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 included 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.

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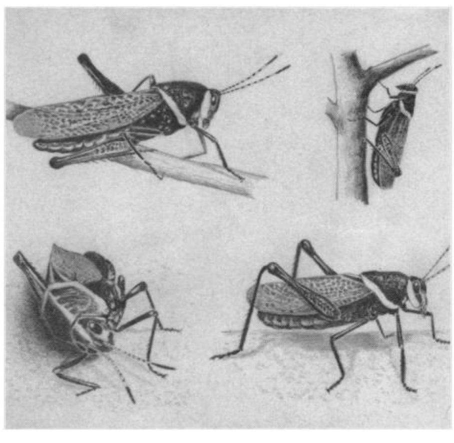
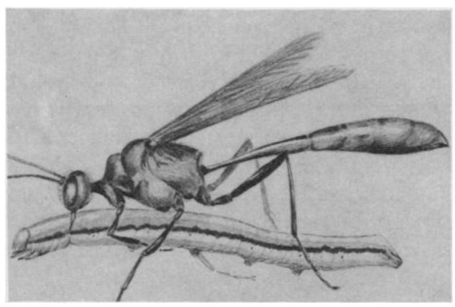
Heat Managers

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 examples 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] meat and controversy aplenty to provoke discussion here.

Though I recommend the book enthusiastically, I do want to note some shortcomings. Comparative physiology is changing in its analytical methods and conceptual framework. The outlook of Heinrich's account is primarily retrospective, rather than prospective. Therefore it sometimes misses opportunities that newer developments have provided. In spite of its taxonomic organization, it does not use phylogenetically based analyses, sometimes to the detriment of its interpretations. Endothermy in moths, for instance, is postulated to have evolved independently numerous times. We need to be assured that ancestors of different endothermic groups were in fact ectothermic and that not all currently endothermic groups had a common endothermic ancestor. If after such analysis independent evolution is demonstrated to be likely, then a variety of studies on convergent evolution and mechanism become feasible. Analytical possibilities and general interest in the results enlarge as a consequence. As another example, Heinrich argues (following Wigglesworth) that wings in all insects are homologous and evolved from the gills of a previously aquatic form. This view requires that the ancestral lineage of all winged insects was primitively terrestrial, evolved into aquatic forms whose larvae possessed the requisite gill characters, and then returned to a fully terrestrial lifestyle prior to diversification. This pterygote ancestor would presumably have been somewhat similar to a modern ephemeropteran (mayfly). Cladograms with relevant synapomorphies mapped onto them are now standard fare in comparative studies. Both these assertions, about endothermy and wing evolution, would have greatly benefited from such illustrations and the rigor they bring to evolutionary interpretations.

Though the book frequently discusses the evolution of the characters described, it is from a relentlessly adaptationist perspective, freely intuiting selective forces that presumably shaped all manner of physiological and morphological characters. Constraints on adaptation and alternative explanations are rarely considered. Assertions with these limitations have not found favor in the broader community of evolutionary biologists and tend to isolate comparative physiologists from the mainstream of evolutionary thought. Also disappointing is the scope of future directions suggested. To his credit, Heinrich does not call for more of the same and in fact lists several areas of past research that he considers unlikely to be highly productive in the future. What he does call for, however, is a focused examination of specific questions, such as the thermoregulatory role of narrow waists in wasps and patterns of hemolymph circulation during warm-up and flight. This would have been an opportunity to point to more general directions and questions in ecology and evolution that might be illuminated by research in insect thermal biology. An example of such research is the investigation of tradeoffs during thermal adaptation currently being pursued by Raymond Huey and Ary Hoffmann using fruit flies as a model experimental system. Pursuit of narrow goals is likely to perpetuate an insular outlook and to isolate comparative research, to everyone's detriment.

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The Horse Tree

Fossil Horses. Systematics, Paleobiology, and Evolution of the Family Equidae. BRUCE J. MACFADDEN. Cambridge University Press, New York, 1992. xii, 369 pp., illus. $74.95.

As trusty mounts or rodeo broncs, pets, team animals, and sources of hair, leather, meat, and milk, horses fascinate us all. They, their still-living allies the asses, zebras, and onagers, and the recently extinct quagga are members of a single genus, *Equus*. *Equus* belongs to a formerly more diverse branch of the mammalian order Perissodactyla. The various living rhinos and tapirs also belong to the Perissodactyla but are distant horse cousins. The most familiar facts about fossil horses are that the earliest horses were about the size of fox terriers but have generally gotten larger, that horses used to have more toes on their feet, and that horses became extinct about 11,000 years ago in the New World and were reintroduced by the Spanish. However, fossil horses also tell us much about how evolution works and are excellent guide fossils for dating sedimentary rocks and for working out biogeography. Like our own genealogies, the history of horses is rich in information. Horse remains can be found as fossils as far back as about 55 million years ago, before which we know of close relatives but don't call them horses. For all but the last 10,000 years or so of this long span, various lineages of horses were primarily North American in distribution, but some spread to Eurasia and Africa by way of the Bering Land Bridge on several occasions. Horses also briefly entered South America in the Pliocene and Pleistocene, after the Panama isthmus connected the two American continents.

If we start with the familiar still-living *Equus* and work backward to little *Eohippus* (or *Hyracotherium*) at the beginning of the Eocene, we get a long line of names: *Equus*, *Merychippus*, *Parahippus*, *Miohippus*, *Mesohippus*, *Epihippus*, *Orohippus*, *Eohippus*. This is often taken as the main line of horses, but of course that view is from the surviving twig of the horse tree toward the roots. Viewed from the roots, the horse family tree is full of equally "important" major branches, each evolving at a different and variable rate and all but one now extinct. To deal with all these branches and stages of evolution, systematists have more or less arbitrarily allocated species of the horse family to genera and other higher taxa. In addition to the single living genus *Equus* with its half-dozen living and many extinct species, there are more than 30 commonly recognized extinct horse genera, some representing lineages and some representing mere stages of evolution but all designated on the basis of such features as the number of toes, size, degree of molarization of the anterior cheek-teeth, facial fossae, crown height of the cheek-teeth, and, most of all, the crown patterns, of the cheek-teeth. Thus teeth, which are the commonest fossils, have played a very important but not exclusive role in the working out of horse phylogeny. As with beavers, microtine rodents, and certain primates, a vast pile of boring literature has built up, documenting the horse family tree in ever finer detail. Specialists mine the pile for some of the best evidence for evolution and for its mechanisms, but the work can be daunting.

" '*Eohippus* and *Eohomo*' sketch done in 1876 at the Yale Peabody Museum during a meeting between Thomas Henry Huxley and O. C. Marsh." [From *Fossil Horses*; courtesy of the Yale Peabody Museum of Natural History]

In contrast, MacFadden offers a readable and even provocative status report and summary of what is known about the multibranched horse family tree over