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CHAPTER 1

Shells and the Questions of Biology

Few works of architecture can match the elegance and variety of the shells of molluscs. Beauty is reason enough to appreciate and study shells for their own sake, but shells offer much more. As molluscs grow, they enlarge their shells little by little, and in doing so inscribe in their shells a detailed record of the everyday events and unusual circumstances that mark their lives. Moreover, the fossil record that chronicles the history of life is replete with the shells of extinct species. We can therefore learn about the conditions of life and death of molluscs not just in our own world, but in the distant past. The sizes, shapes, and textures of shells inform us about the way skeletons are built and how animals respond to the hazards around them.

The molecular biologist Sidney Brenner once observed that there are three fundamental questions we can ask about a biological structure.* How does it work? How is it built? How did it evolve? These questions apply to structures at all levels of the organic hierarchy, from proteins to cells to whole animals, populations, and ecosystems.

The first of Brenner's questions is one of mechanics and effectiveness of design. What is the relationship between structure and function, and how well does the structure work under given conditions? What are the mechanical principles and the circumstances that dictate the possibilities and limitations of adaptive design?

The second question deals with the rules of biological design. What are the rules by which individual organisms develop and grow, and how do they work? What limits do they impose on the diversity of forms encountered in nature? How, and under what circumstances, can change be brought about within the established pattern as defined by the rules? What happens when the rules are broken or relaxed, and when can this occur?

The third line of inquiry is historical. All living and fossil species trace their ancestry back to a single entity in the incredibly distant past. What was the course of this evolution, and what factors were important in charting it? To what extent does a species bear the stamp of history, and how much do its characteristics reflect the conditions

* Horace F. Judson, *The Eighth Day of Creation*, Simon and Schuster, New York; p. 218.

in which it finds itself? When and how does evolutionary change occur, and how is this change constrained by the rules of construction and by the environment in which organisms live?

In the context of shells, these three fundamental questions can be effectively framed in economic terms. We can think of shells as houses. Construction, repair, and maintenance by the builder require energy and time, the same currencies used for such other life functions as feeding, locomotion, and reproduction. The energy and time invested in shells depend on the supply of raw materials, the labor costs of transforming these resources into a serviceable structure, and the functional demands placed on the shell. For secondary shell-dwellers, which generally cannot enlarge or repair their domiciles, the quantity and quality of housing depend on the rate at which shells enter the housing market and on the ways and rates of shell deterioration. The words "economics" and "ecology" are especially apt in this context, for both are derived from the Greek *oikos*, meaning house. In short, the questions of biology can be phrased in terms of supply and demand, benefits and costs, and innovation and regulation, all set against a backdrop of environment and history.

Shells are, of course, more than houses. For many molluscs and most secondary occupants, they are also vehicles, which are often specifically adapted to various modes of locomotion such as crawling, leaping, swimming, and burrowing. Moreover, shells in some instances function as traps for prey and would-be intruders, as offensive weapons of attack, as signals for attracting mates, and even as greenhouses for culturing plant cells that help feed the animal. The various functional demands are apt to be incompatible with each other. The architecture of any one shell reflects not only the compromises among these functional requirements, but also the costs of construction and maintenance, the rules governing growth, and the mark of evolutionary ancestry. Just as the houses of people vary greatly from place to place and over the course of history, so the shells of molluscs bear the marks of geography and time. Costs of construction vary according to geography and habitat; so do the kinds and abundances of predators, the availability of food, the rate of growth, and any number of other factors important in the lives of shell-bearers. Ecologists who wish to understand how population sizes of living species are regulated may be content to document these variations in the biosphere today, but for the evolutionary biologist interested in chronicling the economic history of life, it becomes essential to determine how costs, benefits, and resources have varied over the course of geologic history, and to infer how the course of evolution has been influenced by the interplay between the everyday economic forces and the much less frequent large-scale changes in climate and tectonics that have affected the planet. Such evolutionary insights will be important in attempts to forecast and manage biological change as humans extend their control over the biosphere.

An economic treatment of biology is, of course, not new. Cost-benefit analysis has pervaded much of the literature in evolutionary ecology for the last 25 years. My approach, however, differs from that of most others who have concerned themselves with the economy of nature. The prevailing doctrine has been that organisms are optimally designed to maximize the intake of resources while minimizing costs and risks. If organisms fall short of the optimum, an appeal is generally made to factors that are either unknown or unmeasured. The underlying assumption is always that natural selection—the process by which genes conferring higher survival or reproduction are favored—produces the best design possible given the circumstances in which a population lives.

I find this point of view profoundly antievolutionary. When individual organisms vie for resources—mates, food, living quarters, safe places, and the like—the winner is superior in some way to the loser, as ultimately measured in survival and reproduction. Sometimes being better means being very good indeed, but in other circumstances success is achievable with what, in absolute terms, appears to be only a modest effort. By thinking of selection as favoring a better organism rather than as favoring the best organism, we are at once dismissing the notion of an adaptational ideal. Optimality implies a directedness, even a purpose, for whose existence there is no evidence whatever. Humans can think up strategies and tactics in order to improve their lives or to enhance their own causes, but natural selection acts only in the here and now and is therefore fundamentally different from long-range purposeful planning. Evolutionary change can track environmental change but cannot forecast or plan for it.

The order of topics in this book departs slightly from Brenner's sequence of questions, because it recapitulates the pathway by which I came to the study of shells. From my earliest acquaintance with shells in the Netherlands, I was drawn to the regularity of form that even the simplest and most ordinary shells displayed. Having picked up only empty shells, I saw them as abstract objects. The fact that animals built them and inhabited them was unknown to me. The first part of the book is therefore an exercise in geometry. From a description of shell form, I shall proceed to the rules of construction and arrive at a model that explains some of the basic features of shell architecture.

In the Netherlands I had become accustomed to the chalky and rather sloppily ornamented clam shells that washed up in great profusion on the North Sea beaches. Shortly after coming to the United States, I had the great fortune to be in Mrs. Colberg's fourth-grade class in Dover, New Jersey. The windowsills of her classroom held a display of the shells she had gathered on her travels to the west coast of Florida. My first glimpse of these shells is deeply etched in memory. Here were elegantly shaped clam and snail shells, many adorned with neatly arranged ribs, knobs, and even spines. Not only were the shell interiors impossibly smooth to the touch, but the olive and cowrie shells were externally so polished that I was certain someone had varnished them. The contrast with the drab chalky shells from the Netherlands was remarkable. Why, I wondered, were warm-water shells so much prettier than the northern shells? When a classmate brought in some shells from the Philippines, which were even more spectacular in their fine sculpture and odd shapes, my curiosity was aroused even more. I resolved to begin collecting shells and to read as much as I could find about them.

The geography of shell form has remained a matter of interest for me ever since. It forms the point of departure for the rest of the book. I begin by examining the economic costs of shell construction, and proceed by asking how these costs vary with geography and habitat. Next I review what we know about how shells work, and ask how the factors with which shell-bearers must cope vary with latitude and other geographic and habitat gradients. Differences in shell architecture among molluscan assemblages from different oceans lead into an exploration of how historical factors have conspired to make molluscs and other animals in some parts of the world functionally more specialized than in others. This inquiry, in turn, expands into an architectural and functional history of molluscs from the time of the first appearance of the group in the Early Cambrian, some 530 million years ago, to the present. I close with some suggestions about what we can learn about our own species from the lessons of the history of life.

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References to illustrations are in italics.