

BRYCE KENDRICK

At Kananaskis, I gave a very brief talk listing features, other than ontogeny, of conidia and conidiogenous cells which could be used to classify Fungi Imperfecti. Conidium shape was one.

The shape of an object is generally one of the first of its attributes to be used in describing it because, in our strongly visual approach to life, it is one of the first things we perceive. This has been equally true for microscopic objects like the conidia of hyphomycetes. Some groups of Saccardo's classification are distinguished by their production of "helico-," "stauro-," and "scoleco-spores." At the generic and specific levels much more limited or discrete shape concepts are used: spherical, ovoid, ellipsoid, biconic, curved, flame-shaped, etc. We have tended to use these characters without questioning, because they were convenient and accessible. But as the taxonomic spotlight shifts from mature morphology to ontogeny, we should re-examine shape from two angles: (i) What are the mechanisms which produce the myriad of shapes we know? (ii) How stable a feature is shape - how much is it genetically controlled, and therefore how taxonomically valid is it?

I have an answer of sorts for the first question. As to the genetic control of the factors involved, I know nothing. But the postulation of a possible mechanism must precede any answer to the second question. Let me say at once that I am concerned here only with the over-all shape of a spore, not with acellular appendages, outgrowths, or ornamentations. Further, I am concerned only with conidia

Department of Biology, University of Waterloo, Waterloo, Ontario, Canada.

*I wrote this brief chapter in hopes of stimulating a little rethinking and a little new thinking among students of the Fungi Imperfecti. I have subsequently discovered Professor N. F. Robertson's presidential address to the British Mycological Society (*Trans. Brit. Mycol. Soc.* 48 [1965]: 1-8) in which he makes some comparable suggestions. I am pleased to have arrived independently at somewhat similar views to those held by Professor Robertson, but I am disturbed that relatively little progress appears to have been made in solving the problems he raised in 1965.

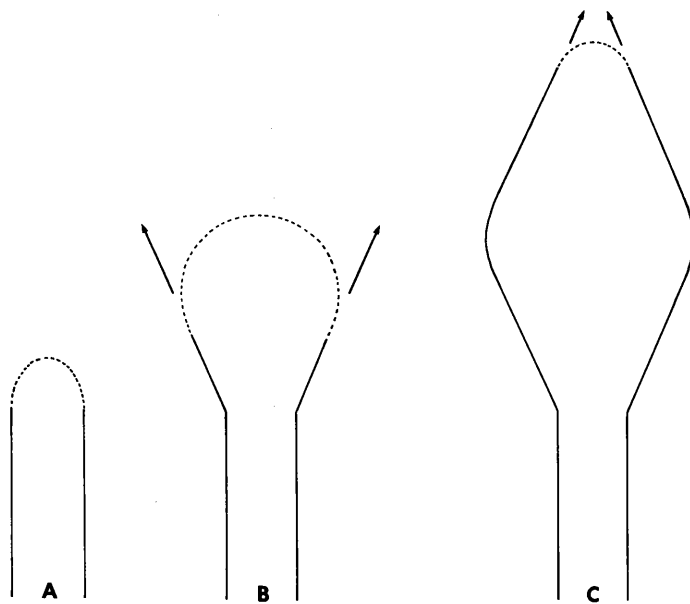


Figure 20.1. A: Diagram of hyphal tip; the dotted line indicates the hemispherical "unset" wall. B: During spore widening, wall setting lags behind blowing out; there is more than a hemisphere of unset wall. Wall setting is proceeding along the tangents shown by the arrows. C: During spore narrowing, wall setting is proceeding along the tangents shown by the arrows.

which are produced entirely by apical growth; this excludes those in which considerable secondary swelling or intussusception of new wall material occurs, as in *Basipetospora*, *Cladobotryum*, and *Amblyosporium*.

A simple analysis of the situation with which I am concerned here will suppose that one fluid (protoplasm) is bounded by a membrane (the cell wall) beyond another fluid (air or water). As far as the cell wall is concerned, I assume for the sake of simplicity in model-building that it may exist in two conditions, which I will call "unset" and "set." For the purposes of this discussion, the "set" wall is inelastic and incapable of further deformation except by rupture due to tension, and is subject to secondary enzymatic softening. The "unset" wall is elastic and can stretch in response to pressure differentials. One further assumption is made for simplicity's sake: that there is at any given moment a sharp line of demarcation between set and unset wall (in reality there must usually be a zone rather than a line).

The first and simplest case is the growing hyphal tip (Figure 20.1 A). It is important to remember that all other fungal manifestations at the apices of hyphae are derived from this case. The hyphal tip can be represented as a cylinder of set wall with a hemispherical cap of unset wall (the shape dictated by surface tension) at its

hyphal growth proceeds, fluid pressure generated within the hypha finds expression at the unset tip, tending to blow it out like a balloon. If the diameter of the hypha is to remain relatively constant, then wall setting must move forward at exactly the same rate as the tip is blowing out.* Conidium production (and the production of many other basically hyphal structures) may be regarded as a result of a change or series of changes in the relationship between rate of blowing out and rate of wall setting. Let us now consider a number of specific examples.

1. The spherical conidium. Here I assume that while blowing out continues, wall setting ceases temporarily. When the conidium has reached full size, rapid and uniform wall setting occurs all over its surface, and the internal growth pressure either ceases or is diverted elsewhere. The area of the hyphal tip which remains or becomes unset at the beginning of this process may vary from the full width of the hypha, as in the case just outlined, down to a very small circular spot (Figure 15.1), and all intermediate cases may be found, giving rise to conidia with basal scars of different widths - in fact, everything from Subramanian's "gangliospor" to Hughes's "blastospore."

When a conidium is not ultimately spherical (the shape dictated by surface tension, minimizing surface area for any given volume), I assume this deviation to be due either to differential growth or to differential wall setting. Since the latter is much easier to deal with in a model system, I shall expand on its various expressions.

2. The long, cylindrical conidium. This may originate from a narrow base, but essentially it repeats the phenomenon of hyphal growth: tip blowing out just keeping pace with wall setting.

3. The conidium widest in the middle, tapered towards both ends. This shape may be due to two shifts in the relationship between rate of wall setting and rate of blowing out. Initially, wall setting lags behind blowing out by a slight but relatively constant amount. There will thus be more than a hemisphere of unset wall (Figure 20.1 B), and setting will thus move along the tangent drawn in the figure. Later, the rate of wall setting overtakes the rate of blowing out, and exceeds the latter by a slight but relatively constant amount. Now there will be less than a hemisphere of unset wall (Figure 20.1 C), and setting will move along the tangent drawn in the figure, steadily narrowing the conidium to its apex.

4. The curved cylindrical conidium. The curvature may be the result of slightly advanced wall setting on one side of the growing apex (the outside of the curve), or slightly retarded wall setting on the other (the inside of the curve), or a combination of both processes going on simultaneously.

5. The "helicospor," coiled in two dimensions. When the differential in wall-setting rates on opposite sides of the apex gradually becomes more extreme, and is so maintained over an extended period of elongation growth, the conidium may become spirally coiled in two dimensions.

*Note how different this process is from the "allometric" growth of most higher plant cells, in which there is increase in both length and width, while the relative growth rates of the two dimensions remain constant.

6. The "helicospore," coiled in three dimensions. In this case, the asymmetrical wall setting must be in two directions: skewed "back/front" as well as "right/left".

It seems to me that all these examples, and more, could be analysed mathematically, using calculus and fluid mechanics; that the dynamic processes of wall setting and the changing equilibria between blowing out and wall setting could be simulated on an analogue computer; and that ultimately the techniques of computer graphics could be tapped to give visual simulations whose driving function could be rapidly corrected as the simulations approached or diverged from the pattern. In this way we may arrive at some understanding of the forces involved in conidium formation. Work on such computer models is proceeding in my laboratory.

George Wald (*Scientific American*, September 1958) wrote: "Confronted with a phenomenon in living organisms, the biologist has always to ask three key questions, each independent of the others: the question of mechanism (how does it work?), the question of adaptation (what does it do for the organism?), the question of embryogeny and evolution (how did it come about?) ... one does not understand only when all three have been answered."

For the Hyphomycetes, the answers lie in the future, but we must at least ask the questions.