Chapter 1

Heterostylous Genetic Polymorphisms: Model Systems for Evolutionary Analysis

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1 Introduction

Heterostyly is a genetic polymorphism in which plant populations are composed of two (distyly) or three (tristyly) morphs that differ reciprocally in the heights of stigmas and anthers in flowers (Fig. 1). The style-stamen polymorphism is usually accompanied by a sporophytically controlled, diallelic self-incompatibility system that prevents self- and intramorph fertilizations, and a suite of ancillary morphological polymorphisms, particularly of the stigmas and pollen of floral morphs. Heterostyly is reported from approximately 25 angiosperm families and has usually been viewed as a floral device that promotes outcrossing, hence reducing the harmful effects of close inbreeding in plant populations.

Since the pioneering work of Darwin and Hildebrand in the last century (see Chap. 2), evolutionary biologists have been intrigued by the complex sexual arrangements of reproductive organs in heterostylous plants. "In their manner of fertilisation" Darwin wrote of *Lythrum* species (Darwin 1865), "these plants offer a more remarkable case than can be found in any other plant or animal." How heterostyly originated, what selective forces maintain the polymorphism, and why it often becomes evolutionarily modified into other breeding systems are questions often posed by workers investigating heterostylous groups. The attention heterostyly has received during this century, considering its infrequent occurrence, resides in several outstanding features that has made it a model system for addressing a variety of questions in evolutionary biology.

First, heterostyly is a simply inherited polymorphism in which the floral morphs are easily identified under field conditions. Population studies using ecological genetic approaches (Ford 1964) therefore offer attractive opportunities for investigations of the natural selection, maintenance, and breakdown of heterostyly (Crosby 1949; Bodmer 1960; Weller 1976a; Barrett 1985a). Second, experimental field studies of the pollination biology of heterostylous plants have enabled analysis of the function and adaptive significance of the polymorphism (Ganders 1979; Barrett 1990). Studies of this type are facilitated by the limited number of mating groups in heterostylous populations and the conspicuous size differences of pollen produced by the floral morphs. These features enable measurements of a variety of reproductive processes associated with pollen transport that are more difficult to investigate in monomorphic species (Barrett and Wolfe 1986). Finally, because of the more

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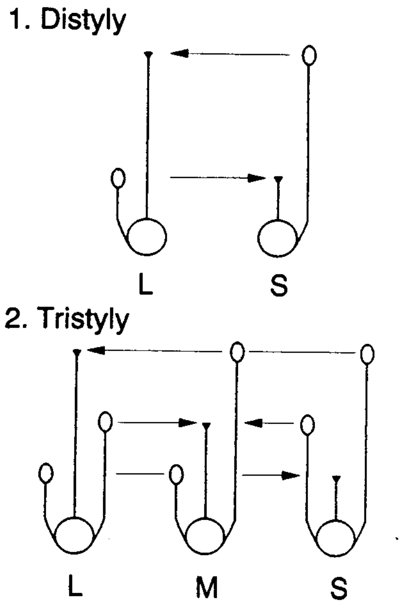

Fig. 1. The heterostylous genetic polymorphisms distyly and tristyly. Legitimate (compatible) pollinations are indicated by the *arrows*, other pollen-pistil combinations are termed illegitimate and usually result in reduced or no seed set. L, M, and S refer to the long-, mid- and short-styled morphs, respectively. Distyly is controlled by a single locus with two alleles. The L morph is usually of genotype *ss* and the S morph *Ss*. In tristyly, the most common mode of inheritance involves two diallelic loci (*S* and *M*), with *S* epistatic to *M*. See Chapter 5 for further details of the inheritance of heterostyly

obvious links between genes, development, morphology, and fitness, in comparison with most other reproductive adaptations, the polymorphism provides opportunities for integrated studies in genetics, development, and population biology. Thus, heterostylous plants provide a rich source of material for evolutionary biologists and represent one of the classic research paradigms for neo-Darwinian approaches to the study of evolution and adaptation.

In this chapter the main themes covered in the book are briefly introduced in the order in which they appear. I begin by examining the nature of heterostyly, its morphological and developmental characteristics, and how it is inherited. This is followed by a consideration of models for the evolution and selection of heterostyly and discussion of the functional basis and reproductive consequences of the floral polymorphisms. The evolutionary breakdown of heterostyly is then reviewed and the chapter concludes by outlining research avenues likely to prove profitable in the future. Throughout, an attempt is made to highlight contrasting viewpoints, cover literature not dealt with in other chapters, and raise unanswered questions to assist forthcoming work on heterostyly.

2 Nature and Occurrence

Research workers differ in opinion regarding the types of variation considered essential for defining a given species as heterostylous. For Darwin and most subsequent workers, particularly those with a genetical perspective, the term heterostyly has usually been reserved for plants with both a reciprocal arrangement of stigma and anther heights (hereafter reciprocal herkogamy) and a diallelic incompatibility system (as illustrated in Fig. 1). Following this view, the litmus test for proof of the occurrence of "true" heterostyly has been the demonstration, by controlled pollinations, of the presence of an intramorph incompatibility system in a species with reciprocal herkogamy. Early on, however, Hildebrand (1866) used the term heterostyly in a strictly morphological sense, and because of recent discoveries, discussed below, there seem to be good grounds for using this approach.

Although the majority of heterostylous plants possess reciprocal herkogamy, diallelic incompatibility, and various ancillary floral polymorphisms, research over the last few decades (reviewed in Barrett and Richards 1990) has revealed a significant number of cases where plants with style length polymorphisms exhibit various combinations of heterostylous and "non-heterostylous characters". The latter include strong self-compatibility, multiallelic incompatibility, monomorphic stamen heights, and an absence of ancillary polymorphisms (Table 1). In some cases taxa with unusual character combinations are related to heterostylous taxa (e.g., *Linum grandiflorum*); in other cases (e.g., *Epacris impressa*) they are not. Because of the spectrum of variation associated with plants displaying style length polymorphisms, it would seem to make more sense to reserve the term heterostyly for species that are polymorphic for a reciprocal arrangement of stigma and anther heights at the population level. At the same time, however, it should be recognized that reciprocal herkogamy can vary greatly in expression (J.H. Richards, D.G. Lloyd, and S.C.H. Barrett, unpubl. data), be associated with various compatibility and incompatibility systems, and need not be accompanied by a suite of ancillary floral polymorphisms.

The number of families containing heterostylous species has grown with increased botanical exploration, particularly of tropical regions. On the other hand, many species originally reported as heterostylous have on closer examination proven to be otherwise (e.g., *Mirabilis, Phlox, Veronica* see Barrett and Richards 1990). Taxonomists working with herbarium specimens have often confused interpopulation discontinuities in floral organ size or developmental variability with heterostyly. Figure 2 illustrates the taxonomic distribution of heterostyly among Dahlgren's superorders of angiosperms (Dahlgren 1980). In Chapter 6, Lloyd and Webb estimate that the polymorphisms are likely to have evolved on at least 23 separate occasions and possibly more if heterostyly has arisen more than once in a family (e.g., Rubiaceae, Anderson 1973).

Two additional families (Ericaceae and Polemoniaceae) may also belong on the list of families containing heterostylous taxa. Recently, R.J. Marquis (unpubl. data) has documented style and stamen length variation in populations of the long-lived shrub *Kalmiopsis leachiana* (Ericaceae) from S. Oregon. Some populations apparently contain two floral morphs differing in style length and stamen height, while others are composed of a single floral morph. Within dimorphic populations style

Table 1. Character combinations in plants with style length polymorphisms

Taxon	Stamen position	Incompatibility	Ancillary polymorphisms	Reference
1. Stylar dimorphism				
Primula vulgaris	Dimorphic	DSI	+++	Darwin (1877)
Linum grandiflorum	Monomorphic*	DSI	++	Darwin (1877)
Villarsia parnassiifolia	Monomorphic	DSI + MSI?	++	Ornduff (1986)
Amsinckia grandiflora	Dimorphic	SC	++	Ornduff (1976)
Quinchamalium chilense	Monomorphic	SC	++	Riveros et al. (1987)
Anchusa officinalis	Monomorphic	MSI	+	Philipp and Schou (1981)
Epacris impressa	Monomorphic	MSI	–	O'Brien and Calder (1989)
Chlorogalum angustifolium	Monomorphic	SC	–	Jernstedt (1982)
2. Stylar trimorphism				
Lythrum salicaria	Trimorphic	DSI	+++	Darwin (1865)
Eichhornia paniculata	Trimorphic	SC	++	Barrett (1985b)
Narcissus triandrus	Trimorphic	MSI	–	S.C.H. Barrett D.G. Lloyd and J. Arroyo (unpubl.data)

DSI = diallelic self-incompatibility, MSI - multiallelic self-incompatibility, SC = self-compatible. Ancillary polymorphisms: +++ well developed, ++ moderately developed, + weakly developed, – absent. *But see chapter 3, Table 1 and Chapter 6, page 166.

length variation is more pronounced than anther height variation and pollen from the two floral morphs is uniform in size. Flowers of *K. leachiana* are atypical for a heterostylous species in being bowl-shaped, although this condition does occur in distylous *Fagopyrum* and *Turnera* (see Chap. 6).

The second putative case of a new heterostylous family involves *Gilia nyensis* (Polemoniaceae). In a floristic treatment of the Polemoniaceae for various western states of the USA, Cronquist reported heterostylous populations of this species from Nye County, Nevada (Cronquist et al. 1984). Recently, D. Wilken (pers. commun.) has investigated these populations and found that they contain long- and short-styled morphs in approximately equal proportions. Studies of the pollen and stigmas of the two morphs failed to reveal any significant dimorphisms.

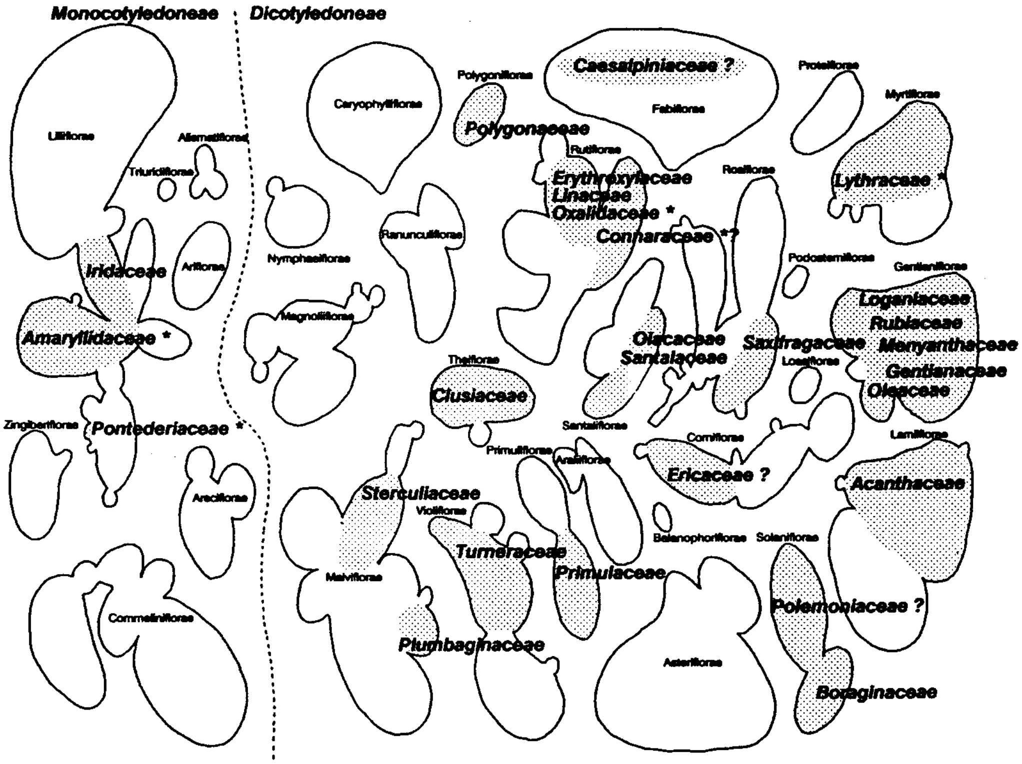

Fig. 2. Taxonomic distribution of heterostyly among the superorders of angiosperms according to Dahlgren's classification of the angiosperms (Dahlgren 1980). Families are positioned within superorders according to Dahlgren's placement of orders and families. Families with tristylous species are indicated by an *asterisk*, those in which the presence of heterostyly needs confirmation are indicated by a *question mark*

3 Structure and Development

The defining features of heterostyly involve morphological polymorphisms. Yet in comparison with the wealth of genetic and ecological work on heterostyly there is a paucity of detailed structural and developmental data for most heterostylous groups. Information on the reciprocal arrangement of stamens and styles and the array of ancillary polymorphisms in heterostylous taxa is comprehensively reviewed by Dulberger in Chapter 3. She points out that population biologists have devoted considerable attention to investigating the adaptive significance of reciprocal herkogamy, with less effort devoted to determining the function of structural differences between pollen grains and stigmas of the floral morphs. Considerable scope would appear to exist for manipulative experiments that investigate the role of stigma and pollen polymorphisms in affecting the capture, hydration, and germination of compatible and incompatible pollen in different heterostylous groups. Dulberger develops earlier views (Mather and de Winton 1941; Dulberger 1975a,b) that the polymorphic properties of pistils and pollen most likely participate directly in the incompatibility mechanism of heterostylous plants, with style length differences involved in the synthesis of incompatibility specifities. While not denying some role for morphological polymorphisms in promoting cross-pollination, she emphasizes their primary function as mechanisms to prevent inbreeding through incompatibility. This unified view of heterostyly is based on the assumption that there is functional integration of morphological, developmental, and biochemical components of the entire syndrome.

A somewhat different perspective on the morphological components of heterostyly is presented by Lloyd and Webb in Chapters 6 and 7, which deal with the evolution and selection of heterostyly, respectively. They follow Yeo (1975) and Ganders (1979) in rejecting a single primary function for the different components of the heterostylous syndrome and instead consider that the function of the various morphological polymorphisms should be considered separately. Lloyd and Webb view the morphological components of heterostyly principally as adaptations that influence different aspects of the pollination process, rather than as a mechanism to avoid inbreeding. Some traits (e.g., reciprocal herkogamy) actively promote cross-pollination, while other polymorphisms (e.g., of pollen and stigmas) function to reduce levels of self-pollination and self-interference.

Attempts to determine the relationships between the structure and function of different polymorphic traits would be aided by developmental studies of heterostylous plants. Despite some early investigations on this topic (Stirling 1932, 1933, 1936; Schaeppi 1935; Bräm 1943) there has been little modern work, using SEM techniques, that has attempted to define the developmental processes responsible for structural differences between the floral morphs, particularly in distylous plants. In Chapter 4, Richards and Barrett review the existing information, primarily from tristylous families, and outline a variety of growth models to account for differences in style and stamen length in heterostylous plants. They suggest that comparative developmental studies of heterostylous groups with inter- and intra-specific floral variation would be valuable to determine whether recurrent associations among heterostylous characters (e.g., long styles, large stigmas, and long stigmatic papillae) are manifestations of common developmental processes. This type of study would be particularly interesting in taxa (e.g., *Palicourea, Amsinckia, Fauria*) where the normal associations are either lacking or reversed in certain species or populations. Anomalies of this type are reviewed by Dulberger in Chapter 3.

Comparative developmental approaches in heterostylous groups displaying variation in breeding systems (e.g., tristyly and distyly in *Lythrum* and *Oxalis*, distyly and dioecy in *Cordia* and *Nymphoides*, and heterostyly and homostyly in most groups) would help to determine the kinds of developmental modifications that underlie shifts in mating patterns. Since changes of this type are frequently associated with the evolution of reproductive isolation (Barrett 1989a), developmental data may shed light on controversies surrounding the morphological and genetic basis of speciation in plants (Gottlieb 1984; Coyne and Lande 1985).

4 Genetics and Molecular Biology

Early experimental studies on heterostyly were largely genetical in nature and concerned with determining the inheritance of the polymorphism. Many leading geneticists (e.g., W. Bateson, R.A. Fisher, J.B.S. Haldane, A. Ernst, A.B. Stout, K. Mather), working in the early to mid-periods of this century, were attracted to working on distyly and tristyly as a model system for studies on inheritance, linkage, recombination, epistasis, supergenes, and polymorphic equilibria. These investigations made a significant contribution to the overall growth of Mendelian and population genetics, and because of this work, heterostyly is frequently presented in textbooks on genetics and evolution as one of the classic examples of a balanced genetic polymorphism involving supergenes.

The inheritance of heterostyly has now been determined for 13 genera in 11 families; this work is reviewed by Lewis and Jones in Chapter 5. The most striking feature of the data on inheritance is the uniformity of one diallelic locus *S, s* in distyly and two loci *S, s* and *M, m* in tristyly, and the dominance of the short-styled morph in both systems. Interestingly, models of the evolution of heterostyly by Lloyd and Webb in Chapter 7 provide an explanation for this common pattern of inheritance of the long- and short-styled morphs in most heterostylous plants. Only three exceptions to the dominance of the short-styled morph have been reported. These occur in *Limonium, Hypericum* and *Oxalis* (see Chap. 5).

Recently, Bennett et al. (1986) have proposed a three-locus model for the control of style length in tristylous *Oxalis rosea* (and see Leach 1983). In this species some short-styled plants are dominant to non-short-styled plants (mid- or long-styled plants) while others are recessive. Breeding experiments demonstrated that the short-styled morph is governed by two gene pairs (*A, a* and *S, s*). In plants segregating for *A, a* on an *SS* background, short styles are recessive, while in plants segregating for *S, s* on an *aa* background, short styles are dominant. Genotypes for the three style morphs under the three-locus model are given in Table 2. The model raises the possibility that in other species of *Oxalis*, with the conventional two diallelic locus control of tristyly [e.g., *O. valdiviensis*, Fisher and Martin (1948) and members of the section *Ionoxalis*, Weller (1976b)] a third locus is present but fixed in the homozygous recessive condition (*aa*). Whether a third locus occurs in other tristylous families is

Table 2. Genotypes for the long-, mid-, and short-styled morphs of *Oxalis rosea* according to the three-locus model of Bennett et al. (1986)

Long-styled morph	Mid-styled morph		Short-styled morph
AASSmm	*AASSMM*	*AaSSMm*	*aaSSMM*
AASsmm	*AASSMm*	*AsSsMM*	*aaSSMm*
AAssmm	*AASsMM*	*AaSsMm*	*aaSSmm*
AaSSmm	*AASsMm*	*AassMM*	*aaSsMM*
AaSsmm	*AAssMM*	*AassMm*	*aaSsMm*
Aassmm	*AAssMm*	*aassMM*	*aaSsmm*
aassmm	*AaSSMM*	*aassMm*	

not known, but the data for *O. rosea* are of some interest in view of D. Charlesworth's suggestion that a third gene may have been involved in the evolution of tristyly (Charlesworth 1979).

Despite progress on the inheritance of style length there are still major gaps in our understanding of the genetical architecture of heterostyly. While generalizations concerning supergene control of heterostyly are frequently made, the evidence comes largely from A. Ernst's extensive work on *Primula* reviewed in Chapter 5. The supergene model may be applicable to most distylous plants; however the number and organization of loci controlling characters of the syndrome are likely to vary among different groups. Whether supergenes are involved in the control of tristyly remains a contentious issue (Chap. 4 and 5). Studies of the genetics of semi-homostylous variants in tristylous taxa would be valuable in addressing this problem. While semi-homostylous variants in *Eichhornia* spp. (S.C.H. Barrett unpubl. data) and *Decodon verticillatus* (C.G. Eckert and S.C.H. Barrett unpubl. data) do not behave as though they have arisen by recombination, those in *Pemphis acidula* (D. Lewis, pers. commun.) appear to do so. Studies of the genetics of homostyle and semi-homostyle formation in heterostylous plants are of general significance to studies of mating-system evolution because floral modifications influencing selfing rate are often under major gene control. This enables tests of theoretical models which frequently assume this mode of inheritance for mating-system modification (Wells 1979; Holsinger et al. 1984; Lande and Schemske 1985).

Modifier genes nonallelic to major genes governing the morphological and physiological features of heterostyly appear to be widespread in heterostylous species. In self-compatible species genes of this type may be of evolutionary significance because of their influence on mating systems. Wide variation in stamen and style length in *Amsinckia* and *Turnera* species directly influences the outcrossing rate of populations (Ganders et al. 1985; Barrett and Shore 1987; S. Belaoussoff and J.S. Shore, unpubl. data). In *Turnera ulmifolia* quantitative genetic studies have demonstrated that this variation is polygenically controlled (Shore and Barrett 1990). The genetic basis of floral variation in *Amsinckia* is unknown, but would certainly be worth investigating since it appears likely that selection on this variation is responsible for the multiple origins of selfing in the genus. Variation in the strengh of self-incompatibility is also common in heterostyly species but its genetic basis has rarely been investigated (but see Beale 1939; DeWinton and Haldane 1933; Mather 1950; Barrett and Anderson 1985; Shore and Barrett 1986) despite its obvious significance for the mating system of populations. Leaky or cryptic systems of self-incompatibility may enable the adjustment of outcrossing levels, depending on the supply of outcross and self-pollen delivered to plants by pollinators.

Recent advances in molecular biology offer exciting new opportunities for understanding more about the genes that control heterostyly. As yet no work on the molecular genetics of heterostyly has been undertaken, but it seems probable that molecular techniques will soon be employed in addressing questions concerned with the number, location, organization, and regulation of genes controlling floral organogenesis and incompatibility. One of the goals of these studies should be the elucidation of molecular mechanisms underlying the contrasting development processes (see Chap. 4) that give rise to the different phenotypes of the floral morphs. The availability of a range of recombinant genotypes (see Chap. 5) and other variants with altered floral traits may be useful in this regard. Elsewhere, molecular studies of floral mutants in *Arabidopsis* and *Antirrhinum* have provided novel insights into the genetic control of flower development in these species (Schwarz-Sommer et al. 1990). If approaches used in these taxa can be successfully transferred to heterostylous plants, they are likely to resolve many unanswered questions concerning the genetic architecture and development of heterostyly.

For molecular studies of heterostyly to be successful, it is necessary that the genes governing the floral polymorphisms are identified and their DNA sequences obtained by molecular cloning techniques. This has been achieved for several *S* alleles in both gametophytic and sporophytic systems of homomorphic incompatibility (reviewed by Haring et al. 1990). Sequences of *S*-glycoproteins in *Nicotiana* and *S* locus-specific glycoproteins in *Brassica* show little similarity, supporting the early suggestion by Bateman (1952) of independent origins for the two systems of homomorphic incompatibility. Comparisons of DNA sequences from different families, particularly those containing taxa with both diallelic and multiallelic incompatibility (e.g., Boraginaceae) may provide the most convincing evidence concerning the evolutionary relationships, if any, of heterostyly to other systems of incompatibility. Studies of this type would be based on the assumption that there are genes specifically for diallelic incompatibility in heterostylous plants analogous in function to those found in families with homomorphic incompatibility. However, if, as Lloyd and Webb suggest in Chapter 6, diallelic incompatibility arises separately in each floral morph, through selection on pollen performance in a particular style length, the search for specific incompatibility genes may be a fruitless exercise since a common molecular mechanism may not exist.

Once sequence data become available for genes controlling heterostylous characters, attempts can be made to characterize how, when, and where the genes are expressed in development. Of particular interest in this regard will be to determine whether the same genes, organized and expressed in a similar way, are responsible for floral differentiation in different heterostylous groups. A supergene model involving several tightly linked genes is most often used to explain the close association between heterostylous characters. However, other genetic models should also be considered, particularly those that involve regulatory genes. Such genes could act to generate the polymorphism by switching development along alternate pathways, or by controlling hormonal gradients responsible for differential organ growth in a morph- or tissue-specific manner, analogous to sex-limited gene expression. With such models, physical linkage of genes controlling the syndrome of floral traits is unnecessary. Models of this type might be particularly useful for explaining the unique properties of tristylous polymorphisms. Although at present these issues fall within the realm of speculation, the rapid progress in development of molecular techniques makes it likely that in the future it may be relatively straightforward to locate and characterize the genes controlling heterostyly. When this is done, we may find that different genetic systems control similar phenotypic expressions in unrelated heterostylous families.

5 Origin and Evolution

Heterostyly has originated on more than 20 separate occasions among angiosperm families (Fig. 2), yet understanding its evolutionary development remains one of the most difficult problems in plant breeding-system evolution. Perhaps this is because the course of evolution in heterostylous groups, "may have been complex and circuitous" (Fisher 1958). A major stumbling block has been our inability to identify, among close relatives of heterostylous taxa, patterns of floral variation which clearly represent stages in the assembly of the polymorphisms. Apart from the Plumbaginaceae, where Baker's studies suggest the build-up of distyly in several steps, beginning with diallelic incompatibility (Baker 1966), in most families the polymorphisms appear to arise de novo, without obvious clues as to the intermediate stages involved. In this respect heterostyly differs from other polymorphic sexual systems, such as dioecy, where variation patterns among related taxa have enabled inferences on the evolutionary pathways involved in the separation of sexes (Bawa 1980).

Our ability to identify stages involved in the evolution of heterostyly, depends on the particular model that is being evaluated. Most modern workers (for exceptions see Anderson 1973; Richards 1986, p. 254) have favored the view that diallelic incompatibility precedes the evolution of reciprocal herkogamy in heterostylous plants (Baker 1966; Yeo 1975; D. Charlesworth and B. Charlesworth 1979; Ganders 1979; Lewis 1982; and Chap. 5). However, Lloyd and Webb in Chapters 6 and 7 revive Darwin's original idea (Darwin 1877) that reciprocal herkogamy developed first, followed by the evolution of an intramorph incompatibility system[2]. Theoretical models of the evolution of distyly, by D. Charlesworth and B. Charlesworth (1979) and Lloyd and Webb (Chap. 7), differ in the ancestral conditions invoked and in the sequence in which heterostylous characters are assembled (Fig. 3). The models therefore make different predictions about the evolutionary build-up of heterostyly and the types of variation patterns likely to be found in the immediate ancestors of heterostylous plants. In this respect both models differ from Mather and DeWinton's (1941) suggestion that the morphological and physiological components of heterostyly arise simultaneously.

The phylogenetic status of self-compatible heterostylous taxa is of particular interest in evaluating models for the evolution and function of heterostyly. In recent years, more cases have been reported in which the morphological components of the polymorphism are accompanied by high levels of self-fertility. Several genera, most notably *Amsinckia* (Ray and Chisaki 1957), *Cryptantha* (Casper 1985), *Eichhornia* (Barrett 1988a), *Melochia* (Martin 1967), *Nivenia* (Goldblatt and Bernhardt 1990), *Quinchamalium* (Riveros et al. 1987), and the monotypic *Decodon* (C.G. Eckert and S.C.H. Barrett unpubl. data) contain species that are highly self-compatible. It has usually been assumed that this condition is derived through relaxation and eventual

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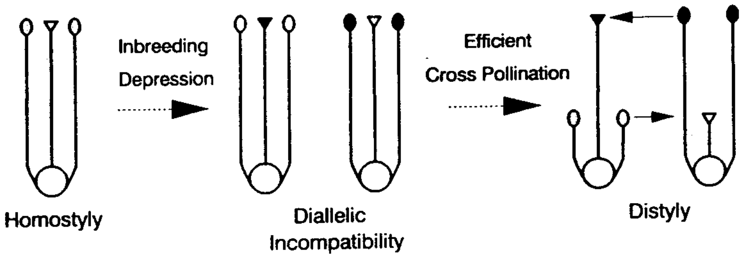
[2] Some disagreement exists over the interpretation of Darwin's views on this point. Yeo (1975, p. 149) states "He did, however, suggest (Darwin 1877, p. 262) that the parent-species of heterostyled plants were "in some degree self-sterile"...... In other words, Darwin thought incompatibility came first and heterostyly followed". However, while Darwin may have considered that the ancestors of heterostylous plants exhibited some degree of self-sterility, it is quite clear from the discussion on pp. 260–268 (Darwin 1877) that he believed the evolution of the intramorph incompatibility system *followed* the establishment of reciprocal herkogamy.

1. Selfing Avoidance Model



2. Pollen Transfer Model

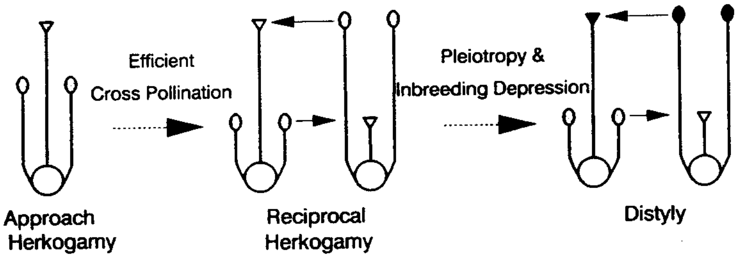


Fig. 3. The two major models of the evolution of distyly. The anti-selfing model follows D. Charlesworth and B. Charlesworth (1979) and the pollen transfer model is developed by Lloyd and Webb in Chapters 6 and 7. The models differ in the ancestral phenotypes invoked, the sequence of establishment of reciprocal herkogamy and diallelic incompatibility, and the emphasis placed on different selective forces. Only major stages in the models are shown for simplicity. Phenotypes with *uniform* pollen and stigmas are self-compatible, those with *shaded* pollen or stigmas are self-incompatible

loss of diallelic incompatibility (Ganders 1979). Genes modifying the strength of incompatibility commonly occur in heterostylous species (see above), and in some of the genera listed above related taxa possess normally functioning diallelic incompatibility systems. However, Lloyd and Webb's model of the evolution of heterostyly (Chap. 7) predicts the occurrence of self-compatible heterostylous populations as an ancestral condition in heterostylous groups (Fig. 3). This contrast with the Charlesworths' model (D. Charlesworth and B. Charlesworth 1979) where self-compatible heterostyly is always likely to be a derived condition. Sound phylogenetic data on the relationships between self-compatible and self-incompatible heterostylous taxa would therefore be useful in evaluating the validity of these models.

Another fertile area of relevance to models of the evolution of heterostyly concerns the apparent association between heterostylous polymorphisms and multiallelic self-incompatibility in *Anchusa* (Dulberger 1970; Schou and Philipp 1984), *Narcissus* (Fernandes 1935; Dulberger 1964; Bateman 1954a; Lloyd et al. 1990) and possibly *Villarsia* (Ornduff 1988). This association is unexpected under a model in which diallelic incompatibility evolves first and reciprocal herkogamy functions to reduce illegitimate pollen transfer between the small number of mating groups associated with this type of incompatibility. However, this association can be accommodated under Lloyd and Webb's model since the selective forces they invoke to explain the evolution of reciprocal herkogamy are independent of whether the ancestral condition is self-incompatible or self-compatible.

The most complex problem concerned with the origins of heterostyly is the evolution of tristyly. Briggs and Walters (1984) recently remarked that "speculation about the evolution of the tristylous condition... is likely to be the hobby of the man who plays three-dimensional chess!". Notwithstanding this pessimistic view, some limited progress has been made on the topic. D. Charlesworth (1979) has developed a quantitative model for the evolution of tristyly and several features of her model have subsequently proven to be correct for particular tristylous groups (Bennett et al. 1986; Kohn and Barrett 1992). In addition, Richards and Barrett (Chap. 4) have investigated the developmental basis of tristyly and attempted to integrate this information with existing knowledge about the inheritance of the polymorphism. Their studies question the commonly held assumption that two separate anther whorls are a necessary precondition for the evolution of tristyly. Before more progress on this topic can be made, however, the question of whether supergenes exist in tristylous species and whether the *S* and *M* loci represent duplicated loci must be answered (Richards 1986; Olmstead 1989). In addition, basic data on the morphology, genetics, and incompatibility relationships from taxa in two additional families[3] (Amaryllidaceae and Connaraceae) recently reported as tristylous (see Chap. 6) are required to determine which features they share with the more widely known tristylous families reviewed by Weller in Chapter 10.

Patterns of floral variation in *Narcissus* (Amaryllidaceae) are particularly intriguing for models of the evolution of tristyly because species possessing stylar monomorphism, dimorphism and trimorphism occur (Fig. 4). Recent work on floral variation in *Narcissus* populations in southern Spain (S.C.H. Barrett, D.G. Lloyd and J. Arroyo unpubl. data) indicates that species with monomorphic populations (e.g., *N. bulbocodium*) exhibit approach herkogamy with two stamen levels; dimorphic populations (e.g., *N. assoanus*) are polymorphic for stigma height with two stamen levels at similar heights; and trimorphic populations (e.g., *N. triandrus*) exhibit reciprocal herkogamy, with three distinct stigma and stamen heights. The functional significance of this variation, and whether it represents stages in the evolutionary build-up of tristyly, are not known. Once again, sound phylogenetic information on species relationships, as well as field studies of the reproductive biology of populations, are required to assess this possibility.

6 Function and Adaptive Significance

Models of the evolution of heterostyly not only differ in the sequence in which morphological and physiological components of the polymorphisms are thought to arise, but also in the emphasis placed on different selective forces (Fig. 3). Most modern workers interpret heterostyly as an outbreeding mechanism. Following this

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[3] Note added in proof, M.S. Zavada and T.K. Lowrey (unpubl. ms.) have recently reported the possible occurrence of tristyly in the south African shrub *Dais continifolia* L. (Thymelaeceae). The three floral morphs differ in style length, stigmatic papillae size and pollen exine sculpturing.

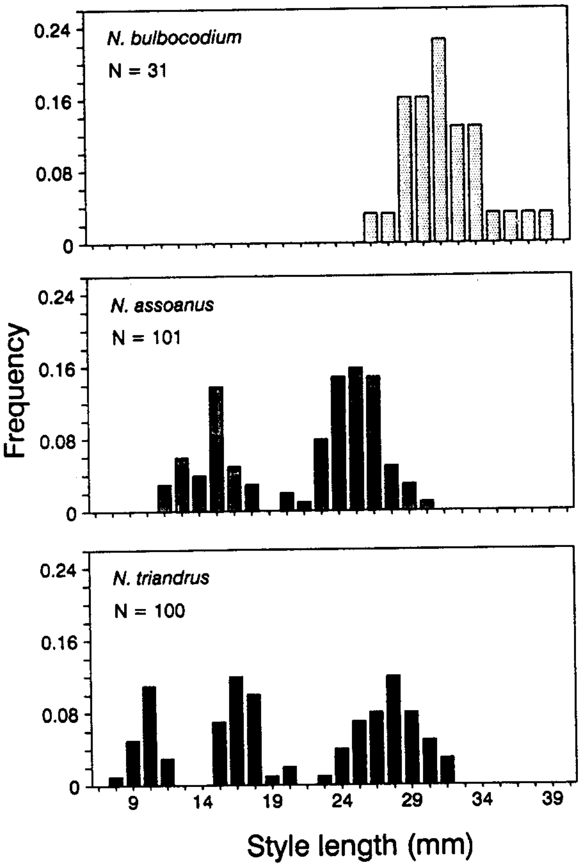

Fig. 4. Patterns of style length variation in *Narcissus* species from southern Spain. The distributions are based on a random sample of flowers collected from a single population of each species. *Narcissus bulbocodium* is monomorphic, *N. assoanus* is dimorphic and *N. triandrus* is trimorphic for style length. (Unpubl. data of S.C.H. Barrett, D.G. Lloyd and J. Arroyo)

view, diallelic incompatibility evolved first as a selfing avoidance mechanism, with inbreeding depression the primary selective force. According to this hypothesis, reciprocal herkogamy then arose secondarily to promote efficient pollen transfer between incompatibility types, hence reducing pollen wastage (see Chap. 7).

Although diallelic incompatibility prevents self-fertilization it also prevents intramorph mating; and, because of the small number of mating groups in heterostylous populations, the extent to which outbreeding is promoted is severely restricted in comparison with multiallelic incompatibility systems. This observation led Darwin (1877), and more recently Lloyd and Webb (in Chaps. 6 and 7), to question whether heterostyly is likely to have evolved primarily as an outbreeding mechanism. Instead, they suggest that reciprocal herkogamy evolved prior to incompatibility to promote efficient pollen transfer between individuals. Incompatibility may then develop secondarily as a pleiotropic byproduct of selection for increased pollen competitive ability on the style type to which pollen is most frequently transferred. Lloyd and Webb (Chap. 7) also show that diallelic incompatibility can be selected as an anti-selfing device, arising when most interplant pollen transfer is already intermorph as a result of reciprocal herkogamy. Thus the cost of diallelic incompatibility, in terms of lost ability to fertilize plants of the same incompatibility type, is reduced.

What evidence exists for Darwin's hypothesis that the function of reciprocal herkogamy is to actively promote efficient cross-pollination between anthers and stigmas of equivalent height in the floral morphs? In Chapter 7, Lloyd and Webb review a variety of experimental studies on the pollination biology of heterostylous populations that have attempted to investigate the adaptive significance of reciprocal herkogamy. Through the development of a novel procedure for analyzing pollen deposition patterns on naturally pollinated stigmas they demonstrate, in contrast to the conclusions of previous workers, these data from earlier studies actually provide impressive support for the Darwinian hypothesis that heterostyly functions to promote legitimate pollination.

A recent study by Kohn and Barrett (1992), using genetic markers and the experimental manipulation of garden arrays of tristylous self-compatible *Eichhornia paniculata*, investigated the two primary hypotheses (anti-selfing and improved cross-pollination) concerned with the function of reciprocal herkogamy. Outcrossing rates, levels of intermorph mating and morph-specific male and female reproductive success were compared in replicate trimorphic and monomorphic populations. They found that both outcrossing rates and seed set were higher in all three morphs in trimorphic than in monomorphic populations (Fig. 5). A large proportion (95%) of outcrossed matings in trimorphic populations were due to intermorph mating. Floral polymorphism therefore increased both outcrossing rate and seed set but the magnitude of the differences varied significantly among the floral morphs. If the ancestral condition in heterostylous groups resembled the long-styled morph, as suggested by Lloyd and Webb in Chapters 6 and 7, then the large increase in seed set in this morph when in trimorphic arrays (see Fig. 5) suggests that the selective basis for the evolution of floral polymorphism may have been increased pollen transfer, rather than higher levels of outcrossing.

Although much has been written concerning the adaptive significance of heterostylous characters (reviewed in Chaps. 3, 6, and 7), little work has been conducted in natural populations where both plants and pollinators have been experimentally manipulated. Yet heterostylous plants offer excellent opportunities for this type of work which is critical for testing adaptive hypotheses (see Chap. 7). By altering the floral morphology (e.g., emasculated versus intact flowers) and morph structure of populations (monomorphic versus polymorphic, homostylous versus heterostylous morphs) hypotheses that invoke fitness differences based on floral morphology can be tested experimentally. In these experiments, use of a variety of techniques previously employed in field studies of heterostylous populations should enable quantitative data to be collected on each of the elementary stages in the pollination and mating process. These include data on the foraging behaviour of pollinators (Weller 1981; Husband and Barrett 1991a), pollen removal from flowers (Wolfe and Barrett 1989; L.D. Harder and S.C.H. Barrett, unpubl. data), pollen deposition on pollinators (Olesen 1979; Wolfe and Barrett 1989) and intact and

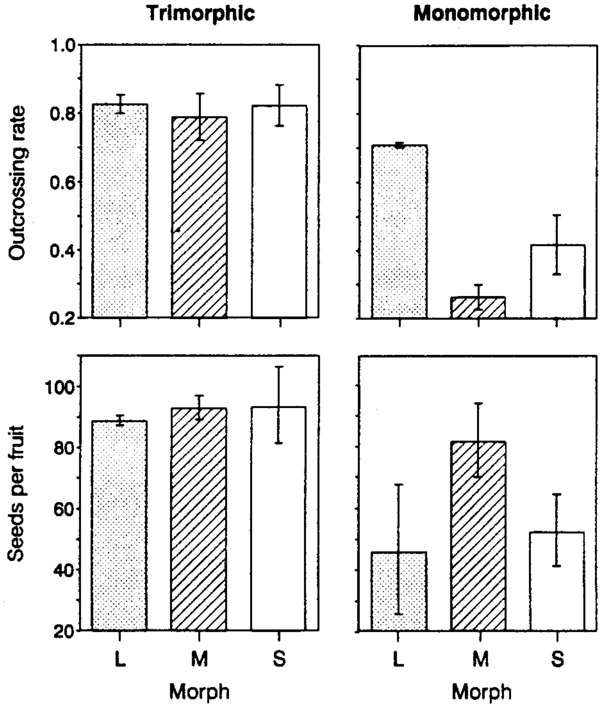

Fig. 5. Mean morph-specific outcrossing rates and seed set in experimental trimorphic and monomorphic populations of tristylous, self-compatible, *Eichhornia paniculata*. Bars represent two standard errors based on three replicate populations of each treatment. (After Kohn and Barrett 1992)

emasculated flowers (Ganders 1974; Barrett and Glover 1985), pollen carryover (Feinsinger and Busby 1987), pollen tube growth (M.B. Cruzan and S.C.H. Barrett, unpubl. data), and mating system parameters including rates of outcrossing (Glover and Barrett 1986), disassortative mating (Ganders 1975a; Barrett et al. 1987), correlated mating (Morgan and Barrett 1990), and male reproductive success (Kohn and Barrett 1992).

In Chapters 6 and 7, Lloyd and Webb introduce an additional selective force that could account for the evolution of floral polymorphisms associated with the heterostylous syndrome. They suggest that various ancillary characters associated with pollen and stigmas may encourage cross-fertilization by reducing the likelihood of mutual interference between the reproductive functions of stamens and carpels within flowers. The recognition that reproductive success occurs through both female and male function in hermaphrodite flowers, and that conflicts may arise between the two, is associated with a growing awareness that various facets of plant reproduction can be viewed from the perspectives of sexual selection and sex allocation theory (Charnov 1982).

In Chapter 8, Casper examines the application of sex allocation theory to heterostylous plants by focusing attention on how heterostyly may function in ways that are unrelated to its role as an incompatibility system. The idea that fitness through female and male function might differ between the morphs in heterostylous species is reviewed. In addition, the issues of the optimal allocation to pollen and seed production in the floral morphs and the selective mechanisms by which morph ratios may be controlled are addressed. Sex allocation models of heterostyly have not been subjected to empirical tests, but Casper discusses a range of studies that address a major assumption of the models; that plants have the ability to control offspring morph ratios through genes unlinked to the heterostyly loci.

Unfortunately, although morph-specific differences in reproductive traits are ubiquitous in heterostylous populations (reviewed in Chaps. 3 and 8), their adaptive significance and influence on fitness gain through female and, particularly, male function are largely unknown. The major limitation to assessing the role of sexual selection in heterostylous plants is a lack of data on male reproductive success. Most of the evidence that the floral morphs might specialize in functional gender comes from comparisons of maternal reproductive characters (reviewed in Chap. 8). A recent attempt to measure the functional gender of floral morphs in tristylous *Eichhnornia paniculata* using genetic markers demonstrated large differences in male reproductive success, particularly between the long- and short-styled morphs (Kohn and Barrett 1992). Short-styled plants consistently sired more mid-styled offspring than long-styled plants. Whether this type of mating asymmetry commonly occurs in tristylous populations is not known, but similar kinds of gender differences are a prerequisite for models concerned with evolution of dioecism from heterostyly (see below).

7 Pollen-Pistil Interactions

Studies of pollen-pistil interactions in heterostylous plants (reviewed in Chaps. 3 and 6) demonstrate that the general properties of diallelic incompatibility systems are fundamentally distinct from those found in multiallelic homomorphic systems. As Dulberger points out in Chapter 3, a variety of different inhibition sites for incompatible pollen tubes, including the stigma, style and ovary, are evident in heterostylous plants. A characteristic feature of most heterostylous taxa in which pollen tube growth has been investigated is the difference in sites of inhibition between the floral morphs (Gibbs 1986).

Recent studies of pollen tube growth following legitimate and illegitimate pollinations in distylous *Primula* spp. (Wedderburn and Richards 1990) and tristylous *Pontederia* spp. (Anderson and Barrett 1986; Scribailo and Barrett 1991) clearly demonstrate the absence of a unitary rejection response, as occurs in homomorphic systems. In *P. sagittata* inhibition sites are particularly complex and depend on the specific pollen size-style length combination that is employed (Fig. 6). The occurrence of variable inhibition sites in heterostylous plants is used as evidence by Lloyd and Webb (Chap. 6) to argue that incompatibility reactions in heterostylous plants may have evolved separately in each floral morph and, as a result, need not share a common molecular basis involving matching recognition factors in the pollen and style. Observations on pollen-pistil interactions in heterostylous plants, com-

A.

Pollen	Style L	Style M	Style S
l	**13.7**	7.2	1.7
m	7.9	**7.6**	1.7
s	1.1	1.0	**1.3**

B.

Pollen	Style L	Style M	Style S
l	**81.2**	72.6	7.4
m	11.1	**91.8**	27.5
s	0.7	16.4	**78.4**

Fig. 6 A,B. Pollen-pistil interactions in self-incompatible, tristylous *Pontederia sagittata*. **A** Mean distance (mm) at which pollen tubes terminate growth in the style following controlled pollinations. **B** Mean percentage seed set. Values in *bold type* are the legitimate combinations. [After **A** Scribailo and Barrett (1991) and **B** Glover and Barrett (1983)]

bined with taxonomic information on the distribution of heteromorphic and homomorphic incompatibility, provide evidence against the view that diallelic incompatibility evolved by degeneration of a multiallelic system until only two alleles remained (Crowe 1964; Muenchow 1982; Wyatt 1983).

Another facet of pollen-pistil interactions, reviewed by McKenna in Chapter 9, concerns the potential for microgametophytic competition to occur in heterostylous plants as a consequence of differences between the floral morphs in style length and pollen size. Gametophytic selection is also discussed by Casper in Chapter 8 in her evaluation of mechanisms that may contribute to the regulation of floral morph ratios in heterostylous populations.

Several approaches have been used in studies of pollen competition in heterostylous plants. These include: (1) Mixed pollinations and progeny tests to determine whether pollen carrying alternate alleles at loci governing style length differs in competitive ability (Tseng 1938; Baker 1975; Barrett et al. 1989). (2) Marker gene and pollen tube growth studies to determine whether differences in the competitive ability of self versus outcrossed or legitimate versus illegitimate pollen occur in self-compatible species (Weller and Ornduff 1977; Glover and Barrett 1986; Casper et al. 1988; M.B. Cruzan and S.C.H. Barrett, unpubl. data). (3) Use of the style length polymorphism as an experimental system for determining whether the intensity of pollen competition (data of McKenna in Chap. 9) or pollen precedence (Graham and Barrett 1990) varies with style length. (4) Studies of the inhibitory effects of prior application of incompatible pollen on compatible pollen tube growth and seed set (Shore and Barrett 1984; Barrett and Glover 1985; Nicholls 1987; Murray 1990; Scribailo and Barrett 1992). This latter phenomenon, known as "stigma or stylar clogging", can be viewed as one aspect of pollen-stigma interference discussed above. Considerable scope for future studies on pollen competition exist in heterostylous plants. Although functional work on heterostyly has focused primarily on the pollination process, it is clear that a variety of post-pollination mechanisms can potentially influence the mating system and morph structure of heterostylous populations.

Studies of pollen-pistil interactions in self-compatible heterostylous taxa are particularly important because of the question of whether self-compatibility is an ancestral or derived condition in heterostylous groups (see Sect. 5 above). Progeny data from *Amsinckia* spp. (Weller and Ornduff 1977; Casper et al. 1988) and *Eichhornia paniculata* (Glover and Barrett 1986 and Fig. 7) indicate significant differences in the siring ability of legitimate and illegitimate pollen when applied in mixtures. This type of phenomenon has been referred to as cryptic incompatibility. It is not clear, however, whether the mechanisms responsible for discrimination between the different pollen types in these species simply represent a weak expression of diallelic incompatibility or whether other aspects of pollen-pistil interactions are involved. Do these species exhibit a rudimentary and primitive form of diallelic incompatibility of the type anticipated in Lloyd and Webb's model of the evolution of heterostyly? Or are these species secondarily self-compatible, through the action of modifier genes that have weakened, but not completely abolished, a pre-existing diallelic incompatibility system? Studies of additional taxa are needed to determine whether differences in the siring ability of legitimate and illegitimate pollen tubes commonly occur in self-compatible heterostylous plants.

8 Maintenance and Breakdown

Mating types in self-incompatible plants are maintained in populations by frequency-dependent selection. In taxa with homomorphic incompatibility the number and frequency of mating types can only be determined by extensive crossing programs. Data are thus limited to a handful of species (Emerson 1939; Bateman 1954b;

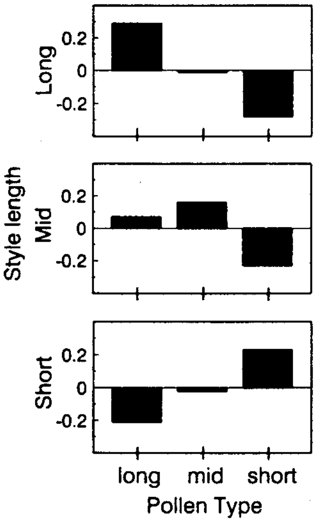

Fig. 7. Fertilization success of pollen from long-, mid-, and short-level anthers when applied in mixtures to stigmas of the long-, mid-, and short-styled morphs of *Eichhornia paniculata*. Genetic markers were used to determine the fertilization success of different pollen types in the mixtures. A value of O indicates random fertilization. (Unpubl. data of M.B. Cruzan and S.C.H. Barrett)

Sampson 1967; Campbell and Lawrence 1981; Karron et al. 1990). In contrast, considerable information on population structure is available for both distylous and tristylous species, because of the small number of mating types and the ease with which they can be identified (reviewed in Chap. 8). Equilibrium morph ratios of 1:1 should be reached in one generation in self-incompatible distylous populations because of the simple mode of inheritance and disassortative mating. In tristylous species, however, the more complex pattern of inheritance results in a slower approach to equilibrium, and morph frequencies at any given time are more strongly influenced by the genotypes of individuals initiating populations and the effects of finite population size (Morgan and Barrett 1988). In large tristylous populations at equilibrium, however, a 1:1:1 ratio of floral morphs will prevail, provided that all morphs have equal fitness, and some degree of disassortative mating occurs (Heuch 1979).

Population surveys of distylous species frequently report equality of the floral morphs (isoplethy) although exceptions are known (e.g., *Primula vulgaris*, Crosby 1949, but see Richards and Ibrahim 1982; *Lythrum* spp., Ornduff 1978; *Hedyotis nigricans*, Levin 1974; *H. caerulea*, Ornduff 1980). Morph frequencies in populations of self-compatible species (e.g., *Amsinckia* spp., Ganders 1975a; *Quinchamalium chilense*, Riveros et al. 1987) or those with extensive clonal growth (e.g., *Oxalis* spp., Mulcahy 1964; *Nymphoides indica*, Barrett 1980; *Menyanthes trifoliata*, F.R. Ganders, unpubl. data) frequently display unequal morph ratios (anisoplethy) because of morph-specific differences in selfing rate or founder effects.

Large scale surveys of floral morph frequencies in tristylous species indicate a variety of complex patterns. Figure 8 illustrates data from four species (*Lythrum salicaria, Decodon verticillatus, Pontederia cordata* and *Eichhornia paniculata*). The striking feature of the data is that despite similar modes of inheritance of tristyly (Chap. 5 and unpubl. data of S.C.H. Barrett and C.G. Eckert) morph frequencies in each species differ in unique ways that reflect their contrasting life history, population ecology, and mating systems. Theoretical models and computer simulation studies of the population dynamics of tristyly in these species have provided insights into the relative importance of stochastic and deterministic forces in explaining morph frequencies (Heuch 1980; Barrett et al. 1983; Morgan and Barrett 1988; Barrett et al. 1989; Eckert and Barrett, 1992).

Equilibrium floral morph frequencies in heteromorphic species with putative multiallelic incompatibility systems (e.g., *Anchusa, Narcissus*) are likely to be quite different from species with diallelic incompatibility. This is because the floral polymorphisms are apparently unlinked to loci controlling incompatibility. In *Villarsia parnassiifolia*, Ornduff (1988) has suggested that incompatibility alleles may be linked to loci controlling morphological polymorphisms in the long-styled morph, but not in the short-styled morph. Where morphological and physiological characters are unlinked, morph frequencies will depend on the relative fitness of the floral phenotypes as female and male parents. This is likely to be largely determined by the pollination biology of populations. In *Anchusa officinalis*, the long-styled morph predominated in all eleven populations sampled by Philipp and Schou (1981). A similar pattern was evident in 10 out of 11 dimorphic and trimorphic populations of *Narcissus* spp. surveyed in southern Spain (S.C.H. Barrett, D.G. Lloyd, and J. Arroyo unpubl. data). Interestingly, the long-styled morph also predominates in the only two

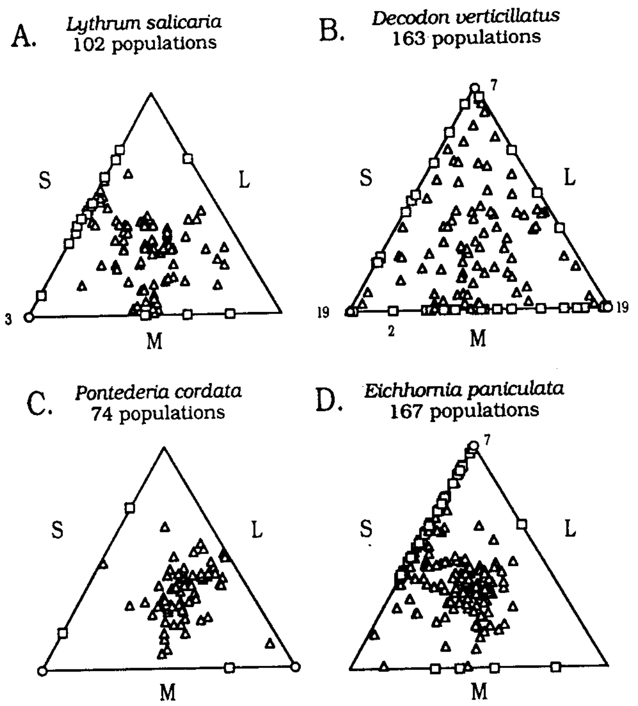

Fig. 8A-D. Floral morph frequences in populations of four tristylous species. **A** *Lythrum salicaria*, **B** *Decodon verticillatus*, **C** *Pontederia cordata*, **D** *Eichhornia paniculata*. *Triangles* represent populations with three floral morphs, *squares* are populations with two floral morphs, and *circles* are populations containing a single floral morph. Isoplethy is equidistant from all axes and the distance of a symbol from each axis is proportional to the frequency of the morph in a population, e.g., *triangles* close to the *S* axis have a low frequency of the short-styled morph. [*Lythrum salicaria* and *Decodon verticillatus*, Eckert and Barrett (1992); *Pontederia cordata*, Barrett et al. (1983); *Eichhornia paniculata*, Barrett et al. (1989) and (unpubl. data)]

well-documented nonheterostylous species with stigma height polymorphisms (*Chlorogalum angustifolium*, Jernstedt 1982; *Epacris impressa*, O'Brien and Calder 1989).

These data suggest that the long-styled phenotype commonly has a selective advantage over the short-styled phenotype, a finding consistent with the overall prevalence of approach herkogamy and rarity of reverse herkogamy in angiosperm families (Webb and Lloyd 1986). Field studies of the pollination biology and mating systems of taxa with stigma height polymorphisms are of special interest because of Lloyd and Webb's suggestion (Chaps. 6 and 7) that this type of variation may represent an early stage in the evolution of heterostyly. Critical testing of their model requires a demonstration that significant levels of disassortative mating occur in populations polymorphic for stigma height.

Surveys of morph frequencies in heterostylous populations have provided valuable clues on the evolutionary processes responsible for the breakdown of heterostyly. In Chapter 10, Weller reviews some of this work in his discussion of the ways that tristyly has become evolutionarily modified in the Lythraceae, Oxalidaceae and Pontederiaceae. Two contrasting evolutionary pathways are most commonly found in these families; the evolution of distyly, by loss of one of the style morphs (Lythraceae and Oxalidaceae), and the evolution of predominant self-fertilization via semi-homostyly. Other modifications include the evolution of facultative apomixis in *Oxalis dillenii* ssp. *filipes* (Lovett Doust et al. 1981), and the possibility of gender specialization in *Sarcotheca celebica* (Lack and Kevan 1987) and *Decodon verticillatus* (C.G. Eckert and S.C.H. Barrett unpubl. data). In addition, Lemmens (1989) has recently reported tristyly, distyly, homostyly, and dioecy in various genera of tropical Connaraceae and suggested that evolutionary trends in this family are similar to those documented in the Lythraceae and Oxalidaceae. Population studies of these genera and other putatively heterostylous taxa of tropical origin (reviewed in Barrett and Richards 1990) are needed to confirm the true nature of their breeding systems.

A variety of evolutionary modifications have also been documented in distylous groups (reviewed in Ganders 1979; Richards 1986; Barrett 1988b). These include the shift from outcrossing to different degrees of selfing through the evolution of homostyly (e.g., *Amsinckia*, Ganders et al. 1985; *Psychotria*, Hamilton 1990; *Turnera ulmifolia*, Fig. 9), the development of apomixis in *Limonium* (Baker 1966) and *Erythroxylum* (Berry et al. 1991), and the evolution of various forms of gender specialization including gynodioecy (*Armeria*, Baker 1966; *Nymphoides*, Vasudevan Nair 1975) and dioecy (primarily in the Rubiaceae, Menyanthaceae and Boraginaceae; Baker 1958; Ornduff 1966; Opler et al. 1975; Lloyd 1979; Beach and Bawa 1980; Muenchow and Grebus 1989; Charlesworth 1989). These shifts in breeding behavior provide a rich, but to date largely untapped, source of experimental material for studies aimed at determining the ecological and genetic basis of mating-system evolution in plants.

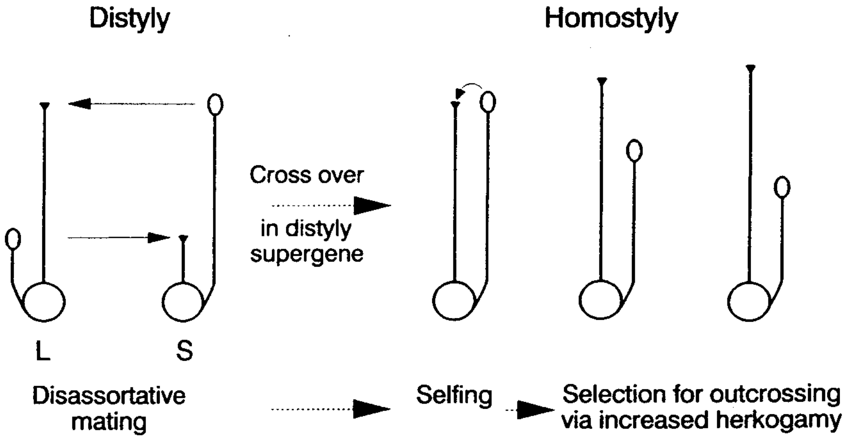

Fig. 9. Model of the evolutionary breakdown of distyly to homostyly in the *Turnera ulmifolia* complex after Barrett and Shore (1987). Homostylous populations vary in stigma-anther separation; the variation is polygenically controlled (Shore and Barrett 1990) and influences the outcrossing rate of populations (S. Belaoussoff and J.S. Shore, unpubl. data)

Most progress on the evolution of mating systems in heterostylous groups has been made by investigating the selective forces responsible for the dissolution of heterostyly to homostyly (reviewed in Richards 1986; Barrett 1989b). The frequent breakdown of floral polymorphism to monomorphism in distylous and tristylous groups represents a model system for studies of the evolution of self-fertilization in plants. This is because the direction of evolutionary change is usually unambiguous, genetic modifications are often simply inherited (Chap. 5), and alterations in floral morphology that influence breeding behavior are usually of large phenotypic effect and therefore readily detected under field conditions. These features have aided both theoretical modeling and experimental studies of natural and artificial populations (B. Charlesworth and D. Charlesworth 1979; Piper et al. 1986; J.R. Kohn and S.C.H. Barrett unpubl. data). To disentangle the selective forces responsible for the evolution of self-fertilization, however, data on selfing rates, inbreeding depression, male and female fertility, patterns of sex allocation, and the genetic basis of mating system modification are required (D. Charlesworth and B. Charlesworth 1981, 1987; Lande and Schemske 1985; Barrett and Eckert 1990). In addition, an understanding of the ecological and demographic circumstances under which selfing variants are favored is also needed (Lloyd 1980; Holsinger 1991).

Some of this information is available for the best-studied heterostylous groups (e.g., *Primula*, Piper et al. 1984, 1986; Curtis and Curtis 1985; Richards 1986; Boyd et al. 1990; *Eichhornia*, Barrett 1979; Barrett et al. 1989; Morgan and Barrett 1989; Barrett and Husband 1990; Husband and Barrett 1991a,b; *Turnera*, Shore and Barrett 1985, 1990; Barrett and Shore 1987; and *Amsinckia*, Ray and Chisaki 1957; Ganders 1975a,b; Ganders et al. 1985), and several lines of evidence indicate that homostyles can experience a selective advantage under conditions where pollinator service is unreliable. However, where fitness components have been compared in heterostylous and homostylous morphs, considerable variation in both space and time has been evident, complicating simple interpretation based on reproductive assurance alone. Long-term studies of the demographic genetics of mixed populations of short-lived taxa are most likely to provide convincing evidence of the selective mechanisms responsible for the evolution of self-fertilization in heterostylous taxa.

9 Conclusions

A century of research on heterostyly has passed since the publication in 1877 of Charles Darwin's book *The Different Forms of Flowers on Plants of the Same Species*, which summarized his extensive investigations of distylous and tristylous plants. The subsequent period can be divided into two phases, differing in research emphasis. The first, lasting until the 1960s, largely involved genetic and biosystematic studies by European workers on a small number of herbaceous taxa (e.g., *Primula, Lythrum, Oxalis, Linum,* and taxa of Plumbaginaceae). At the time, this work was part of mainstream genetics and aided the development of theories concerned with the regulation of recombination and evolution of genetic systems (Darlington 1939; Darlington and Mather 1949; Grant 1975).

Since then, the growth of population biology and increased opportunities for tropical research have stimulated a diversification of approaches involving a broader range of heterostylous taxa. Over the past two decades field investigations of the reproductive ecology and genetics of populations, in concert with the development of theoretical models, have enabled some testing of specific hypotheses concerned with the evolution and breakdown of heterostyly. In addition, structural and developmental studies and work on pollen-pistil interactions have provided the necessary morphological and physiological context for investigations concerned with the adaptive significance of floral polymorphisms.

Although considerable headway has been made during the past century in understanding various aspects of the evolution and breakdown of heterostyly, most of the work has focused at or below the species level. As a result, most interpretations have been conducted in an ahistorical context with little evidence, aside from character correlations, on the number of times characters may have evolved, or the direction and temporal sequence of character transformation. In order that hypotheses on evolutionary pathways in heterostylous groups can be tested more rigorously, phylogenetic analyses using cladistic techniques must be undertaken (Donoghue 1989). Studies of this type are likely to benefit from recent advances in molecular systematics which have provided an array of molecular characters that can be used in phylogenetic reconstruction (Felsenstein 1988; Palmer et al. 1988). Molecular data are of particular value because the characters used to assess relationships are likely to be independent of changes in morphological traits associated with breeding-system evolution. High levels of homoplasy in morphological characters can complicate attempts at phylogenetic reconstruction, particularly those involving character syndromes associated with floral evolution (Eckenwalder and Barrett 1986).

Phylogenetic analysis of heterostylous families in which specific evolutionary hypotheses have been proposed concerning breeding-system variation would be particularly worthwhile. These include: Plumbaginaceae — is the sequence of character build-up for the heterostylous syndrome proposed by Baker (1966) supported? Rubiaceae — has distyly originated more than once in the family, as suggested by Anderson (1973), and how often has it broken down to dioecy? Boraginaceae — what are the phylogenetic relationships between distylous taxa with and without diallelic incompatibility and between these taxa and those with multiallelic incompatibility? Lythraceae and Oxalidaceae — how often has tristyly broken down to distyly in each family, and are similar pathways involved? Finally, phylogenetic analysis would be especially valuable for determining the character syndromes of the immediate ancestors of heterostylous genera. Such information is important for understanding why and how heterostyly has evolved in particular families and provides the necessary historical background for microevolutionary studies of the selection process.

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References

Anderson JM, Barrett SCH (1986) Pollen tube growth in tristylous *Pontederia cordata* L. (Pontederiaceae). Can J Bot 64:2602–2607

Anderson WR (1973) A morphological hypothesis for the origin of heterostyly in the Rubiaceae. Taxon 22:537–542

Baker HG (1958) Studies in the reproductive biology of West African Rubiaceae. J West Afr Sci Assoc Fr 4:9–24

Baker HG (1966) The evolution, functioning and breakdown of heteromorphic incompatibility systems I. The Plumbaginaceae. Evolution 18:507–512

Baker HG (1975) Sporophyte-gametophyte interactions in *Linum* and other genera with heteromorphic self-incompatibility. In: Mulcahy DL (ed) Gamete competition in plants and animals. North Holland, Amsterdam, pp 191–200

Barrett SCH (1979) The evolutionary breakdown of tristyly in *Eichhornia crassipes* (Mart.) Solms (water hyacinth). Evolution 33:499–510

Barrett SCH (1980) Dimorphic incompatibility and gender in *Nymphoides indica* (Menyanthaceae). Can J Bot 58:1938–1942

Barrett SCH (1985a) Ecological genetics of breakdown in tristyly. In: Haeck J, Woldendorp JW (eds) Structure and functioning of plant populations II. Phenotypic and genotypic variation in plant populations. North Holland, Amsterdam, pp 267–275

Barrett SCH (1985b) Floral trimorphism and monomorphism in continental and island populations of *Eichhornia paniculata* (Spreng.) Solms (Pontederiaceae). Biol J Linn Soc 25:41–60

Barrett SCH (1988a) Evolution of breeding systems in *Eichhornia* (Pontederiaceae): A review. Ann M Bot Gard 75:741–760

Barrett SCH (1988b) The evolution, maintenance and loss of self-incompatibility systems. In: Lovett Doust J, Lovett Doust L (eds) Plant reproductive ecology patterns and strategies. Oxford Univ Press, Oxford, pp 98–124

Barrett SCH (1989a) Mating system evolution and speciation in heterostylous plants. In: Otte D, and Endler J (eds) Speciation and its consequences. Sinauer, Sunderland, MA, pp 257–283

Barrett SCH (1989b) Evolutionary breakdown of heterostyly. In: Bock JH, and Linhart YB (eds) The evolutionary ecology of plants. Westview Press, Colorado, pp 151–170

Barrett SCH (1990) The evolution and adaptive significance of heterostyly. Trends Ecol Evol 5:144–148

Barrett SCH, Anderson JM (1985) Variation in expression of trimorphic incompatibility in *Pontederia cordata* L. (Pontederiaceae). Theor Appl Genet 70:355–362

Barrett SCH, Eckert CG (1990) Variation and evolution of mating systems in seed plants. In: Kawano S (ed) Biological approaches and evolutionary trends in plants. Academic Press, Lond New York, pp 229–254

Barrett SCH, Glover DE (1985) On the Darwinian hypothesis of the adaptive significance of tristyly. Evolution 39:766–774

Barrett SCH, Husband BC (1990) Variation in outcrossing rates in *Eichhornia paniculata*: The role of demographic and reproductive factors. Plant Spec Biol 5:41–56

Barrett SCH, Richards JH (1990) Heterostyly in tropical plants. Mem N Y Bot Gard 55:35–61

Barrett SCH, Shore JS (1987) Variation and evolution of breeding systems in the *Turnera ulmifolia* L. complex (Turneraceae). Evolution 41:340–354

Barrett SCH, Wolfe LM (1986) Pollen heteromorphism as a tool in studies of the pollination process in *Pontederia cordata*. In: Mulachy DL, Mulcahy GB, Ottaviano E (eds) Biotechnology and ecology of pollen. Springer Berlin Heidelberg, New York, pp 435–442

Barrett SCH, Price SD, Shore JS (1983) Male fertility and anisoplethic population structure in tristylous *Pontederia cordata* (Pontederiaceae). Evolution 37:745–759

Barrett SCH, Brown AHD, Shore JS (1987) Disassortative mating in tristylous *Eichhornia paniculata* (Spreng.) Solms (Pontederiaceae). Heredity 58:49–55

Barrett SCH, Morgan MT, Husband BC (1989) The dissolution of a complex genetic polymorphism: the evolution of self-fertilization in tristylous *Eichhornia paniculata* (Pontederiaceae). Evolution 43:1398–1416

Bateman AJ (1952) Self-incompatibility systems in angiosperms I Theory. Heredity 6:285–310

Bateman AJ (1954a) The genetics of *Narcissus* I-sterility. Daffodil Tulip Year Book 1954:23–29

Bateman AJ (1954b) Self-incompatibility systems in angiosperms II *Iberis amara*. Heredity 8:305–332

Bawa KS (1980) Evolution of dioecy in flowering plants. Annu Rev Ecol Syst 11:15–40

Beach JH, Bawa KS (1980) Role of pollinators in the evolution of dioecy from distyly. Evolution 34:1138–1143

Beale GH (1939) Further studies of pollen-tube competition in *Primula sinensis*. Ann Eugenics 9:259–268

Bennett JH, Leach CR, Goodwins IR (1986) The inheritance of style length in *Oxalis rosea*. Heredity 56:393–396

Berry PE, Tobe H, Gómez JA (1991) Agamospermy and the loss of distyly in *Erythroxylum undulatum* (Erythroxylaceae) from northern Venezuela. Am J Bot 78:595–600

Bodmer WF (1960) Genetics of homostyly in populations of *Primula vulgaris*. Philos Trans R Soc Lond Ser B 242:517–549

Boyd M, Silvertown J, Tucker C (1990) Population ecology of heterostyle and homostyle *Primula vulgaris*: growth, survival, and reproduction in field populations. J Ecol 78:799–813

Bräm M (1943) Untersuchungen zur Phänalyse und Entwicklungsgeschichte der Blüten von *Primula pulerulenta, P. cockburniana* und ihrer F_1-Bastarde. Arch Julius Klaus-Stift Vererbungsforsch Sozialanthropol Rassenhyg 18:235–259

Briggs D, Walters SM (1984) Plant variation and evolution, 2nd edn. Cambridge Univ Press, Cambridge

Campbell JM, Lawrence MJ (1981) The population genetics of the self-incompatibility polymorphism in Papaver rhoeas I. The number of S-alleles in families from three localities. Heredity 46:69–79

Casper BB (1985) Self-compatibility in distylous *Cryptantha flava* (Boraginaceae). New Phytol 99:149–154

Casper BB, Sayigh LS, Lee SS (1988) Demonstration of cryptic incompatibility in distylous *Amsinckia douglasiana*. Evolution 42:248–253

Charlesworth B, Charlesworth D (1979) The maintenance and breakdown of heterostyly. Am Nat 114:499–513

Charlesworth D (1979) The evolution and breakdown of tristyly. Evolution 33:486–498

Charlesworth D (1989) Allocation to male and female function in hermaphrodites, in sexually polymorphic populations. J Theor Biol 139:327–342

Charlesworth D, Charlesworth B (1979) A model for the evolution of heterostyly. Am Nat 114:467–498

Charlesworth D, Charlesworth B (1981) Allocation of resources to male and female function in hermaphrodites. Biol J Linn Soc 15:57–74

Charlesworth D, Charlesworth B (1987) Inbreeding depression and its evolutionary consequences. Ann Rev Ecol Syst 18:237–268

Charnov EL (1982) The theory of sex allocation. Princeton Univ Press, Princeton, New Jersey

Coyne JA, Lande R (1985) The genetic basis of species differences in plants. Am Nat 126:141–145

Cronquist A, Holmgren AH, Holmgren NH, Reveal JL, Holmgren PK (1984) Intermountain flora, vol 4. N Y Bot Gard, New York

Crosby JL (1949) Selection of an unfavourable gene-complex. Evolution 3:212–230

Crowe LK (1964) The evolution of outbreeding in plants I. The angiosperms. Heredity 19:435–457

Curtis J, Curtis CF (1985) Homostyle primroses re-visited I. Variation in time and space. Heredity 54:227–234

Dahlgren RMT (1980) A revised system of classification of the angiosperms. Bot J Linn Soc 80:91–124

Darlington CD (1939) The evolution of genetic systems. Cambridge Univ Press, Cambridge

Darlington CD, Mather K (1949) The elements of genetics. Allen and Unwin, Lond

Darwin C (1865) On the sexual relations of the three forms of *Lythrum salicaria*. J Linn Soc Lond 8:169–196

Darwin C (1877) The different forms of flowers on plants of the same species. Murray, Lond

DeWinton D, Haldane JBS (1933) The genetics of *Primula sinensis* II segregation and interaction of factors in the diploid. J Genet 27:1–44

Donoghue MJ (1989) Phylogenies and the analysis of evolutionary sequences, with examples from seed plants. Evolution 43:1137–1156

Dulberger R (1964) Flower dimorphism and self-incompatibility in *Narcissus tazetta* L. Evolution 18:361–363

Dulberger R (1970) Floral dimorphism in *Anchusa hybrida* Ten. Isr J Bot 19:37–41

Dulberger R (1975a) *S*-gene action and the significance of characters in the heterostylous syndrome. Heredity 35:407–415

Dulberger R (1975b) Intermorph structural differences between stigmatic papillae and pollen grains in relation to incompatibility in Plumbaginaceae. Proc R Soc Lond Ser B 188:257–274

Eckenwalder JE, Barrett SCH (1986) Phylogenetic systematics of the Pontederiaceae. Syst Bot 11:373–391

Eckert CG, Barrett SCH (1992) Stochastic loss of style morphs from tristylous populations of *Lythrum salicaria* and *Decodon verticillatus* (Lythraceae). Evolution (in press)

Emerson S (1939) A preliminary survey of the *Oenothera organensis* population. Genetics 24:524–537

Feinsinger P, Busby WH (1987) Pollen carryover: experimental comparisons between morphs of *Palicourea lasiorrachis* (Rubiaceae), a distylous, bird-pollinated, tropical treelet. Oecologia 73:231–235

Felsenstein J (1988) Phylogenies from molecular sequences: inference and reliability. Annu Rev Genet 22:521–565

Fernandes A (1935) Remarque sur L'hétérostylie de *Narcissus triandrus* et de *N. reflexus*. Brot Bol Soc Broteriana Ser 2, 10:278–288

Fisher RA (1958) The genetical theory of natural selection, 2nd edn. Dover Publications, New York

Fisher RA, Martin VC (1948) Genetics of style length in *Oxalis*. Nature (Lond) 177:942–943

Ford EB (1964) Ecological genetics. Methuen, Lond

Ganders FR (1974) Disassortative pollination in the distylous plant *Jepsonia heterandra*. Can J Bot 52:2401–2406

Ganders FR (1975a) Mating patterns in self-compatible distylous populations of *Amsinckia* (Boraginaceae). Can J Bot 53:773–779

Ganders FR (1975b) Heterostyly, homostyly and fecundity in *Amsinckia spectabilis* (Boraginaceae). Madroño 23:56–62

Ganders FR (1979) The biology of heterostyly. N Z J Bot 17:607–635

Ganders FR, Denny SK, Tsai D (1985) Breeding system variation in *Amsinckia spectabilis* (Boraginaceae). Can J Bot 63:533–538

Gibbs PE (1986) Do homomorphic and heteromorphic self-incompatibility systems have the same sporophytic mechanism? Plant Syst Evol 154:285–323

Glover DE, Barrett SCH (1983) Trimorphic incompatibility in Mexican populations of *Pontederia sagittata* Presl. (Pontederiaceae). New Phytol 95:439–455

Glover DE, Barrett SCH (1986) Variation in the mating system of *Eichhornia paniculata* (Spreng.) Solms (Pontederiaceae). Evolution 40:1122–1131

Goldblatt P, Bernhardt P (1990) Pollination biology of *Nivenia* (Iridaceae) and the presence of heterostylous self-compatibility. Isr J Bot 39:93–111

Gottlieb LD (1984) Genetics and morphological evolution in plants. Am Nat 123:681–709

Graham SW, Barrett SCH (1990) Pollen precedence in *Eichhornia paniculata* (Pontederiaceae): a tristylous species. Am J Bot 77:54-55 (abstract)

Grant V (1975) Genetics of flowering plants. Columbia Univ Press, New York

Hamilton CW (1990) Variations on a distylous theme in Mesoamerican *Psychotria* subgenus *Psychotria* (Rubiaceae). Mem N Y Bot Gard 55:62–75

Haring V, Gray JE, McClure BA, Anderson MA, Clarke AE (1990) Self-incompatibility: a self-recognition system in plants. Science 250:937–941

Heuch I (1979) Equilibrium populations of heterostylous plants. Theor Popul Biol 15:43–57

Heuch I (1980) Loss of incompatibility types in finite populations of the heterostylous plant *Lythrum salicaria*. Hereditas 92:53–57

Hildebrand F (1866) Ueber den Trimorphismus in der Gattung *Oxalis*. Monatsber Königl Preuss Akad Wiss Berl 1866:352–374

Holsinger KE (1991) Mass action models of plant mating systems I. The evolutionary stability of mixed mating systems. Am Nat (in press)

Holsinger KE, Feldman MW, Christiansen FB (1984) The evolution of self-fertilization in plants: a population genetic model. Am Nat 124:446–453

Husband BC, Barrett SCH (1991a) Pollinator visitation patterns in populations of tristylous *Eichhornia paniculata* in northeastern Brazil. Oecologia (in press)

Husband BC, Barrett SCH (1991b) Colonization history and population genetic structure of *Eichhornia paniculata* in Jamaica. Heredity 66:287–296

Jernstedt JA (1982) Floral variation in *Chlorogalum angustifolium* (Liliaceae). Madroño 29:87–94

Karron JD, Marshall DL, Oliveras DM (1990) Numbers of sporophytic self-incompatibility alleles in populations of wild radish. Theor Appl Genet 79:457–460

Kohn JR, Barrett SCH (1992) Experimental studies on the functional significance of heterostyly. Evolution (in press)

Lack A, Kevan PG (1987) The reproductive biology of a distylous tree, *Sarcotheca celebica* (Oxalidaceae) in Sulawesi, Indonesia. Biol J Linn Soc 95:1–8

Lande R, Schemske DW (1985) The evolution of self-fertilization and inbreeding depression in plants I. Genetic models. Evolution 39:24–40

Leach CR (1983) Fluctuations in heteromorphic self-incompatibility systems. Theor Appl Genet 66:307–312

Lemmens RHMJ (1989) Heterostyly in Connaraceae. Acta Bot Neerl 38:224–225

Levin DA (1974) Spatial segregation of pins and thrums in populations of *Hedyotis nigricans*. Evolution 28:648–655

Lewis D (1982) Incompatibility, stamen movement, and pollen economy in a heterostylous tropical forest tree, *Cratoxylum formosum* (Guttiferae). Proc R Soc Lond Ser B 214:273–283

Lloyd DG (1979) Evolution towards dioecy in heterostylous populations. Plant Syst Evol 131:71–80

Lloyd DG (1980) Demographic factors and mating patterns in angiosperms. In: Solbrig OT (ed) Demography and evolution in plant populations. Blackwell, Oxford, pp 67–88

Lloyd DG, Webb CJ, Dulberger R (1990) Heterostyly in species of *Narcissus* (Amaryllidaceae), *Hugonia* (Linaceae) and other disputed cases. Plant Syst Evol 172:215–227

Lovett Doust J, Lovett Doust L, Cavers PB (1981) Fertility relationships in closely related taxa of *Oxalis*, section Corniculatae. Can J Bot 59:2603–2609

Martin FW (1967) Distyly, self-incompatibility, and evolution in *Melochia*. Evolution 21:493–499

Mather K (1950) The genetical architecture of heterostyly in *Primula sinensis*. Evolution 4:340–352

Mather K, DeWinton D (1941) Adaptation and counter-adaptation of the breeding system in *Primula*. Ann Bot II 5:297–311

Morgan MT, Barrett SCH (1988) Historical factors and anisoplethic population structure in tristylous *Pontederia cordata*: a re-assessment. Evolution 42:496–504

Morgan MT, Barrett SCH (1989) Reproductive correlates of mating system variation in *Eichhornia paniculata* (Spreng.) Solms (Pontederiaceae). J Evol Biol 2:183–203

Morgan MT, Barrett SCH (1990) Outcrossing rates and correlated mating within a population of *Eichhornia paniculata* (Pontederiaceae). Heredity 64:271–280

Muenchow GE (1982) A loss-of-alleles model for the evolution of distyly. Heredity 49:81–93

Muenchow GE, Grebus M (1989) The evolution of dioecy from distyly: reevaluation of the hypothesis of the loss of long-tongued pollinators. Am Nat 133:149–156

Mulcahy DL (1964) The reproductive biology of *Oxalis priceae*. Am J Bot 51:915–1044

Murray BG (1990) Heterostyly and pollen-tube interactions in *Luculia gratissima* (Rubiaceae). Ann Bot 65:691–698

Nicholls M (1987) Pollen flow, self-pollination and gender specialization: factors affecting seed set in the tristylous species *Lythrum salicaria* (Lythraceae). Plant Syst Evol 156:151–157

O'Brien SP, Calder DM (1989) The breeding biology of *Epacris impressa*. Is this species heterostylous? Austr J Bot 37:43–54

Olesen JM (1979) Floral morphology and pollen flow in the heterostylous species *Pulmonaria obscura* Dumort (Boraginaceae). New Phytol 82:757–767

Olmstead RG (1989) The origin and function of self-incompatibility in flowering plants. Sex Plant Reprod 2:127–136

Opler PA, Baker HG, Frankie GW (1975) Reproductive biology of some Costa Rican *Cordia* species (Boraginaceae). Biotropica 7:243–247

Ornduff R (1966) The origin of dioecism from heterostyly in *Nymphoides* (Menyanthaceae). Evolution 20:309–314

Ornduff R (1976) The reproductive system of *Amsinckia grandiflora*, a distylous species. Syst Bot 1:57–66

Ornduff R (1978) Features of pollen flow in dimorphic species of *Lythrum* section Euhyssopifolia. Am J Bot 65:1077–1083

Ornduff R (1980) Heterostyly, population composition, and pollen flow in *Hedyotis caerulea*. Am J Bot 67:95–103

Ornduff R (1986) Comparative fecundity and population composition of heterostylous and non-heterostylous species of *Villarsia* (Menyanthaceae) in western Australia. Am J Bot 73:282–286

Ornduff R (1988) Distyly and monomorphism in *Villarsia* (Menyanthaceae): some evolutionary considerations. Ann Mo Bot Gard 75:761–767

Palmer JD, Jansen RK, Michaels HJ, Chase MW, Manhart JR (1988) Chloroplast DNA variation and phylogeny. Ann Mo Bot Gard 75:1180–1206

Philipp M, Schou O (1981) An unusual heteromorphic incompatibility system: distyly, self-incompatibility, pollen load and fecundity in *Anchusa officinalis* (Boraginaceae). New Phytol 89:693–703

Piper JG, Charlesworth B, Charlesworth D (1984) A high rate of self-fertilization and increased seed fertility of homostyle primroses. Nature (Lond) 310:50–51

Piper JG, Charlesworth B, Charlesworth D (1986) Breeding system evolution in *Primula vulgaris* and the role of reproductive assurance. Heredity 56:207–217

Ray PM, Chisaki HF (1957) Studies of *Amsinckia* I. A synopsis of the genus, with a study of heterostyly in it. Am J Bot 44:529–536

Richards AJ (1986) Plant breeding systems. Allen and Unwin, Lond

Richards AJ, Ibrahim H (1982) The breeding system in *Primula veris* L. II. Pollen tube growth and seed set. New Phytol 90:305–314

Riveros M, Arroyo MTK, Humana AM (1987) An unusual kind of heterostyly in *Quinchamalium chilense* (Santalaceae) on Volcán Casablanca, southern Chile. Am J Bot 74:1831–1834

Sampson DR (1967) Frequency and distribution of self-incompatibility alleles in *Raphanus raphanistrum*. Genetics 56:241–251

Schaeppi H (1935) Kenntnis der Heterostylie von *Gregoria vitaliana* Derby. Ber Schweiz Bot Ges 44:109–132

Schou O, Philipp M (1984) An unusual heteromorphic incompatibility system III. On the genetic control of distyly and self-incompatibility in *Anchusa officinalis* L. (Boraginaceae). Theor Appl Genet 68:139–144

Schwarz-Sommer Z, Huijser P, Nacken W, Saedler H, Sommer H (1990) Genetic control of flower development by homeotic genes in *Antirrhinum majus*. Science 250:931–936

Scribailo RW, Barrett SCH (1991) Pollen-pistil interactions in tristylous *Pontederia sagittata* (Pontederiaceae) II. Patterns of pollen tube growth. Am J Bot (in press)

Scribailo RW, Barrett SCH (1992) Effects of compatible and incompatible pollen mixtures on seed set in tristylous *Pontederia sagittata* (Pontederiaceae). Unpubl. manuscript

Shore JS, Barrett SCH (1984) The effect of pollination intensity and incompatible pollen on seed set in *Turnera ulmifolia* (Turneraceae). Can J Bot 62:1298–1303

Shore JS, Barrett SCH (1985) The genetics of distyly and homostyly in *Turnera ulmifolia* L. (Turneraceae). Heredity 55:167–174

Shore JS, Barrett SCH (1986) Genetic modifications of dimorphic incompatibility in the *Turnera ulmifolia* L. complex (Turneraceae). Can J Genet Cytol 28:796–807

Shore JS, Barrett SCH (1990) Quantitative genetics of floral characters in homostylous *Turnera ulmifolia* var. *angustifolia* Willd. (Turneraceae). Heredity 64:105–112

Stirling J (1932) Studies of flowering in heterostyled and allied species Part 1. The Primulaceae. Publ Hartley Bot Lab 8:3–42

Stirling J (1933) Studies of flowering in heterostyled and allied species Part 2. The Lythraceae: *Lythrum salicaria*. Publ Hartley Bot Lab 10:3–24

Stirling J (1936) Studies of flowering in heterostyled and allied species Part 3. Gentianaceae, Lythraceae, Oxalidaceae. Publ Hartley Bot Lab 15:1–24

Tseng HP (1938) Pollen-tube competition in *Primula sinensis*. J Genet 35:289–300

Vasudevan Nair R (1975) Heterostyly and breeding mechanism of *Nymphoides cristatum* (Roxb.) O. Kuntze. J Bombay Nat Hist Soc 72:677–682

Webb CJ, Lloyd DG (1986) The avoidance of interference between the presentation of pollen and stigmas in angiosperms II Herkogamy. N Z J Bot 24:163–178

Wedderburn F, Richards AJ (1990) Variation in within-morph incompatibility sites in heteromorphic *Primula* L. New Phytol 116:149–162

Weller SG (1976a) Breeding system polymorphism in a heterostylous species. Evolution 30:442–454

Weller SG (1976b) The genetic control of tristyly in *Oxalis* section *Ionoxalis*. Heredity 37:387–393

Weller SG (1981) Pollination biology of heteromorphic populations of *Oxalis alpina* (Rose) Kunth (Oxalidaceae) in southeastern Arizona. Bot J Linn Soc 83:189–198

Weller SG, Ornduff RO (1977) Cryptic self-incompatibility in *Amsinckia grandiflora*. Evolution 31:47–51

Wells H (1979) Self-fertilization: advantageous or disadvantageous? Evolution 33:252–255

Wolfe LM, Barrett SCH (1989) Patterns of pollen removal and deposition in tristylous *Pontederia cordata* L. (Pontederiaceae). Biol J Linn Soc 36:317–329

Wyatt R (1983) Pollinator-plant interactions and the evolution of plant breeding systems. In: Real L (ed) Pollination biology. Academic Press, Orlando Florida

Yeo PF (1975) Some aspects of heterostyly. New Phytol 75:147–153