LITERATURE REVIEWS

Readers are invited to submit reviews of current literature relating to origins. Mailing address: ORIGINS, Geoscience Research Institute, 11060 Campus St., Loma Linda, California 92350 USA. The Institute does not distribute the publications reviewed; please contact the publisher directly.

FEWER ANSWERS THAN QUESTIONS

RATES OF EVOLUTION. 1987. K.S.W. Campbell and M.F. Day, editors. London, Boston and Sydney: Allen and Unwin. 314 p.

Reviewed by L. James Gibson, Geoscience Research Institute

This is another of the books produced in the current debate over evolutionary processes, but it is not simply another rehash of Neo-Darwinism. Much of its interest stems from the rich mix of authors whose specialties range from paleontologists to molecular biologists and more. Each of the 16 chapters, written by one or two authors, was initially presented at a seminar held at the Australian National University at Canberra in February 1985. Each chapter begins with a useful abstract, and ends with a bibliography. The text is well-supplemented with line drawings and tables. I noticed only a few, insignificant typos.

The first 5 chapters are devoted to discussions of paleontological material. Included are a chapter by D. M. Raup on the use of fossils in studies of evolutionary rates, and a chapter by M. R. Walter discussing the origins of the major groups of living organisms. These are followed by separate chapters on the origin and evolution of mollusks (B. Runnegar), echinoderms (K S. W. Campbell & C. R. Marshall) and angiosperms (E. M. Truswell). The majority of the authors of these chapters seem impressed by the relatively sudden appearance of major groups in the fossil record, although it does not appear that punctuated equilibrium is the dominant explanation. Rather, there is a general dissatisfaction with current theories, and a search for new understanding, a feeling which extends through nearly the entire book.

One of the most interesting points made in the paleontological section is based on the discussion of echinoderms. The authors of Chapter 4 state (p 80-82) that the classes of echinoderms do not converge morphologically towards their times of origin. In other words, they were morphologically as distinct at their first appearance as they are today. If evolution proceeds by gradual divergence from a common ancestor, one would expect the degree of divergence to increase over time. Apparently this has not happened with the classes of echinoderms.

The remainder of the book is dominated by genetics, including population genetics, developmental genetics, and molecular genetics. The reader will surely be impressed that many biologists have concluded that the traditional basis of evolutionary theory, population genetics, has not led to an understanding of significant evolutionary change, although it may work well for explaining fluctuations of gene frequencies within a given population. Many of the writers seem to feel that the real basis of evolutionary change will be found in developmental genetics, although this field is not well understood at present.

In Chapter 6, P. G. Williamson discusses the relative importance of extrinsic stabilizing selection versus intrinsic genetic constraints in species stability. He argues that neither ordinary stabilizing selection nor genetic constraint adequately explain evolution. He proposes that intraspecific competition is the primary factor responsible for maintaining species integrity. In this view relaxation of intraspecific competition, as during a population flush, permits morphologically deviant individuals to survive. Such individuals are normally eliminated, not because they are unable to cope with the physical environment, but because stronger individuals of the same species crowd them out. Implicit in this hypothesis is the concept that morphological change is most likely during a population flush, such as might occur if a small number of individuals were to survive a major catastrophe and repopulate an area.

In Chapter 7, D. T. Anderson discusses the problem of development in evolution. The stability of the developmental process, producing similar individuals in radically different environments, seems to indicate that major morphological change cannot occur rapidly. Development is so complex a process that a major disruption would not produce a viable individual. Anderson seems to feel that the way to understand evolutionary change is to determine the cause for the extraordinary conservatism of the developmental process.

Chapter 8 reads somewhat like a lament that population biology has not been able to contribute significantly to understanding morphological change. The two areas are either irrelevant to each other, or have yet to be connected. The author, I. R. Franklin, does not seem to be sure which is the case.

P. R. Baverstock and M. Adams report in Chapter 9 on their work comparing various measures of difference among groups of Australian mammals, birds, and snakes. They report that the degree of morphological similarity among species is not a reliable predictor of the degree of molecular or chromosomal similarity. For example, certain bat species are so similar they cannot be easily distinguished, yet have large molecular differences. On the other hand, certain species of cockatoos are easily distinguishable morphologically, yet their molecular diversity is relatively low. The authors conclude that rates of chromosomal and morphological evolution vary enormously, while molecular evolution is closer to being relatively constant, and suggest that morphology may be determined by only a small fraction of the genome.

In Chapter 10, J. A. Thomson discusses the relationship of development to morphological change, and argues that developmental genes are "compartmentalized", that is, their activity is localized to specific regions of the embryo. Effects of changes in one gene of a complex of genes would be limited to a particular region of the body, resulting in morphological changes that would be rapid but limited. Thus major phenotypic change could occur without disruption of body function. This position seems to contrast sharply with that of the author of Chapter 7.

The importance of population genetics in evolutionary theory is defended by H. L. Carson in Chapter 11. According to Carson:

> *Dramatic changes in the phenotypic and genotypic characters in populations can be experimentally accomplished in as few as five generations of natural selection.*

This may be true, but whether the characters involved are important in evolution is another question. Carson feels that homeotic mutants are not likely to be important in macroevolution because of disturbance to the developmental system. In his view, mutations are the stuff of evolution. Many mutations, perhaps most, appear to be due to mobile genetic elements, rather than to spontaneous changes in the genetic code. Carson points out that, in the absence of selection, random mutational change will cause a character to become unstable and decay until it reaches a level where selection again operates to maintain the character. It has always puzzled me that a person can state such a belief, and yet also believe that new characters can somehow be formed gradually. An incipient organ cannot be selected for unless it is useful. This requires that it be functional and integrated with the rest of the organism's physiology.

In Chapter 12, A. R. Templeton presents data, largely from studies of Hawaiian *Drosophila*, to show that the rate of evolution may be influenced by the type of genetic system of a species, and by the number of individuals that gave rise to the population. Ordinary autosomes are diploid in both sexes, X chromosomes are haploid in males and diploid in females, and mitochondrial DNA is inherited as a maternal haploid. By comparing the degree of divergence for different modes of inheritance, one may obtain clues about the history of the group. According to previous studies, speciation events are most likely when the founding population of four or fewer individuals experiences a rapid increase in population size. Templeton concludes that if mitochondrial and nuclear DNA show similar divergences for two species, the species have probably become isolated by barrier formation (vicariance). If the extent of divergence is quite different, it is likely that founder events were important in the speciation process.

Most evolutionary explanations for the existence of diploidy and recombination suggest they are positively selected for because they provide a mechanism for supplying variation on which natural selection can act. In Chapter 13, D. C. Reanney argues for just the opposite, that they have been selected because they can act to protect the genome against errors. As Reanney points out, information is not improved by random errors. Reanney suggests two mechanisms for protection of the genome against errors: redundancy, both within the genetic code (codons) and in multiple copies of genes; and genetic subdivision, as in RNA viruses with split genomes, and in eukaryotes with split genes. According to Reanney, most mutations in eukaryotes are due to mobile genetic elements, not to errors in copying.

J. Langridge examines several theories of evolution in Chapter 14, including those relating to vitalism, mutation, selection, and directionality. He recognizes that natural selection acting on random genetic variation can account for variation in populations and even between species, but it seems that some other factors may be important in establishing the differences between families and higher taxonomic categories. Langridge dismisses vitalism, stating that there is no reason to think that life requires anything other than the known laws of physics and chemistry. Langridge notes that most organisms contain a great deal of genetic variability, much of which is nearly neutral to selection. The source of the variability, at least in *Drosophila*, seems to be mobile genetic elements. Langridge suggests that mutations in regulatory genes are the mutations important in evolution, but states that the way in which organisms adapt seems more obscure now than before the recent advances in molecular genetics.

On the relationship of an organism to its environment, Langridge suggests that some genetic changes may be induced by the environment, in addition to being selected by the environment. Direction in evolution is due to increasing complexity which reduces the number of alternatives available for future changes. Therefore, evolution may occur relatively rapidly when a new feature first appears, but slows down as the new feature is modified and improved. It is clear that the author considers that a new and expanded view of evolution is needed.

The inadequacy of Neo-Darwinian population genetics is again underscored in Chapter 15 by G. L. G. Miklos and B. John. They argue that most DNA is irrelevant to morphology, pointing out that the study of polymorphisms in structural genes has told us nothing of significance to evolutionary change. In their view, developmental genetics holds the key to the problem, and the appropriate method to solve the problem is to study how cells interact during development, then to search for possible genetic controls over cell movement. Examples discussed include *Drosophila* homeo boxes, and neural cell lineages in arthropods and roundworms. Advances in molecular biology make plausible the hypothesis that evolution may be driven by "molecular drive" rather than selection. In molecular drive, the phenotypes of all individuals in a population may change in concert, due to the synchronous homogenization of one or more multigene families in all individuals of the population. This change may be brought about by mobile genetic elements. This explanation gets around the problem of how a random change occurring in one or a few individuals can be spread and become established in a population, particularly if the change is significant phenotypically.

In the final chapter, J. H. Campbell discusses the relationship of gene structure to evolution. Pointing out that natural selection acts mainly against change rather than promoting change, Campbell argues that as an organism advances evolutionarily, it acquires greater ability to promote further evolutionary advancement. He does contribute to the clarification of what is meant by the term "evolution" by comparing four uses of the term: changes in gene frequency, changes in gene structure, specialization of a structure, and evolutionary advancement. Neo-Darwinism is preoccupied with the first usage of the term, but the explanation for increasing complexity must lie with the last. Readers would be benefitted if authors clearly indicated which sort of change they were referring to, as they seem of radically differing validity.

In summary, I found this book highly worthwhile reading. Not only does the book contain much useful information, but the diversity of authors and opinions adds much to its interest. My thinking has been stimulated by the contents, but I have not yet figured out how its title was chosen.