for supposing that the Crab Nebula originated with the brilliant "guest star" observed by the Chinese and Japanese in A.D. 1054; if, as Williams suggests, the nebula could equally well have originated in the first half of the 12th century, one of the most satisfying tales in the history of science will have to be rewritten.

A good festschrift should, above all, give pleasure. This one will be read with delight, the more so as its contributors display their learning with a grace and lightness of touch that their mentor will surely appreciate.

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A Fossil Group

The Ammonoidea. The Evolution, Classification, Mode of Life and Geological Usefulness of a Major Fossil Group. Proceedings of a symposium, York, England, Aug. 1979. M. R. HOUSE and J. R. SENIOR, Eds. Published for the Systematics Association by Academic Press, New York, 1981. xvi, 594 pp., illus. $86.50. Systematics Association Special Volume No. 18.

Ammonoid cephalopods hold pride of place in late Paleozoic and Mesozoic biostratigraphies, and their chambered shells provide some of the most instructive material for evolutionary studies to be found among the shelled invertebrates. As a consequence, research on ammonoids is vigorous and the literature is immense and widely scattered. Insight into the entire group comes largely from summaries like those in part L of the *Treatise on Invertebrate Paleontology* (R. C. Moore, Ed., Geological Society of America and University of Kansas Press, 1957) or "Molluski-Golovonogie I" of the *Osnovy Paleontologii* (V. E. Ruzhencev, Ed., Izdatel'stvo Akademii Nauk SSSR, 1962). *The Ammonoidea* supplements and updates those volumes by summarizing principal research accomplishments of the last 20 years.

The Ammonoidea is divided almost equally into three parts. The first six papers deal with classification and evolutionary development; the second six with organization and mode of life; and the final eight with biostratigraphy and distribution. The individual chapters are keynote addresses given at a 1979 Systematics Association symposium on ammonoidea. They vary in style, philosophy, and coverage, but all are authoritative.

In chapters on origin, classification, and evolution, authors of Devonian, Carboniferous, and Triassic contributions treat the Ammonoidea as a subclass, whereas Permian, Jurassic, and Cretaceous workers regard the group as an order. Major ammonoid taxa (orders or suborders) are largely the same as in part L of the *Treatise*, but concepts of several are changed through addition, subdivision, or rearrangement. For example, House regards bactritids as primitive ammonoids and includes them as a suborder of the Anarcestida, noting that this moves the question of ammonoid origins back a step, probably to straight orthocerid nautiloids with ventral siphuncles. Authors dealing with Jurassic and Cretaceous ammonoids introduce welcome changes through abandonment of the concept of iterative "replenishment" of the Ammonitina by successive homeomorphic waves from the conservative Phylloceratina and Lytoceratina. Origin of Carboniferous ammonoids from cheiloceratacean Prionoceratidae, the only group to survive the Devonian, seems well established, as is origin of most Triassic ammonoids from the Xenodiscidae. Tozer notes that the Phylloceratida provide the only clear link between ammonoids of the Triassic and those of the Jurassic. Donovan, Callomon, and Howarth, however, reject the idea that all Jurassic ammonoids developed from the Phylloceratina, but they cannot identify lines of descent by which early Jurassic forms developed from Triassic predecessors.

In the section on organization and mode of life, Birkelund concludes from her consideration of shell structure and siphuncular morphology that economy of mass was a primary factor governing shell construction and that differences in siphuncular construction reflect ecologic differences. Wiedmann and Kullmann emphasize the importance of sutural ontogeny, show that sutural phylogeny is related, and conclude that the law of recapitulation applies. Callomon shows that evidence of dimorphism is widespread in Jurassic ammonoids but has not yet been systematically assembled for Cretaceous ones. Lehmann reviews interpretations of aptychi and anaptychi and discusses jaw apparatuses, radulae, crop contents, and ink sacs. Chamberlain summarizes studies of the relationship between hydromechanical design and adaptive locomotor strategies; and Klinger speculates on buoyancy control and ecology in certain heteromorphs. Some of these studies are obviously more advanced than others, but all the features considered have obvious systematic and evolutionary significance.

Because ammonoid biostratigraphy and distribution have been so thoroughly studied, the final section of the book adds little conceptual novelty. However, Ziegler's comments about potential infirmities in Jurassic ammonite biostratigraphy, coupled with earlier comments by Donovan, Callomon, and Howarth on the difficulty of identifying notoriously homeomorphic Jurassic ammonites, should caution those who cite Jurassic ammonite biostratigraphy as the ideal.

The book is well made, has few typographic errors, and is a fitting tribute to the late Bernhard Kummel, to whom it is dedicated. The contents suggest that the revised version of part L of the *Treatise*, in preparation by the same authors, will be a substantial improvement over the first edition.

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Marine Ecology: Status Report

Analysis of Marine Ecosystems. A. R. LONGHURST, Ed. Academic Press, New York, 1981. xxii, 742 pp., illus. $125.

The study of ecosystems as such, rather than simply of component species, is still in a formative stage in which investigators are exploring in many directions with no generally agreed-upon approach. Longhurst has taken up the challenge of assembling and editing a thick volume on the state of the science that encompasses many of the active lines of research on marine ecosystems today. A section of the book is devoted to particular geographical types of ecosystems: high and low latitudes, upwellings, continental shelves, and coral reefs. A second section is devoted to functional aspects of marine ecosystems, such as autotrophy, grazing and predation, and variability in space and time. A final section deals with simulation and experimental studies, in other words with models of all kinds.

Although the book is written by 30 authors, writing more or less independently, a number of themes run through it, giving us insight into what the collective authorship views as important. The integration of physical and chemical oceanography with the study of the biological aspects of ecosystems is impressive. Ecologists clearly recognize that they must understand and reckon with the physicochemical regime. Within that

set of considerations there is recurrent mention of fronts and other regions of locally significant physical activity. Though this may be a fad of the moment, fronts certainly are regions of unusual biological activity and therefore deserve attention. At the same time, they are dynamically complex physical phenomena that have been understood only recently. Several authors consider the roles of nonliving particulate and dissolved organic matter in a way that reflects accurately the current controversies about their roles in the flow of energy through marine ecosystems. This subject is being reopened as new and powerful chemical methods are applied to some long-standing questions about the composition, residence time, origin, and fate of the largest pools of organic matter in the ocean.

The exposition leaves the reader to accept or resolve some contradictions. The unevenness and contradiction from one chapter to another accurately reflect the state of marine ecosystem research. Indeed, no general agreement exists about such basic questions as the structure of food webs, the interaction of their component populations, or whether current methods successfully measure rates of ecosystem processes. Various authors make a case for the special significance of large organisms in one chapter and that of microorganisms in another. The tendency toward bias in favor of certain organismal or trophic groups, which must be inherited from the days when organisms, not ecosystems, were the only formal subjects of study, is seen even in the section on modeling. Most extant models emphasize some specific food chain, usually grazing and predation, and in that they may be less than ecosystem models. Such condensation is not a limitation inherently imposed by computing capabilities, and it tells us how little we understand ecosystem processes.

Though no chapter is devoted specifically to fisheries, a number of the authors are fisheries specialists. Basic questions that have significance for fisheries management are considered, usually in the context of ecosystem function or ecosystem analysis rather than as strictly practical considerations. In this as well as in other respects, the editor avoids creating a cookbook. Methods are discussed primarily in those circumstances where their development has been a crucial and current part of important basic advances or where potential shortcomings in methods may be limiting our understanding.

The coverage and balance among subjects are good. The treatment assumes that the reader needs no descriptive introduction to the ocean or its populations. The chapters are succinct, with citations of more detailed reviews and other relevant literature. The book was obviously produced without delay, because it is up to date with many 1979 and 1980 citations. Topics of current interest are emphasized, and many matters of controversy are discussed. The volume will be especially valuable to graduate students and to investigators who seek an overview of the current state of ecosystem analysis in the marine biome.

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Polymorphism and Selection

Genetic Variability. CHRISTOPHER WILLS. Clarendon (Oxford University Press), New York, 1981. xiv, 312 pp., illus. $49.50.

A principal theme of *Genetic Variability* is that virtually unlimited amounts of polymorphism can be maintained by selection. Wills argues that the neutral theory has gained credibility largely because the "many compelling arguments that neutral alleles should be the most numerous are the result of the properties of the multiplicative selection model." With multiplicative selection, loci have independent effects on viability so that the average fitness of a population decreases exponentially with the number of loci maintained by selection. He would like to bury this multiplicative bugbear once and for all but feels "how tenacious the grip of the multiplicative way of thinking has been and how difficult . . . for population geneticists to escape from it."

The escape proposed is a multifactorial model in which genes do not determine "fitness" but rather "fitness potential" and in which natural selection acts on fitness potential in much the way an animal breeder practices directional selection—to save the best and cull the rest. Wills is a proponent of balancing selection, and his favorite multiple-factor model is "balancing rank-order truncation selection" or brots (my acronym), in which the fitness potential of an organism is proportional to its number of heterozygous loci. Much of the book deals with the implications of brots as inferred mainly from numerical analysis and computer simulation, and few implications are surprising: (i) a large number of segregating loci can be maintained by selection because the selection coefficient per locus varies inversely as the square root of the number of segregating loci; (ii) inbreeding depression is relatively mild and can be accounted for by a residuum of unconditionally harmful alleles that act in multiplicative fashion; (iii) chromosomes do not "crystallize" as a result of buildup of linkage disequilibrium; and (iv) there may be selection for increased recombination. To be sure, brots predicts that a much higher proportion of polymorphisms should have alleles at intermediate frequencies than is actually observed, but this problem is dispensed with by invoking heterogeneous environments and genotype-environment interaction to skew the equilibrium frequencies.

Some readers may object because the brots model is discussed to the virtual exclusion of many other multiple-factor possibilities. Others may question the brots model itself. In assuming that fitness potential is proportional to the number of heterozygous loci, doesn't the model beg the question of the selective maintenance of genetic variation? What is the biological justification of such a model? After all, allozyme polymorphisms are even more widespread in haploid *Escherichia coli* than they are in diploid organisms (R. K. Selander and B. R. Levin, *Science* **210**, 545 [1980]), which suggests that heterozygosity per se may be irrelevant to their maintenance. Yet Wills develops the case for balancing selection in his detailed discussions of hemoglobin structure and function, blood groups, G6PD, and HLA. These minireviews are excellent summaries of a diversity of molecular and epidemiological data relevant to human population genetics. Extrapolation from these few loci to the entire genome requires a leap of selectionist faith, but Wills expresses confidence that the few well-studied human polymorphisms will prove to be typical.

Wills concludes on a pessimistic note because, in the end, "it seems unlikely that we will ever be able to determine with certainty what proportion of alleles in a population is neutral and what proportion is subject to selection." My own view is that the sharp dichotomy between neutral and selected alleles is unnecessary and rather artificial. In the first place, alleles can be important in adaptation and nevertheless change in frequency because of random genetic drift, and Wills himself cites founder effects among the Yanomama Indians as an example. Second, alleles at loci with small effects on characters under stabilizing selection are slightly deleterious