DEVELOPMENT

Life from Repeated Parts

Lauren Ancel Meyers

What do proteins, vertebrate limbs, and random Boolean networks have in common? They stand among the dazzling array of so-called modules discussed in the volume *Modularity in Development and Evolution*, edited by two pioneers at the interface between evolutionary and developmental biology, Gerhard Schlosser (at the University of Bremen) and Günter Wagner (at Yale University). Biologists invoke concepts of modularity to explain, for example, how a single closely related cluster of genes can guide the formation of the fish skeleton, fly brain, and human arm. In common English, modularity means being composed of standardized units that can be used variably and flexibly. As the 23 chapters in the volume demonstrate, modularity appears in neuroscience, developmental biology, and evolutionary biology in a wide range of forms. The varied uses of the term may simply reflect our tendency to decompose the world into parts, or they may indicate a general principle of biological organization.

Modularity in Development and Evolution

Gerhard Schlosser and Günter P. Wagner, Eds.

University of Chicago Press, Chicago, 2004. 610 pp. $90, £63. 0-226-73853-1. Paper, $35, £24.50. ISBN 0-226-73855-8.

The compelling consensus that emerges from this volume places biological modularity on firm scientific footing. Loosely speaking, biological modules are consortia that act autonomously to produce a single form or function and are redeployed within and across species, thereby creating novelty and fueling the development and evolution of biological complexity. This concept is somewhat abstract, because modules occur at multiple levels of biological organization from single molecules up to entire organisms. Although each chapter offers its own flavor of modularity, the authors appear to share an intuition that can be summarized by three criteria: The constituent components of a module should be physically proximate (like the cells within a single embryonic domain of the central nervous system) or temporally correlated (like the expression of the genes in the *Pax-Six-Eya-Dach* network during vertebrate muscle, eye, and ear development). The parts of a module should contribute to a common trait (e.g., the fully developed *Drosophila* wing) or a common process (e.g., activation of the hedgehog signaling pathway during metazoan development). And variations on the resulting trait or process should occur repeatedly within an organism and across the tree of life (like the basic helix-loop-helix protein or the genetic components of the wingless signaling pathway).

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The volume's many versions of modularity occasionally conflict. Most of the differences, however, are simply matters of terminology. For example, Somogyi *et al.* insist that modules at a common level of organization must be entirely disjoint (sharing no common components), while in the next chapter Thieffry and Sánchez celebrate the repetition of components across modules. The contributors all concur that going from a few simple components to a panoply of life-forms is a hallmark of modularity, but they dispute what we should call the module—the inputs or output.

There is genuine disagreement on the practical implementation of modularity. How do we recognize a module? One approach is statistical. We can search for collectives that have much higher internal than external connectivity. For example, quantitative trait loci studies and gene expression analyses can identify suites of genes that most strongly correlate with a prespecified trait. In an insightful chapter, Von Dassow and Meir take a fundamentally different approach and propose a more parsimonious criterion that defines a module as the set of components that are both necessary and sufficient to produce the trait in question. We can discover essential and eliminate extraneous parts through experimental combinatorics or, as they demonstrate, through quasi-experimental exploration of a detailed mathematical model of the system.

At its heart, this endeavor is motivated by the observation that a relatively small set of building blocks seems to underlie the enormous complexity of life. Yet the link between modularity and evolution is surprisingly elusive. There are two profound questions. First, how does modularity give rise to biological diversity? Several entire chapters are devoted to the mechanisms that enable modules to be simultaneously sensitive and insensitive to their developmental milieux—that is, to have robust internal dynamics and external interactions that are easily modified to produce novel features. The key to evolvability, however, is the genetic autonomy of modules. Mutations to the genetic underpinnings must impact only the module itself; otherwise, its evolution may be hampered by the evolution of extraneous traits. The editors point out that autonomy with respect to developmental processes does not guarantee this form of genetic autonomy. They therefore draw a distinction between developmental and evolutionary modularity and focus our attention on the intersection of the two. However, it may have been more productive to insist on a single integrated concept of modularity.

The second and more challenging question regarding the relation between modularity and evolution is, how does modularity arise in the first place? One might be tempted to conflate the two questions and argue that the evolutionary advantage of modularity—the ability to combine and modify existing parts into more favorable assemblies—is enough to explain its ascent via natural selection. But evolutionary theory tells us emphatically that it is not. Natural selection cannot promote traits that only promise novelty in future generations but do not offer any immediate benefits. The thought-provoking chapters by Force *et al.* and Wagner and Mezey offer several alternative theories. For example, modularity may be correlated with genetic architectures that confer stability toward environmental noise and therefore may arise as a by-product of natural selection for such robustness.

Modularity in Development and Evolution offers a thoughtful dialogue about the very existence of modularity along with clear examples of modules from a wide range of disciplines and practical tutorials on the identification of modules through quantitative population genetics, statistical clustering analyses, and dynamical modeling. With the development of high-throughput molecular technologies and realistic computer mod-

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els of gene networks, the study of modularity is coming into its own. This volume provides a timely step forward.

AGRICULTURE

Changing Genes to Feed the World

David Pimentel

In *Mendel in the Kitchen*, Nina Fedoroff (an expert in plant molecular biology and genetics at Pennsylvania State University) and Nancy Brown (a science writer) present a clearly written history of plant breeding that focuses on the new field of the genetic engineering of crops. They emphasize the many contributions that genetically modified organisms (GMOs) now make toward increasing food supplies while at the same time raising the nutritional levels of some foods.

Mendel in the Kitchen
A Scientist's View of Genetically Modified Foods
by Nina Fedoroff and Nancy Marie Brown
Joseph Henry Press, Washington, DC, 2004. 366 pp. $24.95, C$32.95. ISBN 0-309-09205-1.

In the initial chapters, the authors review early plant breeding research, such as the development of hybrid corn, that featured the transfer of genes within crop species. This approach made enormous contributions to fostering the growth of crop yields during the Green Revolution. Crop improvements developed through plant breeding were responsible for approximately 40 percent of the increase in yields; the remaining 60 percent stemmed from greater inputs in fossil-fuels energy, fertilizers, and pesticides. Between 1950 and 1983, yields of crops (especially cereal grains) doubled to quadrupled. On a global scale, grains provide approximately 80 percent of the calories consumed by humans. Thus, the Green Revolution was vital for feeding billions of people around the world.

Though highly successful, these efforts at improving the qualities and yields of crop plants through breeding were relatively slow compared with the advances propelled by subsequent developments in the fields of molecular biology and genetic engineering. Formerly, plant breeders had to depend on manipulating (through the establishment and crossing of selected lineages) the genetic material within a particular crop to increase yields. Now, genetic engineering technology provides a means by which beneficial genes can be relatively rapidly transferred between different plant species or even taken from essentially any other organism and introduced into crops. For example, as the authors point out, this technology has been used to improve the resistance of winter rye, carrots, and other crops to freezing conditions.

However, to date plant breeding, genetic engineering, and other agricultural technologies have not been able to keep pace with the continuing growth in the global human population. (The current population numbers nearly 6.5 billion, and each day there are more than a quarter million additional people to be fed.) The World Health Organization recently reported that around the world more than 3.7 billion people are now malnourished—the largest number in history. Contributing to this nutritional problem are declines in per capita cereal grain production that, according to data collected by the United Nations Food and Agriculture Organization, began in 1984 and continue to the present.

Several places in the book, Fedoroff and Brown emphasize the value of developing herbicide-tolerant crops to help increase yields by controlling weeds. Although raising such genetically engineered crops can reduce weed infestations, there is little evidence the new technology is significantly more effective for weed control than current approaches that combine the use of herbicides and tillage. Nevertheless, companies working on GMOs (which include many firms with substantial interests in agricultural chemicals) have placed a heavy emphasis on developing herbicide-tolerant crops. This focus has contributed to the increased use of herbicides to control weeds and the resulting increase in environmental pollution.

Although they discuss freezing tolerance in crops, the authors do not mention a related issue: the tremendous opportunities that genetic engineering offers for developing perennial grains. At present, most agricultural grains are annual crops, which means the soil has to be tilled and the fields replanted every year. These tasks require the annual investment of an enormous amount of energy, both fossil and human energy. The annual tillage also contributes to the serious soil erosion afflicting croplands in the United States and elsewhere around the world. If perennial grains were developed, farmers might have to replant only once every five or six years. This use of biotechnology would be especially beneficial for many farmers in developing countries, who currently may have to spend more than 400 hours per hectare hand-tilling their fields before planting their crops.

Transgenic success. By 2002, Bt varieties (which contain an insecticidal protein transferred from the bacterium *Bacillus thuringiensis*) accounted for more than a third of the field corn in the United States.

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I found the authors' criticisms of organic agriculture surprising. They report that yields from organic farming are significantly lower than those for most conventionally grown crops and therefore conclude that a shift toward organic foods would require significantly more cropland. This is not the case. Long-term experiments (lasting 22 years) conducted at the Rodale Institute that compared conventional corn and soybean production with two different organic technologies found that the yields were approximately the same. In fact, during drought years corn yields from the organic treatments were significantly higher than those from the recommended conventional approach. The organic farming technologies also offered the advantage of avoiding applications of insecticides and herbicides, whereas conventional corn production uses more insecticides and herbicides than any other crop grown in the United States. Overall, organic approaches would reduce the use of fossil energy in corn production by about 30 percent and substantially increase the organic matter in the soil. The authors' discussion of organic farming emphasizes its potential drawbacks while neglecting the opportunities it offers to conserve fossil energy resources, reduce soil erosion, and reduce global warming.

The criticisms expressed here reflect my disagreement with the authors' positions on several topics covered in the book. But they should not overshadow the fact that Fedoroff and Brown present a strong case that plant breeding and genetic engineering have made and will continue to make substantial contributions to our food supply. Certainly, increased awareness and appreciation of the potential benefits of GMO research will enlarge the scope to cover additional dimensions, such as the development of perennial grain crops. Researchers from many disciplines, social scientists, and any readers desiring a broad perspective of the rewarding applications of genetics in agriculture will find *Mendel in the Kitchen* most helpful.

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