Evolution and the egg

Multicellularity

Most multicellular organisms pass through a single-cell stage from which they then develop. This feature may render them more evolvable.

Lewis Wolpert and Eörs Szathmáry

Evolution has had at least 20 separate attempts at forming multicellular organisms. Plants, animals and fungi are the most spectacular and complex achievements of this kind. There are essentially two ways to make a simple multicellular entity out of single cells: either a single cell divides and its offspring stick together, or several solitary cells aggregate to form a colony. Division and adhesion is characteristic of multicellular forms of aquatic origin, whereas aggregation is typical in terrestrially derived colonies.

What is multicellularity? An overall coordination of at least some key function is a necessary and sufficient condition for a colony of cells to qualify as multicellular. According to this view, most bacterial colonies are not multicellular, as they lack this overall coordination, despite occasionally undergoing self-organized, patterned growth. It is the presence of developmentally differentiated cell types in a colony that makes it truly multicellular.

It is advantageous for the unit of reproduction (the propagule) to be as small as possible (that is, a single cell), as the uniformity thus created will reduce the likelihood of conflict between cells. Mutation — the engine of evolution — will upset this uniformity, and selection against mutation may favour propagules of different sizes. Mutants that affect the organism but benefit the cell (such as those that lead to cancer) cannot be effectively selected out of large propagules, so their occurrence would favour a single-celled propagule. By contrast, uniformly deleterious mutants that affect the survival of both cell and organism can be successfully selected out of a multicellular organism, so their occurrence would favour propagules that are larger than a single cell.

Yet there may be another factor at work. Development from a single cell — an egg — may have been essential for multicellular organisms to have evolved, as they have, into such an enormous variety of different forms. Could an asexual form of reproduction, involving budding (somatic embryogenesis) as in hydra, have given rise to so many complex new forms? This is not a question of competition between cells in the multicellular organism, but an issue that relates to developmental processes that generate the form of the organism. And the answer is no.

The first step in the development of a complex organism is the establishment of a pattern of cells with different states that can differentiate along different pathways. One mechanism for pattern formation is based on positional information: cells acquire a positional identity that is then converted into one of a variety of cellular behaviours, such as differentiating into specific cell types or undergoing a change in shape and so exerting the forces required for the formation of different structures. This and other patterning processes require signalling between and within cells, leading ultimately to gene activation or inactivation. Such a process can lead to reliable patterns of cell activities only if all the cells have the same set of genes and obey the same rules. During evolution, it is the change in genes that leads to the creation of new patterns of development.

In a hydra-like organism that only reproduces by asexual budding, it is impossible to evolve significant changes. There is no way that the genes in the huge number of cells involved in budding can change at the same time, and mutations in individual cells mean that they no longer share the behavioural rules of the majority. It is only through a coherent developmental programme, with all cells possessing the same genes, that organisms can evolve, and this requires an egg.

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Ova development: even the extinct elephant bird's egg represented a single-celled genetic bottleneck.

There are multicellular organisms, such as the cellular slime moulds, that develop by aggregation and not from an egg, but their patterns of cell behaviour have remained very simple for hundreds of millions of years. The evolution of more complex organisms increases the pressure to use an egg as a propagule.

An obvious but erroneous objection to our idea is that we are confusing the intrinsic disadvantage of asexuality, as discussed by population geneticists, with that of having a large propagule. Try to imagine a sexual life cycle that incorporates a large propagule. Each cell in the propagule would have to be fertilized by an individual sperm cell — otherwise the propagule would still be one that develops from a single fertilized egg. These multiple fertilizations would generate within-organism variation that would immediately generate a huge conflict. But this returns us to the question of whether it would be possible to evolve complex development with somatic embryogenesis that happens to be asexual.

We consider it practically impossible to have many asexual, differentiated cell lineages mutating in all sorts of directions in genetic space and yet retain the ability to evolve into viable new forms. This may not be completely impossible but, taking the broad view in evolutionary terms, organisms that develop from an egg would displace those that do not. Sexual reproduction also has long-term advantages, and follows easily and naturally once that life cycle of an organism is committed to egg production. ■

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