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Preface to a Discussion Meeting entitled Evolution of biological diversity: from population differentiation to speciation, held at the Royal Society on 9 and 10 July 1997

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PREFACE

The patterns of diversity in the natural world that inspired Darwin to ponder the 'origin of species' have continued to challenge evolutionary biologists ever since. We now know that biological diversity is the product of population differentiation and speciation, but, what causes populations to differentiate and new species to form? This volume is based on a recent Royal Society Discussion Meeting on the evolution of biological diversity. It proved to be a particularly timely meeting since it brought together evolutionary biologists from a variety of disciplines and with different perspectives on the central theme, and provided an opportunity to discuss recent advances. This volume is by no means a comprehensive treatment of the biology of speciation but it does provide a diversity of data, ideas and views on what is currently a very exciting and vigorous field.

Any consideration of biological diversity must be based on the knowledge of variation within and amongst populations. W. Amos and J. Harwood explore the causes and consequences of genetic variation within species and consider the implications for speciation, while R. K. Butlin and T. Treganza review levels of genetic polymorphism. R. K. Butlin and T. Treganza note that there are large differences in genetic variability within, and genetic distances among, various species, thus demonstrating that species are not equivalent units of genetic diversity. Genetic variation has been documented primarily using allozymes, and while this method is a good predictor of phenotypic divergence and of postmating isolation between populations and species it provides only a weak indication of the extent of premating isolation, probably because of the rapidity of sexual selection.

Given that the relationship between genetic differentiation and the evolution of reproductive isolation is not a straightforward one, what are the factors that promote speciation? Natural selection is clearly important and D. S. Wilson uses his work on pumpkinseed sunfish to illustrate how it can generate differences between individuals within a population. S. A. Foster *et al*. discuss the role of natural selection in driving speciation in the three-spined stickleback, noting that the same correlations between phenotype and fitness may be evident at a range of taxonomic levels. Natural selection can also have indirect effects on the likelihood of speciation, and one of these, arising as a consequence of variation in geographic range size, is considered by K. J. Gaston. Darwin predicted that species with larger geographic range sizes would be more likely to speciate, though recent work suggests that the probability of speciation is in fact greater for species with small to intermediate range sizes. Developmental processes offer further insights into speciation and D. Tautz and K. Schmid consider how the genes that regulate ontogenetic pathways may be involved in the generation of adaptive phenotypes.

The importance of natural selection during speciation is indisputable. Sexual selection has, in contrast, been overlooked until relatively recently. As J. A. Coyne and H. A. Orr observe, it was only at the end of the 1970s that its significance was fully appreciated. T. G. Barraclough and his colleagues use robust, phylogenetically based null models to examine the patterns of diversity among extant animal groups. Their work reveals that sexual selection by female choice in birds accelerates the rate at which reproductive isolation arises, and thereby increases speciation rates and ultimately species richness. Other issues in speciation, such as the role of geography in generating reproductive isolation and the relationship between phenotypic variation and species range, are also amenable to investigation with their approach.

T. Price reinforces the significance of sexual selection by exploring, again in birds, the means by which sexually selected traits become species recognition traits, and the role of sexual selection during adaptive radiation. He notes that sexual selection is likely to play an important part in generating premating isolating mechanisms throughout an adaptive radiation.

Sexual selection usually implies female choice. There are, however, circumstances in which females, as a result of the battle of the sexes in which both partners endeavour to maximize their reproductive fitness, may not be able to exercise this choice. The sexual conflict that results has profound evolutionary consequences in its own right. G. A. Parker and L. Partridge conclude that females may act as a force favouring premating isolation while males can sometimes have the opposite effect. Speciation is expected to occur at a higher rate if females are winning the battle.

This theme is echoed by A. E. Magurran who documents extensive morphological and genetic variation amongst populations of guppies, in Trinidad. Guppies have become a classic example of evolution in action; and marked heritable changes in morphology, behaviour and life history can occur after only a few generations of altered selection. Yet, despite this potential for rapid evolution, and the existence of highly differentiated populations, speciation has not occurred in this group. Sexual conflict may provide the key to understanding this puzzle. The combination of increased male mobility in pursuit of copulations, and sneaky mating attempts which undermine female choice, may be sufficient to raise gene flow to levels that counteract the population differentiation that sexual and natural selection generates.

Coyne and Orr show that the genetics of speciation involve the origin and mechanics of reproductive isolation. Real progress has been made over the last few years, in part by the realization that it is vital to concentrate on tractable questions rather than the intriguing but unanswerable ones that used to exercise evolutionary biologists. Coyne and Orr highlight a number of important challenges for the future. These include the investigation of taxa that have hitherto been neglected, and the evolution of prezygotic, particularly ecological, isolation, which has received less attention than postzygotic isolation.

But what about the generation of higher-order patterns of diversity? S. J. Gould presents the case for species selection and draws on the experiences of Gulliver, who, during his travels, discovered that there was more than one way to perceive the world. Likewise, Gould claims that the hegemony of Darwinism has hindered us from perceiving the importance of selection at higher levels, at least in creating long-term evolutionary trends.

The various papers in the volume illustrate the diverse and innovative approaches that speciation biologists have adopted to study a process that occurs on a time scale largely beyond direct human experience. On average, as J. J. Sepkoski Jr notes, we can expect the formation of three new species in the global biota every year. Few of us, however, can hope to witness the moment when reproductive isolation first occurs. The fossil record has always proved a rich repository of information for evolutionary biologists, and, as Sepkoski demonstrates, it continues to offer new insights into the evolution of biological diversity. For example, he observes that there has been a general decline in rates of speciation in major taxa throughout their histories, although rates tend to remain higher among members in tropical regions. S. Conway Morris also draws on the fossil record to review the evolution of diversity in ancient ecosystems. The interplay of abiotic and biotic factors in generating these patterns of diversity needs further elucidation but, as Conway Morris sadly concludes, it is clear that our own species is working towards the destruction of the richest biota the world has ever seen. Questions concerning the evolution of biological diversity will continue to offer many challenges to future biologists; let us hope that much of the existing biological diversity can be preserved for our scientific descendants to study.

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