BOOK REVIEWS

Vertebrates Ashore

Amniote Origins. Completing the Transition to Land. STUART S. SUMIDA and KAREN L. M. MARTIN, Eds. Academic Press, San Diego, CA 1996. x, 510 pp., illus. \$74.95 or £55. ISBN 0-12-676460-3.

Until recently, there has been no concerted effort to evaluate and synthesize the myriad of paleontological and neontological data bearing on the origin of the amniote egg, or indeed, of the Amniotes—the group comprising the reptiles, birds, and mammals—them-

selves. This volume attempts to fill the void.

The earliest tetrapods, the crocodile-like labyrinthodont amphibians, probably evolved from large, "fleshyfinned" (crossopterygian) bony fish during the mid-Paleozoic era, about 375 to 400 million years ago. Thereafter, one of the most impor-

tant evolutionary rubicons in the radiation of terrestrial vertebrates was the development of the amniotic egg. With its protective shell and extensive extraembryonic membranes, the amniotic egg greatly facilitated reproduction in non-aqueous environments and effectively opened vast regions of both mesic and xeric terrestrial environments to vertebrate colonization.

At the volume's outset, Laurin and Reisz present a novel cladistic analysis in which lepospondyl amphibians (including a variety of mostly salamander-like Paleozoic forms, as well as living salamanders and frogs) are interpreted as being much more closely related to the earliest amniotes than assumed previously. However, many of Laurin and Reisz's most significant nodes lack solid objective support (see R. L. Carroll, Bull. Mus. Hist. Nat. Paris 4ème sér., 17, 389-445 [1995]). In addition, many of the character transformations used to support lepospondyl-amniote affinity were either frequently achieved in other clades, were subject to common reversal, or are anatomically improbable (for example, a major reduction in number of presacral vertebrae and re-elaboration of the proatlas in three separate lineages).

Laurin and Reisz's use of cladograms is also instrumental in their rejection of Carroll's widely accepted hypothesis that early amniotes were small and oviparous. However, the earliest known ancestors of amniotes were, in fact, small (\sim 100-mm-snout-to-vent length), and the fossil record of early amniotes clearly documents progressive size increase.

Carroll's model of protoamniotes is accepted in later chapters in this volume by Packard and Seymour and by Stewart. In the course of comprehensive reviews of a variety of amphibian/amniote developmental fea-



Reconstruction of *Eocaptorhinus laticeps*, a Late Paleozoic amniote. Length, about 30 centimeters. [From Sumida's paper in *Amniote Origins*; after Heaton and Reisz, 1980]

tures, these authors point out that the early development of a small, shelled egg deposited on land would have been necessary to facilitate diffusion of oxygen to the developing embryo as well as to provide mechanical support. Additionally, Stewart points out that recent embryological studies conclude that the probable excretory function of the primitive allantois, an extraembryonic membrane synapomorphous for amniotes, is also consistent with ovipary in protoamniotes.

Several chapters deal, at least indirectly, with alterations in the skin that probably accompanied the development of complete terrestrialism in amniotes. In an especially informative chapter, Frolich reviews osmoregulatory and mechanical properties of tetrapod skin. Interestingly, he concludes that the major adaptive feature of amniote skin was reduction of the dermis and elaboration of a low-mass epidermis, largely for resistance to mechanical abrasion rather than for waterproofing. Curiously, in another chapter Martin and Nagy suggest that epidermal waterproofing and an extensive dermal armor for resistance to mechanical abrasion were major attributes of the skin in early amniotes.

Two chapters are devoted to physical aspects of the Paleozoic world. A careful com-

pilation of Mid- to Late Paleozoic biogeography is provided by Berman, Sumida, and Lombard. Given the close proximity of Late Paleozoic landmasses, the apparent cosmopolitan or near cosmopolitan distribution of many taxa is not unexpected. However, the authors themselves point out that the paucity of fossil deposits dating from this period poses a severe limitation to more detailed conclusions about factors facilitating and limiting distribution of virtually all Late Paleozoic taxa.

Graham, Aguilar, Dudley, and Gans review evidence that, compared to today's atmosphere, the Late Paleozoic Era atmosphere contained higher concentrations of oxygen but lower levels of carbon dioxide. Unfortunately, the authors fall prey to the common misconception that higher levels of atmospheric oxygen content somehow signify that Paleozoic vertebrates maintained higher levels of activity than would be possible today. This is unfounded: at the current "low" levels of atmospheric oxygen, all ex-

tant tetrapods maintain fully saturated levels of arterial oxyhemoglobin, and even significant increases in aerial oxygen content would have little effect on blood oxygen carrying capacity.

The book also includes several chapters on early tetrapod locomotion, herbivory, and trophic apparatus. Unfortunately, it lacks a concluding synthesis or overview, and the

reader is left with little, if any, direction for resolution of the conflicting hypotheses set forth in the text. Nevertheless, *Amniote Origins* provides a useful, if uneven, foundation for future biologically oriented investigations of the origin of amniotes.

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Nerve Cells with Names

The Neurobiology of an Insect Brain. MAL-COLM BURROWS. Oxford University Press, New York, 1996. xvi, 682 pp., illus. \$100 or £55. ISBN 0-19-852344-0.

The devastation of native crops by locust plagues was a major problem in the governance of the British Empire, and the Anti-Locust Research Center was established in Britain to make these animals available for study to control their spread. The diverse behaviors that enable locusts to migrate en masse (they can walk, jump, and fly) drew the attention of scientists (first among them Graham Hoyle beginning in the 1950s) interested in investigating how their nervous systems generate such a panoply of motor actions with a limited number of nerve cells, and locusts have become the subjects of some of the most fascinating work done in contemporary neuroscience. As is documented in this overview of the literature on locust neurobiology, the field has expanded enormously, particularly in the last 20 years, in the areas of neuroethology, cellular neurophysiology, developmental neurobiology, and neuropharmacology. The author has not only made major contributions in most of these areas but read voluminously. The book contains introductory chapters on the anatomy, development, and pharmacology of the nervous system, which form the basis for

subsequent chapters on the physiology and connectivity of the neurons that generate specific behaviors. As the reader is led through the primary literature, superb illustrations summarize areas of research in sufficient detail to be useful both to those in the field and to others, such as molecular biologists and roboticists, curious about how nerve cells develop and function.

A key advantage for research offered by the nervous systems of locusts (and other arthropods) is that many of the nerve cells are unique and identifiable; that is, a given neuron can be found in different individuals and studied repeatedly. The cellular properties and synaptic connections of these neurons can there-

fore be understood within the context of the animal's structure and behavior more readily than is the case with vertebrate systems. In Burrows's excellent section on jumping, for example, a novice reader can be introduced to the single fast extensor tibia motoneuron (FETi), which innervates the hindleg muscle that generates the force of the jump. The jump is produced by a complex, but energy-efficient, mechanism: as the FETi becomes active, the leg is locked in a flexed position by excitation of neurons to the opposing flexor muscle. This allows for storage of energy from the extensor contraction in bending of the exoskeleton (and a tenfold amplification of the power output). The actual jump is then triggered by sudden inhibition of the flexors and release of the lock, involving interneurons that receive inputs of a number of different sensory modalities. The upshot of this circuitry is an extremely forceful jump delayed by the time required to develop the force (it is easy to catch a locust or grasshopper during the co-contraction phase but probably not after lift-off).

The sections on other behaviors are equally intriguing and extensive. The excellent chapter on flight may leave many amazed at the plasticity in the connectivity of such a "simple" system. Other behaviors such as oviposition can be elicited by activating an isolated part of the nervous system, implying that there really is a "computational module" at the animal's rear end. And the discoveries continue, notably in the work of Harald Wolf and Ansgar Büschges, who are publishing recordings from some interneurons in freely behaving animals.

One of my reservations about the volume is that it is mistitled, having for the most part little to do with the brain (the words "vision" and "chemoreception" are not in the index) and really being about a



A locust shortly before jumping. [©James C. Cokendolpher; Fran Heyl Associates]

chain of ganglia that are the equivalent of a spinal cord and brainstem. Second, some points need correction (locusts are not holometabolous, as stated). Finally, the format the author has chosen for discussing the results of many studies (interweaving facts, insights, and opinions with relatively few source citations) makes demands on the reader's confidence in him. There is also a bilious, "off-with-theirheads" spirit in the discussion of some studies that seems inappropriate in a review volume whose goal is to encourage research in the field. So I suggest taking the book as a source of inspiration rather than as the final word on a subject. However, it does summarize an outstanding and singular body of work and attests to the value of studying animals whose neurons you can get to know personally.

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Browsings

Atomic Histories. Rudolf E. Peierls. AIP Press, Woodbury, NY, 1997. xviii, 378 pp., illus. \$32.95. ISBN 1-56396-243-8. Masters of Modern Physics.

A reprinting of some 60 nontechnical essays including sketches of eminent physicists, commentary on atomic energy and arms control, and reflections on other matters that concerned the late author, one of the pioneers of the atomic bomb.

Imagined Worlds. Freeman Dyson. Harvard University Press, Cambridge, MA, 1997. viii, 215 pp., illus. \$22. ISBN 0-674-53908-7. The Jerusalem-Harvard Lectures.

Five wide-ranging essays in which the author uses "stories, imagined and real, to explore the interplay of science and technology with evolution and ethics."

Six Not-So-Easy Pieces. Einstein's Relativity, Symmetry, and Space-Time. Richard Feynman. Helix (Addison-Wesley), Reading, MA, 1997. xxx, 152 pp., illus. \$25 or C\$34. ISBN 0-201-15025-5.

Expositions of vectors, symmetry in physical laws, the special theory of relativity, relativistic energy and momentum, space-time, and curved space extracted from Feynman's *Lectures in Physics*, with introductory material by Roger Penrose and others.

State of the World 1997. A Worldwatch Institute Report on Progress Toward a Sustainable Society. Lester R. Brown *et al.* Norton, New York, 1997. xviii, 229 pp., illus. \$25 or \$C32.99, ISBN 0-393-04008-9; paper, \$13.95, ISBN 0-393-31569-x.

The fourteenth in a series of annual reports, presenting nine essays on topics including "the legacy of Rio," preservation of cropland, prevention of chronic disease in developing countries, security in the post-Cold-War era, and "the ozone experience."

Unifying Biology. The Evolutionary Synthesis and Evolutionary Biology. Vassiliki Betty Smocovitis. Princeton University Press, Princeton, NJ, 1996. xxiv, 231 pp., illus. \$29.95 or £25. ISBN 0-691-03343-9.

A historiographic consideration of the coalescence of evolutionary biology as a discipline and its "construction of the grandest narrative of Western culture, the modern story of evolution."

Views of the Cell. A Pictorial History. Joseph G. Gall. American Society for Cell Biology, Bethesda, MD, 1997. 128 pp., illus. \$29. ISBN 1-57814-001-3.

Sixty microscopic views, 1630–1950, that have appeared on the cover of the journal *Molecular Biology of the Cell*, with brief accounts of the classic work they represent.