

The editors and authors have given us a splendid rendition of details, bringing together widely scattered information. Yet I missed the big picture. The editors should have shown how these case histories relate to global eustasy and regional epeirogeny.

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Biography of Our Planet

Oasis in Space. Earth History from the Beginning. PRESTON CLOUD. Norton, New York, 1988. xviii, 508 pp., illus. \$29.95. Commonwealth Book Fund Program.

Geologists are lucky people. They get to travel to all sorts of odd, beautiful spots, away from the urban miasma. They study that most wonderful, strange, and improbable of subjects, the earth. They can tell true tales of polar bears, hippos, and encounters with cannibals. They even get to go to committee meetings without wearing ties.

Preston Cloud is one of the luckiest of geologists: he saw the planet in the days before its ecological ruin; he has seen his discipline grow to a hard, if less amusing, science with a firm theory of the earth; he has seen innumerable rocks (the best geologist is often the one who has seen the most rocks) and much mud; and, mirabile dictu, he has had a chance to write it all down for us.

Oasis in Space is a paean to the glory of the earth. It is a fine exposition of the history of our planet, written in a chatty style that hides deep learning and wise judgment. The book is a biography of the planet, and it pays more than usual attention to the infancy, childhood, and youth of the earth. The first section recounts the beginnings of the planet and introduces the fundamental logical tools of geology, together with the concept of geological time. This is followed by an account of the next 3 billion years, or most of what is commonly (but not by Cloud) called the Precambrian. Woven into this history of the biosphere is a discussion of the more physical aspects of geology: plate tectonics, climatology, and so on. The final chapters recount the more familiar tale of a planet inhabited by metazoa: a biosphere dominated by plants and animals. Within this saga of trilobites, fish, dinosaurs, and humans, the author interleaves many other topics: mountain building and continental collision, evolution and extinc-

tion, oil and climate, forcing factors and the question whether a gale in a junkyard would ever assemble a B-29 bomber.

There is much meat in the book, and the material is eclectic and up-to-date; there is even mention of RNA enzymes, not normal matter for a geology text. There are many set-piece expositions of such varied subjects as the origin of ironstones and the history of the atmosphere, plate tectonics, the theory of evolution, and the nature of mass extinction. Throughout the book the argument is detailed and careful: there is little of the vacuity common in general geology texts. The book should appeal to hordes of students (though it may be too advanced for first-year students) and to scientists who are not geologists. It may even revitalize those professional earth scientists like myself who are so worn down by the interminable business of grant application and implementation that we forget the splendor of our home. Though one may disagree with some of Cloud's opinions and dispute some of his conclusions, this is a book worth reading well and well worth buying. And what a wonderful title!

Now, like most field geologists, I must end with a Cloud story and a moral. He visited us once, years ago, in the Zimbabwean bush. Our camp was by a pool occupied by bathing maidens at one end and a large hippo on a sandbank at the other. Cloud, being a geologist, went straight for

the end with the hippo. Now large hippos are not safe—they kill many people, bite you in three, and stomp on the remains—but Preston was fearless. He advanced steadily onto the sandbank in his inexorable investigation of nature, while we watched, worried, and considered rescue. The hippo arose and angrily prepared to charge. Fortunately, at the very last moment it yielded and ran off with a great splash, and *Oasis in Space* could be written. The moral, inevitably, is that of Cloud's last chapter: mankind now rules the earth and nature is in retreat.

But hippos do not just sleep on sandbanks. Hippos have incongruously tiny tails, which do more than keep off flies. When a hippo defecates, which it does with great éclat, the co-evolutionary tail whirs around like a fan. The dung hits it, is spread far and wide, and nurtures the riverbank habitat. Here is the parting message of Cloud's book: when we remove the hippo we also leave the riverbank, the river, and the world much the worse. Our planet is in crisis. *Oasis in Space* is a summation of the insight gained by earth scientists in this century. Earth science has solved the problem of how the planet works in physical terms; our challenge now is to understand and manage the biosphere, our home, before it is destroyed.

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Sexual Reproduction

The Evolution of Sex. An Examination of Current Ideas. RICHARD E. MICHOD and BRUCE R. LEVIN, Eds. Sinauer, Sunderland, MA, 1987. x, 342 pp., illus. \$55; paper, \$29.95.

The near ubiquity of sexual reproduction has long attracted the attention of evolutionary biologists. Why should so many species engage in the complicated behavioral and physiological processes needed to bring together gametes from two distinct individuals, and possess the elaborate genetic machinery involved in producing recombination between the maternal and paternal genomes during the production of these gametes? It would seem much easier simply to engage in "some harmless mode of vegetation," as Edward Gibbon once put it. Since the development of the modern evolutionary synthesis in the 1930s and '40s, thinking about the evolutionary significance of sex and genetic recombination has been dominated by the idea that the long-term survival of the population or species is promoted by the ability of sexual reproduction to gener-

ate new combinations of alleles at different loci and thereby accelerate the rate of evolution. On this view, asexual taxa are more vulnerable to extinction in the face of a changing environment and so are poorly represented among extant species of higher plants and animals. During the past 15 years or so, this type of interpretation has come under increasing challenge, and considerable effort has been expended in developing models of selection on genes that modify the mode of reproduction or the frequency of genetic recombination, with the course of evolutionary change being determined by the changes in frequency of these genes within populations.

The early phases in the development of this viewpoint were reviewed by George Williams (*Sex and Evolution*, 1975) and John Maynard Smith (*The Evolution of Sex*, 1978). Since then, a number of significant further theoretical developments have occurred, and an ambitious attempt to test the earlier models against the evidence provided by the taxonomic distribution and ecological corre-

lates of modes of reproduction has been made by Graham Bell (*The Masterpiece of Nature*, 1982). Michod and Levin's volume is a collection of papers by leading contributors to this field and provides an excellent overview of the current state of affairs. A characteristically wry judgment on this is passed by Joseph Felsenstein (p. 75): "There is a continuing flow of new theories and variants of existing theories, but there seems to be no major new source of data, no illuminating new experiment, no barrier to progress in other fields. The problem has simply flared up again and will probably gutter out after a while."

Readers of this book will probably come away with considerable sympathy for this judgment. Though a great deal of ingenuity has been expended on the development of a wide variety of theoretical models, it has proved extraordinarily difficult to test them critically against the data. All too often, the facts can be interpreted in various different ways, and investigators have shown a tendency to take the consistency of a set of observations with their pet theory as proof of its validity, without being careful to rule out the alternatives. For instance, Bell proposes that sexual reproduction enables more efficient exploitation of heterogeneous environments and asserts (p. 136) that "sex is associated with old, stable, complex environments. These are the circumstances in which environmental heterogeneity . . . and mutually antagonistic relationships between species . . . are likely to be the most pronounced." He omits to mention that a similar pattern of association will be produced by the fact that asexual or self-fertilizing individuals may experience a relatively higher level of reproductive success than sexual individuals in sparsely populated habitats or in temporary habitats colonized by a few propagules, where the probability of mating encounters is low.

Nevertheless, a number of genuine conceptual advances have been made as a result of recent work, and these are brought out in several of the papers in this volume. There is no doubt that the study of the evolutionary biology of reproductive systems is now a much richer and intellectually rewarding field than it was 20 years ago, when it was stultified by uncritical acceptance of the group-selectionist views of writers such as Darlington and Stebbins. We are now confronted by a great diversity of well-formulated models for the evolutionary advantages of genetic recombination, reviewed here in papers by Bell, Brooks, Crow, Felsenstein, Maynard Smith, and Seger and Hamilton. The heretical view that genetic recombination is basically a mechanism for the repair of mutational damage is expressed forcefully

in the papers by Holliday and by Bernstein, Hopf, and Michod. Levin argues persuasively that bacterial conjugation is a by-product of the advantage to plasmids of transfer between hosts and that transformation is probably a mechanism for repair of mutational damage. Hickey and Rose go further (probably too far) and argue that sex in eukaryotes results from the selective advantage to parasitic DNA of transfer between hosts.

What is one to make of this diversity of viewpoints? In trying to sort the wheat from the chaff, it would seem wise to be clear about whether or not certain facts rule out particular theories. In examining the possibility that genetic recombination is purely a mechanism for repair of mutational damage, especially double-strand chromosome breaks as argued by Bernstein *et al.*, one surely has to consider the fact that meiotic recombination is absent in males of many species of Diptera, in males of haplodiploid species, and in females of at least some species of Lepidoptera. Any repair advantage to recombination must have been small in comparison to the forces favoring its elimination in these genetic systems. In *Drosophila*, the hatchability of eggs approaches 100% under optimal conditions, and in the haplodiploid wasp *Habrobracon* the productivity of fertilized and unfertilized eggs is similar. Both these facts suggest that mortality due to spontaneous chromosome breaks is low. Maynard Smith gives further reasons (p. 112) for concluding that "the evolution of recombination cannot be explained by the immediate requirements of DNA repair, of methylation, of gene conversion, or of disjunction in meiosis." This conclusion seems almost inescapable to me.

If this is so, then we are confronted with the difficult task of distinguishing between the numerous possible mechanisms for the evolution and maintenance of non-zero rates of genetic recombination. The papers on this topic certainly do not come to a unanimous decision on this point, and it may well be that a multiplicity of factors is involved. However, the near universality of recombination in organisms with DNA genomes and the existence of surrogate mechanisms such as multicompartmental genomes in RNA viruses (which are mentioned here only in Crow's lucid contribution but surely deserve more discussion) suggest that at least one universally acting force is responsible. Furthermore, such a force must operate effectively throughout the genome in order to account for the relative uniformity of rates of recombination per nucleotide site within a given species, with the exception of regions of the genome where it is advantageous for recombination to be suppressed

(such as between the sex chromosomes). The process that seems to me to come closest to meeting these requirements is that originally proposed by Crow and greatly extended by Alexei Kondrashov. They have shown that there is a selective advantage to genetic recombination in a population at equilibrium between selection and mutation to deleterious alleles at a large number of loci, when the net impact on log fitness of adding a new mutation increases with the number of mutations already present in an individual.

It may be objected that a universally acting selective force favoring recombination and sexuality cannot account for the occurrence of asexual taxa and the undoubted correlations between asexuality and ecology. However, asexuality has consequences other than the suppression of recombination, such as the assurance of reproductive success mentioned above and the advantage accruing from the "cost of meiosis." In addition, the long-term effects of asexuality in leading to increased rates of extinction due to the irreversible accumulation of mutations by Muller's ratchet or to failure to evolve sufficiently fast will further distort the taxonomic picture.

It is therefore extremely dangerous to derive conclusions concerning the adaptive significance of recombination from comparative evidence on reproductive modes, as is done in the papers by Ghiselin, Bell, Seger and Hamilton, and Shields. As is pointed out by David Lloyd in his perceptive contribution (p. 251), "If the features and distribution of outcrossed, self-fertilized and asexual species are to be understood, a more eclectic approach is required." Despite these strictures, this book provides a valuable source of information and ideas on the evolution of sex and will unquestionably be consulted by all those interested in this field.

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A Theoretical Framework

The Evolution of Individuality. LEO W. BUSS. Princeton University Press, Princeton, NJ, 1988. xvi, 203 pp., illus. \$40; paper, \$12.95.

Although the title of Leo Buss's book sounds like it could belong to a Southern California pop psychology tract, the subject of the book is much more fundamental and significant—the evolutionary origin of the individual as the unit of selection in multicellular plants and animals. Historically this