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 book grows out of Weismann's late-19th-century arguments on the significance of germ line segregation during development, but its intellectual viewpoint arises from the last decade's intense controversies on the adequacy (not validity) of the Modern Synthesis as an explanation for evolutionary phenomena, particularly the often heated controversies about units of selection and the possibility that natural selection may act at multiple levels in the biological hierarchy. The high point of this volume is undoubtedly Buss's derivation of a conceptual paradigm for developmental patterns, based on the idea that ontogenetic patterns and specific developmental phenomena such as induction and programmed cell death are best viewed as the consequences of selection on cell lineages within an embryo to limit their replication and to isolate the germ line from potential somatic mutations. This is, in my opinion, the theoretical framework that embryologists have searched for during the last hundred years, rationalizing the common patterns seen early in ontogeny, the great diversity of patterns in later ontogeny, and the commonness of heterochrony as a mechanism of evolutionary change. Buss's exploration of this thesis is the major strength of this book, fitting topics as diverse as developmental patterns, life cycle evolution in parasites, and the dominance of diploidy in both metaphytes and metazoans into a single framework.

Given the importance and potential power of the ideas in this book, it is unfortunate that it has as many flaws as it does. One gets the impression that it was prepared in haste; typographical errors are distressingly frequent, the rows and columns have been interchanged in figure 2.17, making it difficult to follow the argument in the caption, the alga in figure 4.11 is misidentified, and footnote 40 in chapter 2 is totally unrelated to the text and obviously misplaced. The design of the book, with the printed text spanning only two-thirds of the page, leaves the impression that the publisher has attempted to make the book appear longer than it really is. Many of the figures were apparently included more for their esthetic value than for their ability to clarify and illuminate the text, and the figure captions are exceptionally cryptic; if the reader is not already familiar with the information in the figure, the captions will rarely help. Some of the book's central terms are used in ways counter to the common understanding of most biologists. "Heritability," for example, is defined (p. 69) as "the capacity to yield a new multicellular individual," and the word "variant" is apparently used both in the sense of a mutation and to describe the results of cellular differentiation. The citations are in footnote style rather than standard biological format, often making it difficult to determine the specific reference if, for example, it was first cited 20 pages before. The logic underlying some of Buss's arguments is occasionally rather strained, and the reader is continually frustrated by the desire for more examples and more explicit attempts to test the predictions derived from these arguments, but this criticism is perhaps better seen as indicative of the intellectual excitement Buss's ideas engender than as a weakness of the volume in hand. With more documentation and a greater exploration of the implications of these ideas this could easily have been the most important book in biology in this decade, but even with its flaws it should be on the list of required reading for all evolutionary and developmental biologists.

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A Sole Survivor

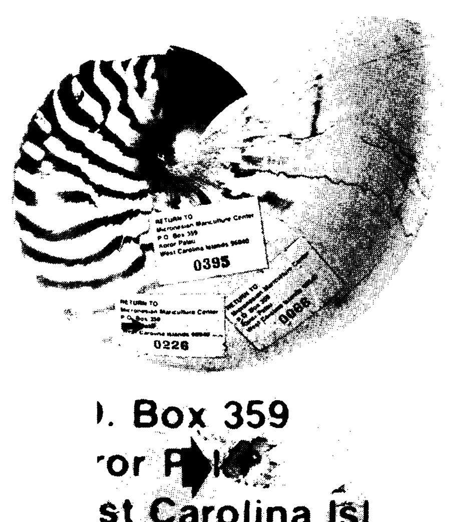
The Natural History of Nautilus. PETER DOUGLAS WARD. Allen and Unwin, Winchester, MA, 1987. xiv, 267 pp., illus. $34.95.

Nautilus. The Biology and Paleobiology of a Living Fossil. W. BRUCE SAUNDERS and NEIL H. LANDMAN, Eds. Plenum, New York, 1988. xxviii, 632 pp., illus., + plates. $95. Topics in Geobiology, vol. 6.

Nautilus is a small, ecologically unimportant genus of deep-water tropical invertebrates. If it were like most other such genera, one would be lucky to find even a single obscure paper devoted to it during any given year. Why, then, should *Nautilus* merit the publication of two full-length books in a single year? The answer is simple. As the single surviving genus of cephalopods with a chambered external shell, *Nautilus* is the only key we possess for unlocking the biology of the hundreds of fossil nautiloids and ammonoids that were so prominent in the seas of the Paleozoic and Mesozoic eras. Moreover, *Nautilus* offers a fascinating contrast in its physiology and mode of life to the other living cephalopods—squids, octopuses, and cuttlefishes—in which the shell is either internal or lost entirely.

The two books under review—one a single-authored synthesis by P. D. Ward, the other a multi-authored collection of papers edited by W. B. Saunders and N. H. Landman—cover much the same ground and reveal remarkably few points of disagreement. Both provide much new information as well as incisive reviews of previously published work. Ward emphasizes buoyancy control and shell growth, together with extensive observations on the ecology of the living species on forereef slopes in the tropical western Pacific. Several physiological aspects only briefly touched upon by Ward receive more extensive treatment in the Saunders-Landman volume, which also contains chapters on many other topics including ecology, reproduction, shell microstructure, and taxonomy.

The picture of *Nautilus* that emerges from these two books is of a low-energy animal that, compared to other cephalopods, swims and grows slowly and hatches as an unusually large (25-millimeter-diameter) juvenile. Whereas most other cephalopods have an extraordinarily sophisticated visual system, the comparatively simple camera-obscura eyes of *Nautilus* appear to play a subordinate sensory role to the highly developed olfactory and tentacular sense organs. Vertical movement in the water column is made possible by a complex buoyancy-control mechanism, in which liquid is pumped into and out of the shell chambers by the siphuncle. The rate of liquid removal from the chambers, which varies according to depth and temperature as well as with the thickness and permeability of the siphuncular wall, controls diverse aspects of the life of *Nautilus*, including growth rate and the ability of the animal to respond rapidly to sudden changes in its density. The maximum depth at which *Nautilus* can live is



Mature *Nautilus belauensis* "trapped three times in 1977 off Mutremdiu Point, Palau (shell diameter 216 mm." The arrow on tag 0226 points to *Octopus* boring. [From W. B. Saunders *et al.*, "Predation on *Nautilus*," in *Nautilus: The Biology and Paleobiology of a Living Fossil*]