

ties are perceptive and clearly drawn. He also does a skillful job of presenting the context of particular paleontological problems, such as the significance of *Archegosaurus* and the reptilian ancestry of birds. Curiously, given his professed intentions, his account is weakest when he tries to relate these personal and scientific narratives to broader social and economic causes.

Desmond pushes his revisionism too far, and most readers will no doubt find parts of his argument more intriguing than convincing. But he raises important questions, and he explores new areas in the history of paleontology as well as brings a new perspective to some of the old. Certainly it is long past time for a reassessment of Huxley and Owen. For that reason alone, anyone interested in the initial reception of the theory of evolution will find this book interesting if not entirely satisfying.

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## Speciation

**Mechanisms of Speciation.** Proceedings of a meeting, Rome, May 1981. CLAUDIO BARIGOZZI, Ed. Liss, New York, 1982. xiv, 548 pp., illus. \$88. Progress in Clinical and Biological Research, vol. 96.

It is likely that the topic of speciation is more thoroughly awash in unfounded and often contradictory speculation than any other single topic in evolutionary theory. That, at least, is the most compelling conclusion to which a reading of this symposium leads.

Of the 25 papers in the volume, several, whatever their merits, do not bear on the subject of speciation; many merely describe chromosomal and other differences among related species (for example, those by Coluzzi, Capanna, Battaglia, and Ehrendorfer); and, though some authors (notably Mayr, Stebbins, Ayala, White, Templeton, Gottlieb, Carson, and Dover) have interesting things to say about conceptual issues, their views for the most part have already been published widely. The volume apparently has not been edited by anyone whose primary language is English. It is not a substantial contribution to the literature on speciation.

There are some points of interest, of course. Mayr introduces the term "peripatric" (not parapatric) speciation to de-

scribe his 1954 model of genetic reorganization in small populations. Stebbins advances reasons for thinking that "sub-microscopic structural differences" in chromosomes are the major mechanism of speciation in plants. Powell draws attention to the possible role of microorganisms in inducing sterility of hybrids between populations of their hosts. Riley cites evidence that simple genetic changes may trigger mispairing of chromosomes that differ in their organization of satellite DNA, and White argues that differences in such repeated sequences are not the basis of hybrid sterility. Carson asserts that chromosome reorganization is incidental in speciation rather than causal, whereas Nevo believes that "chromosomal speciation . . . is generally prevalent in mammals." Carson believes that speciation and indeed anagenetic adaptive change require the stochastic disorganization and subsequent reorganization of a highly integrated gene pool that resists selection; in contrast, Gottlieb affirms the widely held (but challenged) view that reproductive isolation and adaptation can evolve independently and that the one is not prerequisite to the other.

The highly contradictory and often fuzzy thinking that invests speciation theory appears to have several bases. First, there is a common tendency to suppose that any genetic differences found between species have been instrumental in their genesis, even if the differences may have developed merely in concert with, or subsequent to, reproductive isolation, and even if there is no evidence that they contribute to reproductive isolation. For example, chromosomal differences that reduce hybrid fertility by 50 percent or more nevertheless permit extensive gene flow between the populations. If, as is often the case, the populations exchange genes to a far lesser extent, the structural differences are likely merely to have accompanied speciation, rather than to have driven it as White seems to believe. (Incidentally, White misconstrues Futuyma and Mayer's argument (*Syst. Zool.* 29, 254 [1980]) against stasipatric speciation; we did not argue that negatively heterotic chromosome rearrangements are unlikely to be fixed, but only that they cannot spread in a large panmictic population as the stasipatric model supposes.) Similarly, there is no reason to think, as some authors in this volume seem to, that allozyme differences between populations are relevant to the evolution of reproductive isolation. In the same vein, the existence of repeated DNA se-

quences that differ between species but are homogeneous within species might warrant a "molecular drive" hypothesis of the kind Dover advances, but there is as yet no reason to think that these sequences are instrumental in speciation, or that speciation requires a mechanism as novel and speculative as the one Dover offers.

Second, speciation theory is still encrusted by myths that have little basis. Neither theoretical nor empirical population genetics supports the idea that a population founded by few individuals is substantially reduced in heterozygosity. There is little empirical evidence, and, as Templeton remarks, little theoretical reason to expect, that speciation often entails the reinforcement of premating isolating mechanisms, though this idea persists in this volume.

Third, speciation theory is strongly colored by the highly holistic view of the species as an integrated, coadapted gene pool that resists selection. Clearly epistasis and genetic correlations do exist, so this view is not entirely without support. But this concept of species has been counterproductive in certain ways: it has tended to discourage useful reductionist approaches to speciation, and it has led to a proliferation of almost mystical hypotheses for which no mechanistic bases have yet been identified. Thus on the basis of absolutely no evidence we find authors in this volume postulating that speciation is caused by changes in regulatory genes (whatever they may be), by regulatory effects of repeated sequences (which have not been demonstrated), or by chromosome rearrangements that protect gene complexes against recombination; that speciation invariably requires a drastic reduction in population size; that species progressively lose the capacity for further speciation as their gene pools progressively congeal. But virtually all the evidence for genetic homeostasis and coadaptation (reviewed here by Carson) is susceptible to a less holistic interpretation, and, after all, populations do respond readily to selection.

With the exception of Templeton's admirable essay, this book hardly addresses at all the simpler models that can account for speciation. Many species are isolated only by ethological or other premating barriers, which none of the authors treats in detail. Such barriers can arise quite simply, as Templeton stresses, by adaptive divergence or by sexual selection (see for example Lande, *Proc. Natl. Acad. Sci. U.S.A.* 78, 3721 [1981]), and Kirkpatrick, *Evolution* 36, 1 [1982]).

Hybrid sterility is often merely a consequence of mispairing of chromosomes: this aspect of speciation, then, will surely require merely an understanding of the molecular basis of chromosome pairing. Chromosome pairing may or may not be affected by repeated sequences, but it will almost certainly prove susceptible to a reductionist, rather than holistic, interpretation of the genome. And it is certainly possible (see M. Nei, in *Population Genetics and Ecology*, S. Karlin and E. Nevo, Eds., Academic Press, 1976) to develop simple models of genetic divergence that account for inviability or failure of gametogenesis in hybrids. Often, as Templeton notes, only a few segregating units participate in postzygotic incompatibility. Thus, rather than search for the basis of incompatibility in the integration of the whole genome, we need to model, and especially to identify at the biochemical level, critical developmental pathways in which incompatibilities arise in consequence of simple genetic changes. Neither the reductionist models of population genetics nor those of biochemistry figure prominently in this volume, but it is in such models that progress in speciation theory undoubtedly lies.

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## Biological Chemistry

**Stereochemistry.** CH. TAMM, Ed. Elsevier, New York, 1982. x, 342 pp., illus. \$65. New Comprehensive Biochemistry, vol. 3.

This volume is a collection of seven chapters of nearly equal length devoted to aspects of stereochemistry especially relevant to biochemistry and molecular biology. Each chapter has an extensive list of references, generally to work published in the 1970's; some references to papers published in 1980 and 1981 are included. The book contains a large number of carefully prepared and informative figures.

In an introductory chapter B. Testa outlines the basic principles and defines the nomenclature that can be used to describe the geometry of biochemical substrates. In addition to the conventional classification of isomers with contrasting molecular geometries as enantiomeric and diastereomeric stereoisomers, Testa describes the isomeric classification proposed by Mislow that is based

upon the nature of the interactions of all atoms in a molecule, bonded and non-bonded. This analysis emphasizes the correspondence that exists between atoms in diastereomeric stereoisomers and in constitutional isomers. Since isometric comparisons are an important feature in biological stereoselectivity, their introduction in a book directed to biological scientists should be valuable. The chapter also clearly defines such terms as "chiral," "prochiral," "asymmetric," "dissymmetric," "enantiotopic," and "diastereotopic" groups and faces, symmetry planes and rotation-reflection axes, and chiral planes and axes. In addition to the customary stereochemical descriptions of tetrahedral centers, Testa introduces the stereochemical implications of pentacoordinate and hexacoordinate centers. Basic stereochemical nomenclatures (R, S, pro-R, pro-S, and so on) used to describe stereoisomers and stereoheterotopic groups are defined and illustrated.

Testa emphasizes that conformational isomers and configurational isomers are defined by differences in the energy barriers that separate the differing molecular geometries, configurational isomers being separated by "high energy" barriers and conformational isomers by "low energy" barriers. Therefore, in contrast to the sharp intrinsic division between enantiomers and diastereomers, the division between conformational and configurational isomers must allow for overlapping designations. A significant portion of the chapter is devoted to conformational isomerism, in both acyclic and five- and six-membered cyclic systems. Testa analyzes differences in the barriers to rotation about differing bond types (carbon-carbon and heteroatom-heteroatom single bonds and so on) and considers the process of heteroatom inversion upon the interconversion of conformers.

In a second introductory chapter R. Bentley illustrates how the basic concepts and terminology described by Testa can be applied in analyses of biochemical systems. In a description of the historical development of this field, Bentley makes the interesting observation that a "three-point attachment" mechanism to account for the differentiation of enantiomers by drug receptors was proposed by Easson and Stedman in 1933, 15 years before Ogston used a three-point attachment to illustrate how enzymes could differentiate between the enantiotopic *a,a* groups of a  $C_{aabc}$  center. Bentley also emphasizes the important point that actual three-point attachments are not required for differentiation

between enantiomeric molecules or enantiotopic groups. What is required is the possibility of creating diastereomeric relationships. Thus, three-point attachment should be considered part of a convenient diagram, not a stereochemical principle.

Bentley illustrates various chemical and biochemical procedures that have been used in investigations of stereoselectivity. For example, the interconnecting experiments and methodologies used to establish the stereoselectivities of citrate biosynthesis, the stereoselectivities of various dehydrogenases toward the diastereotopic 4'-hydrogens of NADH and NADPH, and the stereoselectivity of malate synthetase with respect to acetyl substrates with chiral methyl groups are all reviewed in detail.

Chapters by H. G. Floss and J. C. Vederas on reactions catalyzed by pyridoxal phosphate, by P. A. Frey on enzyme-catalyzed substitutions at the phosphorus atom of phosphates, and by J. Rétey on reactions involving vitamin B<sub>12</sub> effectively build upon the foundation developed in the introductory chapters. The chapter by Floss and Vederas comprehensively reviews the experiments that have established stereoselectivities for each class of reaction mediated by pyridoxal phosphate. These data are analyzed in terms of the proposals of Dunathan, that the bond to be cleaved will be oriented perpendicular to the plane of the conjugated  $\pi$  system of the pyridoxal moiety and that the binding sites for the pyridoxal phosphate cofactor of all enzymes are derived from one primordial enzyme, thereby creating a common structure and resulting in reactions upon a single face of the bound cofactor. The extensive experimental evidence supporting these proposals and the limited results in apparent conflict with them are both critically evaluated. The chapter by Frey describes the methods that have been used in the stereospecific syntheses and stereochemical analyses of substrates with chiral phosphate groups. Representative studies are then described that establish the stereoselectivities of four different classes of enzymes, phosphohydrolases, phosphotransferases, nucleotidyltransferases, and ATP-dependent synthetases. The results are interpreted in terms of stereochemical evidence for single-displacement or for double-displacement, Ping-Pong, mechanisms. The chapter by Rétey consists of a review of the stereochemical course of coenzyme-B<sub>12</sub>-catalyzed rearrangements and a summary of the stereoselectivities manifest in the biosynthesis of