there is a gulf between observables (character states used in systematics) and the units that play causal roles in evolution. Developmentally oriented evolutionary biologists seek a causal understanding and definition of homology that differs profoundly from the phylogenetic systematists' definition. As Donoghue remarks, "the choice of a definition is, at least in part, a means of forcing other scientists to pay closer attention to whatever one thinks is most important"; but fortunately "attention to the variety of legitimate concerns... is not entirely dependent on the choice of a definition."

Within biology, is ambiguity (or richness) of meaning endemic to ecology and evolutionary biology? Is it a sign of unclear thought, of weakness in the science? Are the functional-biological disciplines, such as molecular biology and physiology, "harder" sciences marked by greater conceptual and semantic clarity? This seems unlikely, given the issues uncovered by philosophers of science in their preoccupation with both evolutionary biology and physics, which between them embrace a fair spectrum of "hardness." Are terms such as "function," "induction," and "recombination," "hormone," "enzyme," and "biochemical pathway," or, for that matter, "eye," "lung," and "malate dehydrogenase," all staunchly unambiguous? Or would an analysis of keywords in functional biology be as thoughtprovoking as the volume that Keller and Lloyd have assembled?

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Biogenesis: Some Like It Hot

Marine Hydrothermal Systems and the Origin of Life. Report of SCOR Working Group 91. N. G. HOLM, Ed. Kluwer, Norwell, MA, 1992. iv, 242 pp., illus. \$133. Reprinted from *Origins of Life and Evolution of the Biosphere*, vol. 22 (1992).

"Heat has been justly regarded the mother of all generations," wrote Jean-Baptiste Lamarck in his 1804 Philosophie Zoologique. He added that "it cannot be doubted that suitable portions of inorganic matter, occurring amidst favourable surroundings, may by the influence of Nature's agents, of which heat and moisture are the chief, receive an arrangement of their parts that foreshadows cellular organization, and thereafter pass to the simplest organic state and manifest the earliest movements of life." Deep-sea hydrothermal vents fit well this description: they are hot, they are rather wet, and, according to several contributors to this volume, they are the spot where life may have begun four billion years ago.

In 1977 an expedition led by John B. Corliss found the first active hydrothermal vent in an oceanic ridge not far away from the Galápagos Islands. The lure of deep-sea hot springs is not limited to their proximity to one of the holy shrines of evolutionary biology. As is made clear in the opening chapter by Nils G. Holm, hydrothermal vents are truly remarkable places: the imag-



Giant clams, crabs, and other organisms from the Galápagos hydrothermal vent. [Visuals Unlimited; F. Gaill, Woods Hole Oceanographic Institution]

es obtained by small submersibles and remote-controlled vehicles equipped with video cameras have revealed spectacular landscapes with black smokers surrounded by stinking, red-blooded clams, blind white crabs, and flocks of sulfur-metabolizing bacteria swimming in dark waters. The discovery of this unique submarine world rapidly awoke in some scientists a sense of the primordial, and speculation on the role of vents in the origin and early evolution of life was soon sparked.

The first detailed hypothesis suggesting a hydrothermal emergence of life was published in a 1981 supplement of *Oceanologica Acta* coauthored by Corliss, John A. Baross, and Sarah E. Hoffman. Although none of these three has contributed to it,

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some of their basic ideas appear to culminate with the publication of this book, which includes the papers written by the members of a working group formed in 1988 under the auspices of the Scientific Committee on Oceanic Research to study from an interdisciplinary perspective the possible connection between deep-sea hydrothermal vents, abiotic synthesis of organic compounds, and the appearance of life.

At first glance, submarine hydrothermal systems appear to be ideally suited for creating life. More than a hundred vents are known to exist along the active tectonic areas of the Earth, and at least in some of them huge amounts of catalytic clays and minerals interact with an aqueous reducing environment rich in H₂, H₂S, CO, CO₂, and possibly HCN, CH₄, and NH₃, which are known to react under possible prebiotic conditions to produce amino acids, purines, and other biochemical monomers. As Roy M. Daniel documents, deep-sea hot springs are also an important source of many new hyperthermophilic autotrophic and heterotrophic bacteria that seem to thrive quite happily at temperatures between 80° and 110°C. Their discovery raises once more the issue of the physical limits to the growth and survival of organisms, but is also of considerable evolutionary significance. Molecular phylogenies based on ribosomal RNA and other biological macromolecules have shown that all heat-loving prokaryotes occupy the short, deepest branches of universal evolutionary trees; that is, they are the oldest recognizable organisms. Hyperthermophily, primitiveness, and submarine volcanic springs seem to fit together like hand in glove.

An abyssal, hot hydrothermal vent instead of Darwin's warm little pond? Not everybody accepts this possibility. A few years ago Stanley L. Miller and Jeffrey L. Bada argued that the high temperature leads rapidly to an irreversible hydrolysis of organic compounds and thus to very short lifetimes for amino acids, nitrogen bases, and other biochemical molecules that are generally assumed to have been essential for the first organisms. This appears to be an insurmountable obstacle for any theory attempting to explain the emergence of life under hot vent conditions. However, the skeptical attitude of Miller, Bada, and others has worked as an intellectual challenge for several contributors to this book, who discuss in considerable detail the possibility of abiotic synthesis of life precursors in hydrothermal systems, advocating nonequilibrium conditions, supercritical fluids, and the percolation of water through catalytic mineral assemblages. It is unlikely that life is originating de novo in extant marine vents, but, as James P. Ferris notes, the issue of the prebiotic significance of these

deep-sea environments should be addressed not only by theoretical analysis and realistic experimental simulations but also by *in situ* searches for non-biological amino acids and chemical intermediates that are known to be specific markers of different abiotic synthetic processes.

On the other hand, the fact that hyperthermophilic organisms are located at the base of evolutionary trees does not necessarily imply that they represent the starting point of biological evolution. Life at boiling temperatures requires a number of biochemical adaptations that are not easy to envisage in the first living systems. Heat-loving bacteria seem to prevent thermal denaturation of their genetic material by twisting their DNA in the right-hand direction, leading to a positive supercoiled double-stranded chain. This unique topological conformation of DNA is generated by reverse gyrase, an ATP-dependent enzyme found only in hyperthermophilic microorganisms. Recent studies by Patrick Forterre and his associates at the University of Paris-Sud in Orsay have shown that reverse gyrase is a combination of a DNA helicase and a DNA topoisomerase, two enzymes involved in the replication of DNA of mesophilic organisms like Escherichia coli, yeast, and ourselves. As Forterre and his collaborators have argued, the most likely interpretation of their discovery is that reverse gyrase is the result of a gene fusion event that took place before the appearance of heat-loving bacteria but after the origin of life, once DNA genomes and the enzymes involved in their unwinding and replication had evolved. Hyperthermophily is an ancient trait, but most likely it is a secondary adaptation that appeared during an early stage of biological evolution at which we are beginning to get a glimpse.

This conclusion does not lessen the significance of hydrothermal vents in shaping the Archean environments in which early life evolved. There is considerable evidence that four billion years ago the Earth was subjected to a period of intense bombardment by asteroids, meteorites, and comets. It has been argued that such catastrophic collisions raised the terrestrial surface temperature to sterilizing levels. Under such conditions submarine hot vents may have been a haven for life. In the primitive, shimmering environment, only the resilient offspring of earlier organisms that had already adapted to boiling temperatures such as those found in hydrothermal springs would have survived. It is unfortunate that this hypothesis, which has gained adherents among planetary scientists, is only mentioned in passing in this volume.

This book, which is the first comprehensive summary of the arguments suggesting a submarine hydrothermic origin of life, would have been uniquely balanced if it had in-

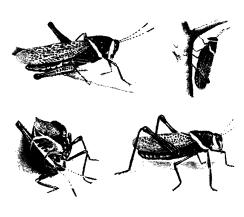
cluded contributions from scientists who reject such a possibility. Discussion of the prebiotic role of deep-sea hot springs has become as heated as the water flowing from the ridges of the Earth's mantle, and as a result zealous overstatement is part of the spirit of some of the authors of this book. Though I do not see a direct, causal connection between the origin of life and hydrothermal vents, I share the fascination of the authors of this volume with these unique environments. As summarized in the final chapter, there are many research opportunities and unsolved problems in this field (including the search for hyperthermophilic nucleated one-celled organisms, which may or may not exist). There is evidence of extensive igneous activity during the early Archean, and seafloor hydrothermal vents were probably operating long before life appeared on our planet. The study of their modern counterparts and their unique ecosystems will undoubtedly bring considerable insight into the geochemical cycles of the early Precambrian, as well as into key aspects of the evolution of hyperthermophily, chemoautotrophy, and symbiosis and other issues equally important to the understanding of early biological evolution. Antonio Lazcano

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Heat Managers

The Hot-Blooded Insects. Strategies and Mechanisms of Thermoregulation. BERND HEINRICH. Harvard University Press, Cambridge, MA, 1993. 601 pp., illus. \$75.

Thermometer crickets, heated and air-conditioned beehives, moths with body temperatures of mice: all these intriguing exam-



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ples of insect thermal biology were known at the beginning of this century. Still it was the common view, until about two decades ago, that insects were uninterestingly passive in regard to their body temperatures. Many kinds of insects are now known to be capable of regulating body temperature with considerable precision during activity, using metabolically generated heat. Although insects have not produced endothermy along the lines of mammals and birds, that is, at rest in the absence of muscle activity, they have evolved an astonishingly great diversity of novel thermoregulatory types and thermal responses, new examples of which are still being discovered.

The principal architect of the revision of our understanding of insect thermal biology is Bernd Heinrich, and this book is his summary of the development and current state of the field. It is a personal tour through the subject by a very knowledgeable, if sometimes opinionated, guide. Heinrich details his and others' research with an immediacy and intensity that actually convey the excitement of being the first person to discover a biological phenomenon. The book is organized according to taxon, discussing general aspects of the thermal biology of each group and summarizing relevant research results. For the specialist, these latter summaries are very useful; for the more casual reader, looking for stories about wonderful animals, they are easily glossed over. This book is destined to become the definitive text on insect thermoregulation: there is no competition, and it is so comprehensive and thoughtful that it is doubtful that any successor will soon be forthcoming. I particularly recommend it for use in graduate seminars in comparative physiology; there is

Above, "Wasp (Ammophila sp.) dragging a caterpillar to its burrow. Its narrow waist is ideally suited for counter-current heat exchange as blood travels between the hot thorax and the cool abdomen, but as of yet the possibility that it acts in this way has not been investigated." [From *The Hot-Blooded Insects*]

Left, "Thermoregulatory postures of the lubber grasshopper Taeniopoda eques. Heating postures are flanking (top left) and ground-flanking (bottom left). Heat avoidance postures are shade-seeking (top right) and stilting (bottom right)." [From The Hot-Blooded Insects; drawings from photographs by D. W. Whitman, 1987]