

quences of such relationships may be special. Though this idea is not new, Bekoff presents it in a manner that not only informs, criticizes, synthesizes, and suggests new research possibilities but also inspires and entertains.

If I must criticize *Parental Care in Mammals*, I would say that I found Karyl Swartz and Leonard Rosenblum's "The social context of parental behavior: a perspective on primate socialization" disappointing in its deliberate deemphasis of data and insights gained from fieldwork, uncritical use of the concept of function, and inaccurate reporting of certain studies. The book might have also benefited from discussions of the role of cognitive factors in parent-offspring relationships and from consideration of the contribution that developmental studies have made to the understanding of social relationships in general. Nevertheless, this is a welcome and long-awaited volume. Though not all the ideas will be new to seasoned researchers, it will be of use to a wide audience of scholars and advanced students.

CAROL M. BERMAN

*Department of Anthropology,
State University of New York,
Buffalo 14261*

Evolutionary Change

Evolution and Speciation. Essays in Honor of M. J. D. White. WILLIAM R. ATCHLEY and DAVID S. WOODRUFF, Eds. Cambridge University Press, New York, 1981. x, 436 pp., illus. \$49.50.

The 20 essays in this collection honoring M. J. D. White range from research papers of relatively narrow focus to broad reviews of major topics in evolutionary biology. They provide an excellent sampler of detailed work on and overviews of speciation and evolution.

The first essay is an informative and entertaining biographical sketch of White by William Atchley. The remaining essays are grouped into three categories: cytology and cytogenetics, hybrid zones, and speciation and evolution. In addition to representing the general areas in which White has made major contributions, many of the essays deal with experimental systems or ideas originally developed by him. For example, several deal in whole or in part with work performed on morabine grasshoppers, and thus can be regarded as extensions of White's pioneering and continuing studies on this group. On the theoretical side, White's model of stasipatric

speciation plays a prominent role in a great many of the essays. Stasipatric speciation occurs when a chromosomal rearrangement that is adaptive or neutral when homozygous but deleterious when heterozygous becomes fixed in a local population, principally through the action of genetic drift and inbreeding, and perhaps meiotic drive. Once fixed in a local population, hybrids between individuals from this population and members of the species outside it suffer from the heterozygote disadvantage, thereby reducing gene flow and potentially producing selection against hybridization. Speciation occurs if such selection against hybridization is effective in reinforcing the reduction in gene flow or if the reduction in gene flow is so great that differentiation can occur at the remainder of the genome. White has argued that the events leading to such chromosomal fixation can occur well within the original species distribution, leading to a "stasipatric" distribution of ancestral and derived species. This model represents a major departure from the once widely accepted Mayrian dogma that speciation is universally due to the erection of geographical barriers and that peripheral populations predominate in the speciation process.

Although the essays are in honor of White, they do not always agree with his interpretations. For example, most of the essays discussing stasipatric speciation present arguments against parts or all of his model. This occurs as early as the first essay following the biographical sketch. In that essay, Bernard John reexamines the taxonomic and cytogenetic data on the Australian grasshopper genus *Vandiemenella*, White's premier example of stasipatric speciation. John points out that the data are not all clear-cut. First, are the chromosomal taxa really species or just races? Second, some of the natural "interracial" (by White's definition of races) hybrids of this group show as much, if not more, reduction in fecundity as some of the "interspecific" (once again, by White's definitions) crosses. Third, it is not clear how much of the hybrid inferiority is due to chromosomal as opposed to genotypic differences. Finally, John argues—in direct contradiction to White—that there is no evidence that pericentric inversions of the X (the chromosomal feature most often used by White to distinguish "species" in this group) reduce heterozygote fertility as required under the stasipatric model. John then goes on to question the cytogenetic data base of some of White's other examples of stasipatric speciation.

Elsewhere in the book, Barton and

Hewitt (to give but one example) present several theoretical difficulties with the stasipatric model, the most important being that a cline involving a single chromosomal change is not a strong barrier to gene flow for the rest of the genome even if heterozygotes are only half as fertile as homozygotes. This makes it unlikely that a chromosomal change could trigger differentiation in the remainder of the genome. This conclusion implies that the stasipatric model must rely principally upon reinforcement of the chromosomal barrier through selection favoring pre-mating barriers. The hypothesis of reinforcement is discussed in several of these essays, but most extensively in "a critical review" by Murray Littlejohn. Although Littlejohn thinks reinforcement is not impossible, he argues that it can occur "only under a rather restricted range of conditions" (p. 328) and points out (as do other contributors) that virtually none of the classic examples of reinforcement have withstood closer scrutiny. Thus, stasipatric speciation through reinforcement of the chromosomal hybrid inferiority is also rather unlikely. White's model, therefore, does not fare well in many of these essays in his honor.

The essay that seems to support White's model of stasipatric speciation most strongly is Guy Bush's "Stasipatric speciation and rapid evolution in animals." However, the major point of this essay is that chromosomal rearrangements "can play an important role in repatterning developmental pathways that lead to striking phenotypic change" (p. 203). Bush argues that chromosomal rearrangements are therefore a frequent route through which major innovative adaptations arise. If this is true, the adaptive associations of the rearrangements would predominate in evolutionary importance over their role as a barrier to gene flow (recall the Barton and Hewitt essay). Given strong adaptive consequences, a chromosomal rearrangement could rapidly go to fixation in a species despite hybrid inferiority, thereby causing karyotypic evolution within the species but not speciation. Moreover, if a chromosomal cline were established, it would most likely be due to a fitness cline in the effects associated with the major developmental modifications induced by the chromosomal rearrangement, rather than to hybrid inferiority caused by meiotic difficulties. Thus, as the extent to which a chromosomal rearrangement alters developmental pathways increases, the importance of meiotic hybrid inferiority in determining the evolutionary fate of the rear-

range decreases. This makes stasipatric speciation even more unlikely. Chromosomal rearrangements would still be important in evolution and speciation, to be sure, but the mechanisms determining their fates would be quite different from the stasipatric model envisioned by White.

Many of the contributors to this volume not only disagree with White but disagree with each other as well upon a great many issues. For example, John also addresses the question of phenotypic effects raised by Bush. He makes a distinction between the "exophenotype" (the traits resulting from the pattern of development and metabolism) and the "endophenotype" (the factors regulating the genetic composition of gametes and zygotes produced by an individual) and argues (p. 30) that "chromosome change is not sensibly related to exophenotypic change" but rather is related to endophenotypic change. This view is in direct opposition to the view portrayed in Bush's essay. Both authors buttress their arguments with much documentation; Bush refers to specific cases in which chromosomal rearrangements alter sex determination or enzyme levels, and John gives examples in which meiotic properties are altered with no exophenotypic change; John points out that in many groups morphological change is not correlated with chromosomal change, but Bush counters that the adaptive significance of the rearrangements is often not morphological but physiological; and so on. The reader can only conclude that sometimes rearrangements do influence the exophenotype and sometimes they do not. The critical question then becomes, which type plays the more important role in evolution and speciation—that is, is the primary evolutionary significance of karyotypic evolution to be found in the endophenotype or in the exophenotype? Perhaps there is no single answer to this question. As is well known, a particular type of chromosomal rearrangement might have very different endophenotypic consequences in different groups: for example, inversions that act merely as crossover suppressors in *Drosophila* can create unbalanced gametes in mammals. Could not the same be true for exophenotypic consequences? In addition, there might be interactions between the type of chromosomal effects and the exact mode of speciation. One of the principal contributions of White's stasipatric model to general evolutionary theory was to reintroduce pluralism into the explanation of speciation. White never regarded stasipatric speciation as a re-

placement for geographical speciation, but rather as an additional mode. Moreover, he emphasized that certain groups, because of their population structure and type of cytogenetic constraints, would be more predisposed toward stasipatric speciation than others. In general, as White himself has argued, there is no reason to suppose that different modes of speciation behave identically with respect to chromosomal evolution. Such a pluralistic view is also called for in resolving the apparent conflict between the views of chromosomal evolution put forth by John and Bush: they do not need to be regarded as alternatives.

The way in which chromosomal change affects evolution is but one of several issues discussed in this volume upon which sharp disagreements are evident. I do not regard this as a weakness of the volume, but rather as its principal strength. I took great delight in (and learned much by) juxtaposing the many well-written and well-documented but diametrically opposing arguments and conclusions that appear among the essays of this volume. The volume is therefore not only informative but stimulating as well, for the essays conjure up more questions than answers. The reader cannot help being made aware of the excitement and flux of ideas that characterize current evolutionary theory and models of speciation—an excitement and flux stirred up in no small part by the writings of Michael White.

ALAN R. TEMPLETON

Department of Biology,
Washington University,
St. Louis, Missouri 63130

Marine Invertebrates

Advances in Marine Biology. Vol. 18, The Biology of Mysids and Euphausiids. JOHN MAUCHLINE. Academic Press, New York, 1980. x, 682 pp., illus. \$93.

Euphausiid biology is currently a topic of considerable interest, and Mauchline's new book is accordingly well timed. The prospect of millions of dollars being spent on the study of the Antarctic krill *Euphausia superba* through such large multinational projects as BIOMASS and FIBEX and the possibility of euphausiids entering our lives as frozen shrimp tails for the rich and shrimp pastes and flour for the poor ensure that this updated book on the biology of euphausiids (and incidentally of mysids) will find a ready market of grateful readers. Mauchline's task was to review the

literature on euphausiids that has appeared since his earlier (1969) treatise, written with L. R. Fisher; that volume dealt exclusively with euphausiids and was published as volume 7 of the *Advances in Marine Biology* series. Literature surveys often tend to be dull, in part because authors attempt the impossible task of making sense of a spotty, often incoherent array of publications. Occasionally Mauchline's interesting style fades when he considers works that should never have been published but nevertheless must be cited in a catholic if not eclectic review. His ire shows in an occasional acknowledgment that "it is difficult to see the usefulness of these experiments, but . . ." If the book suffers any shortcoming, it is this attempt to consider all the literature. Mauchline's knowledge of mysids and euphausiids would seem adequate to allow him to present a synthesis of how these animals live, an approach that would give him an opportunity to point out gaps and directions in research. He has instead chosen the format of a comprehensive review of the literature, and as a consequence his account of the biology lacks the snap of conciseness.

Though Mauchline's first love is euphausiids, he has published several papers on mysids, and he has used the occasion of this book to present a review of the mysid literature as well. The contrast of these two sections is interesting because they represent science for satisfaction and curiosity (mysids may be important in the ecological economy of the sea but are unimportant in the dollar economy of either grantees or food producers) versus big-dollar science (there may be enough *Euphausia superba* in the Antarctic to sustain a fishery—krillery?—that would surpass the 60 to 70 million tons that is the total catch of all the world's fishing fleet). Mauchline writes of mysids for his own satisfaction, and the result is an excellent, welcome compendium that supplants and extends the earlier 1951 work of the Tattersalls.

In this book, as in the earlier Mauchline and Fisher volume, the treatment proceeds from taxonomy and distribution (one new species of euphausiid described since 1969 and one synonymized to keep the total at 85), to larval morphology, to feeding (a topic treated anecdotally or qualitatively simply because quantitative studies of feeding of either mysids or euphausiids are almost nonexistent), vertical migration (still enigmatic), on through to growth and maturity. With regard to this last topic Mauchline departs from his role of reviewer to