1
Introduction: genes, dreams and structural rearrangements

Post-mating effects, especially as observed in hybrid sterility and 'hybrid break-down' are largely incidental to the speciation process. They do not appear to serve to actively reinforce reproductive isolation . . . I feel that a de-emphasis on post-mating isolation in animals may serve as a major step in the unification of speciation theory in plants and animals.

(Carson, 1985, pp. 387–88)

Of all the mechanisms which have gained man's attention, those responsible for producing the enormous biological diversity which surrounds us have been paramount. One needs to look no further than the historical record to see that not only was the cataloguing of plant and animal species and their variation a significant pastime for our predecessors, but the origins of these forms were of the greatest importance.

Some of the most outstanding examples of biological cataloguing are the 20 000-year-old cave paintings of Australia's aboriginal tribes. These paintings depict the diversity of species which were hunted, or encountered during aboriginal man's everyday existence. They also show forms which were purely imaginary and which were manifestations of phenomena which could not be readily explained; among these the lightning man, *namarrgon*, is commonly seen.

One of the features of aboriginal rock art is an intense interest in the internal structure of organisms. While such characteristics were undoubtedly a byproduct of a definite gastronomic bent, there is little doubt that a commonality of form between species was also recognized. Thus, reproductive organs, gastro-intestinal systems, circulatory systems, muscle blocks, tendons and bones can be seen in their X-ray art of vertebrates. In both aboriginal ceremony and myth, many of these structures were antecedents of new biological forms; not a far cry from Adam's rib. Equally, spiritual figures portrayed in ancient rock art, such as the rainbow serpent, were implicated in the creation of new species. Here the interaction between this mystical reptile and the land forms it encountered on its

travels, initiated both the speciation process and spread the populations of man and other organisms. The oral history of these people portrayed in legend and ceremony confirms this creationism in its purest form; from the earth.

Yet, there is little difference between this and the formalized creationism which was introduced into the structured religions, be they Hellenism, Buddhism or Christianity, some 18000 years later. Most of us are familiar with Christian creationist views on the origin of plant and animal species. The myths of the dreamtime exalted in aboriginal rock art and Old Testament views on the origins of life, both share a necessity for the intervention of an outside force to explain what could not be readily understood. While the creationists believe in a six-day miracle, at least the aboriginal dreamtime was temporally sequential, depending on the travels of the rainbow serpent.

The fact that these views are still being intoned and taken up by a growing number of people, tells us that science has failed to get its message across to a large section of the community: those who depend on faith and the literal interpretation of analogies as their guide to survival. Thus, the very strength of evolutionary theory, the vast database encompassing so many fields of biology, has become its greatest weakness. The fragmentation of approach to that common theory has resulted from an array of new techniques, each of which has established itself as an independent entity with its own discordant views on evolutionary processes and an extensive literature to support it. It might be seen as a sad comment that in the two hundred years since Linnaeus first described species as biological entities, there is still no universally accepted definition of what a species is. Nevertheless, this is a natural consequence of the fragmentation of disciplines and the particular requirements which each science has for a species definition. Any army would have considerable difficulty in defending itself when lines of communication are so overextended.

In the years which have elapsed since 1978 when Michael White wrote *Modes of Speciation*, a vast body of data has been published on every aspect of speciation theory. Among the many contributions, the most valuable, in terms of our under-standing of the genetics of speciation, have come from two areas. The first of these involves the study of fertility and viability effects of structural chromosomal rearrangements on interracial and interspecific hybrids. This type of information can provide a direct assessment of the role of chromosome change in speciation. The second area includes the application of biochemical and molecular techniques which have only recently been developed, or applied to problems of plant and animal speciation. Multidisciplinary investigations can provide a most valuable perspective into the evolution of particular species complexes. For example, a lineage of chromosome races or species may be investigated chromosomally with standard preparations, C, G, Ag, or fluorescence banding with numerous fluoro-

chromes using chromosomes derived from lymphocyte cultures. Liver and other tissues may be analysed electrophoretically for 60 presumptive loci, and the mitochondrial DNA (mtDNA) or ribosomal DNA (rDNA) may be sequenced or mapped with restriction endonucleases. Similarly, immunogenetic techniques such as the microcomplement fixation of serum albumin, which requires just a few drops of blood, can ascertain the relationships between these forms and establish the time of their evolutionary divergence. With any luck at all, studies on the comparative morphology of members of this complex can then be made. A suite of techniques providing alternative or corroborative phylogenies for the evolution of a species complex can give a direct assessment on both the degree and timing of genetic divergence and an array of perspectives on the evolution of that complex. Moreover, since all of these techniques can be applied to samples obtained from the same specimens, the impact of the findings is maximized. Comprehensive data are indispensable, and when independent data sets are corroborative in their findings, the conclusions which may be reached are often indisputable.

Despite the substantial body of new and exciting cytogenetic, biochemical and molecular data, and the accrued information of a hundred years of plant and animal cytogenetic research, *Modes of Speciation* was the last published volume which provided an insight into chromosomal speciation theory. Numerous recently published books or conference proceedings, have either downgraded the significance of chromosomal speciation, or simply ignored it in favour of speciation by genetic differentiation (see the introductory quotation to this chapter). Indeed, the volumes presented by this essentially North American coterie of like-minded geneticists would lead the reader to think that much of the data presented in this book did not exist. Consequently, I have attempted to correct this imbalance by providing a broad and integrated view on the concept of chromosomal speciation and the overwhelming amount of evidence which now supports it.

One of the recent developments associated with increased emphasis on genetic and molecular research into speciation, has been an amplified attack on the biological species concept (BSC). This concept remains as the most used species definition despite having been under relatively constant criticism since its introduction. The more recent arguments used against the BSC originated from two core areas. First, the application of biochemical and molecular techniques has revealed the existence of numerous genetically distinct populations within species. Many systematists with a cladistic interest feel that distinct populations of this type should be recognized as species. Consequently, there is a push from this direction to recognize evolutionary and phylogenetic species concepts. The second area of attack on the BSC was made by those who view species as having evolved by purely allopatric means, involving the gradual accumulation of genetic

differences. These authors have argued against the concept of chromosomally induced speciation and the likelihood that such changes can form reproductive isolating mechanisms. They also consider such mechanisms to be incidental to the speciation process. Since this is the very basis of the BSC and some evolutionary species concepts, this can be viewed as a significant area of conflict. In the second chapter of this book, species concepts are considered and the question of the most appropriate species concept is addressed.

In the third chapter, particular aspects of the process of allopatric speciation in isolated populations are examined. The key question as to how reproductive isolation can be attained by genic differentiation is approached from three perspectives. First, a basis for comparison is made by defining our understanding of what reproductive isolation is and by describing the nature of genic variation within and between speciating lineages. The second approach has used the large number of hybridization and genetical analyses in *Drosophila* to establish a relationship between genic and reproductive isolation. The third perspective briefly examines the possibility of speciation with major genetic divergence and an apparent absence of reproductive isolation. This is contrasted with rapidly attained reproductive isolation in some flowering plants.

A contrasting form of allopatric speciation involving the revolutionary conditions associated with founder populations is considered in the fourth chapter. Not only do these conditions provide for rapid genetic differentiation, but they also introduce the likelihood of the fixation of chromosomal rearrangements which can act as reproductive isolating mechanisms. The concept of the founder population is most important to the possibility of chromosomal speciation. It is not surprising that the founder effect is itself a matter of debate. The different models of founder effect and related concepts are discussed and the predictions, in terms of population structure and impact on genetic variability, are assessed.

One of the major problems facing evolutionary biologists has been the appreciation of what types of chromosomal rearrangements are associated with speciation. Too many attacks have been made on chromosomal speciation concepts by those who are unaware of a distinction between balanced polymorphisms and negatively heterotic rearrangements. In the fifth chapter of this volume, those chromosomal rearrangements which may be and also those which cannot be involved in the speciation processes are considered. In the second part of this chapter, theoretical studies which have used chromosomal databases encompassing a considerable variety of structural rearrangements, and which have been widely quoted as supporting or refuting chromosomal speciation hypotheses, are also examined.

The sixth chapter is subdivided into two basic areas which explain aspects of the fixation of chromosomal rearrangements in isolated populations. The first of those is to consider factors responsible for the predominance and high incidence

of particular forms of chromosomal rearrangements in chromosomally speciating complexes, such as mutation rate, the direction of change and meiotic drive. The second section considers some of the theoretical models which have been advanced to explain how negatively heterotic rearrangements can reach fixation in isolated populations.

The great body of evidence derived from chromosomally speciating lineages is presented in Chapters 7 and 8. In the former, the fertility and viability effects of structural rearrangements are examined in two situations. The first of these considers spontaneous mutations in domesticated species. The second, and largest, section involves the consideration of natural and laboratory hybrids between members of chromosomally speciating lineages. The impact of chromosomal rearrangements on the fertility and viability of these hybrids is described in considerable detail.

This theme is followed in Chapter 8 where complexes of species which have been examined both chromosomally and genetically by either protein electrophoresis or some form of molecular analysis are compared. A simple framework for comparison has been constructed, where lineages of species are categorized as ancient or recent. The simplest of questions is asked. In these speciating complexes, does the evidence suggest whether the chromosome race has been formed before or after genetic differentiation? That is, an attempt is made to determine the primacy of chromosomal divergence in an allopatric population, and thus establish chromosomal speciation.

Chapter 9 examines the major models which have been advocated for chromosomal speciation and discusses their relative advantages and disadvantages. These are divided into three categories, based purely on the proposed area of origin. That is, whether the speciation event occurred within or outside of the parental species distribution, or within the hybrid zone. Twelve different models for internal and external chromosomal speciation are critically examined. Similarly, three different modes of speciation in hybrid zones are considered.

The development of molecular techniques and their application to speciation research has greatly changed our understanding of that process and previously unheard of evolutionary mechanisms have been described. Chapter 10 discusses the major areas of molecular research with a view to explaining existing cladogenic processes. Two questions are asked. First, can molecular turnover mechanisms provide processes by which indistinguishable populations can establish postmating isolating mechanisms which are sufficiently powerful to enable speciation to occur? Second, have molecular mechanisms been detected which can enhance the formation and fixation of chromosomal rearrangements, or genetic divergence, thus providing additional support for existing modes of speciation? Answers to these questions were developed through the analysis of the pattern of concerted

evolution and the process of molecular drive. The evolutionary impact of genomic turnover mechanisms is considered.

The eleventh and last chapter provides a résumé of the concepts and conditions necessary for chromosomal speciation and touches briefly on the analysis of hybrid zones, on the role of chromosomal evolution in macroevolution, and the evolutionary significance of chromosomal speciation.

Hopefully, this volume will correct the perceived imbalance in speciation theory which currently exists. Chromosomal speciation remains as one of the two most significant forms of speciation and, as the growing body of evidence now shows, it is one of the most common.

2
The species – what's in a name?

> The unit of evolution is the terminal taxon, the isolated interbreeding population which is an objective reality. All living beings belong to a terminal taxon, but whether or not a given species is a terminal taxon is unpredictable, being dependent on future discovery.
>
> (Løvtrup, 1979, p. 388)

Perhaps the short quotation from Løvtrup (1979) which introduces this chapter best sums up the dilemma faced by biologists and does so in the simplest possible way. This most basic of biological problems, that of defining what a species is, appears to be no more resolvable today than it was two hundred years ago. Indeed, it could be argued that the situation is deteriorating, since with the development of sophisticated biochemical and molecular techniques and their application to biological populations, the nexus between a morphologically recognizable species and that isolated, interbreeding population which is Løvtrup's 'terminal taxon' is being forced further and further apart.

It is no exaggeration to say that the history of science is littered with discarded species concepts. This might well be due to the fact that our perception of what a species is necessarily changes with the additional knowledge which we have gained. While there is little doubt that Agassiz' (1857) view of a species as 'thoughts of the creator which are real' would gain little acceptance today, at least in the scientific community, it might be surprising that Darwin's own view of a species may suffer the same fate. Darwin regarded species as open systems with fluid borders which could only be subjectively delimited. The different species concepts recognized today all involve closed systems with what are at least generally definable borders.

It is not the intention of this chapter to provide an historical view of what a species is. Mayr (1963, 1982a), Dobzhansky (1970), Ghiselin (1974) and Slobodchikoff (1976) can provide the reader with a surfeit of information on this subject. It is more important to understand the species concepts which are either in current use, or which have at least been proferred as usable models. Not all of these will be included here since the aim of this chapter is to provide a working basis for

this volume. Thus, an attempt is made to define the biological species concept and to integrate the ramifications of criticisms made against this model. Equally, the validity of certain possible replacements for the BSC are critically examined, as are alternative approaches such as the evolutionary species concept and derivations of this.

2.1 The Linnaean species, morphology and systematics

It is no idle comment to say that Linnaeus (1707–78) was the father of modern systematics. He introduced the facility of binomial nomenclature, and the view that every organism must belong to the lowest taxonomic entity, the species. Nevertheless, while Linnaeus put forward the basic framework for classification and used it to categorize vast numbers of organisms, he was also a creationist who maintained that biological species were real entities created by God.

> There are as many species as the infinite being created diverse forms in the beginning, which, following the laws of generation, produced as many others but always similar to them: Therefore there are as many species as we have different structures before us today.
>
> (Linnaeus, 1751, in Mayr, 1982a, p. 258).

A consequence of this attitude is the belief that species are well-defined and constant in form. While this is out of tune with both evolutionary theory and observed variation, there is little doubt that if man is to hope to catalogue the organisms present around him, he can only reasonably describe those entities which are perceived as being different. Thus, the vast majority of species which were described during the drive to categorize the world's fauna, which occurred in the nineteenth and early twentieth centuries, relied on the morphological species concept. Indeed, most species described by today's taxonomists are also morphological species described under the rules of the International Commission of Zoological Nomenclature or its botanical equivalent.

The date 1 January 1758, was arbitrarily fixed by the zoological code as the starting point of zoological nomenclature, for this date coincided with the publication of Linnaeus' *Systema Naturae* (10th edition) and Clerck's *Aranei Svecici*. Zoological nomenclature is the system of scientific names applied to taxonomic units of animals known to occur in nature. The code regulates the naming of taxa in the family, genus and species groups. Names regulated by the code are attached to a name-bearing type specimen, and in the case of the species this is the holotype. The code was introduced as a means of regulating nomenclature following the confusion which occurred after the introduction of Linnaeus' binomial

naming system and was simply a means of regulating priority and removing synonymy.

Two of the definitions which have been used to define the morphospecies are 'established by morphological similarity regardless of other considerations' (Cain, 1954), and in a parody Mayr (1963, p. 31) suggested that:

> Natural populations considered by general consent to be species are morphologically distinct. Morphological distinctness is thus the criterion of species rank. Consequently, any natural population that is morphologically distinct must be recognized as a separate species.

With open-ended definitions of this form the morphological species concept posed a suite of typological problems. In some cases, polymorphic variants within a species have been defined as species; in others different sexes of a species have themselves been defined as species; and further, morphologically different populations have been regarded as species.

Mayr (1963) attacked the use of morphospecies because the concept ignores the primary role of reproductive isolation and concentrates on the secondary role of morphological differences. He argued that the vulnerability of the purely morphological species concept in sexually reproducing species can be shown by:

1 The presence of conspicuous morphological differences among conspecific individuals and populations (intraspecific variation). That is, where there are often greater differences between individuals, or populations, than between related species.
2 The virtual absence of morphological differences among some sympatric populations (sibling species), that otherwise have all the characteristics of good species, being reproductively isolated from each other.

Nevertheless, despite these anomalies the morphological species remains as the baseline for the taxonomic description of our flora and fauna. They must remain so for they are tangible, recognizable units which can be diagnosed by their innate form. However, most modern biologists also place the species they deal with in the context of their biological distinctiveness. Thus, while such biological species may not be described as taxonomic entities, they are sometimes described as biological entities.

2.2 Biological species concepts

2.2.1 The biological species concept (BSC) (Mayr, 1942, 1963)

Any definition of a species must cope with the fact that speciation is an ongoing process and, as such, the analysis of existing species at any instance of time must reveal a continuum of variation, ranging from species with profound morphological differences between them, through every stage of differentiation, to those populations which are beginning to diverge and are showing the earliest stages of doing so. Traditional systematists who only recognize morphological species because of the self-imposed limitations of the Linnaean binomial system, would regard all of these entities, including cryptic and sibling species, as intraspecific variation. Such an approach ignores the biological reality of much of the variation we encounter.

The emergence of the biological species can be traced back to the early nineteenth century and this has been done most eloquently by Dobzhansky (1970) and Mayr (1982a). The key decision which created the BSC was the recognition by Dobzhansky (1937) that the process responsible for species formation was the development of reproductive isolating mechanisms. A host of definitions have been produced based on this most fundamental character:

> Species are groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups
>
> (Mayr, 1942, p. 120).
> ['actually or potentially' was deleted from Mayr's 1969 definition].

and

> That stage of the evolutionary process at which the once, actually or potentially interbreeding array of forms becomes segregated in two or more separate arrays which are physiologically incapable of interbreeding
>
> (Dobzhansky, 1937, p. 312).

and

> Species are ... systems of populations; the gene exchange between these systems is limited or prevented in nature by a reproductive isolating mechanism or perhaps by a combination of several such mechanisms
>
> (Dobzhansky, 1970, p. 357).

and

> The sum total of the races that interbreed frequently or occasionally with one another, and that intergrade more or less continuously in their phenotypic characters, is the species
>
> (Grant, 1963).