

Contents

Preface	xv
Copyright acknowledgements	xix
1 Introduction: genes, dreams and structural rearrangements	1
2 The species – what’s in a name?	7
2.1 The Linnaean species, morphology and systematics	8
2.2 Biological species concepts	10
2.2.1 The biological species concept (BSC) (Mayr, 1942, 1963)	10
2.2.2 The biological species concept mark II (Mayr, 1982a)	13
2.2.3 The recognition species concept (Paterson, 1978, 1985)	14
2.2.4 The cohesion species concept (Templeton, 1989)	16
2.3 Evolutionary species concepts	19
2.3.1 Simpson’s (1961) evolutionary species concept	19
2.3.2 Wiley’s (1978) evolutionary species concept	21
2.3.3 The ecological species concept (Van Valen, 1976)	23
2.3.4 The phylogenetic species concept (Cracraft, 1983)	25
2.4 Concluding remarks	27
3 Genic differentiation, reproductive isolation and speciation in allopatric populations	31
3.1 Reproductive isolation: dichotomous views	31
3.2 Genic variation	34
3.3 Differentiation of central and peripheral populations: inversion polymorphism and genic effects	37
3.4 Stages of genic differentiation during allopatric speciation	40
3.4.1 Lewontin’s approach (1974)	40
3.4.2 Ayala’s view (1974, 1975)	42
3.4.3 The dichotomy	43

3.4.4	Species hybrids, genic differentiation and reproductive isolation	45
3.4.5	Another view	48
3.4.6	Rapid reproductive isolation in some flowering plants	49
3.5	Concluding remarks	51
4	Genetic revolution or gradual reform? Expectations of the founder effect	54
4.1	The shifting balance theory (Wright, 1932, 1982a, b)	54
4.2	The founder effect (Mayr, 1954, 1982b)	57
4.3	The flush–crash–founder cycle (Carson, 1975, 1982a)	60
4.4	The founder–flush model (Carson, 1968; Carson and Templeton 1984)	61
4.5	The organizational theory of speciation (Carson, 1982a, 1985)	62
4.6	Genetic transilience (Templeton, 1980, 1982)	63
4.7	The dilemma: is it shifting its balance or foundering?	65
4.8	Genetic variability and the founder effect	68
5	Chromosomal rearrangements as post-mating isolating mechanisms	72
5.1	Types of structural rearrangements implicated in reproductive isolation	73
5.1.1	Potentially negatively heterotic changes	73
5.1.1.1	<i>Tandem fusions</i>	74
5.1.1.2	<i>Robertsonian fusions and reciprocal translocations</i>	75
5.1.1.3	<i>X-chromosome effects – a special case?</i>	79
5.1.1.4	<i>Inversions</i>	80
5.1.2	Neutral or adaptive changes	84
5.1.2.1	<i>Heterochromatin addition</i>	84
5.1.2.2	<i>Chromosomal polymorphism</i>	86
5.2	Chromosome change and speciation: the theoretical approach	87
5.3	Concluding remarks	90

CONTENTS

xi

6	The fixation of chromosomal rearrangements in isolated populations	92
6.1	Chromosomal mutation rate	93
6.2	Random or non-random chromosomal rearrangements	95
6.3	Simultaneous multiple chromosome rearrangements	102
6.4	Meiotic drive	104
6.4.1	Sex chromosome drive	105
6.4.2	Supernumerary chromosome drive	108
6.4.3	Meiotic drive for autosomal rearrangements: examples from animals and plants	109
6.4.3.1	<i>Segregation distortion in Drosophila melanogaster</i>	109
6.4.3.2	<i>Grasshoppers</i>	110
6.4.3.3	<i>The sheep blowfly (Lucilia cuprina)</i>	111
6.4.3.4	<i>The common shrew (Sorex araneus)</i>	111
6.4.3.5	<i>Blue foxes (Alopex lagopus)</i>	112
6.4.3.6	<i>Mus domesticus</i>	112
6.4.3.7	<i>t-haplotype in Mus</i>	113
6.4.3.8	<i>Flowering plants</i>	114
6.5	Theoretical perspectives on fixing deleterious structural rearrangements in founding populations	117
6.6	Concluding remarks	122
7	The impact of structural hybridity on fertility and viability	126
7.1	Fertility effects induced by chromosome changes	126
7.2	Spontaneous mutations	128
7.2.1	Pigs (<i>Sus scrofa</i>)	129
7.2.2	Cattle (<i>Bos taurus</i>)	130
7.2.3	Sheep (<i>Ovis</i> species)	132
7.2.4	Domestic fowl (<i>Gallus domesticus</i>)	133
7.2.5	The importance of investigation into spontaneous mutations	133
7.3	Hybridization studies: simple and complex systems	135
7.3.1	Fertility effects of fusion heterozygosity in <i>Mus domesticus</i>	135
7.3.1.1	<i>Single Robertsonian fusions</i>	139
7.3.1.2	<i>Multiple independent Robertsonian fusions</i>	141
7.3.1.3	<i>Multiple Robertsonian fusions with monobrachial homologies</i>	142
7.3.1.4	<i>Reciprocal translocation in Mus</i>	144
7.3.1.5	<i>Genic variation in Mus</i>	146
7.3.2	<i>Rattus sordidus</i> complex	148

7.3.3	Muntjac deer	149
7.3.4	Horses (<i>Equus</i> species)	151
7.3.5	Interspecific hybridization in the Bovidae	153
7.3.5.1	<i>Dik-diks</i>	153
7.3.5.2	<i>Bos hybrids</i>	154
7.3.6	Lemurs	156
7.3.7	Rock wallabies	159
7.3.8	<i>Caledia captiva</i>	161
7.4	An overview	164
7.4.1	Chromosomally induced hybrid infertility	164
7.4.2	Genic effects on fertility: more apparent than real?	168
8	Genic change and chromosomal speciation	171
8.1	Chromosomal and genetic differentiation: the relationship	171
8.2	Genic changes in speciating complexes distinguished by fusions, fissions and rearrangements sharing brachial homologies	174
8.2.1	Class 3. The <i>Rhogeessa tumida-parvula</i> complex	175
8.2.2	Class 3. The <i>Proechimys guairae</i> species group	176
8.2.3	The genus <i>Rattus</i>	176
8.2.3.1	Class 3. The <i>Rattus rattus</i> complex	177
8.2.4	Class 3. The <i>Gerbillus pyramidum</i> complex	179
8.2.5	Class 4. The <i>Spalax ehrenbergi</i> complex	180
8.2.6	Class 3. The <i>Acomys cahirinus</i> complex	183
8.2.7	Class 3. The <i>Gehyra variegata-punctata</i> complex	185
8.2.8	Class 3. The <i>Sceloporus grammicus</i> complex	187
8.2.9	Class 3. The <i>Phyllodactylus marmoratus</i> complex	189
8.3	Genic changes in speciating complexes characterized by both neutral chromosomal changes and also by negatively heterotic rearrangements	191
8.3.1	The genus <i>Thomomys</i>	191
8.3.2	The <i>Peromyscus maniculatus</i> complex	194
8.3.3	The <i>Sorex araneus</i> complex	198
8.4	Concluding remarks	200
8.4.1	Genic expectations in chromosomally speciating populations	200
8.4.2	The primacy of chromosome change in speciation	202

CONTENTS

xiii

9 Chromosomal speciation	208
9.1 Internal modes of chromosomal speciation	210
9.1.1 The triad hypothesis (Wallace, 1953)	211
9.1.2 Stasipatric speciation (White <i>et al.</i> , 1967; White, 1968, 1978a, b)	213
9.1.3 Chain processes in speciation (White, 1978b)	216
9.2 External models for chromosomal speciation	220
9.2.1 Saltational speciation (Lewis, 1966)	222
9.2.2 Quantum speciation (Grant, 1971)	224
9.2.3 Parapatric speciation and model 1B: speciation by the founder effect (Bush, 1975)	226
9.2.3.1 <i>Speciation by the founder effect: type 1B</i>	226
9.2.3.2 <i>Parapatric speciation</i>	227
9.2.4 Alloparapatric speciation (Key, 1968, 1974, 1981)	229
9.2.5 Chromosomal transience (Templeton, 1981)	231
9.2.6 Primary chromosomal allopatry (King, 1981, 1984)	232
9.2.7 Speciation by multiple centric fusions which share monobrachial homologies	234
9.2.8 A dual-level model for speciation by pericentric inversion (King, 1991)	238
9.3 Speciation by hybridization	240
9.3.1 Hybrid recombination (Templeton, 1981)	240
9.3.2 Polyploidy, parthenogenesis and hybridogenesis	241
9.4 Concluding remarks	243
10 Molecular mechanisms and modes of speciation	245
10.1 Concerted evolution: the pattern	246
10.1.1 Molecular drive: the process	249
10.1.1.1 <i>Unequal chromatid exchange</i>	250
10.1.1.2 <i>Gene conversion</i>	251
10.1.1.3 <i>Transposition</i>	251
10.1.1.4 <i>Replication slippage</i>	252
10.1.1.5 <i>RNA-mediated transfer of genetic information</i>	252
10.1.2 Molecular drive as a mode of speciation	254
10.2 Genomic transposition	255
10.2.1 Selfish DNA	255
10.2.2 Hybrid dysgenesis	256
10.2.3 Do transposable elements induce speciation?	258

10.2.4	The induction of chromosomal rearrangements by transposable elements	260
10.3	Does repetitive DNA have a regulatory function?	264
10.4	Concluding remarks	265
10.4.1	Can molecular turnover mechanisms provide a means of establishing post-mating isolating mechanisms in undifferentiated populations powerful enough to enable speciation?	265
10.4.2	Can molecular mechanisms enhance the formation and fixation of chromosomal rearrangements or genetic divergence and thus support existing mechanisms for speciation?	267
11	Conclusions and perspectives	269
11.1	An overview	269
11.2	A jaundiced view	276
11.2.1	Chromosomal hybrid zones and gene flow	276
11.2.2	Are present-day geographic distributions a valid tool for determining past evolutionary events?	277
11.2.3	Chromosomal or genetic reproductive isolation?	279
11.2.4	The relationship between chromosomal change and morphological change	280
11.3	Hybrid zones	280
11.4	Punctuated equilibrium: a speciationist's view of evolution	285
11.5	End view	289
	References	291
	Name index	319
	Subject index	322