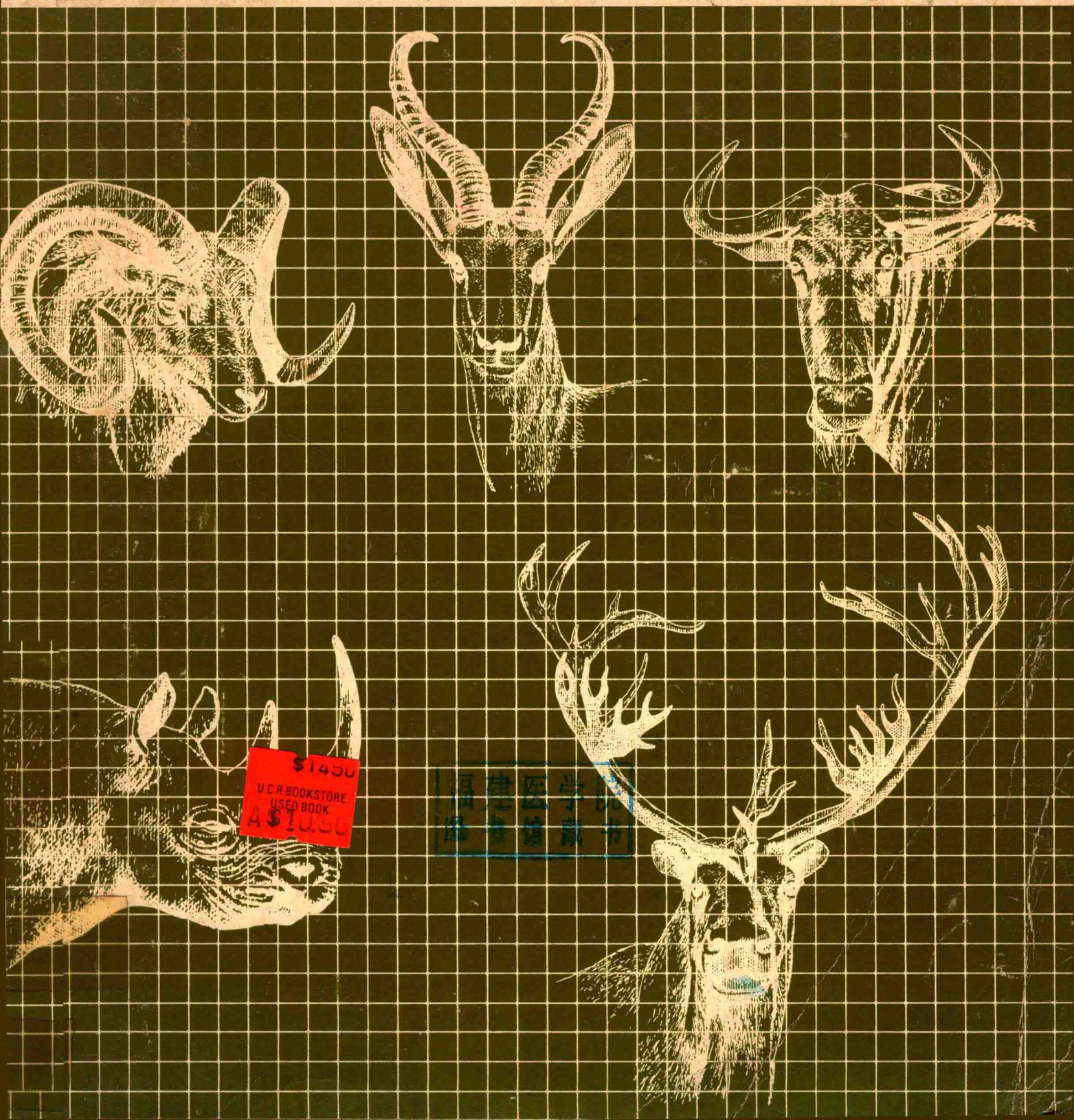


SCIENTIFIC
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VERTEBRATES: Adaptation

With Introductions by Norman K. Wessells



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Readings from
**SCIENTIFIC
AMERICAN**

VERTEBRATES: Adaptation

With Introductions by
Norman K. Wessells
Stanford University



W. H. Freeman and Company
San Francisco

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PREFACE

The unprecedented triumphs of molecular biology since the 1950s tend to make us forget the broad and ancient base on which modern life sciences are built. As we succeed in constructing mechanistic interpretations of life processes, it is sobering to realize how perceptive and accurate were the observations of those phenomena made hundreds of years ago. Although the following quotation was written by Pliny the Elder 1900 years ago, nearly every topic in it is discussed in this book and is still under active investigation.

The swiftest of all animals, not only those of the sea, is the dolphin: it is swifter than a bird and darts faster than a javelin, and were not its mouth much below its snout, almost in the middle of its belly, not a single fish would escape its speed. But nature's foresight contributes delay, because they cannot seize their prey except by turning over on their backs. . . . They have a habit of sallying out on to the land for an unascertained reason, and they do not die at once after touching earth—in fact they die more quickly if the gullet is closed up. . . . For a voice they have a moan like that of a human being. . . . The dolphin is an animal that is not only friendly to mankind but is also a lover of music, and it can be charmed by . . . the sound of the water-organ. (Pliny, *Natural History*, IX, vii, viii.)

Today we believe the dolphin's swiftness is due to laminar flow of water over its skin, so that eddies and turbulence do not generate drag. The sallies of whales or dolphins onto beaches may stem from a failure of the echo-locating navigational system to detect shallow, sloping sea bottoms, or may be due to ear parasites that interfere with the hearing of echoes. The dolphin's "voice" is of course an integral part of the echo-locating system and is also used for communication between these remarkably "brainy" cetaceans. And, what else but "nature's forethought" (natural selection in our terms) could explain so well the origin of these adaptations or the equally marvelous ones described throughout this collection of articles from *Scientific American*?

This book and its companion volume—*Vertebrates: Physiology*—(W. H. Freeman and Company, 1980) are about the structures, functions, and adaptations of vertebrates. We shall study molecules, cells, organs, and organisms in these two books, and our purpose will be to see how the parts are orchestrated to yield the functioning individual vertebrate, adapted for its particular niche. Any overview of the kind endeavored in these books must be based on certain biases. The prejudice observed in these books is that it is just as sterile to study only bones and morphology as to concentrate only upon molecules or cells. A student can best achieve real understanding by sampling at all levels of organization, and integrating the knowledge thus obtained to gain a fuller picture of a trout, a toad, or a titmouse.

This book concentrates upon adaptations of vertebrates to the physical and biological world in which they live. Swimming, running, flying, navigating, mating, and communicating are but a few of the activities treated in the various articles from *Scientific American*. Emphasis is placed upon an integrated view of selected vertebrates (crocodiles, seals, kangaroos, and so on), so that the student may gain a better appreciation of how anatomical, physiological, and behavioral features of a vertebrate fit together to yield a creature adapted for a given niche. The companion book, *Vertebrates: Physiology*, provides important background about the most important organ systems and physiological problems of vertebrates, and is meant to be read by the student prior to study of this book.

The two collections of articles are designed to supplement courses in introductory biology, vertebrate biology, comparative anatomy, and physiology. As such, the books are meant to fill some of the gaps and answer some of the questions that might arise from a general survey of vertebrate biology. Orientation to the field and articles is provided by Introductions to the Sections of the book. Although *Scientific American* has not of course published articles on all the subjects that might interest a student, the scope is nevertheless quite broad; therefore references to Offprints on related subjects are included. In addition, a special list of recent references for each section is found in the Bibliography at the end of each book.

I have assumed that teachers and students will be able to consult the *Annual Review of Physiology*, *Biological Reviews*, or *Physiological Reviews*, for many useful papers that are not cited specifically here. The important book by P. W. Hochachka and G. N. Somero, *Strategies of Biochemical Adaptation*, and *Animal Physiology* by R. Eckert and D. Randall, are to my mind the most useful means of amplifying the many intriguing aspects of vertebrate life treated in these *Scientific American* articles. For those needing background in ancient vertebrates and paleontology, the book by B. J. Stahl, *Vertebrate History: Problems in Evolution*, is by far the best balanced evaluation and summary.

Thanks go to the many students in my Vertebrate Biology course at Stanford, whose interest, enthusiasm, and questioning have added so much to the pleasures of teaching. I am also indebted to Sharon Willy for the excellent index. Finally, thanks also go to Lois Wessells for aid and comfort in busy times.

November 1979

Norman K. Wessells

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I

ADAPTATIONS: GENERAL FEATURES

Every species of animal is marvellously cunning for its own interests.

Pliny
NATURAL HISTORY, VIII, xii

ADAPTATIONS: GENERAL FEATURES

I

INTRODUCTION

This book is concerned with the many types of adaptations of vertebrates to the world in which they live. The article "Adaptation" by R. C. Lewontin provides a superb general and theoretical treatment of this subject.

Lewontin emphasizes that the "fit" of organisms to their physical and biological environments may be regarded as a primary result of the evolutionary process. For example, the properties of water, particularly its density, place certain restrictions upon the animal body if rapid locomotion is to be attempted. We see the result in the common shapes of dolphins, penguins, ichthyosaurs (an extinct type of aquatic dinosaur with a body shape nearly identical to that of a dolphin), and seals; all of these distinctive creatures evolved from terrestrial vertebrates that re-entered the sea and adopted it as their primary habitat at different times in vertebrate history. Yet, all have attained the same general body configuration that is compatible with laminar flow, minimal turbulence, and efficient, rapid swimming. It is argued that natural selection has operated to yield this convergence in body shape and the resultant "fit" with the environment.

As Lewontin points out, however, a given characteristic of an organism (its color, size of chin, and so on) may derive from a complex of factors, not solely genetic variation and natural selection acting on the character *per se*. The history of an organism and its lineage, particularly the modes of development it uses to build its organs and tissues, is a key factor that sets limits upon the ways that the organism and its offspring can respond to changing environments. Lewontin emphasizes the pointlessness of attempting to construct ad hoc explanations for every bodily feature in terms of selective pressure. Such a practice could divert attention from real causes. The reader should keep Lewontin's caveats and theoretical framework in mind while studying the various morphological, physiological, and behavioral adaptations that are described in the articles of this book.



by Richard C. Lewontin
September 1978

The manifest fit between organisms and their environment is a major outcome of evolution. Yet natural selection does not lead inevitably to adaptation; indeed, it is sometime hard to define an adaptation

The theory about the history of life that is now generally accepted, the **Darwinian theory of evolution** by natural selection, is meant to explain two different aspects of the appearance of the living world: **diversity and fitness**. There are on the order of two million species now living, and since at least 99.9 percent of the species that have ever lived are now extinct, the most conservative guess would be that two billion species have made their appearance on the earth since the beginning of the Cambrian period 600 million years ago. Where did they all come from? By the time Darwin published *On the Origin of Species* in 1859 it was widely (if not universally) held that species had evolved from one another, but no plausible mechanism for such evolution had been proposed. **Darwin's solution to the problem was that small heritable variations among individuals within a species become the basis of large differences between species. Different forms survive and reproduce at different rates depending on their environment, and such differential reproduction results in the slow change of a population over a period of time and the eventual replacement of one common form by another.** Different populations of the same species then diverge from one another if they occupy different habitats, and eventually they may become distinct species.

Life forms are more than simply multiple and diverse, however. Organisms fit remarkably well into the external world in which they live. They have morphologies, physiologies and behav-

iors that appear to have been carefully and artfully designed to enable each organism to appropriate the world around it for its own life.

It was the marvelous fit of organisms to the environment, much more than the great diversity of forms, that was the chief evidence of a Supreme Designer. **Darwin realized that if a naturalistic theory of evolution was to be successful, it would have to explain the apparent perfection of organisms and not simply their variation.** At the very beginning of the *Origin of Species* he wrote: "In considering the Origin of Species, it is quite conceivable that a naturalist... might come to the conclusion that each species... had descended, like varieties, from other species. Nevertheless, such a conclusion, even if well founded, would be unsatisfactory, until it could be shown how the innumerable species inhabiting this world have been modified, so as to acquire that perfection of structure and coadaptation which most justly excites our admiration." Moreover, Darwin knew that "organs of extreme perfection and complication" were a critical test case for his theory, and he took them up in a section of the chapter on "Difficulties of the Theory." He wrote: "To suppose that the eye, with all its inimitable contrivances for adjusting the focus to different distances, for admitting different amounts of light, and for the correction of spherical and chromatic aberration, could have been formed by natural selection, seems, I freely confess, absurd in the highest degree."

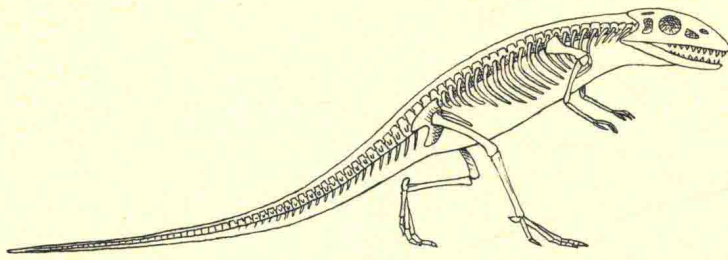
These "organs of extreme perfection" were only the most extreme case of a more general phenomenon: adaptation. Darwin's theory of evolution by natural selection was meant to solve both the problem of the origin of diversity and the problem of the origin of adaptation at one stroke. Perfect organs were a difficulty of the theory not in that natural selection could not account for them but rather in that they were its most rigorous test, since on the face of it they seemed the best intuitive demonstration that a divine artificer was at work.

The modern view of adaptation is that the external world sets certain "problems" that organisms need to "solve," and that evolution by means of natural selection is the mechanism for creating these solutions. **Adaptation is the process of evolutionary change by which the organism provides a better and better "solution" to the "problem," and the end result is the state of being adapted.** In the course of the evolution of birds from reptiles there was a successive alteration of the bones, the muscles and the skin of the forelimb to give rise to a wing: an increase in the size of the breastbone to provide an anchor for the wing muscles; a general restructuring of bones to make them very light but strong, and the development of feathers to provide both aerodynamic elements and lightweight insulation. This wholesale reconstruction of a reptile to make a bird is considered a process of major adaptation by which birds solved the problem of flight. **Yet there is no end to adaptation.** Having adapted to flight, some birds reversed the process: the penguins adapted to marine life by changing their wings into flippers and their feathers into a waterproof covering, thus solving the problem of aquatic existence.

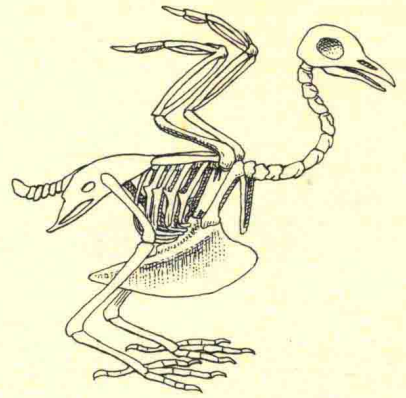
The concept of adaptation implies a preexisting world that poses a problem to which an adaptation is the solution. A key is adapted to a lock by cutting and filing it; an electrical appliance is adapted to a different voltage by a transform-

ADAPTATION is exemplified by "industrial melanism" in the peppered moth (*Biston betularia*). Air pollution kills the lichens that would normally colonize the bark of tree trunks. On the dark, lichenless bark of an oak tree near Liverpool in England the melanic (black) form is better adapted: it is better camouflaged against predation by birds than the light, peppered wild type (top photograph on opposite page), which it largely replaced through natural selection in industrial areas of England in the late 19th century. Now air quality is improving. On a nearby beech tree colonized by algae and the lichen *Lecanora conizaeoides*, which is itself particularly well adapted to low levels of pollution, the two forms of the moth are equally conspicuous (middle). On the lichenized bark of an oak tree in rural Wales the wild type is almost invisible (bottom), and in such areas it predominates. The photographs were made by J. A. Bishop of the University of Liverpool and Laurence M. Cook of the University of Manchester.

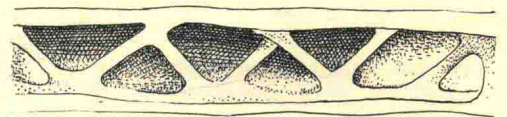
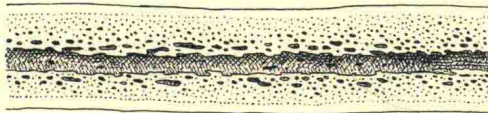
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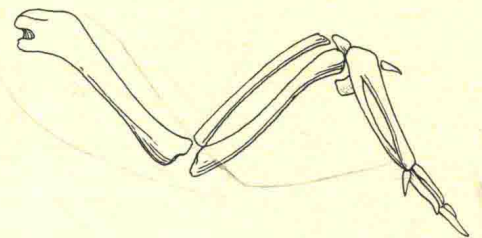
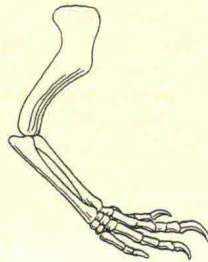
BIRDS



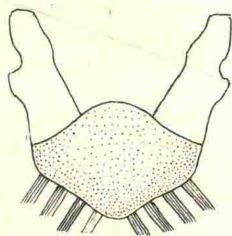
BONE



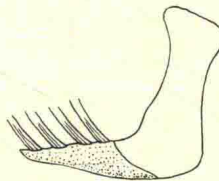
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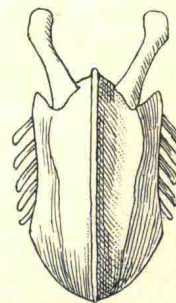
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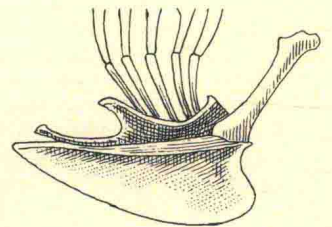
BOTTOM VIEW



SIDE VIEW

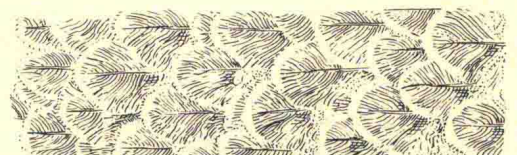
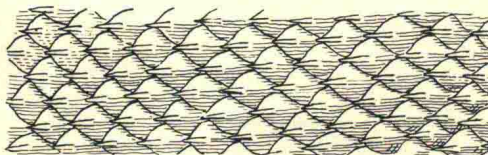


BOTTOM VIEW



SIDE VIEW

SKIN COVERING



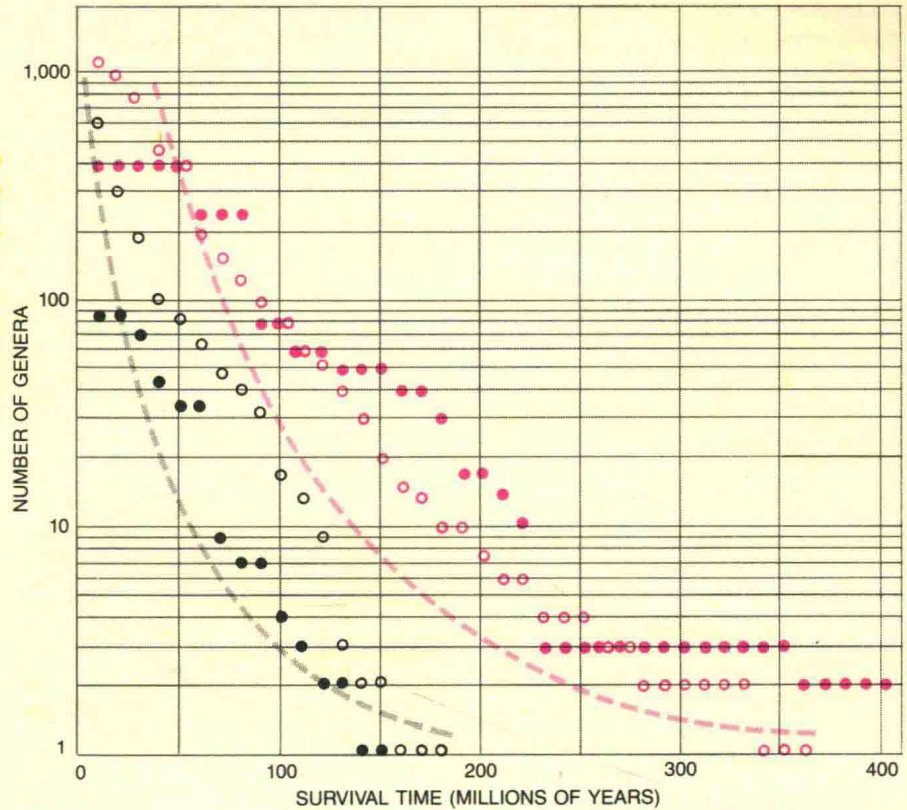
EVOLUTION OF BIRDS from reptiles can be considered a process of adaptation by which birds "solved" the "problem" of flight. At the top of the illustration the skeleton of a modern pigeon (right) is compared with that of an early reptile: a thecodont, a Triassic ancestor of dinosaurs and birds. Various reptile features were modified to become structures specialized for flight. Heavy, dense bone was restruc-

tured to become lighter but strong; the forelimb was lengthened (and its muscles and skin covering were changed) to become a wing; the reptilian sternum, or breastbone, was enlarged and deepened to anchor the wing muscles (even in *Archaeopteryx*, the Jurassic transition form between reptiles and birds whose sternum is pictured here, the sternum was small and shallow); scales developed into feathers.

er. Although the physical world certainly predated the biological one, there are certain grave difficulties for evolutionary theory in defining that world for the process of adaptation. It is the difficulty of defining the "ecological niche." The ecological niche is a multidimensional description of the total environment and way of life of an organism. Its description includes physical factors, such as temperature and moisture; biological factors, such as the nature and quantity of food sources and of predators, and factors of the behavior of the organism itself, such as its social organization, its pattern of movement and its daily and seasonal activity cycles.

The first difficulty is that if evolution is described as the process of adaptation of organisms to niches, then the niches must exist before the species that are to fit them. That is, there must be empty niches waiting to be filled by the evolution of new species. In the absence of organisms in actual relation to the environment, however, there is an infinity of ways the world can be broken up into arbitrary niches. It is trivially easy to describe "niches" that are unoccupied. For example, no organism makes a living by laying eggs, crawling along the surface of the ground, eating grass and living for several years. That is, there are no grass-eating snakes, even though snakes live in the grass. Nor are there any warm-blooded, egg-laying animals that eat the mature leaves of trees, even though birds inhabit trees. Given any description of an ecological niche occupied by an actual organism, one can create an infinity of descriptions of unoccupied niches simply by adding another arbitrary specification. Unless there is some preferred or natural way to subdivide the world into niches the concept loses all predictive and explanatory value.

A second difficulty with the specification of empty niches to which organisms adapt is that it leaves out of account the role of the organism itself in creating the niche. Organisms do not experience environments passively; they create and define the environment in which they live. Trees remake the soil in which they grow by dropping leaves and putting down roots. Grazing animals change the species composition of herbs on which they feed by cropping, by dropping manure and by physically disturbing the ground. There is a constant interplay of the organism and the environment, so that although natural selection may be adapting the organism to a particular set of environmental circumstances, the evolution of the organism itself changes those circumstances. Finally, organisms themselves determine which external factors will be part of their niche by their own activities. By building a nest the phoebe makes the availability of dried grass an important part of its



EXTINCTION RATES in many evolutionary lines suggest that natural selection does not necessarily improve adaptation. The data, from Leigh Van Valen of the University of Chicago, show the duration of survival of a number of living (solid dots) and extinct (open circles) genera of Echinoidea (black) and Pelecypoda (color), two classes of marine invertebrates. If natural selection truly fitted organisms to environments, the points should fall along concave curves (broken-line curves) indicating a lower probability of extinction for long-lived genera. Actually, points fall along rather straight lines, indicating constant rate of extinction for each group.

niche, at the same time making the nest itself a component of the niche.

If ecological niches can be specified only by the organisms that occupy them, evolution cannot be described as a process of adaptation because all organisms are already adapted. Then what is happening in evolution? One solution to this paradox is the Red Queen hypothesis, named by Leigh Van Valen of the University of Chicago for the character in *Through the Looking Glass* who had to keep running just to stay in the same place. Van Valen's theory is that the environment is constantly decaying with respect to existing organisms, so that natural selection operates essentially to enable the organisms to maintain their state of adaptation rather than to improve it. Evidence for the Red Queen hypothesis comes from an examination of extinction rates in a large number of evolutionary lines. If natural selection were actually improving the fit of organisms to their environments, then we might expect the probability that a species will become extinct in the next time period to be less for species that have already been in existence for a long time, since the long-lived species are presumably the ones that have been im-

proved by natural selection. The data show, however, that the probability of extinction of a species appears to be a constant, characteristic of the group to which it belongs but independent of whether the species has been in existence for a long time or a short one. In other words, natural selection over the long run does not seem to improve a species' chance of survival but simply enables it to "track," or keep up with, the constantly changing environment.

The Red Queen hypothesis also accounts for extinction (and for the occasional dramatic increases in the abundance and range of species). For a species to remain in existence in the face of a constantly changing environment it must have sufficient heritable variation of the right kind to change adaptively. For example, as a region becomes drier because of progressive changes in rainfall patterns, plants may respond by evolving a deeper root system or a thicker cuticle on the leaves, but only if their gene pool contains genetic variation for root length or cuticle thickness, and successfully only if there is enough genetic variation so that the species can change as fast as the environment. If the genetic variation is inadequate, the species will become extinct. The genetic resources

of a species are finite, and eventually the environment will change so rapidly that the species is sure to become extinct.

The theory of environmental tracking seems at first to solve the problem of adaptation and the ecological niche. Whereas in a barren world there is no clear way to divide the environment into preexisting niches, in a world already occupied by many organisms the terms of the problem change. Niches are already defined by organisms. Small changes in the environment mean small changes in the conditions of life of those organisms, so that the new niches to which they must evolve are in a sense very close to the old ones in the multidimensional niche space. Moreover, the organisms that will occupy these slightly changed niches must themselves come from the previously existing niches, so that the kinds of species that can evolve are stringently limited to ones that are extremely similar to their immediate ancestors. This in turn guarantees that the changes induced in the environment by the changed organism will also be small and continuous in niche space. The picture of adaptation that emerges is the very slow movement of the niche through niche space, accompanied by a slowly changing species, always slightly behind, slightly ill-adapted, eventually becoming extinct as it fails to keep up with the changing environment because it runs out of genetic variation on which natural selection can operate. In this

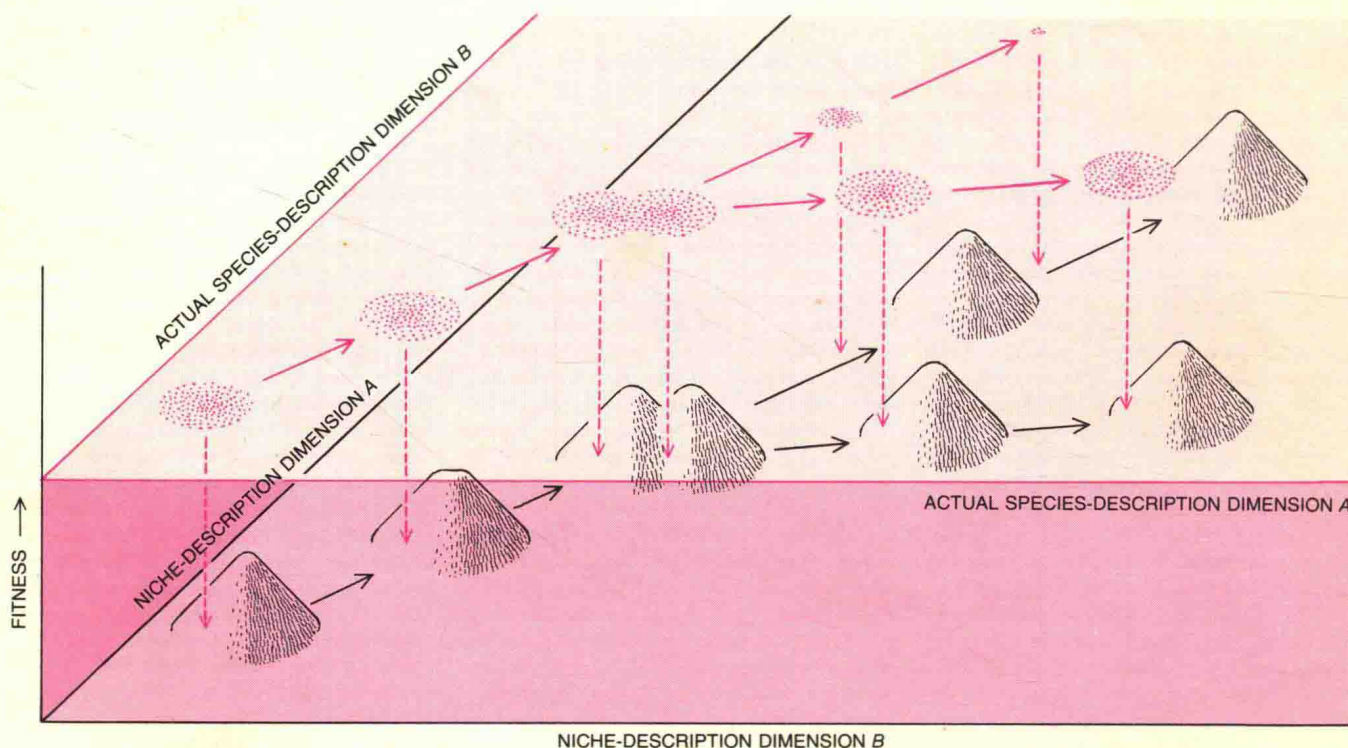
view species form when two populations of the same species track environments that diverge from each other over a period of time.

The problem with the theory of environmental tracking is that it does not predict or explain what is most dramatic in evolution: the immense diversification of organisms that has accompanied, for example, the occupation of the land from the water or of the air from the land. Why did warm-blooded animals arise at a time when cold-blooded animals were still plentiful and come to co-exist with them? The appearance of entirely new life forms, of ways of making a living, is equivalent to the occupation of a previously barren world and brings us back to the preexistent empty niche waiting to be filled. Clearly there have been in the past ways of making a living that were unexploited and were then "discovered" or "created" by existing organisms. There is no way to explain and predict such evolutionary adaptations unless a priori niches can be described on the basis of some physical principles before organisms come to occupy them.

That is not easy to do, as is indicated by an experiment in just such a priori predictions that has been carried out by probes to Mars and Venus designed to detect life. The instruments are designed to detect life by detecting growth in nutrient solutions, and the solutions are prepared in accordance with knowledge

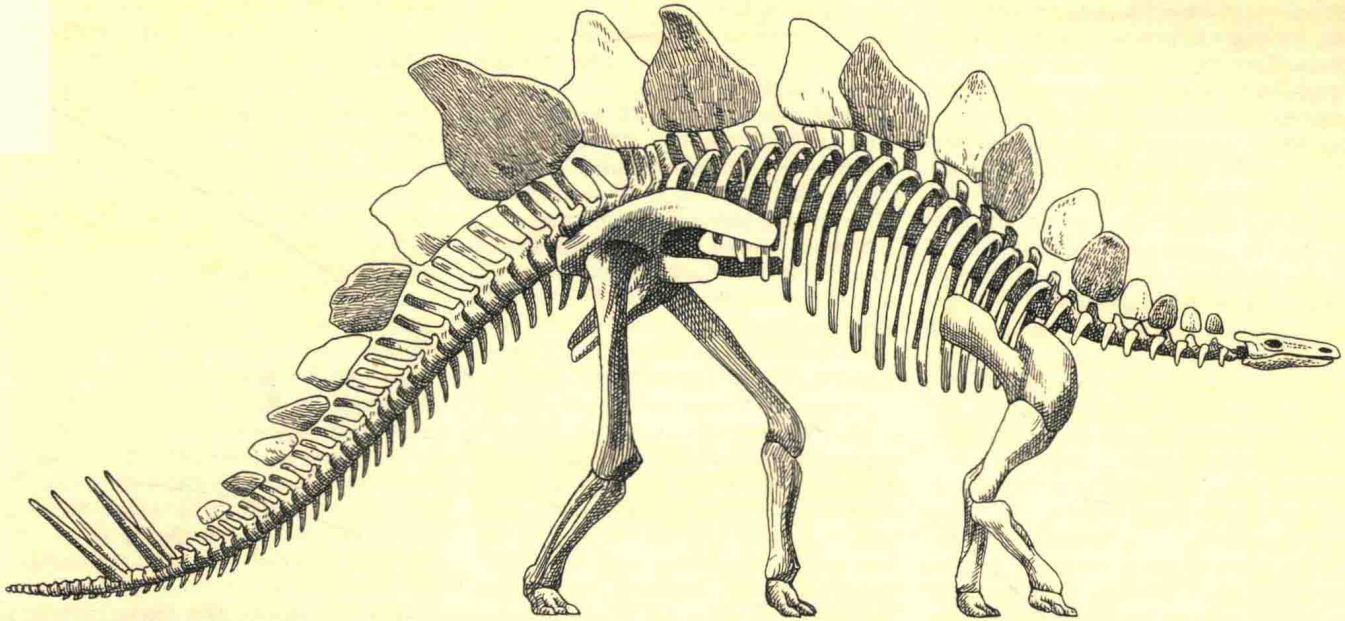
of terrestrial microorganisms, so that the probes will detect only organisms whose ecological niches are like those on the earth. If Martian and Venusian life partition the environment in totally unexpected ways, they will remain unrecorded. What the designers of those instruments never dreamed of was that the reverse might happen: that the nature of the physical environment on Mars might be such that when it was provided with a terrestrial ecological niche, inorganic reactions might have a lifelike appearance. Yet that may be exactly what happened. When the Martian soil was dropped into the nutrient broth on the lander, there was a rapid production of carbon dioxide and then—nothing. Either an extraordinary kind of life began to grow much more rapidly than any terrestrial microorganism and then was poisoned by its own activity in a strange environment, or else the Martian soil is such that its contact with nutrient broths results in totally unexpected catalytic processes. In either case the Mars life-detection experiment has foundered on the problem of defining ecological niches without organisms.

Much of evolutionary biology is the working out of an adaptationist program. Evolutionary biologists assume that each aspect of an organism's morphology, physiology and behavior has been molded by natural selection as a solution to a problem posed by the



SPECIES TRACK ENVIRONMENT through niche space, according to one view of adaptation. The niche, visualized as an "adaptive peak," keeps changing (moving to the right); a slowly changing species population (colored dots) just manages to keep up with the niche, always a bit short of the peak. As the environment changes, the sin-

gle peak becomes two distinct peaks, and two populations diverge to form distinct species. One species cannot keep up with its rapidly changing environment, becomes less fit (lags farther behind changing peak) and extinct. Here niche space and actual-species space have only two dimensions; both of them are actually multidimensional.



STEGOSAURUS, a large herbivorous dinosaur of the Jurassic period, had an array of bony plates along its back. Were they solutions to the problem of defense, courtship recognition or heat regulation? An engineering analysis reveals features characteristic of heat regu-

lators: porous structure (suggesting a rich blood supply), particularly large plates over the massive part of the body, staggered arrangement along the midline, a constriction near the base and so on. This skeleton in the American Museum of Natural History is 18 feet long.

environment. The role of the evolutionary biologist is then to construct a plausible argument about how each part functions as an adaptive device. For example, functional anatomists study the structure of animal limbs and analyze their motions by time-lapse photography, comparing the action and the structure of the locomotor apparatus in different animals. Their interest is not, however, merely descriptive. Their work is informed by the adaptationist program, and their aim is to explain particular anatomical features by showing that they are well suited to the function they perform. Evolutionary ethologists and sociobiologists carry the adaptationist program into the realm of animal behavior, providing an adaptive explanation for differences among species in courting pattern, group size, aggressiveness, feeding behavior and so on. In each case they assume, like the functional anatomist, that the behavior is adaptive and that the goal of their analysis is to reveal the particular adaptation.

The dissection of an organism into parts, each of which is regarded as a specific adaptation, requires two sets of a priori decisions. First one must decide on the appropriate way to divide the organism and then one must describe what problem each part solves. This amounts to creating descriptions of the organism and of the environment and then relating the descriptions by functional statements; one can either start with the problems and try to infer which aspect of the organism is the solution or start with the organism and then ascribe adaptive functions to each part.

For example, for individuals of the

same species to recognize each other at mating time is a problem, since mistakes about species mean time, energy and gametes wasted in courtship and mating without the production of viable offspring; species traits such as distinctive color markings, special courtship behavior, unique mating calls, odors and restricted time and place of activity can be considered specific adaptations for the proper recognition of potential mates. On the other hand, the large, leaf-shaped bony plates along the back of the dinosaur *Stegosaurus* constitute a specific characteristic for which an adaptive function needs to be inferred. They have been variously explained as solutions to the problem of defense (by making the animal appear to be larger or by interfering directly with the predator's attack), the problem of recognition in courtship and the problem of temperature regulation (by serving as cooling fins).

The same problems that arose in deciding on a proper description of the ecological niche without the organism arise when one tries to describe the organism itself. Is the leg a unit in evolution, so that the adaptive function of the leg can be inferred? If so, what about a part of the leg, say the foot, or a single toe, or one bone of a toe? The evolution of the human chin is an instructive example. Human morphological evolution can be generally described as a "neotenic" progression. That is, human infants and adults resemble the fetal and young forms of apes more than they resemble adult apes; it is as if human beings are born at an earlier stage of physical development than apes and do not

mature as far along the apes' development path. For example, the relative proportion of skull size to body size is about the same in newborn apes and human beings, whereas adult apes have much larger bodies in relation to their heads than we do; in effect their bodies "go further."

The exception to the rule of human neoteny is the chin, which grows relatively larger in human beings, whereas both infant and adult apes are chinless. Attempts to explain the human chin as a specific adaptation selected to grow larger failed to be convincing. Finally it was realized that in an evolutionary sense the chin does not exist! There are two growth fields in the lower jaw: the dentary field, which is the bony structure of the jaw, and the alveolar field, in which the teeth are set. Both the dentary and the alveolar fields do show neoteny. They have both become smaller in the human evolutionary line. The alveolar field has shrunk somewhat faster than the dentary one, however, with the result that a "chin" appears as a pure consequence of the relative regression rates of the two growth fields. With the recognition that the chin is a mental construct rather than a unit in evolution the problem of its adaptive explanation disappears. (Of course, we may go on to ask why the dentary and alveolar growth fields have regressed at different rates in evolution, and then provide an adaptive explanation for that phenomenon.)

Sometimes even the correct topology of description is unknown. The brain is divided into anatomical divisions corresponding to certain separable

nervous functions that can be localized, but memory is not one of those functions. The memory of specific events seems to be stored diffusely over large regions of the cerebrum rather than being localized microscopically. As one moves from anatomy to behavior the problem of a correct description becomes more acute and the opportunities to introduce arbitrary constructs as if they were evolutionary traits multiply. Animal behavior is described in terms of aggression, division of labor, warfare, dominance, slave-making, cooperation—and yet each of these is a category that is taken directly from human social experience and is transferred to animals.

The decision as to which problem is solved by each trait of an organism is

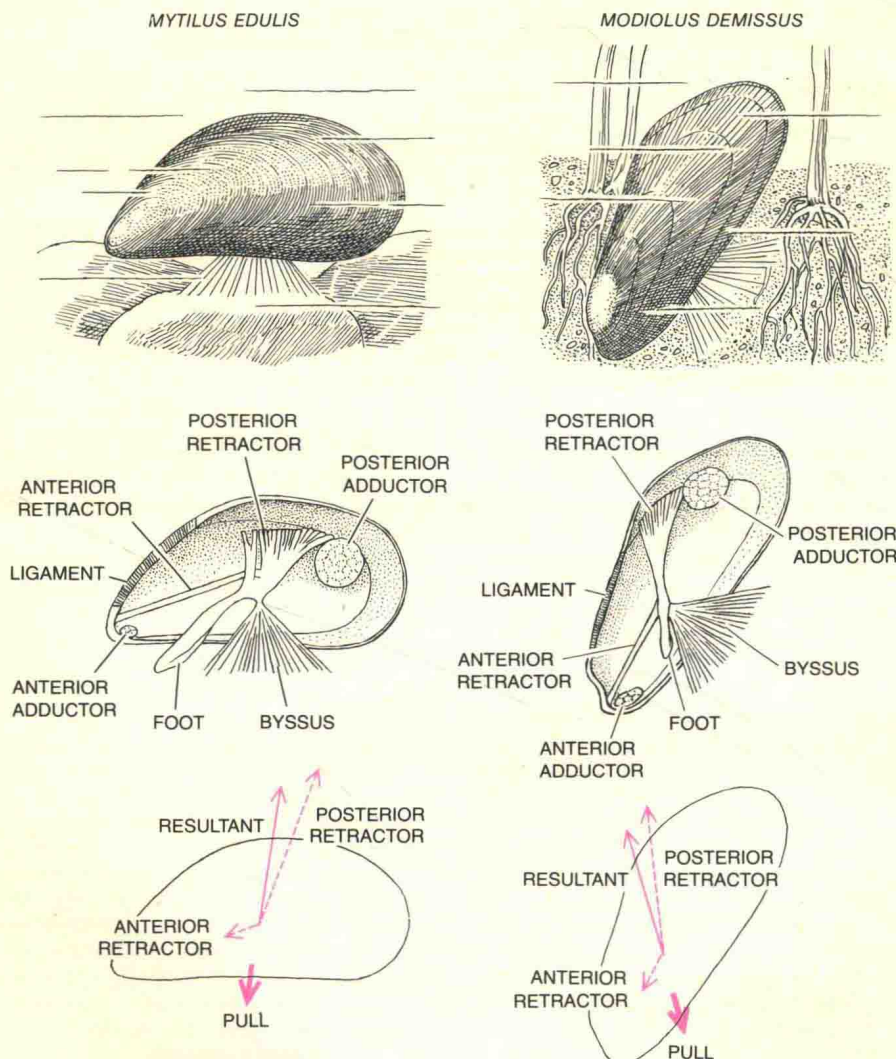
equally difficult. Every trait is involved in a variety of functions, and yet one would not want to say that the character is an adaptation for all of them. The green turtle *Chelonia mydas* is a large marine turtle of the tropical Pacific. Once a year the females drag themselves up the beach with their front flippers to the dry sand above the high-water mark. There they spend many hours laboriously digging a deep hole for their eggs, using their hind flippers as trowels. No one who has watched this painful process would describe the turtles' flippers as adaptations for land locomotion and digging; the animals move on land and dig with their flippers because nothing better is available. Conversely, even if a trait seems clearly adaptive, it cannot be assumed that the species would suffer in

its absence. The fur of a polar bear is an adaptation for temperature regulation, and a hairless polar bear would certainly freeze to death. The color of a polar bear's fur is another matter. Although it may be an adaptation for camouflage, it is by no means certain that the polar bear would become extinct or even less numerous if it were brown. Adaptations are not necessary conditions of the existence of the species.

For extinct species the problem of judging the adaptive status of a trait is made more difficult because both the trait and its function must be reconstructed. In principle there is no way to be sure whether the dorsal plates of *Stegosaurus* were heat-regulation devices, a defense mechanism, a sexual recognition sign or all these things. Even in living species where experiments can be carried out a doubt remains. Some modern lizards have a brightly colored dewlap under the jaw. The dewlap may be a warning sign, a sexual attractant or a species-recognition signal. Experiments removing or altering the dewlap could decide, in principle, how it functions. That is a different question from its status as an adaptation, however, since the assertion of adaptation implies a historical argument about natural selection as the cause of its establishment. The large dorsal plates of *Stegosaurus* may have evolved because individuals with slightly larger plates were better able to gather food in the heat of the day than other individuals. If, when the plates reached a certain size, they incidentally frightened off predators, they would be a "preadaptation" for defense. The distinction between the primary adaptation for which a trait evolved and incidental functions it may have come to have cannot be made without the reconstruction of the forces of natural selection during the actual evolution of the species.

The current procedure for judging the adaptation of traits is an engineering analysis of the organism and its environment. The biologist is in the position of an archaeologist who uncovers a machine without any written record and attempts to reconstruct not only its operation but also its purpose. The hypothesis that the dorsal plates of *Stegosaurus* were a heat-regulation device is based on the fact that the plates were porous and probably had a large supply of blood vessels, on their alternate placement to the left and right of the midline (suggesting cooling fins), on their large size over the most massive part of the body and on the constriction near their base, where they are closest to the heat source and would be inefficient heat radiators.

Ideally the engineering analysis can be quantitative as well as qualitative and so provide a more rigorous test of the



FUNCTIONAL ANALYSIS indicates how the shape and musculature of two species of mussels are adapted to their particular environments. *Mytilus edulis* (left) attaches itself to rocks by means of its byssus, a beardlike group of threads (top). Its ventral, or lower, edge is flattened; the anterior and posterior retractor muscles are positioned (middle) so that their resultant force pulls the bottom of the shell squarely down to the substratum (bottom). *Modiolus demissus* (right) attaches itself to debris in marshes. Its ventral edge is sharply angled to facilitate penetration of the substratum; its retractor muscles are positioned to pull its anterior end down into the marsh. The analysis was done by Steven M. Stanley of Johns Hopkins University.