

Biological organization—A new look at an old problem

The cell theory, or cell doctrine, which states that all organisms are composed of similar units of organization, called cells, was first enunciated in 1839 and has remained one of the foundations of modern biology. This idea predates other great paradigms in biology, such as Darwin's theory of evolution (1859), the rediscovery of Mendel's laws of inheritance (1900), and the establishment of comparative biochemistry (1940). Although ultra-structure research and molecular biology have added much to the cell theory, and it has retained its eminent status in biology, the cell theory faces two ongoing problems.

First, the cell theory began as, and to a great extent remains, a structural idea. This structural view, which is found in most textbooks, describes the components of a cell and their fate in cell reproduction. Today, however, biology focuses on DNA and its informational features, and the description of a cell needs to catch up with this contemporary view of life. The cell is, and needs to be described as, a unit of self-control. That is, the description of a cell needs to incorporate ideas about how information is converted to structure. The second problem with the cell theory is historical: It first gained prominence along with the organismal theory, which is the idea that the organism has its own structural features apart from those of cells. The ensuing debate over which of the two structural theories better explains biological organization, especially in protists, has never been resolved sufficiently by structural criteria.

A resolution to both problems can be found by restating the cell and organismal theories in terms of crite-

ria of self-control and then viewing them as existing at different levels of biological organization. Levels of control is the subject of hierarchical theory; hence, organisms can be better described by a hierarchical than a mainly structural perspective. In this article, I explain the relationship between the cell theory and hierarchical theory. I begin by developing both theories and then try to reconcile them.

The cell theory—organismal theory controversy

In 1838, Theodor Schwann and Matthias Schleiden were enjoying after-dinner coffee and talking about their studies on cells. According to his biographer (Frédéric 1884), when Schwann heard Schleiden describe plant cells with nuclei, he was struck by the similarity of plant cells to cells he had found in animal tissues. The two scientists went immediately to Schwann's lab to look at his slides. Schwann published his book on animal and plant cells (Schwann 1839) the next year, a treatise devoid of acknowledgments of anyone else's contribution, including that of Schleiden (1838). He did, however, summarize his findings into three famous conclusions about cells:

- The cell is the unit of structure, physiology, and organization.
- The cell retains a dual existence as a distinct entity and a building block in the construction of organisms.
- Cells form by free-cell formation, similar to the formation of crystals.

The first two statements are still acceptable, although the third is clearly wrong. Before Schwann's publication, there were two rival theories on how cells form—one claiming free-cell formation and the other claiming cell division. Schwann picked the

wrong one—free-cell formation—because he failed to consider all available theoretical ideas. The correct interpretation of cell formation by division was finally promoted by others and formally enunciated in Rudolph Virchow's powerful dictum *Omnis cellula e cellula* ("All cells only arise from pre-existing cells"; Wilson 1896).

The cell doctrine reached its present-day eminence in 1896 with the publication of E. B. Wilson's *The Cell in Development and Heredity*, which was an accumulation of what was known about the roles of cells in embryology and chromosomal behavior. Nevertheless, some biologists held stubbornly to the idea that nerve organization remained an important exception to the cell theory because some fibers appeared to come from nonliving substances. But even this final resistance to the cell theory succumbed with Ross Harrison's convincing demonstration (Harrison 1907) that neurons in culture arise only from other nerve cells.

The cell is usually investigated by three approaches: characterizing structural components, identifying the biochemical activity of the components, and noting how the components multiply and segregate during cell division. In 1952, a fourth approach to the study of the cell began when the mathematician John von Neumann developed a theory of self-reproducing automata, in which he viewed cells as self-regulating machines. Although others had previously described cells as machines, it was von Neumann who emphasized the importance of internal control and who provided the formalism behind this feature. He proposed that such a machine would have three components: an assembler, to make another automaton; an information tape, to direct the activity of the assembler; and a tape recorder, to

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