduction

Hierarchical transition is a striking feature of the living world. Multicellular organisms arise from single-celled ancestors. Simple embryos give rise to functionally complex adults. Examples of hierarchical transition abound in *Eukarya*, with those in *Animalia* and *Plantae* garnering the most attention in contemporary biology. What about *Fungi*? Despite copious accounts of the evolution and development of *Fungi*, their study is yet lacking in the hierarchical transition literature.

This project expands the current model of hierarchical transition and provides a general model for studying hierarchical transition in the filamentous fungi. This will improve the scope of our current hierarchical transition models and help explain why *Fungi* has all but been ignored in hierarchical transition research. I accomplish this in two parts. First, I defend a hierarchy thesis:

*Hierarchy Thesis:* A differentiated hierarchical whole can arise not only through the integration of individuated parts but also by the individuation of parts within an integrated whole.

The integration model dominates current hierarchical transition literature and evolutionary theory more generally. That this model fits many cases in *Animalia* and *Plantae* may explain the popularity of these cases, and the predominance of the integration model. According to this model, hierarchical transition consists in a transition from independent parts to a unified parts-in-a-whole. Two complicating factors in hierarchical transition by integration dominate the current literature:

*Part-Level-Selection:* If higher fitness of a *parts-in-a-whole* requires lower fitnesses for *parts*, then achieving hierarchy requires establishment of a common benefit and overcoming inter-part competition through cooperation.

*Part-Level-Ecology:* The evolution of a *parts-in-a-whole* takes place in the context of an ecology that supports *parts* so that selective conflicts between *parts* and a *part-in-a-whole* initially (and perhaps later) favor *parts*.

In contrast to the popularity of the integration model, components of the individuation model are employed in one form or another throughout literature on *Plantae* and *Fungi* yet a general model is lacking. It is not surprising then that the place of the individuation model alongside the integration model as a complementary mode of hierarchical transition is hardly recognized. According to the individuation model, hierarchical transition consists in a transition from a unified whole to a unified whole-with-parts. A major implication of this model is that part-hood itself, and not just the independence or integration of parts, can be regulated in evolution and development. Just as parts can integrate to form a whole, so can a whole individuate parts within itself. There are two important evolutionary-developmental implications of the status of part-hood as a phenotype subject to regulation:

*Whole-Level-Selection:* Since a *whole-without-parts* lacks *parts*, achieving hierarchy involves individuating *parts* within a *whole* to produce a *whole-with-parts* in a way that benefits *whole-level* fitness; this does not involve overcoming inter-part selection so long as *parts* are insufficiently individuated.

*Whole-Level-Ecology (Individuation):* The evolution of a *whole-with-parts* takes place in the context of an ecology that supports *wholes* so that if *parts* are

sufficiently individuated to allow inter-*part* selection, this selection takes place in a context that initially (and perhaps later) favors *wholes*.

These two factors have in common a lack of cooperation/conflict posed by inter-part selection and so suggest that regulation of part-hood allows transition without this classic challenge. In addition, a *whole-without-parts* may have ecological advantages resulting from removal of constraints imposed by compartmentalization.

First, without part-hood, wholes can avoid inter-part conflict, the focus of contemporary hierarchical transition literature (based on integration models). Simply put, if a whole has no parts, then there can be no conflict between part-level processes (often put in terms of parts cheating or policing one another) and whole-level processes. Second, without part-hood, wholes can avoid physiological and ecological constraints associated with part-whole organization and growth by addition of parts. In particular, resources, whether nutritive or cytological, are not constrained to compartments or specific regions in a whole-without-parts.

In tandem with the hierarchy thesis, I defend a mycology thesis

*Mycology Thesis:* The filamentous fungi have evolved a developmental cellularization process to meet ecological and reproductive demands for coenocytic growth in early development and cellularization in later development.

This second thesis argues that the individuation model at the center of the first thesis is exemplified by developmental manipulation of cellularity in the filamentous fungi. Indeed, the filamentous fungi offer not just case studies of an exception to current models but an exception comprised of an evolutionarily significant and ecologically

ubiquitous group. In the filamentous fungi, the regulation of part-hood is primarily achieved via a cell cycle that starkly contrasts with that seen in *Animalia*, *Plantae*, and yeast-form members of *Fungi*. In the filamentous fungi the separation of karyokinesis and cytokinesis during cell reproduction allows for growth without formation of discrete compartments or cells. In other words, growth can occur via the expansion of a coenocytic whole, not via the reproduction of discrete cells. Coenocytic as opposed to cellular growth impacts the two evolutionary-developmental implications associated with the regulation of cellularity: inter-part conflict is avoided because the coenocytic whole is not divided into independent parts with potentially differing fates; and the whole-without-parts benefits in its absorptive ecology from the ability to more quickly transport cytoplasm, organelles and nutrients throughout its entirety. Coenocytic growth is advantageous for exploratory growth through substrates, but a more compartmentalized development is advantageous for substrate exploitation and differentiation of complex tissues. To this end, the filamentous fungi regulate the compartmentalization of hyphae in later stages of development and achieve hierarchical transition from a whole to a whole-with-parts.

The thesis is organized as follows. In the first section I elaborate the hierarchy thesis. I schematize the evolutionary-development models underlying the hierarchy thesis and discuss the theoretical implications of hierarchical transition model expanded to encompass both integration and individuation processes. In the second

section I defend the mycology thesis and its relation to the hierarchy thesis in five parts. First, I introduce *Fungi*, briefly discuss the origin and evolution of the filamentous fungi, and introduce an abstracted model of hierarchical transition in the filamentous fungi. Second, I discuss cytological features that contribute to the evolutionary-developmental differences between the major Eukaryotic kingdoms, *Fungi*, *Animalia*, and *Plantae*. In particular, I explain how the filamentous fungi achieve sophisticated control over cellularization (part-hood in this case). Third, I explore the non-cellular growth (whole-without-parts) of filamentous fungi and how they both lack inter-cellular conflict (inter-part conflict) and benefit ecologically from their lack of cellularization (lack of part-hood). Fourth, I elaborate the developmental regulation of cellularity in the filamentous fungi, focusing on septation dynamics. Finally, I explain how the filamentous fungi achieve hierarchical transition via cellularization and differentiation of vegetative mycelia and tissues and of complex fruiting bodies.

## 2. Modeling Hierarchical Transition

Hierarchical transitions can take place within the development of a life cycle (within ontogeny) or within the evolution of a lineage (within phylogeny).

Embryonic cells dividing and forming a fetus is an example of transition in ontogeny (Buss 1987); a clade of unicellular algae giving rise to descendants with division of labor is an example of transition in phylogeny (Kirk 2000). At their most general the individuation and integration models of hierarchical transition treat transitions in ontogeny and transitions in phylogeny as equivalent. In specific cases, the mechanisms involved in these processes may be similar or distinct.

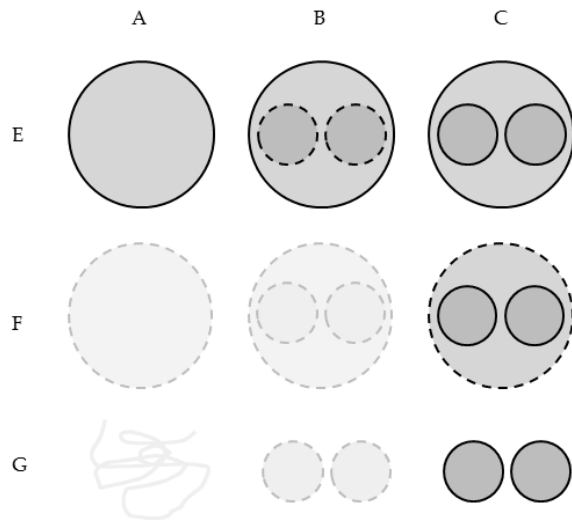
### 2.1 *Integration versus Individuation*

In this project I focus on hierarchical transition taking place from one level to two levels. I refer to the lower of the two levels as the *part* level and the higher of the two levels as the *whole* level. Accordingly, I treat transitions from *parts* to *parts-in-a-whole* and transitions from a *whole* to a *whole-with-parts*. We must keep three things in mind regarding this terminology. First, this *part/whole* language is relative to a given transition, so that for example a single deer could be a *whole* with cellular *parts* in regard to a transition to multicellularity, but that deer and others could be *parts* of a *whole* herd in regard to a transition to social complexity. Second, parts and wholes are evolutionary individuals (they have heritable fitness-relevant properties) and thus not just any object qualifies (Brandon 1982; Godfrey-Smith 2009). (Although a cell may have parts like an endoplasmic reticulum or cytoskeleton, those parts are

not *parts* in the sense used here.) Third, I use the *part/whole* distinction free of the constraints of any given ranking system -- if a whole and its parts each satisfy the evolutionary criterion just discussed then they can qualify as parts and wholes in my sense (on rank freedom in biological hierarchies see Okasha 2011).

We can represent our parts, wholes, and transitions in a 3 x 3 possibility space (see Figure 1). Transitions involving the formation of a whole proceed G-F-E; transitions involving the formation of parts proceed A-B-C. A *part* to *parts-in-a-whole* transition proceeds from paradigmatic parts (CG) to paradigmatic parts partially integrated (CF) to paradigmatic parts integrated into a paradigmatic whole (CE). A *whole* to *whole-with-parts* transition proceeds from a paradigmatic whole (EA) to a paradigmatic whole with partially individuated parts (EB) to a paradigmatic whole with individuated paradigmatic parts (EC). Positions AF, AG, BF, and BG involve neither a paradigmatic part nor a paradigmatic whole. Dynamics involving these positions are outside the scope of this project, but the possibility of other routes to a *whole-with-parts* hierarchy such as AG-BF-CE is intriguing. Prima facie, a system at AF, AG, BF or BG could undergo selection so that a transition could start without a paradigmatic evolutionary individual.





**Figure 1. Possibility Space for Hierarchical Transitions**

Hatched circles represent transitional (non-paradigmatic) stages; faded stages (AF, BF, AG, BG) have neither a paradigmatic part nor a paradigmatic whole.

### 2.1.1 Integration Dynamics and Modeling

We can schematize hierarchical transition via integration with a few steps (see Figure 2A). A transitioning system begins with a single part, such as a cell or an organism. Reproduction of this part results in a group of parts discrete from one another in terms of physical boundaries, physiologies or expression patterns. We can place the modes of integration that can occur during transition into three rough groups. Physiological integration involves establishing physiological connections such as fluid transport canals or cooperative feeding behaviors. Signaling integration involves establishing communication capacities such as cell-cell signal trafficking or pheromone signaling. Physical integration involves establishing physical connections

that may or may not involve physiological or signaling connections. For example, discrete cells may fuse their cell walls, or oysters may clump together. As integration proceeds, two things happen. Firstly, the parts establish a common fate as a whole. In evolutionary terms, this means the whole has a fitness that is (to some degree) independent of the fitnesses of the parts. Secondly, the whole gains the ability to differentiate its parts. This can lead to reproductive specialization and possibly other physiological specializations resulting in complex functional structures.

The status quo model of hierarchical transition involves the transition of a group of independent evolutionary individuals to an integrated, higher-level individual with these lower-level individuals as parts. In his recent synthesis of hierarchical transition theory, Godfrey-Smith writes that "transitions in individuality" involve "a new kind of Darwinian population," a collection of evolutionary individuals (Godfrey-Smith 2009: 110, 122). Although such a new population could arise via transitions to new *wholes* or to new *parts* (as this project argues), Godfrey-Smith and others focus on the former. Thus, Godfrey-Smith writes that hierarchical transition takes place via the integration "of the collective in an overall sense" in the form of division of labor, "mutual dependence (loss of autonomy) of parts," and "maintenance of a boundary between a collective and what is outside it" (Godfrey-Smith 2009: 93). Godfrey-Smith's focus on integration is standard in contemporary theory: Leigh writes that "the most objective mark of evolutionary progress is the series of evolutionary transitions where parts combine

to form larger, more effective wholes" (Leigh 1999: 30); Rainey & Kerr defined a major transition as a "shift from autonomous lower-level entities to differentiated and integrated higher-level entities" (Rainey & Kerr 2011: 141); and Simpson describes transition via integration of parts in successive aggregate, group, and individual phases (Simpson 2011: 201). The transition to multicellularity receives particular attention in this regard: Michod writes that "the evolution of multicellular organisms is the premier example of the integration of lower evolutionary levels into a new, higher-level individual" (Michod 1999: 53); and Calcott writes that the evolution of multicellularity and of eusociality have similar histories in which "formerly solitary individuals got together to form some higher-level cohesive unit" (Calcott 2011: 38).

Contemporary theory focuses on two factors in transitions via integration: cooperation and conflict. Michod summarizes the idea nicely: major transitions "share two common themes: (1) the emergency of cooperation among the lower level units in the functioning of the new higher-level unit, and (2) regulation of conflict among lower-level units" (Michod 1999: 60; cf. Michod 2011). On the one hand, selection reinforces the integration of parts if this leads to a whole-level property that increases part-level fitnesses, a "generation of benefit" (Godfrey-Smith 2009: 124). On the other hand, selection produces inter-part conflicts if the generation of whole-level benefit comes at the cost of part-level benefits. As a result of these opposing processes, "parts join to form larger wholes only if there is a genuine community of

interest among parts, and if circumstances allow the enforcement of this common interest" (Leigh 1999: 30) -- cooperation is vital (Michod 1999: 53; Calcott 2011: 38).<sup>1</sup>

One mechanism for surmounting this difficulty is the eventual weakening of evolutionary individuality on the part ("partial de-Darwinizing") of the lower-level units via selection at the higher level (Godfrey-Smith 2009: 122; cf. Buss 1987).

I suggest that two factors are central to the cooperation-conflict hurdle that transitions via integration face. First, *part-level-ecology* refers to the fact that the environment in which the transition occurs may be the environment that historically shaped the adaptations of the parts. In other words, the "environment of evolutionary adaptedness,"

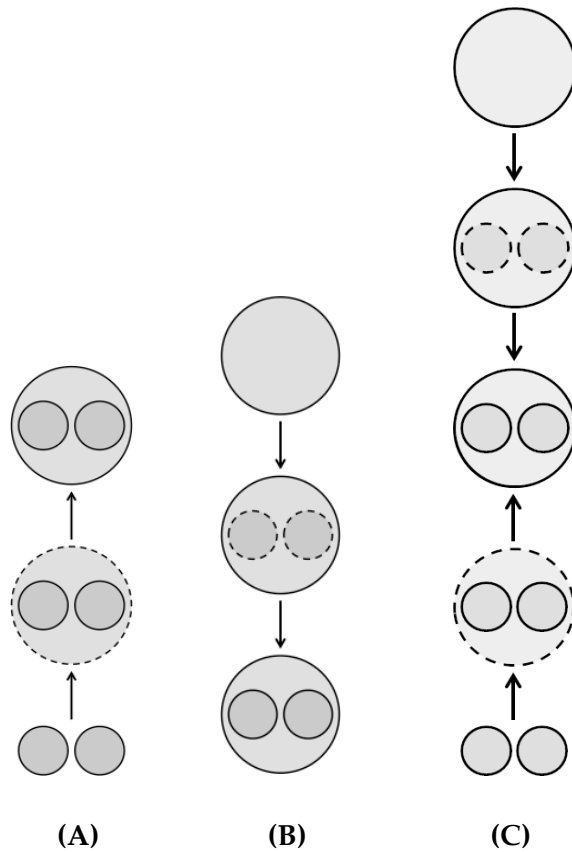
"the environment in which a species lived while its existing characteristics... were being evolved, and... the only environment in which there can be any assurance that activation of a system will be likely to result in the achievement of its biological function" (Bowlby 1969: 82, quoted in Irons 1998: 194),

may be very close to the current, "adaptively relevant environment," "those features of the environment that the mechanism must interact with in order to confer reproductive advantage" (Irons 1998: 198) (cf. Brandon 1990 on historical versus present adaptedness). If this is so, then existing parts are developing and evolving in the context of a *part-level-ecology*. Second, *part-level-selection* refers to the fact that in the cooperation-conflict process that characterizes transition via integration, parts

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<sup>1</sup> In contrast to this theme of cooperation and conflict across levels, Clarke argues that in the case of established modular organisms, "under particular circumstances (circumstances satisfied by many plants) competition at a lower-level can be beneficial for a higher-level individual" (Clarke 2011: 228, 247).

begin as paradigmatic evolutionary individuals and thus have an advantage over the emerging *parts-in-a-whole*. This effect is intensified if these parts also exist in a *part-level-ecology* -- they are eminently evolvable and responsive to natural selection and they exist in an environment to which they have adapted at the part level. I argue below that neither of these complications exists for transitions via individuation.



**Figure 2. Hierarchical Transitions to L1,2**

(A) Hierarchical transition via integration from *parts* to *parts-in-a-whole* (L1 to L1,2); (B) Hierarchical transition via individuation from *whole* to *whole-with-parts* (L2 to L1,2); (C) Hierarchical transition via integration and via individuation on a common axis. Dotted lines represent intermediate stages in part- or whole-hood.

### 2.1.2 Individuation Dynamics and Modeling

I introduce the individuation model to explain hierarchical transition in groups like the filamentous fungi and to complement the integration model.

Although one can find elements of the individuation model in the present literature, this project unifies and elaborates this work into an explicit, general model. We can break the model down into a few steps (see Figure 2B). The system begins with a single part, such as a coenocytic filamentous structure. With an eye towards hierarchical transition, we refer to this initial object as a whole. The components of this whole are highly integrated in the senses just mentioned for the integration model (physical, physiological, signaling). Reproduction or growth within this whole results in expansion or turnover within a still-integrated whole. We can place the modes of individuation that can occur during transition into three rough groups. Physical individuation of parts involves the physical separation of the whole into distinct regions. Physiological individuation of parts involves a reduction in physiological connection between regions of the whole. Signaling individuation of parts involves separation of the whole into regions allowing for distinct origins and destinations of signals, as well as separate signaling channels or environments. Individuation proceeds along two lines. First, the whole divides into parts that (to some degree) have individual evolutionary fates. This means the parts have their own fitnesses that are (to some degree) independent of the fitness of the whole. Second, the parts gain the ability to undertake developmental transformations that are (somewhat) independent from one another. This can lead to reproductive specialization and possibly other physiological specializations resulting in complex functional structures.

From the descriptions of the integration and individual models we can see that they model hierarchical transition in terms of common metrics. Indeed, we can see these two modes of hierarchical transition as starting from opposite ends of an integration-individuation spectrum and ending up near the middle at a point of hierarchical systems comprised of individuated parts integrated into a whole (see Figure 2C).<sup>2</sup> Nonetheless, these two modes of transition differ greatly in terms of their starting conditions and dynamics. I now turn to how part-hood regulation nullifies the importance of central factors in transition via integration (*part-level-selection* and *part-level-ecology*) for transition via individuation and presents a different set of starting constraints (*whole-level-selection* and *whole-level-ecology*).

## **2.2 Regulation of Part-hood**

A key difference between the integration and individuation models of hierarchical transition is the role of part-hood regulation in the latter. Considered abstractly, this regulation may seem no more remarkable than the regulation of whole-hood. However, in evolutionary biology, and in the context of hierarchical transitions to multicellularity, this regulation is hardly considered in contemporary theory. The reliance of hierarchical transition by individuation on the regulation of cellularity, however, reveals deep theoretical roots of the integration/individuation

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<sup>2</sup> It may be that the middle position in Figure 2C is not possible, given in-principle conflicts between the paradigmatic status of a whole and that of its parts (cf. Godfrey-Smith 2009). In this case, the figure might be modified to include six steps, with the middle two representing hierarchical systems with the paradigmatic status of either the whole (lower in the figure) or the parts (higher in the figure) slightly reduced.



distinction. Naturalists, many of them botanists, have long challenged the view that cells are the building blocks of organisms. For example, at the beginning of the twentieth century, Clifford Dobell advocated an *organismal theory* in opposition to this *cell theory*, a developmental view that closely parallels the distinction between individuation and integration:

“Now in a very large number of multinucleate organisms the cytoplasm is subdivided into a number of definite compartments, each of which encloses a nucleus. These cytoplasmic subdivisions together with their enclosed nuclei we may call – following the ordinary usage – cells: and we may say that the organisms themselves display a cellular structure. Very many organisms, however, are uninucleate, binucleate or multinucleate, but show no subdivision of the cytoplasm into compartments containing the nuclei. These organisms may therefore justly be called – when compared with the former group – non-cellular. It is obviously incorrect to call them unicellular, for the cells of cellular animals and plants are subdivisions of whole organisms. Upon this basis, therefore, we may define Metazoa and Metaphyta as organisms possessing a cellular structure: we may define Protista, on the other hand, as organisms possessing a non-cellular structure.” (Dobell 1911: 276)

According to Dobell protists (which he defines broadly as those organisms one usually calls “unicellular”) do not qualify as unicellular organisms because cellularity is a matter of protoplasmic (i.e. involving cytoplasm and nuclei) organization into cells. Dobell replaces the opposition between *many cells* and *one cell* with that between *cells* and *not-cells* (Dobell 1911: 277). In doing so, he opens up the possibility of distinguishing multinucleate, non-cellular organisms from those with only a single nucleus – neither is simply a *cell*.

Now, the debate between cell theorists and organismal theorists is bigger and older than Dobell and his interlocutors, but Dobell's view sums up nicely the imperative that guides the distinction in this thesis between processes of individuation and integration: "The cell must be defined in terms of the organism, and not the organism in terms of the cell." (Dobell 1911: 284-285) (For a thorough historical review of the debate see Reynolds 2007, 2010; Table 1, reproduced from Niklas (1992) provides a nice comparison of the main tenets of each position.) Hierarchical transition by integration sits well with the cell theory definition of an organism in terms of cells – the process starts with *parts* and eventually results in *parts-in-a-whole*. The organismal viewpoint however opens the way for a hierarchical transition by individuation – a *whole* that pre-exists *parts* and eventually gives rise to them in the form of a *whole-with-parts*. (This distinction, of course, goes beyond this particular use of the models with *cells* as parts and *organisms* as wholes.)

Returning to the question of part-hood regulation in hierarchical transition via individuation, I argue that this process shows how such transitions can avoid the problems of *part-level-selection* and *part-level-ecology* posed by transition via integration. In their place, I argue that the starting context of transition via individuation involves *whole-level-selection* and *whole-level-ecology* and as a result does not face the cooperation/conflict hurdle that challenges transition by integration. In addition, a *whole-without-parts* has ecological opportunities not available to

aggregates of parts, although it can forgo this stage and transition to a *whole-with-parts* to achieve hierarchical transition and complex differentiation.

**Table 1. Cell Theory vs. Organismal Theory (after Niklas 1992: 34)**

	<u>Cell Theory</u>	<u>Organismal Theory</u>
Developmental corollaries	<ul style="list-style-type: none"> <li>• All living things are made up of cells</li> <li>• Each cell is an individual of equal morphological rank</li> <li>• Each multicellular organism is an aggregate of cells</li> <li>• The properties of the organism are the sum of the many cells</li> <li>• Ontogeny is the cooperative effort of many cells</li> </ul>	<ul style="list-style-type: none"> <li>• Ontogenesis is the property of the organism as a whole</li> <li>• Growth and differentiation are the properties of the protoplasm</li> <li>• Cell division may or may not involve septation of the protoplasm</li> <li>• If septation occurs, then cells are subordinate parts of the whole</li> <li>• Ontogenesis is the resolution of the the whole into parts</li> </ul>
Phylogenetic corollaries	<ul style="list-style-type: none"> <li>• Unicellular organisms are primitive and "elementary"</li> <li>• Elementary units formed colonial organisms through an acquired failure to separate after multiplication</li> <li>• Cells within colonial organisms became specialized and interdependent, eventually producing the multicellular organisms</li> </ul>	<ul style="list-style-type: none"> <li>• Unicellular and multicellular organisms are nonseptate and septate individuals, respectively</li> <li>• Unicellular and multicellular organisms are homologous</li> <li>• Colonial organisms are derived, not primitive organisms</li> <li>• Division of labor and mechanical benefits were effected by cellularization</li> </ul>

### 2.2.1 Whole-Level-Selection and -Ecology

Without parts, a whole does not face the challenge of part-level-selection conflicting with whole-level-selection. Let us illustrate this with a popular example from evolutionary game theory. We start with individual human hunters (parts) adapted to solitary hunting of rabbits. These hunters may attempt to integrate and pursue a new, whole-level-ecology such as group-hunting of deer. This strategy is available due to the complex differentiation (e.g., division of labor) made possible with a *parts-in-a-whole*. If the hunters do integrate, the whole-level benefits of cooperating to hunt deer may come at the cost of forgoing the part-level benefits of individually hunting rabbits. Not only is rabbit hunting available, but individuals are already adapted to this ecology, so individual-level pressures to avoid cooperation (or cheat other cooperators) may overpower group-level pressures to cooperate and hunt deer. Alternatively, we can start with a whole (very large) organism adapted to hunting deer. If this whole individuates parts, the whole-level-selection benefits of deer-hunting may be magnified if complex differentiation improves the hunting abilities of the whole. However, if individuation is not sufficient to allow parts of the whole to defect and hunt rabbits (thus feeding themselves and not other parts of the whole), then there is no part-level-selection conflicting with whole-level-selection. Because a whole-without-parts lacks a population of parts capable of undergoing part-level-selection, it does not immediately face a selective challenge to hierarchical transition. Instead, the Darwinian population present at the outset is one of wholes,

whose competition with one another is external, unlike the internal competition faced by an aggregation of parts. If parts are eventually individuated sufficiently to allow parts to independently hunt rabbits, at the outset of this new conflict between part-level-selection (for solo rabbit hunting) and whole-level-selection (for cooperative deer hunting) favors the whole since it came to the transition with prior adaptations to a whole-level-ecology.

### **2.2.2 Advantages of Lacking Parts**

The regulation of part-hood opens up the possibility of viewing parts as a constraint. In addition to avoiding inter-part conflicts, a whole-without-parts may take advantage of ecological possibilities that are closed to *wholes-with-parts*. At its most general, this involves developmental strategies that allocate system resources with more spatial freedom than is allowed with compartmentalization. A *whole-without-parts* can transcend the symmetrical allocation of internal resources (e.g., nuclei or ribosomes in the eukaryotic case) imposed by part-hood. For example, in biological systems the physical, physiological, and signaling separations characterizing independent or partially-integrated parts limit the number of possible allocations of resources throughout the whole. Without parts, a whole might asymmetrically allocate resources to favor metabolism or growth in particular regions over others, or to rescue resources from threatened or obsolete regions.

### **2.2.3 Regulating Part-hood to Achieve Complex Differentiation**

Although the regulation of part-hood allows a whole to grow without establishment of parts, this same regulation allows a whole to transition to a *whole-with-parts*. Such a hierarchical transition opens up the opportunity for potentially adaptive complex differentiation. Since this results from developmental regulation, the timing of transition may differ across developmental strategies depending on ecological particulars. The advantages of parts are available to a whole, but part-hood can be up-regulated or down-regulated through development instead of serving as the basis for development itself (i.e., as seen in systems that always grow and reproduce via discrete parts).

### 3. Hierarchical Transition in the Filamentous Fungi

I now turn to the project's second thesis,

*Mycology Thesis:* The filamentous fungi have evolved a developmental cellularization process to meet ecological and reproductive demands for coenocytic growth in early development and cellularization in later development.

I begin with a brief introduction to the origin and evolution of *Fungi* and I introduce a general model for the evolutionary development of filamentous fungi. This sets the stage for my examination of the role of cellular starting points in determining the mode of hierarchical transition available to the filamentous fungi. Next, I examine the factors behind *whole-level-selection* and *whole-level-ecology* that characterize non-hierarchical filamentous development. Finally, I turn to the particular mechanisms that facilitate the hierarchical transition via individuation of the filamentous fungi.

#### 3.1 Origins, Evolution, and Development of Filamentous Fungi

*Fungi*, *Animalia*, and *Plantae*, the three eukaryotic lineages that show hierarchical transition and complex differentiation, shared their most recent common ancestor approximately 1000 million-years-ago (MYA) (Moore 1998: 9-16). *Plantae* later diverged from the most recent common ancestor of *Animalia* and *Fungi*, followed by the final split of that pair.

The basal portions of the fungal phylogeny are not yet satisfactorily resolved, but the root of the tree is thought to be near *Chytridiomycota* (see Figure 3).

Accordingly, "no accepted phylogenetic hypothesis exists for the evolution of form

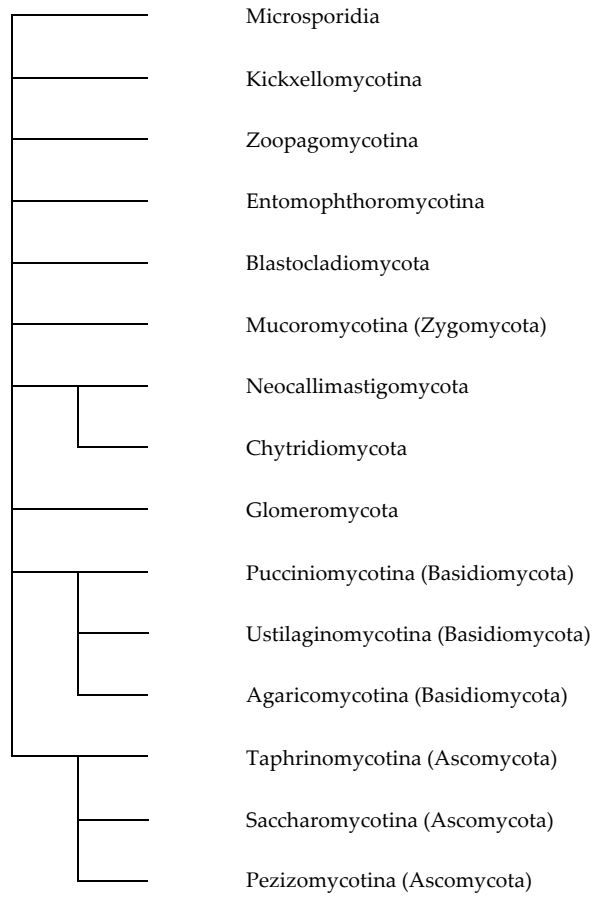
and nutritional mode for the earliest fungi" (James et al. 2006: 819). We can, however, draw several conclusions about the likely ancestors of *Fungi*. Several authors suggest that the last common ancestor of all of *Fungi* was an aquatic, phagotrophic, flagellated, unicellular protist and likely freshwater as opposed to marine (Cavalier-Smith 1987, 2001; Wainright et al. 1993; Lutzoni et al. 2004; James et al. 2006; Steenkamp et al. 2006).

Cavalier-Smith (1987; 2001) proposes an intriguing hypothesis for the evolution of early chytrids from a choanoflagellate-like ancestor. Cavalier-Smith suggests that early chytrids evolved from these ancestors by loss of phagotrophy and gain of a chitin wall (see Figure 4) (cf. Andrews & Harris 2007). This early chytrid maintained a separate flagellate stage in addition to its parasitic or saprotrophic stage. In addition, branched pseudopodia of the chytrid's ancestor may have been converted into branched rhizoids seen across chytrid morphologies. Saprotrophic or parasitic life-styles take advantage of a rigid external wall for attachment to and possible invasion of substrata and hosts. Chytrid morphologies consist in variations on a simple morphology that includes ovoid growth, polarized growth, septation, and dispersion via single-celled propagules (see Figure 5) (Cavalier-Smith 2001; Barr 2001; James et al. 2006).

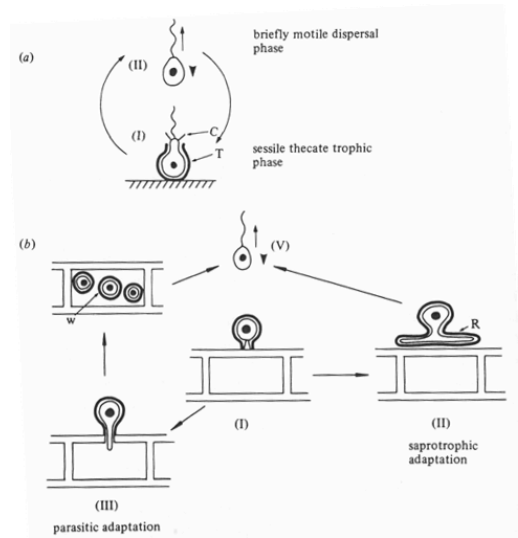
The basic life-style of early chytrids, absorptive nutrition by a rigid-walled vegetative stage, persisted throughout the evolution of *Fungi* and heavily constrained fungal distribution and variation of life-styles (Cooke & Rayner 1984:



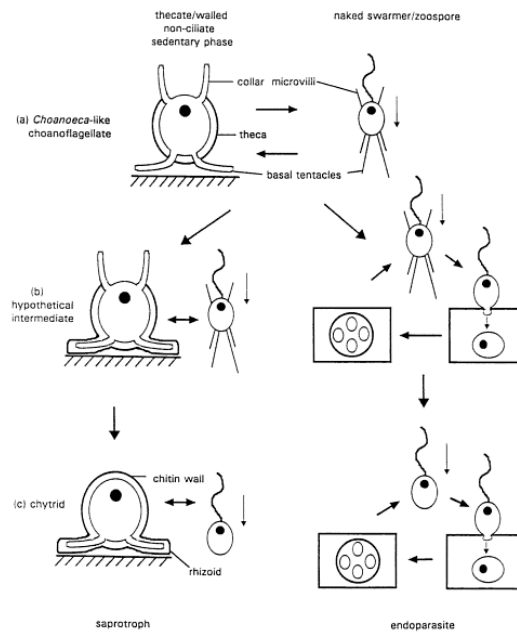
ch.1). In the descendants of chytrid fungi, a major loss of the flagellar stage in development occurred around the time of the fungal invasion of land 550-600 MYA (Moore 1998: 9-16). Filamentous growth and aerially (as opposed to aquatically) dispersed propagules were key for new, terrestrial ecologies (James et al. 2006; Spatafora & Robbertse 2010). Evidence suggests a strong link between the evolution and diversification of land plants and that of the filamentous fungi, via fungal associations with roots of vascular plants to form mycorrhizas and with algae to form lichens (Niklas 1997: ch.3; Moore 1998: ch.1; Redecker & Raab 2006; Bauer et al. 2001: 80). This link is further supported by the strong association with land plants of early, parasitic members of *Basidiomycota*. Finally, with the further evolution of septal morphologies and dynamics in *Dikarya* (*Ascomycota* and *Basidiomycota*) we see the increased role of septation in filamentous growth forms and the appearance of complex, differentiated structures.



**Figure 3. Phylogeny of *Fungi* (after Hibbett et al. 2007)**



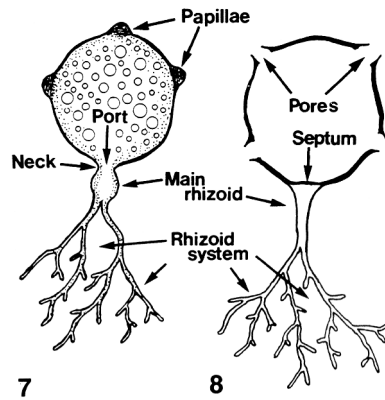
(A)



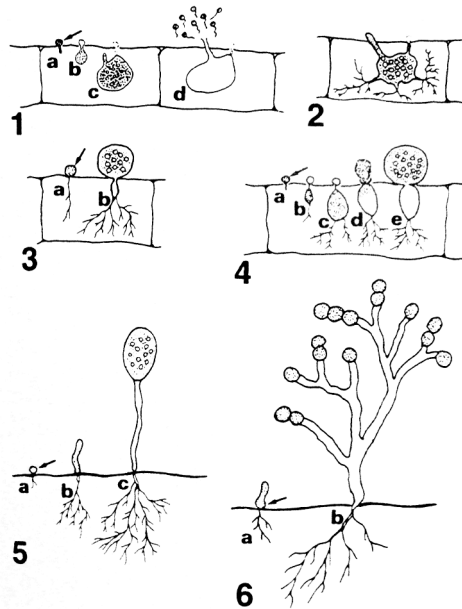
(B)

**Figure 4. Choanoflagellate origin of Chytrids (from Cavalier-Smith)**

Two similar schematics of hypothetical choanoflagellate origins of Chytrids. A sessile trophic stage may develop as a result of increased growth of a rigid outer wall (top of each diagram); this aids the switch to absorptive nutrition via attachment and/or invasion of substrata or hosts (bottom left and right of each diagram). (A) (Cavalier-Smith 1987: 342); (B) (Cavalier-Smith 2001: 27).



(A)

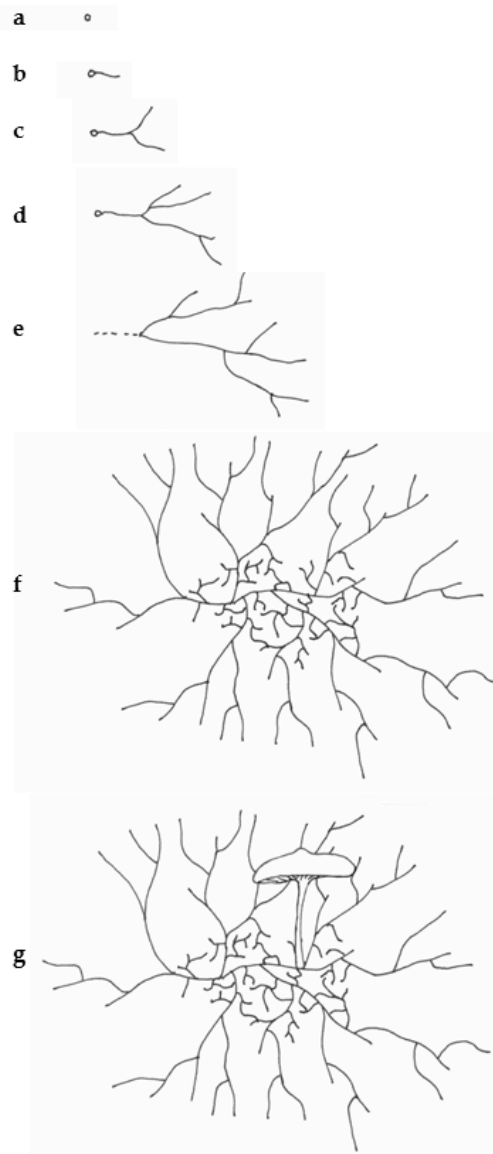


(B)

**Figure 5. Chytrid morphology (Barr 2001a: 97)**

(A) The basic chytrid body embodies the characteristic morphologies of *Fungi*: (i) ovoid growth (thallus, 7-8); (ii) polarized growth (rhizoid and rhizoid system, 7-8); (iii) septation (adventitious septum, 8); and (iv) dispersal of single-celled propagules from a sporocarp (pored thallus, 8). (B) Variations on chytrid morphology (1-4 in host cells; 5-6 on substratum surface).

Before examining the cellular starting points of filamentous fungi in detail, I introduce a general model of the evolutionary development of filamentous fungi based on our brief look at their evolutionary history. In the following sections, I elaborate three central themes of this model: Coenocytic and polarized growth allow filamentous *wholes*; septation allows distinct *parts*; and differentiation produces complex *wholes-with-parts*. The generalized model begins with spore germination (see Figure 6). Germination leads to growth of a non-septate filament. Branching angles and cytoplasmic flow are exploratory. As the mycelium grows, it may compartmentalize hyphal sections behind growing tips, and it may evacuate older cell wall sections via septation. When a nutrient source is found, the mycelium changes its growth pattern, initiating secondary growth near its center. This differentiation involves increased reticulation and septation of filaments. An inner senescent zone may develop where resources are exhausted. The mycelium may grow complex, differentiated fruiting bodies on the inside of the exploitative zone. The mycelium may produce spores via these complex fruiting structures or via simple fruiting structures during other growth stages. I use this general model to capture the spectrum of individuation in filamentous fungi life cycles and also the evolution of individuation in lineages derived from simple, non-hierarchical ancestors. Many life cycles will include only early stages of the model, and many fungi derived from ancestors with pronounced individuation will likewise show less hierarchical transition during ontogeny.



**Figure 6. Generalized Evolutionary Development of Filamentous Fungi**

Stages in ontogeny/phylogeny go from less- to more-individuated starting from the top down. This progression may be viewed as a continuum of individuation wherein fungi with less individuated developmental stages lack lower (more individuated) stages. This progression may also be viewed as the derivation through the fungal phylogeny of more individuated life cycle stages. Specific morphologies are: (a) spore stage; (b) germination and filament growth; (c-d) continued growth and branching; (e) early filaments evacuated via septation (dashed line); (f) secondary growth (with septation) begins in colony center; (g) fruiting body formation (with septation) from secondary growth. (Reproduction via non-differentiated structures is not shown and can result in production of spores, returning the cycle to position 'a'.)

### 3.2 Cellular Starting Points

In The Evolution of Individuality, Buss argues that basic differences in cell morphologies and cycles underlie the distinct evolutionary-developmental patterns seen in *Animalia*, *Plantae* and *Fungi* (Buss 1987). Buss focuses on two ancestral traits that differ among *Animalia*, *Plantae*, and *Fungi*, and provide phyletic constraints<sup>3</sup> for the transitions to multicellularity: cellularization and rigid cell walls (cf. Moore 1998: 28-29). *Animalia*, *Plantae*, and *Fungi* differ in these traits (see Table 2). Of particular relevance to our investigation of hierarchical transition, we will see that filamentous members of *Fungi* differ in terms of their ability to regulate cellularization (part-hood).

Animals are cellularized in that growth consists in multiplication of discrete cells. In addition, animals cells lack rigid walls. Accordingly, animal phylogeny and ontogeny begins with individuated, mobile cells. Plants are cellularized and their cells have rigid walls. Accordingly, plant phylogeny and ontogeny begin with individuated cells but their cells are immobile. Fungi lack cellularization but have rigid walls. To Buss's three groups we may add *Myxomycota*, which satisfy his fourth category: absence of cellularization and absence of rigid cell walls (Gray & Alexopoulos 1968).<sup>4</sup>

On cellularization and cell wall rigidity Buss writes:

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<sup>3</sup> By *phyletic constraints* I mean ancestral (or 'starting') conditions for a clade that predispose it to some phylogenetic or ontogenetic pathways more than others. For a discussion of the term's many uses see McKittrick (1993).

<sup>4</sup> Buss introduces these categories as generalizations characterizing the majority of the so-called 'higher' plants, animals and fungi.

"Quite different limits on the diversity of possible life cycles were ordained by the very different paths which individuality followed in the three multicellular kingdoms. The ancestral characteristics that each clade brought to this fundamental evolutionary transition defined the somatic context in which cell lineages interacted, and thus determined the nature of potential synergisms and conflicts between selection on the level of the cell and that of the individual." (Buss 1987: 121)

The focal interaction for Buss is that between two levels of evolutionary individuals: multicellular organisms and their component cells. His work focuses on the

challenges associated with transitioning from *parts* to *parts-in-a-whole* in animal and plant lineages. In particular, he looks at the trade-offs for individual cells between

solitary life and reproduction, and membership in a multicellular collective with a division of labor and thus possibly no reproduction (for a given cell). This approach

is premised on animal and plant development beginning with the reproduction of discrete cells. However, animals and plants differ with respect to cell mobility.

Animal cells are not constrained by rigid walls. This allows for the sequestration of a germ line distinct from somatic lines but also leaves open the possibility of system-

wide parasitism (e.g., mammalian cancer). Plant cells are constrained by rigid walls and thus plants cannot sequester germ lines as some animals do. On the contrary,

apical meristems maintain totipotency and thus the ability to give rise to tissues of varying types, including reproductive tissues. In contrast to animals, however, plants

are less susceptible to cancerous parasitism since rigid cell walls limit the mobility of aberrant cell lines.



Buss's starting point of cellularization and wall rigidity is central to my account of integration and individuation, but I do not share his focus on the issue of part-whole conflict. I depart from Buss in this regard because the case of animals (his focus) is different from that of fungi, and plants, in an important way. Plants and filamentous fungi are by and large more modular organisms than the animals Buss studies. With modularity comes increased independence and redundancy of parts such that the loss of one or many parts to an aberrant cell lineage is not as detrimental to the whole as it can be in less modular organisms such as the higher animals (Carlile 1995). Of course, the evolution of modular development may itself owe much to the particulars of cellular starting points. The rest of this section focuses on the distinct cellular starting points of *Animalia*, *Plantae*, and *Fungi*.

**Table 2. Cellular Starting Points (modified from Buss 1987: 130)**

Clade	Cellularized	Rigid Cell Walls
Fungi	No	Yes
Plantae	Yes	Yes
Animalia	Yes	No
Myxomycota	No	No

### 3.2.1 Animalia

In animal cells, cytokinesis (protoplasmic division) typically follows karyokinesis (nuclear division). In most cases cytokinesis involves the centripetal contraction of a contractile ring (Goldberg et al. 1998). Rappaport summarizes the process nicely:

“the basic form of cytokinesis starts with a spherical cell containing a central mitotic apparatus. Division entails the formation of a uniform circumferential indentation on the surface that deepens in a plan that intersects with the midpoint of the mitotic apparatus and is oriented perpendicular to its axis. Division ends in the formation of two daughter cells of equal volume.”  
(Rappaport 1996: 1)

When cytokinesis follows the onset of karyokinesis, it begins near the end of mitosis (Rappaport 1996: 3). The axis of cytokinesis is oriented perpendicularly to the mitotic axis, but the overall spatial symmetry of the process ranges from spherical to bilateral. Early development (when division involves cleavage but not growth) is particularly variable across taxa. For example, sea urchin eggs show “near spherical symmetry” whereas ctenophore eggs and some coelenterate eggs undergo “unilateral cleavage” (Rappaport 1996: 10-13). Cytokinesis tends to be more symmetrical in later life stages, although tissue cells can be more irregularly shaped due to adhesion or cell-cell connections (Rappaport 1996: 16). Numerous theories address the mechanics of cytokinesis (Rappaport 1996: 21-55).

Delayed cytokinesis resulting in coenocytic cells is present in *Animalia*.

Delayed cytokinesis occurs irregularly in some coelenterates, but it occurs regularly and precisely in the early development of some arthropods (Rappaport

1996: 307-321). *Collembola* eggs show cytokinesis only after two mitoses; *Drosophila* embryos undergo numerous rounds of somewhat synchronous karyokinesis with regular nuclear spatial arrangement before asymmetric cytokinesis (which Rappaport calls "cellularization").

### 3.2.2 Plantae

As with animal cells, in land plant cells cytokinesis typically follows karyokinesis. In most cases, cytokinesis involves the coordinated centrifugal growth of a phragmoplast and a cell plate (Wright & Smith 2008). Both of these division processes result in cytokinesis.<sup>5</sup> Unlike in animals, where the mitotic spindle position determines the plane of cleavage, in plants the division plane is determined prior to mitosis. In a typical higher plant cell, a cytoskeletal "preprophase band" marks the division plane before mitosis, and breaks down with formation (usually perpendicular to the band plane) of the mitotic spindle. After chromosome segregation, a *phragmoplast* forms between nuclei and serves as the basis for the new cell plate. The phragmoplast grows centrifugally as a torus (a donut-like shape), recycling its components as the cell plate grows from its center. The process ends with the fusion of the cell plate with the maternal cell wall (Wright & Smith 2008: 33-

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<sup>5</sup> The formation of the cell plate may involve formation of cell-cell connections. Speaking from the organismal perspective, Niklas notes that "A multicellular plant thus consists of a single living protoplast incompletely subdivided by an infrastructure of cell walls" (Niklas 1997: 154).

34). This process can occur asymmetrically, such as in vacuolated cells with a laterally located nucleus (Wright & Smith 2008: 50).

### **3.2.3 Fungi**

In this project I draw a distinction between yeast-form and filamentous fungi to roughly distinguish fungi that undergo hierarchical transitions via integration from those that do so via individuation. The actual range of fungal morphology is not so simple. Numerous fungi have dimorphic life cycles – environmental conditions can induce either vegetative growth form. More generally, Gow points out that

“All fungi have some capacity to grow in two basic morphological forms – spheres and tubes – therefore it could be argued that they are all, to some extent, dimorphic.” (Gow 1995b: 402)

The distinction between these two growth forms primarily concerns cell polarity. Analogous cellular processes produce distinct morphologies based on the orientation of growth and wall deposition. If we also consider morphological differences owing to the presence or absence of internal and/or external rigid walls we can divide fungal morphologies into five groups. Following Cavalier-Smith (2001: 7-8; see Figure 6):

- “1. The multinucleate syncytial hypha (often partially divided by septa) that forms an indeterminate branching mycelium, bounded by walls which usually contain chitin fibres in a matrix of  $\beta$ -glucans.
2. The unicellular uninucleate walled yeasts, often with little or no chitin, which have arisen polyphyletically from hyphal ancestors.

3. The chytridiaceous thallus, differentiated into one or more globular nucleated portions and very slender and enucleate rhizoids...
4. A naked cell or coenocyte, which characterises Coelomomycetales and Microsporidia, which probably lost vegetative cell walls through independently endoparasitising insects; both retained chitinous spores for dispersal to new hosts...
5. A determinate multicellular thallus of uninucleate cells, as in Laboulbeniales''

I focus on morphologies 1 and 2 since they serve as good examples of alternative modes of hierarchical transition, and many cases are characterized by complex, differentiated organisms. Morphologies 3, 4, and 5 primarily characterize parasitic species (in some case, derived species) with little hierarchical morphology.

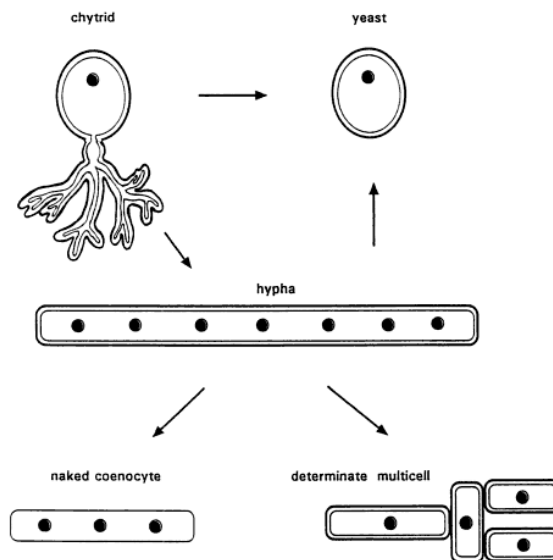


Figure 7. Fungal body forms (Cavalier-Smith 2001: 7)

Two popular experimental model organisms provide a good picture of yeast cells (morphology 2). The reproductive cycle of the fission yeast *Schizosaccharomyces pombe* begins with the initiation of mitosis. Actin is relocated to form an equatorial ring of filaments around the nucleus. After nuclear division, the nuclei migrate to opposite ends of the oblong (and elongated) cell. The primary septum originates in the periplasmic space and grows into the cell, perpendicular to the division plane. (The periplasmic space is between the rigid outer wall and the cell membrane.) Secondary septa form on either side of the primary septum. Finally, the primary septum just deposited is removed, leaving two separated cells (Moore 1998: 52; Wendland & Walther 2006: 106).

Cytokinesis is similar in yeasts like *Saccharomyces cerevisiae* that divide by budding instead of by fission. An acto-myosin ring constricts the connection between the mother and daughter (the bud) and a primary septum is laid down across the bud site, completing cytokinesis. Secondary septa are built between each cell's membrane and the primary septum (Wendland & Walther 2006: 115).

Even with the separation of cytoplasm into two discrete units, yeast cells may remain connected via the budding-site septa. On the one hand, the connecting wall may be partly degraded to separate the two cells (Wendland & Walther 2006: 105). On the other hand, the cells may remain connected. In some yeasts, such as *S. cerevisiae*, this can play a role in pseudo-filamentous growth - exploratory, linear chains of cells (Granek et al. 2011). *S. cerevisiae* and other yeasts can also form

complex, integrated multicellular colonies (Palkova & Vachova 2003, 2006; Vachova et al. 2009; Granek & Magwene 2010).

Cell division in filamentous fungi (morphology 1) is similar in most respects to that in yeasts, animals and plants. The significant difference is the separation of karyokinesis and cytokinesis (Gull 1978; Trinci 1979; Wendland & Walther 2006). The first step in cell reproduction involves karyokinesis. This is sometimes accompanied by primary septum deposition (as it is in yeast cells). However, karyokinesis can occur without primary septum formation, so that a coenocytic multinucleate cell results. In some cases, a primary septum is formed later in the cell cycle, and in others an already-formed primary septum is degraded. A hypha can deposit a secondary septum at the site of an existing primary septum. This constitutes cytokinesis and so results in complete cell division as in the case of yeasts. As with yeasts however the two cells may remain connected via their secondary walls, even if there is no cytoplasmic connection. Deposition of a secondary septum can occur during the reproductive cycle, as it does in yeasts or in spore formation, or it can occur during another stage of the cell cycle.

The separation of karyokinesis and cytokinesis in filamentous fungi is the key to evolutionary development via individuation (not integration). Without the deposition of septa, growing hyphae do not establish strict part-part boundaries and thus do not establish hierarchy. In terms of organismal theory, coenocytic hyphae are non-compartmentalized and thus non-cellular. It is only with later with septation (if

any) that these hyphae compartmentalize and thus establish a part-whole hierarchy. This key difference in cellular starting points between the filamentous fungi and other clades with hierarchical transition leads to the characteristic growth and development of filamentous fungi, to which we now turn.

### **3.3 Filamentous Fungi as Wholes-without-parts**

When it comes to the evolutionary sources of coenocytic growth and polarized growth, we can view both as derived, but developmentally simple innovations. Indeed, *innovation* may be too strong a term, since either growth habit can result from the removal or continuation of ancestral developmental steps (at least in their simple forms). These two changes from ancestral growth modes demonstrate how the removal of obligatory part-hood removes a significant evolutionary-developmental constraint and enables the filamentous growth central to the *whole-without-parts* ecology adopted by the filamentous fungi.

#### **3.3.1 Coenocyt**

As I mentioned in the previous section, coenocytic growth is simple to achieve from an ancestral state with joined karyokinesis and cytokinesis. The lineage has only to lose the formation of septa accompanying karyokinesis. Although the extent of compartmentalization via septation varies in the filamentous fungi (see below for discussion) even regularly septate fungi maintain functional coenocyt (Gregory 1984; Carlisle 1995). Coenocyt enables both "translocation" of water and solutes via "bulk flow" through a filament and "transmigration" of organelles (such



as nuclei) or even the entire protoplasm (thus emptying the rigid outer wall) (Gregory 1984; Jennings 1984; Carlile 1995).

### **3.3.2 Polarized Growth**

Polarized growth occurs throughout the living world and plays an important role in development. As a general phenomenon, Gow writes that cells "exhibit polarized cell development or tip growth when the expansion of the cell surface is focused at one location" (Gow 1995a: 277). In the fungi we see polarized growth in germ tube growth after spore germination (Trinci 1984) and fission or budding processes in yeasts (as discussed above) (Sudbery & Court 2007). In contrast to these limited growth phases in other life cycles, polarized growth is the "main growth form of filamentous fungi" (Fischer 2007).

Coenocytosis aids filamentous growth by allowing for translocation and transmigration of hyphal elements. Importantly, this allows for the structured polarization of organelles that would be restricted within compartments if the filament were fully cellularized. Hyphal growth tips across the filamentous fungi show characteristic polar protoplasmic ordering (Grove 1978; Roberson et al. 2010). Cytoplasmic vesicles cluster at the apex and organelles, including nuclei, cluster posteriorly. In *Dikarya* hyphal growth tips contain a structured "dynamic organizing center," the Spitzenkörper, whose "presence and absence are tightly correlated with

rates of cell growth" (Roberson et al. 2010: 9-11).<sup>6</sup> Transport to the growth point is highly polarized and can involve complex systems (Roberson et al. 2010).

### 3.3.3 Filament Mechanics and Ecology

Filamentous growth provides several mechanical and ecological benefits over cellular or yeast-form growth: steady ratio of surface area to volume throughout extension; favorable mechanics for stress-resistance; favorable mechanics for penetrative growth; and advantages for substrate exploration and protoplasmic transport.

Filamentous growth accomplishes increased size while maintaining a constant surface-area-to-volume ratio (the ratio is  $4/\text{diameter}$  if we ignore the filament cap) (Moore 1998, ch.2). Thus, it presents an alternative to another strategy for increasing size without decreasing this ratio - multicellular growth. Filamentous growth can increase mycelium size, but without a change in the hyphal tip extension rate the only way to increase the overall growth rate is by branching to create more growing tips (Trinci 1978, 1979, 1984; Righelato 1979). The constant surface-area-to-volume ratio and the steady increase of overall surface-area with growth and branching is key for fungal nutrition, which involves food consumption by direct

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<sup>6</sup> Roberson et al. (2010) report that one group outside the *Dikarya* shows Spitzenkörper, *Allomyces* (*Blastocladiomycota*).

contact, enzyme secretion, and substrate absorption (Cooke & Rayner 1984; Roberson et al. 2010).<sup>7</sup>

Hyphal geometry is ideal for a number of mechanical reasons. The radial symmetry of a hollow cylinder is advantageous in settings where filaments are in substrates that limit self-loading stresses (e.g., bending under your own weight) and effectively randomize dynamical loading stresses (Niklas 1992, ch.3). Cylindrical growth also advantageous for resisting symmetrical swelling stresses. Growth of this shape is easy to achieve via uniform growth at the hyphal apex. Hyphal shape also improves penetrative/invasive growth into soil, wood, or host cells. Narrowed growing tips combined with polarized growth make for efficient penetration (Money 2007).

The coenocytic state of the filament also means that a great hyphal length can support tip growth, increasing the growth rate and also allowing for tip growth through substrate regions with little or no local resources (Carlile 1995). This allows for more efficient substrate exploration, and for transmigration of protoplasm away from depleted resource zones to more active areas of the mycelium.

### ***3.4 Filamentous Fungi as Wholes-with-parts***

Filamentous fungi regulate part-hood, and may thus achieve hierarchical transition, via manipulation of septal deposition, modification, plugging, and

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<sup>7</sup> Cooke & Rayner (1984: 49) note that in a resource-rich substratum the benefits of the greater surface-area-to-volume ratio of the yeast growth form may in some cases outweigh the benefits of the exploratory and/or invasive capacity of the filamentous growth form (i.e., where exploratory and/or invasive growth does not improve relative growth rate).

degradation. As with coenocytic and polarized growth habits that characterize filamentous growth in general, septation dynamics, at least in their simple, less derived forms, may be *free innovations* – the cellular machinery for septation is already present in organisms that accompany karyokinesis with cytokinesis by plasma membrane constriction via primary septum formation and cell separation via secondary septum formation. In order to achieve septation from a coenocytic state, an organism has only to active machinery it already has and that it uses for spore formation and irregular septation in the mycelium (for example, to separate a senescent section). The morphology, location and timing of septation can vary in the development of an individual mycelium, and it also varies greatly across taxa (Gull 1978; Wendland & Walther 2006).

Septation in fungi ancestral to *Dikarya* (*Ascomycota* and *Basidiomycota*) is rarely associated with incomplete hyphal compartmentalization (Gull 1978). Septa are present, of course, but they mostly play a role in complete cell division (as in yeast reproduction or in spore formation) or full separation of two sides of a filament. Simple pored septa can be achieved through manipulation and/or early termination of these ancestral septation processes. More complex septation processes such as those in *Basidiomycota* or pore-plugging devices in *Ascomycota* represent more significant departures from ancestral machinery. The typical septum in *Ascomycota* consists in a disc with a simple central pore. Some lineages show elaboration of the pore rim, and others show multi-perforate septa. Many lineages also have Woronin

bodies (see below) associated with septal pores. Septa separation sexual propagules are often more elaborate than those found in vegetative mycelia (Gull 1978).

Septal structure in *Basidiomycota* varies greatly from single-pore septa to complex dolipore septa. Septal structure in the largely parasitic *Pucciniomycotina* typically consists in a disc with a single central pore, although multi-perforate cases are found. Many septa are associated with pore-plugging bodies (see below) (Swann et al. 2001). Septa in *Ustilaniomycotina* are likewise simple and lacking in elaborate structures that characterize *Agaricomycotina* septa. Most members of *Ustilaniomycotina* are parasitic and dimorphic, where the parasitic stage is typically hyphal (Bauer et al. 2001). Septa in *Agaricomycotina* (most of the fungi that make large fruiting bodies such as mushrooms, puffballs, and brackets) are highly structured. The central pore of the septum is swollen ("dolipore") and each side of the pore is associated with a "parenthosome", a "hemispherical perforate cap" that resembles a parenthesis (Gull 1978). Parenthosomes may be uni- or multi-perforate, and their structure may differ within the same organism. During the mating of two monokaryotic hyphae, complex septa may be degraded to form simple-pore septa to allow nuclear migration and the establishment of dikaryotic mycelia.

Primary septation regulation in filamentous fungi plays three major roles: compartmentalization to establish functional cytoplasmic privacy for differentiation; control of organellar and cytoplasmic traffic; and isolation of damaged or senescent regions of a mycelium. Some authors suggest a mechanical role for primary septa as

stabilizing cross-walls, but this is likely a secondary role for septa (i.e., not one with a great effect on fitness) (Gull 1978).

### **3.4.1 Functional Cytoplasmic Privacy**

I mean by functional cytoplasmic privacy the functional separation of one cytoplasmic section from another. In typical animal and plant cells, near-complete separation of cells from one another results in a distinct inside-outside structure of the cytoplasm. This allows for privacy in the sense that expression patterns can be contained within the cell compartments and signaling activities across the cells can be tightly regulated. This does not mean that the cell is unresponsive to external stimuli. Rather, it means that it is capable of undergoing a developmental process different from that of a neighboring cell.

Functional compartmentalization and differentiation may be the primary function of primary septation in hyphae (Gull 1978; Markham 1994; Carlile 1995). The timing of septation formation, modification, and degradation is tightly correlated with mycelial differentiation (see below), and the sophistication of septa is clearly correlated with the sophistication of differentiated structures. On the latter point, Gull writes:

"The existence of septa, particularly perforate septa, gives the higher fungi the potential of colony differentiation and tissue production together with the development of specific cell types. It appears that the more complex the septal structure so the more complex is the type and degree of differentiation allowed... The most highly differentiated fruit-bodies formed by micro-organisms are those produced by the basidiomycetous fungi. These involve complex arrangements of hyphae to produce tissue-like specializations and

cell types. I do not believe that it is coincidental that these organisms also possess the most complex septal form found in the fungi.” (Gull 1978: 88-89)

I explore this relationship further in our discussion below of fungal tissue development.

### **3.4.2 Traffic Control**

Septa play a role in regulating the traffic of organelles and cytoplasm throughout the mycelium. Complete septa can block traffic between hyphal sections, and pored septa may restrict the size of organelles trafficked. In addition to these static roles (although the deposition or degradation of a septum for this purpose would be dynamic) septa can play a dynamic role via pore-plugging. Most plugging occurs in *Dikarya*, although some cases are found in *Zygomycotina* (Markham 1994). Plugs may consist in preformed Woronin bodies or crystalline bodies, or in the de novo formation of plug materials at the septum. Woronin bodies associated with large-pored septa in *Ascomycota* allow for significant translocation through septa but also allow pore closure in response to stress or damage (Gull 1978). Septal plugging also allows for temporary isolation or separation of hyphal sections, which may become permanent by deposition of permanent materials over the plug site (Markham 1994).

### **3.4.3 Segmentation**

By segmentation I mean permanent separation of hyphal sections by primary and secondary septum deposition. This plays a role in spore formation, and as noted

above, isolation of damaged regions, but it may also be used for isolation of senescent or obsolete filaments after protoplasmic evacuation (Gull 1978; Trinci 1978; Markham 1994; Carlile 1995).

### **3.5 Hierarchical Transition in Filamentous Fungi**

Filamentous fungi that achieve differing degrees of hierarchical transition via mycelial septation may develop a variety of complex differentiated structures. This represents the height of individuation in the filamentous fungi (Figure 5) and demonstrates how filamentous fungi can develop cellularity in later ontogeny to produce hierarchical structures similar to those reached by other lineages via progressive integration (Figure 2). The individuation of a fungal mycelium can take the form of network elaboration, simple vegetative tissue formation, or more complex fruiting structure formation.

Complex mycelial networks are restricted to terrestrial filamentous fungi, most the *Dikarya* (Gregory 1984). Mycelial networks elaborate the exploration theme first embodied by filamentous growth. Basic advantages such as polarized growth, concerted growth effort, and evacuation of older segments can be complicated by network factors. These include regulation of septation rate; septation type; branch rate; branch angle; branch location; hyphal fusion ("anastomosis"); and growth rate (Trinci 1978, 1984; Carlile 1995; Prosser 1995; Rayner et al. 1995; Klein 1996).

Branch rate, branch angle, and branch fusion are simple ways to modify network patterns. As seen in the generalized development model (Figures 5), early



exploratory growth is characterized by branching away from the mycelium and a lack of hyphal fusion. Septation is limited to separation from evacuated outer walls or partial compartmentalization of hypha far behind growing tips. This is an efficient strategy for finding resources. However, with exploitative growth around a resource, branch angles and hyphal fusion accomplish a denser, reticulate, and more septate mycelium. This allows for more efficient exploitation of the resource, and also the possibility of simple tissue differentiation.

Vegetative tissues include linear mycelial strands or cords, and rhizomorphs. (Stipes of some fruiting bodies also consist in simple linear tissues (Moore 1995).) Mycelial strands and rhizomorphs can be seen as extremes on a spectrum of linear tissues formed by hyphae (Moore 1995: 431). Strands consist in "parallel aggregates of morphologically similar hyphae" with some septation (Moore 1995: 426). Strands provide larger-scale translocation of fluids and nutrients than can be accomplished by simple filaments. This increases the ability of the mycelium to contribute overall resource consumption to particular growth sites (such as exploratory sections lacking local resources), aids in the support of large fruiting body construction, and plays a significant role in plant-root-associated mycorrhizal networks. In contrast to strands, rhizomorphs are more integrated, compartmentalized, and differentiated. In particular, they have a uniform differentiated morphology characterized by "highly organized apical growth point and extreme apical dominance" (Moore 1995: 430). Rhizomorphs represent the epitome of polarized, penetrative, exploratory growth in

the filamentous fungi. Thus, rhizomorphs are much closer to plant roots in their structure and sophistication than are hyphal strands, which are perhaps closer to root hairs.

Macroscopic reproductive structures additionally involve globose tissues, whether simple survival structures like sclerotia ("pseudoparenchymatous hyphal aggregations") or larger and more differentiated fruiting structures seen in *Dikarya* (Moore 1995). As noted earlier, there is a strong correlation between mycelial and septal sophistication and the sophistication of macroscopic fruiting bodies. From a resource perspective, this makes sense given the nutrients and fluids required to form a large, rigid structure like a bracket or toadstool. However, the complex differentiated tissues that comprise many macroscopic fruiting bodies require tight organization of tissues and compartments of their own in addition to those in supporting mycelial networks (Poggeler et al. 2006; Wosten & Wessels 2006). While clearly unnecessary for the majority of filamentous fungal lifestyles, macroscopic fruiting bodies are remarkably effective at large-scale spore dispersal to effect colonization of distant substrates.

## 4. Conclusion

I have argued that hierarchical transition can proceed via integration or individuation and that the evolutionary development of the filamentous fungi is best understood via the individuation model. The cellular starting point of the filamentous fungi allowed for regulation of part-hood and thus for the developmentally simple features of coenocyt and polarized growth that characterize filamentous morphologies well-suited to absorptive ecologies. Reintroduction of hyphal compartmentalization via septation during vegetative and sexual development allowed the formation of differentiated mycelia and complex tissues. However, this later-stage individuation kept in place the early-stage coenocyt important for vegetative exploration and thus allowed for hierarchical transition unhindered by the classic cooperation/conflict constraint posed by cellularity.

As for the particulars of the filamentous fungi, mycological literature is rife with mentions of correlations between septation and septum complexity on the one hand, and vegetative and sexual complexity on the other, but more study of the precise role of septation is needed. Septal ultrastructure is a popular diagnostic criterion for filamentous fungi phylogenetics (despite repeated appearances and disappearances of different morphologies within some groups), but it seems the careful study of septal timing and its precise role in tissue differentiation is limited to a few model organisms. Such close studies provide much of the impetus for my

application of the individuation model to the filamentous fungi, but consideration of a broader set of case studies would undoubtedly improve the model. The diversity and plasticity of filamentous fungi development makes this group both fascinating and fruitful to study, but also difficult to capture with a simple model.

Despite the limitations of this case study, we see that a striking implication of the control of cellularization in the filamentous fungi is that the evolutionary individuality of parts, in this case cells, is itself a phenotype of the whole that is flexible in evolutionary development. Not only are cells not necessary at the outset of development, but their presence, and thus the compartmentalization of the whole, can be an ecological hindrance. Put more generally, hierarchical transition from *whole* to *whole-with-parts* involves the regulation of part-hood. Transition by individuation avoids the status quo problem of competition amongst parts preventing wholeness by simply starting with wholeness and no part-hood. Without parts, there can be no inter-part conflict. This expansion of the standard hierarchical transition spectrum promises to improve our understanding of the filamentous fungi and related groups such as *Myxomycota*, and also challenges the most basic assumptions at play in our theories of biological hierarchy and the levels of selection.

## References

Abbreviations: *BSV* (Berlin: Springer-Verlag); *MIT* (Cambridge, MA: MIT Press); *CUP* (Cambridge, UK: Cambridge University Press); *PUP* (Princeton, NJ: Princeton University Press); *OUP* (Oxford, UK: Oxford University Press); *UCP* (Chicago: University of Chicago Press); *LCH* (London: Chapman & Hall)

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