Heterostyly in Tropical Plants

SPENCER C. H. BARRETT AND JENNIFER H. RICHARDS

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Abstract

BARRETT, S. C. H. (Dept. of Botany, University of Toronto, Toronto, Ontario, Canada M5S 1A1) and J. H. RICHARDS (Dept. of Biological Sciences, Florida International University, Miami, Florida 33199, U.S.A.). Heterostyly in tropical plants. Memoirs of the New York Botanical Garden 55: 35–61. 1990. Since Darwin's original work, heterostylous breeding systems (distyly and tristyly) have provided a rich source of material for experimental studies of mating system evolution and genetics. Much of our knowledge of heterostyly has come from observations and experiments conducted on herbaceous taxa from the north temperate zone, particularly *Primula* and *Lythrum*. While it does not appear that the basic features of heterostyly differ between temperate and tropical species, the more diverse pollinator assemblages and larger number of woody heterostylous plants in tropical regions may complicate the functioning of the polymorphism, particularly in mass flowering species. Recent studies of several tropical groups indicate a variety of evolutionary modifications of the heterostylous syndrome, including the replacement of distyly by various gender polymorphisms (*Cordia* and several genera of Rubiaceae) and the breakdown of outcrossing to selfing via homostyle formation (e.g., *Turnera ulmifolia*). Many spurious accounts of heterostyly in tropical groups come from inadequate sampling and a misunderstanding of the

basic features of these complex polymorphisms. Suggestions are provided for future ecological investigations of tropical heterostylous plants and attention is drawn to various taxonomic groups that would repay detailed study.

Key Words: heterostyly; mating system evolution; pollinator assemblages; gender polymorphisms.

Introduction

Since the pioneering studies of Darwin (1862, 1877) and Hildebrand (1866), heteromorphic incompatibility systems have attracted the attention of biologists interested in the evolution and adaptive significance of plant reproductive systems. This is because the floral polymorphisms that constitute the heterostylous syndrome are simply inherited, and the genetic modifications that influence mating behavior can be detected easily under field conditions. Populations of heterostylous plants are usually composed of two (distyly) or three (tristyly) self- and intramorph incompatible mating groups that differ primarily in style length, anther height and pollen size. The polymorphisms are reliably reported from 24 phylogenetically diverse angiosperm families, indicating that these complex outbreeding systems are polyphyletic in origin.

Much of our knowledge of heterostyly has been derived from observations and experiments conducted on herbaceous taxa from the north temperate zone. Textbook descriptions of distyly and tristyly are usually based on Darwin's studies of *Primula vulgaris* and *Lythrum salicaria*, respectively. These taxa have also been used by several prominent geneticists as model systems for studies of inheritance, linkage, genetic polymorphism, and supergenes (Bateson & Gregory, 1905; Fisher & Mather, 1943; Ford, 1964; Lewis, 1949). Generalizations about the nature of heterostyly have often been extended from these studies to other families, despite the polymorphism's variable expression and occurrence in many unrelated taxa. In recent years this problem has been remedied, to some extent, as a broader range of plant material, particularly from tropical regions, has come under detailed investigation. This review attempts to integrate new information from tropical studies with existing data to clarify issues concerned with the function and evolution of heterostylous systems.

Although most studies of heterostyly have been conducted on temperate herbaceous species, there are several notable exceptions. Darwin (1877) made important observations on the floral morphology of a range of material sent to him by naturalist correspondents in the tropics. These included the following taxa: *Cordia, Cratoxylum, Eichhornia, Erythroxylum, Nymphoides, Pontederia* and several Rubiaceous genera. Burck (1883, 1884, 1887, 1895) discussed the relationships between distyly and tristyly, as well as the evolution of dioecism from heterostyly, based on studies of *Erythroxylum* and several tropical Rubiaceae. The first experimental pollination studies conducted in the tropics on a heterostylous plant were those carried out in Java on *Psychotria malayana* by Ernst (1932). Later, Baker (1958, 1962) in West Africa and Bir Bahadur (1968) in India examined the reproductive biology and pollination systems of several tropical heterostylous groups, particularly genera of Rubiaceae.

During the past decade, increased botanical exploration of tropical regions coupled with a revival of interest in pollination biology has resulted in a considerable amount of research on tropical heterostylous plants. While it does not appear that the basic features of heterostyly differ in any fundamental way between temperate and tropical species, the more diverse pollinator assemblages and larger number of woody heterostylous plants in tropical regions raise interesting ecological problems concerning the function of the polymorphism in large mass flowering species. In addition, several comparative studies reviewed below have revealed novel variation patterns which require us to broaden our ideas about the pathways of evolution in heterostylous groups.

In this review we first briefly summarize the basic features of the heterostylous syndrome and discuss recent ecological work on the function of the polymorphism using, where possible, examples from tropical species. We then discuss the spectrum of evolutionary modifications that have been discovered in tropical heterostylous groups with a special focus on floral heteromorphisms that do not readily fit into the conventional view of the polymorphism. We conclude by suggesting research areas in need of attention and particular taxonomic groups which we believe would be worth critical in-depth study. Since few comprehensive studies of woody heterostylous groups have been reported, we have broadened our coverage to include both herbaceous and woody tropical plants. For more comprehensive treatments of the subject of heterostylous breeding systems, the reader is referred to the reviews of Vuilleumier (1967), Ganders (1979a) and Richards (1986).

The Heterostylous Syndrome

Although heterostyly was first documented by Clusius in *Primula* in 1583 (van Dijk, 1943), the term was not used widely until Darwin's book on the subject was published in 1877. While Hildebrand (1866) used "heterostyly" in a strictly morphological context, Darwin restricted its use to those taxa in which the style and stamen polymorphisms were accompanied by a self- and intramorph incompatibility system (Fig. 1). Since that time a significant number of heterostylous species have been examined in which the incompatibility system is either weakly developed or non-existent. However, in virtually all cases related heterostylous taxa that possess diallelic incompatibility are known, and it seems probable that self-compatible heterostyly is a derived condition involving relaxation and eventual loss of the incompatibility system (although see Lloyd and Webb, 1990a for an alternative view). We use the term heteromorphic to refer to other systems, such as those in *Narcissus* and *Anchusa*, where incompatibility is multiallelic. The difficulties of providing a universal definition of heterostyly are likely to become more pronounced as additional species are examined, and we discuss these problems more fully below.

Several additional floral polymorphisms can accompany the differences in style length and stamen height in the floral morphs of heterostylous species. These usually involve differences in the size and shape of stigmatic papillae and the size and number of pollen grains produced by the sets of stamens of contrasting height. Other, more restricted, morph-specific polymorphisms which have been reported include differences in corolla size and shape, stylar coloration and pubescence, pollen shape, color, exine sculpturing and storage products, ovule number and seed size. In some cases the degree of polymorphism varies between populations of a species, whereas in others the polymorphisms are stable features of all heterostylous taxa in a family. It is noteworthy that all polymorphisms reported in heterostylous plants involve reproductive structures and, as yet, there is not convincing evidence of morph-specific differences in vegetative characters. The functional significance of most of the floral polymorphisms that occur in heterostylous groups are uninvestigated, despite their obvious value as experimental systems. Presumably, the diversity in expression of floral polymorphisms among heterostylous taxa reflects contrasting selection pressures imposed by different pollinator groups, as well as developmental and phylogenetic constraints specific to particular heterostylous lineages.

The inheritance of distyly has been determined for twelve genera from ten families (Ornduff, 1979a; Shore & Barrett, 1985a). The polymorphisms are inherited as if controlled by a single gene "locus" with two alleles. Except for two genera where the dominance relationships are reversed (Baker, 1966; Ornduff, 1979a), the long-styled morph (hereafter L) is homozygous (ss), while the short-styled morph (hereafter S) is heterozygous (Ss). Evidence from the Primulaceae (Ernst, 1955), Plumbaginaceae (Baker, 1966) and Turneraceae (Shore & Barrett, 1985a) suggests that distyly is controlled by a series of tightly linked genes that comprise a supergene. Self-compatible forms, known as homostyles, with anthers and stigmas at the same level in a flower are interpreted as recombinant phenotypes that have arisen by crossing-over within the supergene. Although homostyles are rarely observed in distylous populations, close relatives of distylous taxa are frequently monomorphic for style and stamen length, and comparative studies in-

dicate that the evolutionary breakdown of heterostyly to homostyly is common (Baker, 1966; Barrett & Shore, 1987; Richards, 1986).

The genetic control of tristyly is more complex, and little is known about how the genes that control the various components of the polymorphism are organized. A similar two-locus (S, M) system has been demonstrated in three families (Lythraceae, Oxalidaceae and Pontederiaceae) in which tristyly has been reliably reported. Under this model the S locus is epistatic to the M locus, and the genotypes for the three style lengths are: long-styled morph (hereafter L) $ssmm$; mid-styled morph (hereafter M) $ssMm$, $ssMM$; short-styled morph (hereafter S) $SsMm$, $SsMM$, $Ssmm$. Variations in linkage relationships, epistasis and polyploidy result in different patterns of inheritance within and among the three families (Fisher & Mather, 1943; Weller, 1976; S. C. H. Barrett, unpublished data). Recently, a three-locus model has been proposed for the inheritance of tristyly in *Oxalis rosea* (Bennett et al., 1986).

In most distylous species the supergene determining the floral polymorphisms also controls a diallelic, sporophytic, physiological self-incompatibility system in which only pollinations between morphs are compatible. These pollinations are referred to as legitimate (Darwin, 1877), while the remaining self- and intramorph pollinations are known as illegitimate pollinations. Tristylous plants usually possess a two-locus, diallelic, sporophytic incompatibility system, but since each plant possesses two stamen levels, not all intermorph pollinations are legitimate. Seed set is normally obtained from pollinations between anthers and stigmas of equivalent height. Legitimate pollinations in distylous and tristylous plants are illustrated in Figure 1.

In most angiosperm families with homomorphic sporophytic incompatibility, pollen is trinucleate and the inhibition of incompatible pollen tubes occurs on the stigmatic surface (Brewbaker, 1967; Nettancourt, 1977). In contrast, heteromorphic species may possess binucleate or trinucleate pollen, and several different sites of pollen tube inhibition have been reported, including the stigma, style and ovary (see Anderson & Barrett, 1986; Gibbs, 1986). One of the most striking features of incompatibility behavior in heterostylous taxa is that the site of

pollen tube inhibition usually differs between the floral morphs. For example, in ten distylous Rubiaceae from tropical lowland wet forest in Costa Rica the site of the incompatibility barrier varied both within and between species (Bawa & Beach, 1983). In the S morph pollen tubes were always inhibited in the stigmatic tissue, whereas in the L morph the site varied between species. In some cases pollen tubes from self- and intramorph pollinations penetrated to the base of the style, although no seed was produced. In tristylous *Pontederia sagittata* from Mexico pollen tube inhibition depends on the particular pollen size-style length combination that is involved. Inhibition occurs in the stylar tissue (L and M morphs) or the ovary (M and S morphs). Ovarian rejection is prezygotic with pollen tube inhibition primarily localized in the region of the micropyle (Glover & Barrett, 1983; Scribailo & Barrett, unpublished data). These observations suggest that the general properties of incompatibility reactions in homomorphic and heteromorphic sporophytic systems may be fundamentally different and cast doubt on the evolutionary derivation of heteromorphic from homomorphic incompatibility (Barrett, 1988a; Gibbs, 1986).

Heterostyly in the Tropics

Heterostyly is not apparently associated with any geographical region, habitat or life form, and there is no indication that the polymorphism is over-represented in tropical relative to temperate areas. The major difference between temperate and tropical heterostylous groups is the larger representation of woody heterostylous taxa in tropical communities. This probably reflects the trend toward woodiness in tropical members of families with both temperate and tropical distributions (Hallé et al., 1978). In temperate regions there are no heterostylous trees and few shrubs, whereas in the tropics many heterostylous genera are exclusively woody (e.g., *Averrhoa, Biophytum, Byrsocarpus, Cordia, Cratoxylum, Erythroxylum, Oplonia,* and many Rubiaceae). Although woody heterostylous plants occur in many different types of tropical vegetation, they are most commonly represented as shrubs or small trees of the sub-canopy of tropical forests. Few species are found as tall trees in the canopy layer (Baker et al., 1983). A list by family of
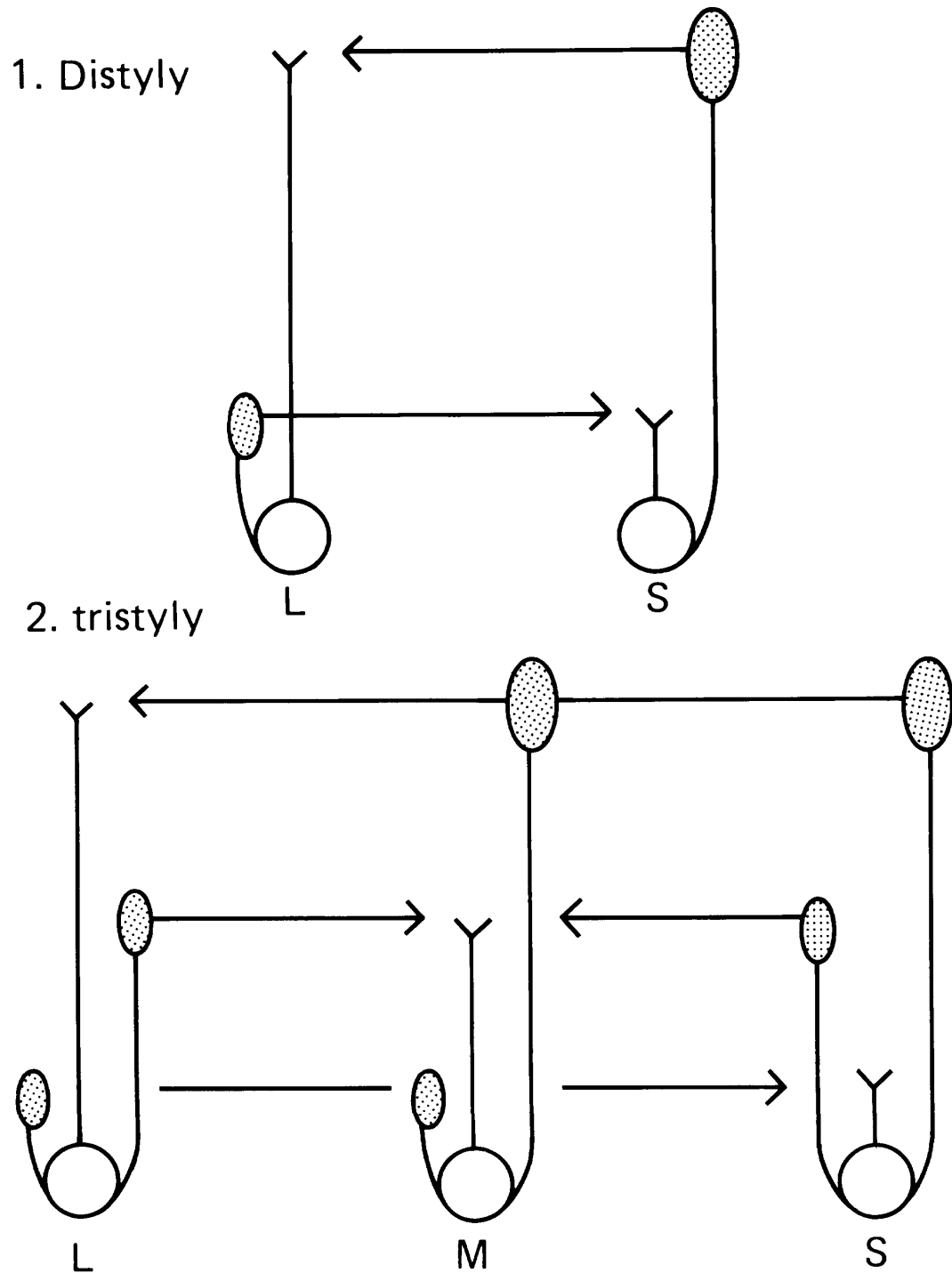
1. Distyly

2. tristyly

Fig. 1. The heterostylous genetic polymorphisms, distyly and tristyly. Legitimate pollinations are indicated by arrows.

primarily tropical genera in which heterostyly is reported is given in the Appendix. Many of the genera are essentially unstudied; where modern work has been conducted, a recent reference is provided.

As a result of the paucity of breeding system studies at the community level in tropical regions, it is premature to generalize about the relative frequency or functional role of heterostyly in comparison with other outbreeding systems. The only studies available are those of Bawa and colleagues for two lowland forest ecosystems in Costa Rica and by Arroyo and colleagues for a secondary deciduous forest and a montane cloud forest in Venezuela. In Costa Rica 2–3% of the woody species in each ecosystem are distylous (K. S. Bawa, unpublished, cited in Baker et al., 1983) whereas in Venezuela two of the 22 species examined in the deciduous forest (Zapata & Arroyo, 1978) and three of the 35 species occurring in cloud forest were distylous (Sobrevila & Arroyo, 1982). These low frequencies are not unexpected, given the rarity of heterostyly in the Angiosperms as a whole.

Owing to the greater range of potential pollinators in tropical as compared with temperate communities, it seems reasonable to predict that tropical heterostylous groups will display more variation in the heterostylous syndrome. The relatively stereotyped floral plans of temperate heterostylous genera such as *Primula, Linum* and *Oxalis* suggest a restricted range of body sizes and behaviors among pollinator groups that visit these taxa. These patterns contrast with those displayed by families such as the Rubiaceae, where adaptive radiation of floral traits to a wide range of pollinators, including bees, moths, butterflies and hummingbirds, has occurred [see Gentry, this volume]. Such evolutionary diversification raises some interesting issues concerned with the function of heterostyly under contrasting pollinator faunas. As yet there has been little detailed work on the pollination biology of tropical heterostylous plants.

Functional Significance of Heterostyly

DISASSORTATIVE POLLINATION

The most widely accepted explanation of the functional significance of heterostyly was originally formulated by Darwin (1877), who hypothesized that the reciprocal placement of stamens and styles in the floral morphs is a mechanical device to promote insect-mediated legitimate pollination. According to the hypothesis, pollen from different stamen levels adheres to specific locations on a pollinator's body, corresponding to the position where compatible stigmas contact the pollinator. The result is phenotypic disassortative pollination among floral morphs.

During the past two decades, the amount of legitimate pollination in natural populations of heterostylous plants has been investigated by using the conspicuous size heteromorphism of pollen produced by different stamen levels. By examining stigmatic pollen loads, the number of legitimate (compatible) and illegitimate (incompatible) pollen grains deposited by pollinators can be estimated. Most studies to date have been conducted on populations of temperate distylous species. Although in many cases authors concluded that their data provided limited support for the Darwinian hypothesis, this interpretation must be questioned because in most cases inappropriate experimental designs were used (Ganders, 1979a; Lloyd & Webb, 1990b). To evaluate whether the stamen-style heteromorphism promotes significant levels of legitimate pollination, the intrafloral illegitimate component of the pollen load should be removed by emasculation (Ganders, 1974). Emasculation is necessary because pollen transfer between anthers and stigmas within a flower is unaffected by the polymorphism, and this component of the pollen load obscures the critical parameter to be measured, the illegitimate outcrossed fraction of the pollen load. In the two studies where this procedure has been adopted, in distylous *Jepsonia heterandra* (Ganders, 1974) and tristylous *Pontederia cordata* (Barrett & Glover, 1985), support for the Darwinian hypothesis was obtained.

Only three pollen flow studies have been conducted on tropical plants. These involve distylous *Cratoxylum formosum* in Singapore (Lewis, 1982) and *Turnera subulata* (*T. ulmifolia* var. *elegans*) in India (Rama Swamy & Bir Bahadur, 1984) and tristylous *Pontederia sagittata* in Mexico (Glover & Barrett, 1983). In each study the investigators found large amounts of illegitimate pollen on open-pollinated stigmas. Because

emasculation was not employed, however, it is not possible to fully evaluate the efficacy of heterostyly in promoting disassortative pollination in these species.

The study of *Cratoxylum formosum* by Lewis (1982) is of particular interest, because the species' novel floral morphology distinguishes it from other heterostylous species. Instead of possessing a limited number of stamens, as is common in most heterostylous taxa, *C. formosum* has numerous (144) anthers. These are arranged in staminal bundles so that more than half the height of the flower is occupied by anthers, and the anther positions are partially concurrent in the two morphs. Lewis describes an unusual method by which the two anther levels are distinguished through stamen bending in the L morph. After the flower has opened, the longer anthers in the L morph bend to the level of the shorter anthers, so that all anthers occupy a narrow disc which corresponds in height to stigmas of the S morph. Anther bending in the L morph coincides with anther dehiscence, and the stamens return to the upright position later in the day, when pollination is complete. Lewis argues that the stamen movement mechanism in the L morph is an important evolutionary innovation which developed to promote effective pollination of the S morph. The pollen load data, however, indicate that in comparison to the L morph the S morph receives few legitimate pollen grains. While stigmas of the L morph capture an average 1200 grains of which 46% are compatible, the S morph receives only 64 grains of which 90.5% are compatible. This disparity between morphs in total pollen capture is the largest reported for a heterostylous species.

POLLEN-STIGMA INTERFERENCE

As in many woody tropical plants, *Cratoxylum formosum* opens thousands of flowers at the same time. Where pollinators forage systematically within a restricted area, this flowering pattern is likely to result in high levels of geitonogamous pollination, raising the issue of whether there are negative influences of illegitimate pollen on seed set. Several workers have considered the potential evolutionary significance of the inhibitory effects of incompatible pollen on seed set in self-incompatible plants (Bawa & Opler, 1975; Zapata & Arroyo, 1978). This effect could be important in heterostylous species because the limited number of mating groups in populations results in stigmas capturing large amounts of incompatible pollen. Lloyd and Yates (1982) and Webb and Lloyd (1986) have recently proposed that the stamen-style polymorphism which characterizes heterostylous plants is a floral mechanism to reduce mutual interference between maternal and paternal reproductive functions. According to this view, one effect of the spatial separation of anthers and stigmas is that it increases maternal fitness by reducing adverse effects of incompatible pollen and allowing more space on the stigma for compatible pollen.

Unfortunately, relatively few experimental studies have demonstrated clear inhibitory effects of incompatible pollen to maternal reproductive function in self-incompatible plants (although see Nicholls, 1987). While, as described above, open pollinated stigmas of distylous *Turnera ulmifolia* and tristylous *Pontederia sagittata* capture large amounts of incompatible pollen, separate investigations of each species have failed to detect any large-scale inhibitory effects of incompatible pollen. In *T. ulmifolia,* Shore and Barrett (1984) found a deleterious effect of self pollen on the performance of cross pollen in the L morph, but this only occurred with the highest deposition level (5 anthers) and after the longest interval of time (3.4 hours) between the application of the two pollens. In *P. sagittata* the L morph is also more susceptible to the inhibitory effects of incompatible pollen, with detrimental effects becoming more significant as the interval of time increases between applications of self and cross pollen (Scribailo & Barrett, unpublished data). No effects were evident in the S morph of *P. sagittata,* but small inhibitory effects were demonstrated in the M morph. However, field studies of both species suggest that these effects would be unlikely to occur in natural populations, since ample legitimate pollen is usually deposited on stigmas soon after the commencement of anthesis. In other mass flowering heterostylous species, however, it is possible that large incompatible pollen loads may have detrimental influences on seed set. These effects may be particularly important in woody heterostylous species of forest environments where, because of high species diversity, individual plant densities may be low. It is noteworthy that in Lewis's study of *Cratoxylum formosum,* conducted in a road-

side plantation, pollen loads of some bees were composed of only one pollen type indicating local foraging. In natural stands, where density could be considerably lower, this situation may be accentuated.

POLLEN CARRYOVER

Despite large floral displays, restricted foraging by pollinators and high illegitimate pollen loads, sufficient legitimate pollen is usually deposited on stigmas of heterostylous plants to effect maximum seed set (Lewis, 1982). This observation suggests that significant pollen carryover occurs in most heterostylous populations, and it has been suggested that the stamen-style polymorphism may function, in part, to enhance pollen carryover (Waser & Price, 1983; Glover & Barrett, 1986b). Thus, floral heteromorphism may reduce pollen wastage on illegitimate stigmas by increasing pollen residency on pollinators and, therefore, increasing the distance that it is transported. Such an effect might be particularly important in species with large floral displays, such as trees or species with extensive clonal growth. By increasing the distance that pollen is dispersed, a greater number of genets are likely to be encountered, resulting in enhanced male fitness. Because pollen size is morph-specific in many heterostylous species, measurements of pollen carryover can be made under field conditions (Wolfe & Barrett, 1989). To evaluate the hypothesis outlined above, comparisons of carryover runs involving a single morph and mixtures of morphs are required. The hypothesis predicts longer pollen carryover (a flatter curve) under heteromorphic sequences than under monomorphic sequences.

In one of the first experimental studies of the pollination ecology of a tropical heterostylous species, Feinsinger and Busby (1987) compared the patterns of pollen carryover in the floral morphs of *Palicourea lasiorrachis*. The species occurs in cloud forests of Central America and is hummingbird pollinated. By assessing compatible pollen tubes in recipient styles, they found that plants of the S morph transferred significantly fewer total pollen grains to flowers of the L morph than vice versa. However, pollen of the S morph was more evenly dispersed among recipient stigmas and travelled further than pollen of the L morph. The difference in amounts of

pollen captured is not the result of the usual pollen production differences between the morphs (see Ganders, 1979a), since in *P. lasiorrachis* the morphs do not vary in this trait. Feinsinger and Busby (1987) suggest that differences in stigma size may contribute to the asymmetric patterns of pollen carryover between the morphs. The stigma of the L morph is much smaller in surface area (3.04 vs. 7.45 mm^2) than that of the S morph. As a result, pollen grains of the S morph are less likely than those of the L morph to be captured by compatible recipient stigmas.

These investigations of pollen flow illustrate the kind of field studies that are required to fully understand the complexities of the pollination process in heterostylous plants. Considering that heterostyly was the first sexual system in plants to be recognized as an ecological phenomena involving pollination biology, it is remarkable how little detailed work has been conducted on the pollination ecology of heterostylous species, particularly in tropical communities.

Evolutionary Modifications

Most families in which heterostyly occurs provide evidence of evolutionary modifications of both the floral morphology and incompatibility system. These changes have important influences on the mating systems of populations and can initiate character divergence and speciation (Barrett, 1989a). Comparative studies of related species have commonly been employed to infer pathways of breeding system evolution in heterostylous groups (Baker, 1966; Ornduff, 1972). Of particular significance are species which display intraspecific variation in floral biology and breeding systems. In these cases population studies can be employed to investigate the selective mechanisms responsible for changes in mating behavior. In addition, the genetic basis of alterations in floral traits and incompatibility systems can be determined using controlled crosses (Weller, 1976; Barrett, 1985a, 1985b; Shore & Barrett, 1986). Intraspecific studies are more likely to provide conclusive evidence of the causes of mating system change, since the possibility of confounding taxonomic differences with factors responsible for evolutionary shifts in breeding pattern is minimized.

Mating systems of heterostylous species can be

modified in two distinct ways: either to an alternative outbreeding system, or, more frequently, to an increased level of inbreeding via self-fertilization. Below, we review several examples of these pathways using recent studies of tropical heterostylous groups. First, however, we consider several cases of taxa in which incomplete sampling, usually of herbarium material, has led to misinterpretations of the true nature of the breeding system. This problem has been particularly evident in tropical groups, where field observations and experimental work have often been lacking.

MISINTERPRETATIONS OF HETEROSTYLY

Many species have been reported as heterostylous but with closer examination have proven to be otherwise. Taxonomists working with herbarium specimens have often confused interpopulation discontinuities in floral organ size or developmental variation with true heterostyly. Asa Gray reported heterostyly in *Phlox subulata,* which has long styles, as a result of lumping it with *Phlox nivalis,* which has short styles (Grant & Grant, 1965). In some cases the reverse situation has arisen, where the floral morphs of heterostylous species have been described as distinct species because of their contrasting floral architectures (e.g., *Quinchamalium,* as discussed by Riveros et al., 1987; *Schismatoclada,* as discussed by Verdcourt, 1958). Some confusion has also arisen concerning the occurrence and true nature of tristyly. Bir Bahadur's surprising claim that tristyly occurs in 57 genera from 14 families (Bir Bahadur, 1978) is clearly based on a misunderstanding of the fundamental features of the polymorphism. However, the unconfirmed reports of tristyly in *Agelaea* (Hemsley, 1956) and *Hugonia* (Robson, 1963) deserve more attention.

Erythroxylum spp. have been described as distylous (Darwin, 1877) and tristylous but in evolutionary transition to distyly (Burck, 1895). Recent experimental studies by Ganders (1979b), including measurements of floral traits and controlled crosses of *E. coca* and *E. novogranatense,* indicate that these species are distylous. Burck's confusion appears to have arisen because the flowers of each morph possess two sets of stamens with slightly different pollen sizes, a characteristic of tristylous species. The stamens, however, particularly of the S morph, display considerable variation in length that is unrelated to incompatibility type, since pollen from both levels within a morph exhibits the same incompatibility phenotype. Variation in stamen height is continuous, making it impossible to divide either morph into sub-groups, except in a completely arbitrary way (Fig. 2). Controlled crosses, conducted by Ganders, revealed the presence of two self- and intramorph incompatible mating groups associated with the style length differences.

A different situation occurs in the notorious tropical aquatic weed *Eichhornia crassipes,* the water hyacinth. Ever since Fritz Müller (1871, 1883) reported L and M morphs of *E. crassipes* in southern Brazil, there has been disagreement as to whether *E. crassipes* is distylous or tristylous. The first report of tristyly was made in the English edition (1883) of "Die Befruchtung der Blumen durch Insekten" by Herman Müller (1873). However, the report is an apparent mistranslation by D'Arcy W. Thompson of the original German edition, where no mention is made of the S morph. Herman Müller and later Darwin (1877) stated that *E. crassipes* was probably trimorphic, basing their statements on the assumption that the missing S morph would be found. Until recently, however, this had not occurred, and most modern workers have considered the species to have lost the S morph and become distylous. Since distyly has evolved from tristyly in other heterostylous families (see below), this seemed quite plausible. Discovery of the "missing" S morph in the Amazon Basin in 1974 (Barrett, 1977a), however, provided conclusive evidence that the species is tristylous. The uneven geographical distribution of floral morphs in *E. crassipes* (Fig. 3) (Barrett & Forno, 1982) cautions against generalizations about the floral biology of a species based on observations from a limited part of its range.

EVOLUTION OF DISTYLY FROM TRISTYLY

Although Burck's suggestion that the breeding system of *Erythroxylum* was in evolutionary transition from tristyly to distyly has proven incorrect, this pathway of evolution has been documented in *Oxalis* and *Lythrum* (Mulcahy, 1964; Ornduff, 1972). Among tropical plants the shrub *Pemphis acidula,* an inhabitant of seashores from
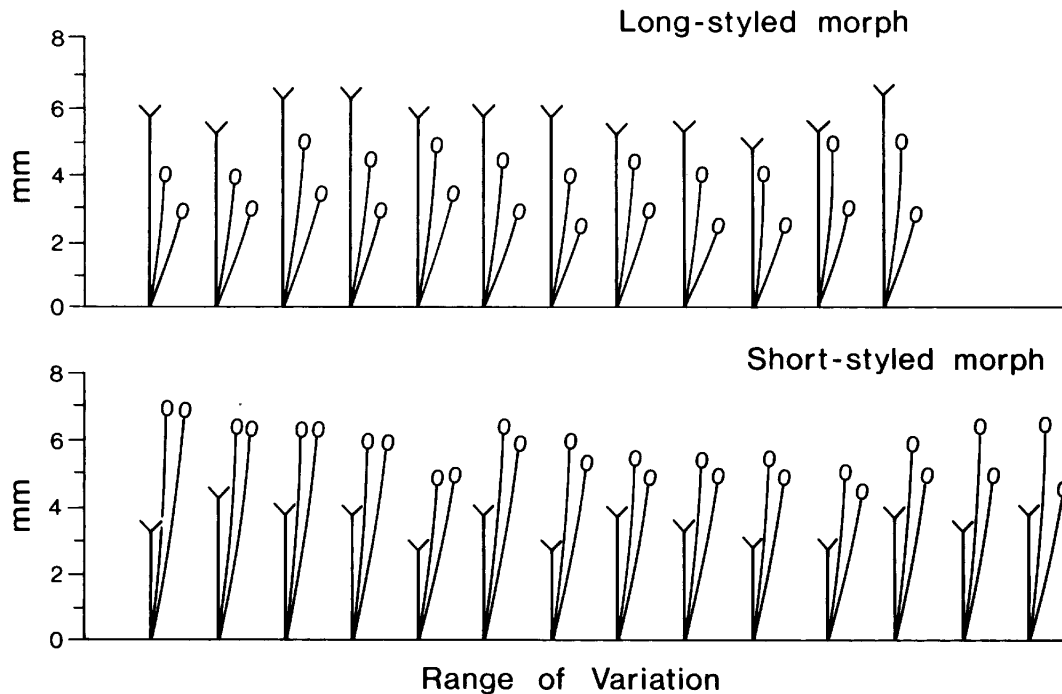
Long-styled morph

Short-styled morph

Range of Variation

Fig. 2. Variation in style and stamen lengths in *Erythroxylum coca*. After Ganders (1979b).

East Africa to the Pacific Ocean, exhibits particularly interesting patterns of variation in floral traits, which Lewis and Rao (1971) and Lewis (1975) interpret as the result of disruptive selective acting on the breeding system. A large number of populations distributed from Africa to Taiwan contain the L and S morphs, but not the M morph. The populations exhibit considerable variation in anther height and pollen size, with both morphs possessing two distinct anther levels. In the L morph, however, mid-level anthers are below the mid position and close to short-level anthers, whereas in the S morph mid-level anthers are close to long-level anthers. Controlled crosses revealed that the two morphs were self- and intramorph incompatible and that pollen originating from different anther levels within a flower exhibits the *same* incompatibility phenotype. These patterns suggest that the M morph has been lost from populations, and selection for changes in the position and incompatibility behavior of mid-level anthers in the remaining two morphs has been associated with this change. A similar process appears to have occurred in populations of *Oxalis alpina* in Mexico and southeast Arizona (Weller, 1986). In both *Pemphis* and *Oxalis* it is unclear what selective forces are involved, and why in both species the M morph is lost from populations.

EVOLUTION OF DIOECISM FROM DISTYLY

Several distylous genera (e.g., *Cordia, Coussarea, Erythroxylum, Mussaenda, Nymphoides, Psychotria*) contain dioecious taxa. This observation led Darwin (1877) to suggest that sexual dimorphism could evolve from heterostyly as a result of gender specialization, with the two floral morphs no longer making equal contributions to offspring through pollen and ovules. Although this breeding system change is quite rare, it has attracted considerable theoretical interest because of the possibilities that the selective forces involved are independent of inbreeding avoidance and outcrossing advantage (Charnov, 1982). The transition is particularly evident in several tropical woody genera of the Rubiaceae and in *Cordia* (Boraginaceae).
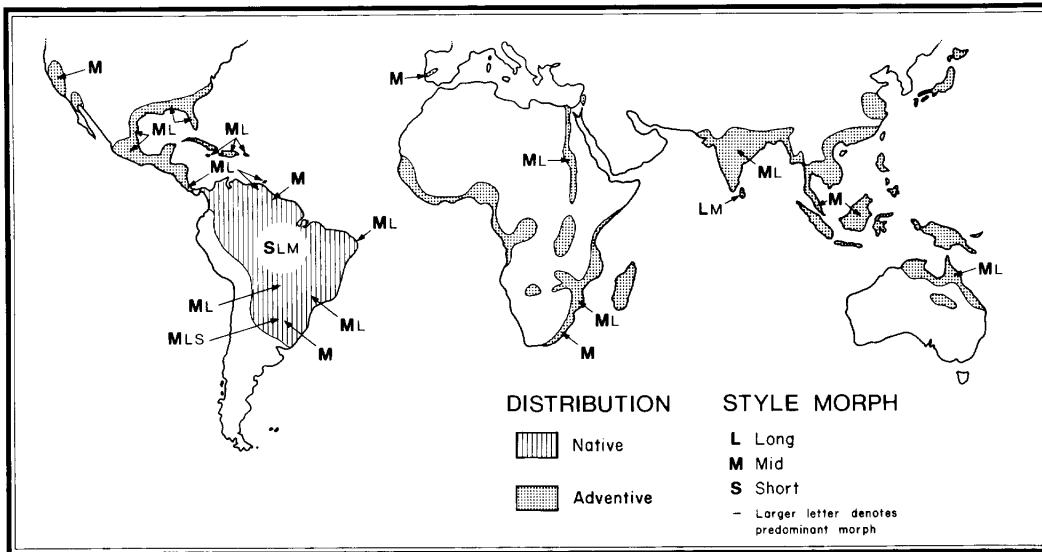
Fig. 3. The geographical distribution of floral morphs in tristylous *Eichhornia crassipes*. Modified from Barrett (1977a) and Barrett & Forno (1982).

Beach and Bawa (1980), following Robertson (1892) and Baker (1958), have proposed that the shift from distyly to dioecy is initiated by a change in the pollinators of distylous populations that disrupts reciprocal pollen flow between individuals of the two floral morphs (Fig. 4). A loss of specialized long-tongued pollinators, for example, would result in undirectional pollen transport from long-level stamens of the S morph to stigmas of the L morph. They postulate that ac-cumulation of sterility mutations affecting pollen and ovule fertility in the L and S morphs, re-spectively, would occur because of disuse of short-level organs. This would result in development of strict femaleness and maleness, respectively, in the two floral morphs. Beach and Bawa (1980) provide two lines of evidence in support of this hypothesis. First, they show that in several cases the evolution of dioecy from distyly has been accompanied by a shortening of corolla tube
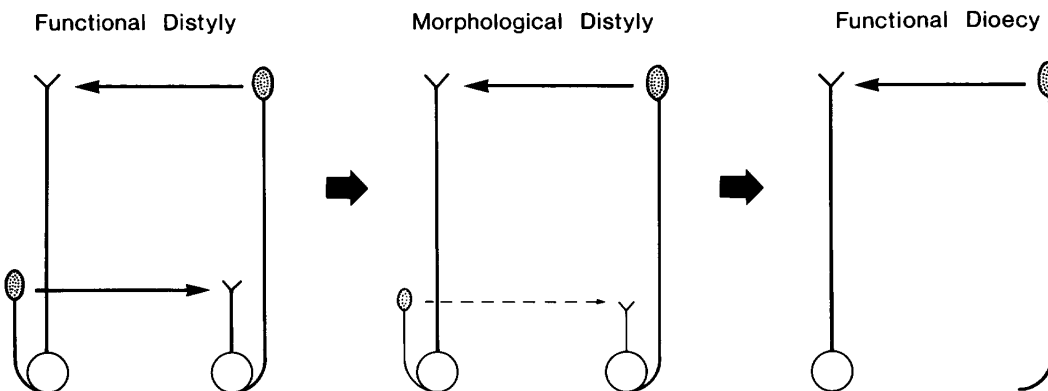

Fig. 4. Model of the evolution of dioecism from distyly following the Bawa & Beach (1980) hypothesis. Note the loss of pollen transport between short-level organs.

length. Secondly, they claim that in all known cases the L morph has evolved into the pistillate plant and the S morph the staminate plant. This pattern is consistent with the hypothesis and not predicted by any other.

Muenchow and Grebus (1989) have recently challenged the Beach and Bawa hypothesis, as well as the long-held belief that femaleness evolves in the L morph and maleness in the S morph. They modelled the spread of sterility mutations in a distylous population and examined: 1) how sensitive the spread of unisexuality was to recombination between the mutations and the distyly "locus"; and 2) whether partial, rather than absolute, loss of specialized pollinators would lead to the evolution of dioecism. Their results indicate that the conditions under which dioecy can evolve from distyly following the Beach and Bawa model are quite restrictive. The change occurs only if the sterility mutations are very tightly linked to the distyly supergene and if the loss of long-tongued pollinators is virtually complete. From a survey of the literature the authors also concluded that, while flowers often become shallower in association with the evolution of dioecism, there was little evidence that the L morph inevitably becomes pistillate and the S morph staminate. However, while it is true that in some genera (e.g., *Coussarea, Nymphoides*) it is difficult to discern from which of the floral morphs the two sexes have originated, in others (e.g., *Mussaenda, Cordia*) this is not the case.

The most informative comparative data come from a study of eight *Cordia* species from Costa Rica (Opler et al., 1975). Among the taxa studied a range of breeding systems was represented, including distyly, subdioecy, dioecy and homostyly. The authors proposed two major pathways of evolution from an ancestral distylous condition, one toward dioecy via gender specialization and the other to self-fertilization via homostyly. Using the fruit set and morph ratio data collected by Opler et al. (1975), Lloyd (1979) formulated phenotypic gender measures for the morphs of five *Cordia* species (Table I). These data illustrate the development of gender specialization that accompanies the evolution of dioecism in *Cordia*. Distylous *C. dentata* and *C. pringlei* exhibit no apparent gender differences, sub-dioecious *C. inermis* and *C. collococca* show considerable gender specialization, and *C. panamensis* is dioe-

cious with the L morph transmitting genes solely through ovules and the S morph acting as a strictly unisexual (constant) male. The transition is accompanied by a change in corolla depth (Table I), suggesting that alterations in the pollinator fauna of *Cordia* species may have played a role in driving the system from distyly to dioecy, as Beach and Bawa (1980) proposed.

Studies of *Cordia* highlight the importance of obtaining fertility measures for the floral morphs in natural populations since conclusions based solely on floral morphology are likely to be erroneous. Ideally, individual fertility measures should be obtained and genetic analysis of plant-to-plant variation in the degree of gender specialization conducted. Although the floral morphs in heterostylous populations often differ in pollen and seed production, relatively few examples of the shift to gender dimorphism are known. Since no accurate measures of *functional gender* are currently available for the morphs of heterostylous plants, it is premature to assume, as many recent authors have done, that gender specialization is a standard expectation in heterostylous populations.

EVOLUTION OF SELF-FERTILIZATION

The most common pattern of evolutionary modification in heterostylous breeding systems involves the breakdown of the polymorphism toward increased self-fertilization and floral monomorphism (Barrett, 1989b). The usual pathway is by the formation of self-compatible homostyles. Homostyles possess stigmas and anthers at the same relative position within a flower and, as a result, are largely self-pollinating and autogamous. Many heterostylous genera (e.g., *Amsinckia, Eichhornia, Lythrum, Melochia, Oxalis*) contain homostylous taxa that are small-flowered, highly self-pollinating and adapted to pioneer environments. This correlation suggests that the shift to selfing has evolved repeatedly in association with the colonization of temporary habitats.

The co-occurrence of floral heteromorphism and monomorphism among related heterostylous taxa can present difficulties for evolutionary interpretation, since taxa that are monomorphic for floral traits may be either ancestral or derived from their heterostylous relatives. The term homostylous was used specifically by Darwin

Table I
Gender specialization in *Cordia* (Boraginaceae)[a]

Species	Breeding system	Corolla length (cm)	L or female		S or male	
			Fruit set	G_P	Fruit set	G_P
C. dentata	distylous	0.85	17	0.443	18	0.557
C. pringlei	distylous	1.9	17	0.471	15	0.529
C. inermis	sub-dioecious	0.27	9.5	0.947	1	0.053
C. collococca	sub-dioecious	0.4	33	0.957	1	0.043
C. panamensis	dioecious	0.45	19	1.000	0	0.000

[a] After Opler et al. (1975) and Lloyd (1979).

(1877) to refer to taxa that were monomorphic and *derived*. One means of distinguishing between the two alternatives is by controlled crosses between heterostylous and monomorphic taxa. If homostyly arises by crossing over within the heterostyly supergene, controlled crosses can reveal specific patterns of residual self-incompatibility in the monomorphic taxa. These patterns would be unexpected in primitively monomorphic taxa (Dowrick, 1956; Baker, 1975).

This approach has been used to clarify the complex patterns of floral variation in the neotropical *Turnera ulmifolia* polyploid complex (Shore & Barrett, 1985b; Barrett & Shore, 1987). In this group of herbaceous perennial weeds two contrasting patterns of floral morphology occur. Populations are either dimorphic or monomorphic for a suite of traits (e.g., style length, anther height, pollen size) associated with their breeding systems. Dimorphic populations exhibit typical features of distyly with strong self-incompatibility and a 1:1 ratio of the L and S morphs (Barrett, 1978). Monomorphic populations are self-compatible with long styles and a range of stamen heights. Populations with long styles and long-level stamens have a morphology that corresponds to the long-homostyle phenotype in *Primula* (Dowrick, 1956). At the other extreme are monomorphic populations with long styles and short-level stamens. These forms are incapable of automatic self-pollination and resemble the typical L morph of distylous populations. This range of variation raises questions concerning the origin and evolutionary relationships among forms within the complex. Is floral monomorphism a derived condition in this case, and if so, has homostyly arisen as a result of recombination within the distyly supergene? (see Shore & Barrett, 1985a). Alternative possibilities are that

some forms are ancestral or have originated directly from the L morph through loss mutation(s) at the self-incompatibility locus. Mutations of this type occur independently of changes in floral morphology and have been reported in several distylous populations of *T. ulmifolia* (Shore & Barrett, 1986).

A crossing program between distylous morphs and three monomorphic taxonomic varieties of *T. ulmifolia* was used to examine the origins of floral monomorphism in the group (Barrett & Shore, 1987). The results provided clear evidence that the three varieties are long homostyles that arose by recombination, since the predicted seed set patterns from the cross-over model were revealed in all phenotypes. Pollen of the S morph was compatible in crosses with homostyles, whereas pollen from the L morph was not. In reciprocal crosses pollen of the homostyles was only compatible in crosses with the L morph (Fig. 5). Thus, although some homostylous populations possess "short-level" stamens, their pollen exhibits the incompatibility reaction of long-level stamens of the S morph.

The finding that each monomorphic variety in *T. ulmifolia* is a long homostyle provides empirical support for Charlesworth and Charlesworth's (1979a) theoretical model of the breakdown of distyly. They demonstrated that if the "allele" determining the S morph is dominant, as in *T. ulmifolia* (Shore & Barrett, 1985a), long homostyles will spread to fixation with greater probability than other self-compatible recombinant phenotypes. In some long homostylous populations of *T. ulmifolia* it appears that selection pressures favoring increased outcrossing have resulted in the reestablishment of herkogamy (separation between stigmas and anthers) as a result of selection on polygenic variation for sta-
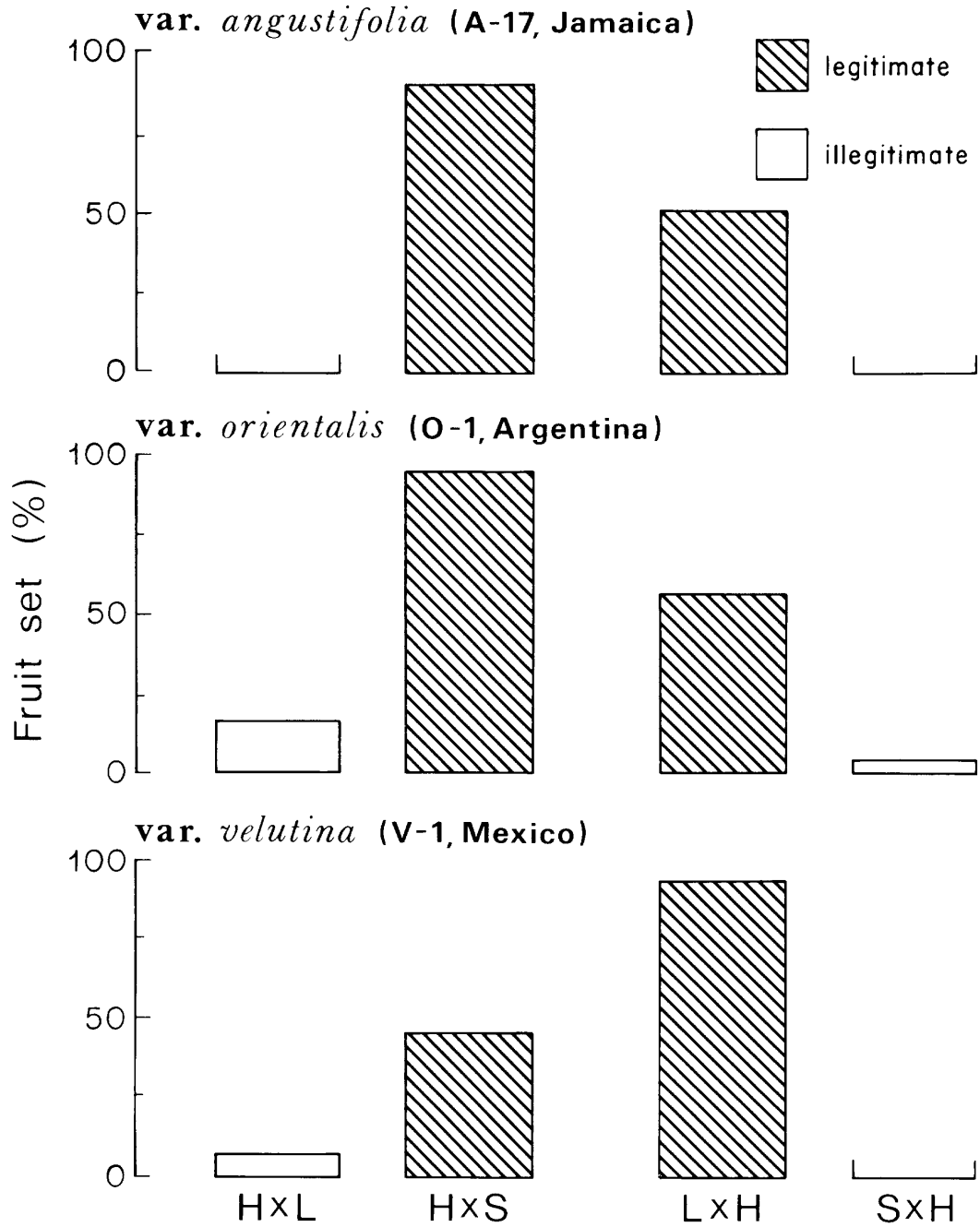
Fig. 5. Compatibility relationships between distylous and homostylous varieties of the *Turnera ulmifolia* complex. Histograms illustrate the percentage fruit set obtained in crosses between the L and S morphs, respectively, and three homostylous (H) varieties. For further details see Barrett & Shore (1987).
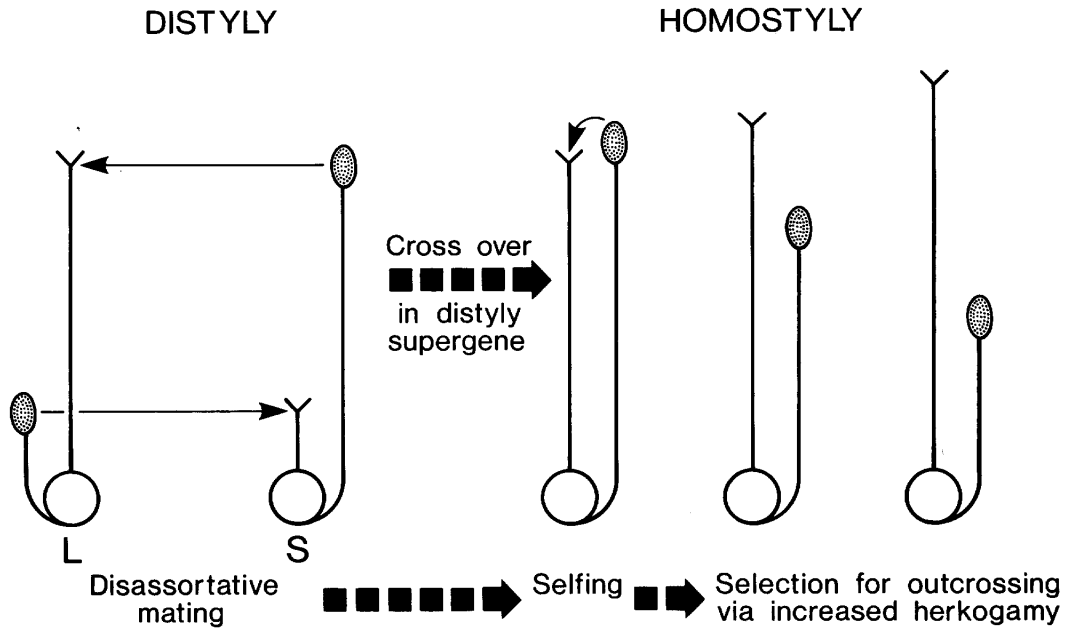
DISTYLY   HOMOSTYLY

Cross over
■ ■ ■ ■ ▶
in distyly
supergene

L   S

Disassortative ■ ■ ■ ■ ■ ▶ Selfing ■ ▶ Selection for outcrossing
   mating   via increased herkogamy

Fig. 6. Model of the evolutionary relationship among distylous and homostylous forms in the *Turnera ulmifolia* complex after Barrett & Shore (1987).

men and style length. The resulting phenotypes are capable of high outcrossing levels (Barrett & Shore, 1987) indicating that the evolution of selfing from outcrossing in the *T. ulmifolia* complex is not necessarily a unidirectional change, as has been postulated for many other groups (Fig. 6).

Floral dimorphism and monomorphism also occur in the hummingbird pollinated *Palicourea fendleri*, a shrub of tropical cloud forests in Venezuela (Sobrevila et al., 1983). These authors reported an unusual population at San Luis composed exclusively of the L morph and isolated geographically from the remaining distylous populations that were investigated. In contrast to plants of the L morph from distylous populations, plants from San Luis were highly self-compatible and produced "thrum-like" pollen. The authors suggested that this form may also have arisen by crossing-over. A controlled pollination study of the type conducted on *T. ulmifolia* would be helpful in substantiating this view, since an alternative possibility is that self-compatibility has arisen through relaxation of self-incompatibility in the L morph. This process commonly occurs in heterostylous plants and may

be particularly likely in isolated populations composed of a single floral morph.

Other Floral Heteromorphisms

We anticipate that with increasing study of tropical groups a greater diversity of floral conditions that involve polymorphisms of reproductive parts will be found. It is therefore desireable to review cases that have been identified as "anomalous", "incomplete", or "spurious" heterostyly and to determine their morphological and functional similarities and phylogenetic affinities with known heterostylous groups. In some cases, as we described above, the problem may be one of incomplete sampling or a misinterpretation of the fundamental nature of heterostyly. In others, however, a distinctive floral syndrome may be involved, as in the case of enantiostyly in the monocotyledonous families Haemodoraceae and Tecophilaeaceae. Experimental studies by Ornduff and Dulberger (1978) and Dulberger and Ornduff (1980) have demonstrated that this condition is a true genetic polymorphism for style
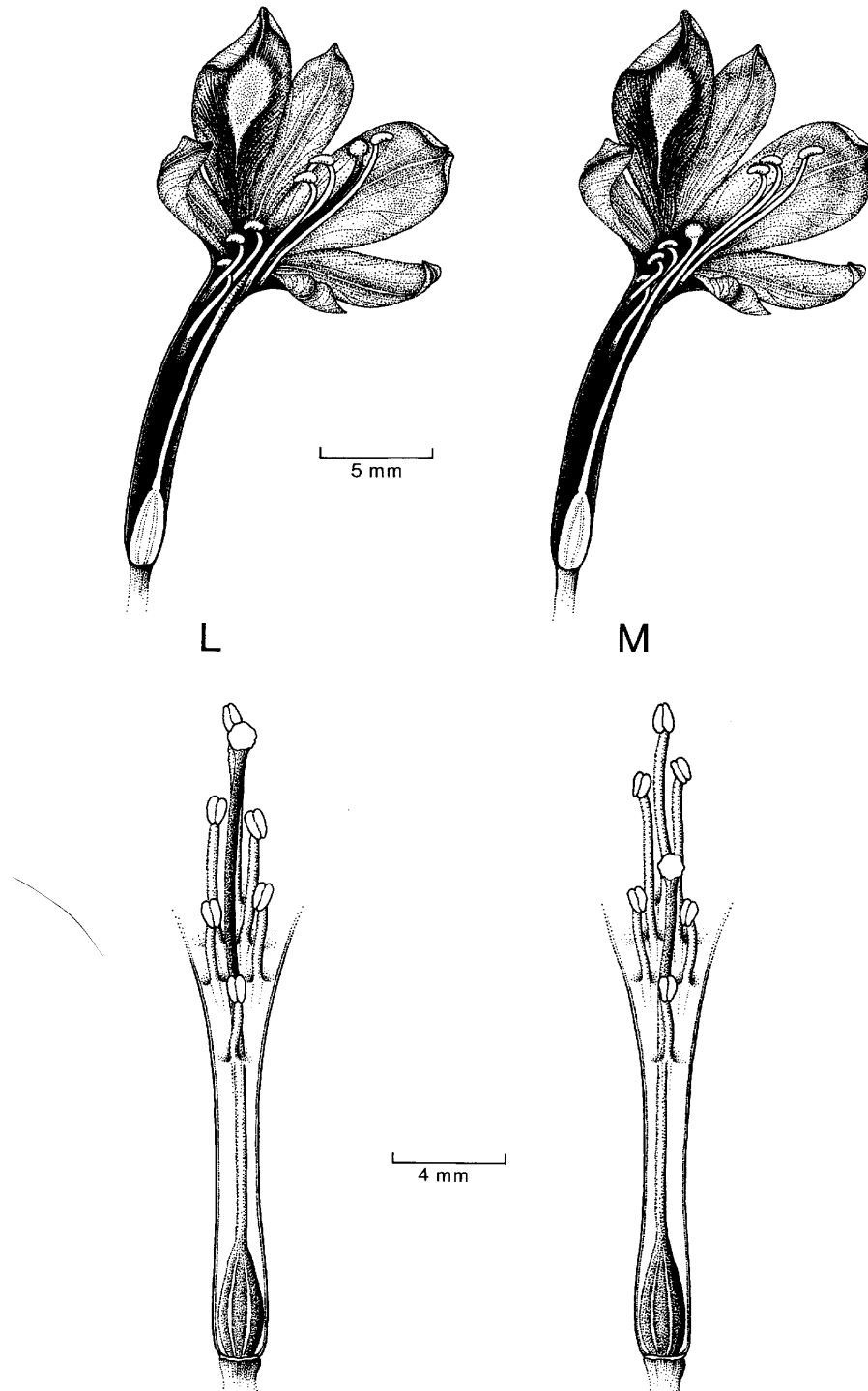
Fig. 7.   Residual floral heteromorphism in *Eichhornia diversifolia*. The two floral morphs L and M are self-pollinating semi-homostyles that have originated from the L and M morphs of an ancestral tristylous system. Note the differences between morphs in style length and style coloration. After Barrett (1988b).

Table II

Reproductive traits in taxa reported to possess "anomalous" heterostyly. Features chosen normally distinguish the floral morphs in heterostylous species

Feature	Anchusa officinalis[a]	Guettarda scabra	Narcissus tazetta	Quinchamalium chilense
Bimodal distribution:				
Stigma height	no	no	yes	yes
Anther height	no	no	no	yes
Stigma-anther	yes	yes	—	—
Incompatibility system	multi-allelic SI	self-compatible	multi-allelic SI	self-compatible
Pollen dimorphism	weak	none	—	yes
Stigma dimorphism	weak	yes	—	—
Genetic control				
L morph ss	yes	—	yes	—
Morph ratio	excess L morph	1:1	—	excess S morph
Source	Schou & Philipp, 1984	Richards & Koptur, unpub.	Dulberger, 1964	Riveros et al., 1987

[a] *Anchusa hybrida* has a similar dimorphism (Dulberger, 1970).

orientation (left or right) that may represent an independent response in these families to selection pressures favoring cross-pollination and/or a reduction of pollen-stigma interference.

RESIDUAL HETEROSTYLOUS CHARACTERS

Where heterostyly has become modified into another type of breeding system such as dioecy or homostyly, confusion can arise if "transitional" populations occur in which residual heterostylous characters persist. In some cases these characters may segregate in populations, giving rise to clear discontinuities in variation pattern. An example involves the largely autogamous aquatic *Eichhornia diversifolia,* a colonizer of temporarily inundated sites throughout much of the neotropics. Most populations contain a single self-pollinating semi-homostylous (one set of anthers adjacent to the stigma) phenotype. In northeast Brazil, however, two distinctive phenotypes co-occur in populations. These phenotypes differ in style length, style coloration and stamen position (Fig. 7). Several lines of evidence indicate that the phenotypes are independently derived from the L and M morphs of an ancestral tristylous system and that the polymorphisms are residual components of the genetic architecture of tristyly. Since the two phenotypes are largely selfing, the polymorphic traits may have little functional significance in contemporary populations. In this example it is relatively straightforward to establish the relationship between the floral polymorphisms and true heterostyly, since close relatives of the genus display the orthodox tristylous syndrome, as well as a range of derived, selfing, semi-homostylous conditions (Barrett, 1985b, 1988b). In several other cases, however, in which stylar heteromorphism has been linked to heterostyly (e.g., *Mirabilis, Veronica*), no relatives are known that are heterostylous, and it is doubtful that the variation has anything to do with the polymorphism.

ANOMALOUS HETEROMORPHISMS

Although heterostylous systems have arisen a number of times in different taxa, the similarity in expression of characters in these taxa may indicate common genetic and developmental pathways. A few heteromorphic species have been reported, however, which have distinctive expressions of style variability combined with unusual incompatibility relations. These probably represent breeding systems that are fundamentally different from heterostyly. A summary of the expressions of typical characteristics of the heterostyly syndrome in these anomalous species is presented in Table II. The table does not include species which show anomalous types of heterostyly but that are related to species in which heterostyly is well-developed, e.g., *Linum grandiflorum.* We have also not included species which have not been well documented. For example,

Cordia sebestena has been variously described as being heterostylous (Opler et al., 1975) or heterocorollic (Percival, 1974; Tomlinson, 1980) and obviously deserves further investigation. Darwin (1877) described *Leucosmia* (=*Phalaria*?) *burnettiana* (Thymelaeaceae) as having a heterostyly similar to *Linum grandiflorum*. Although Ganders (1979a) reports that distyly in the Thymelaeaceae has not been substantiated, this genus might exhibit some other type of stylar heteromorphism. Style length differences between botanical garden collections of *Veronica gentianoides* are apparently inherited as in distyly, but no other heterostylous characters are found. Whether or not the short-styled morph occurs in natural populations of this species is unclear.

Table II shows that, even with the small number of species reported in the literature, there is a great deal of variability in the expression of characteristics typical of heterostylous groups. This variability indicates that these species do not exhibit a single type of stylar polymorphism, as is found in heterostyly. The species cover a wide taxonomic range, including both monocotyledons and dicotyledons. Similarly, both herbaceous and shrubby plants are represented. In all of these species the stylar polymorphism is analogous to distyly. Although two species, *Narcissus triandrus* and *Mirabilis froebelii*, have been suggested as anomalous tristylous systems, both appear to be species with extreme variation in style length (Baker, 1964; Bateman, 1952, 1968). Baker (1964) found that in *Mirabilis froebelii* the ratio of style length to mean stamen length varies continuously, with median ratios the most frequent. This type of analysis, where the distribution in a population of style-stamen length ratios is examined, can reveal stylar heteromorphisms which are not obvious when style or stamen lengths alone are measured.

Species with stylar dimorphisms differ from distylous species in a number of ways. Variation in stigma and anther heights are not as obvious as in distyly. Figure 8 shows the clear separation of morphs in three distylous Rubiaceae when stigma height is plotted against anther height. In the fourth species, *Guettarda scabra*, distinct morphs are not evident. In *Guettarda scabra*, as in *Anchusa officinalis*, neither stigma nor anther height have bimodal distributions, but two groups (Fig. 9) are seen when style-anther relationships within a population are considered (Philipp & Schou, 1981; Richards & Koptur, 1987 and J.

H. Richards, unpublished data). *Quinchamalium chilense* has bimodal stigma and anther height distributions, but in both it and *Anchusa hybrida* stigma and anther positions are not reciprocal in the two morphs, with anther height differing less than stigma height between the morphs (Dulberger, 1970; Riveros et al., 1987). When individuals of *Anchusa officinalis* are grouped into morphs based on their stigma-anther height ratios, a similar lack of reciprocity between morphs is seen (Philipp & Schou, 1981). However, in *Guettarda scabra* average anther and stigma heights are reciprocal in the two morphs (J. H. Richards, unpublished data). In *Narcissus tazetta* stigma height varies bimodally but not anther height. Expression of the secondary characteristics of the heterostylous syndrome, such as pollen and stigma dimorphisms, are also less marked in this group of taxa than in distylous species (Table II).

Species with stylar dimorphisms also differ from distylous species in their incompatibility systems. *Quinchamalium chilense* and *Guettarda scabra* are highly self-compatible (Richards & Koptur, 1987; Riveros et al., 1987), although whether these species have a cryptic self-incompatibility similar to that in *Amsinckia grandiflora* (Weller & Ornduff, 1977) is not known. The other species with stylar dimorphisms are self-incompatible but both intra- and intermorph compatible (Dulberger, 1964, 1970; Philipp & Schou, 1981; Schou & Philipp, 1984). Thus, their incompatibility resembles a homomorphic, multiallelic incompatibility system (Nettancourt, 1977). Unlike most homomorphic systems, however, in which pollen tube inhibition usually occurs on the stigmatic surface or in the style, inhibition in *Anchusa officinalis* and *Narcissus tazetta*, occurs in the ovules (Dulberger, 1964; Schou & Philipp, 1983).

Although the species with stylar dimorphisms differ from distylous taxa in their morphology, in the cases studied (Table II) the genetic control resembles that of distylous groups. Results of crosses are consistent with the floral "morphs" being controlled by a single gene with two alleles and dominance. As is true in most distylous species, the L morph is recessive *ss* (Dulberger, 1964; Schou & Philipp, 1984). The distribution of "morphs" within populations has been studied in *Anchusa officinalis* (Philipp & Schou, 1981), *Anchusa hybrida* (Dulberger, 1970) and *Quinchamalium chilense* (Riveros et al., 1987). A di-
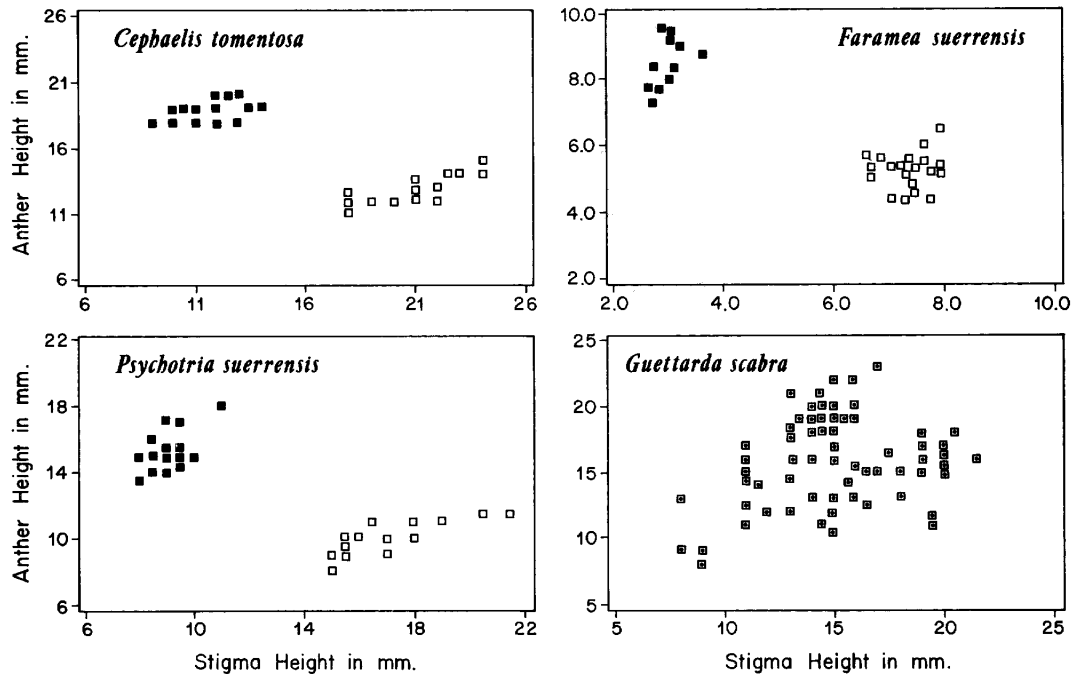
Fig. 8. Scatter plots of stigma and anther heights in four representative genera of the Rubiaceae. Note the clear separation into two groups in distylous *Cephaelis*, *Faramea* and *Psychotria* and the absence of groups in *Guettarda* (J. H. Richards, unpublished data).

stylous population would be expected to have an isoplethic (1:1) ratio of L and S plants. In *Anchusa officinalis* L plants are always in excess, whereas in *Anchusa hybrida* the ratio varies from S excess (one population), through isoplethy (three populations), to L plants in excess (one population). In *Quinchamalium chilense* S plants are always in excess.
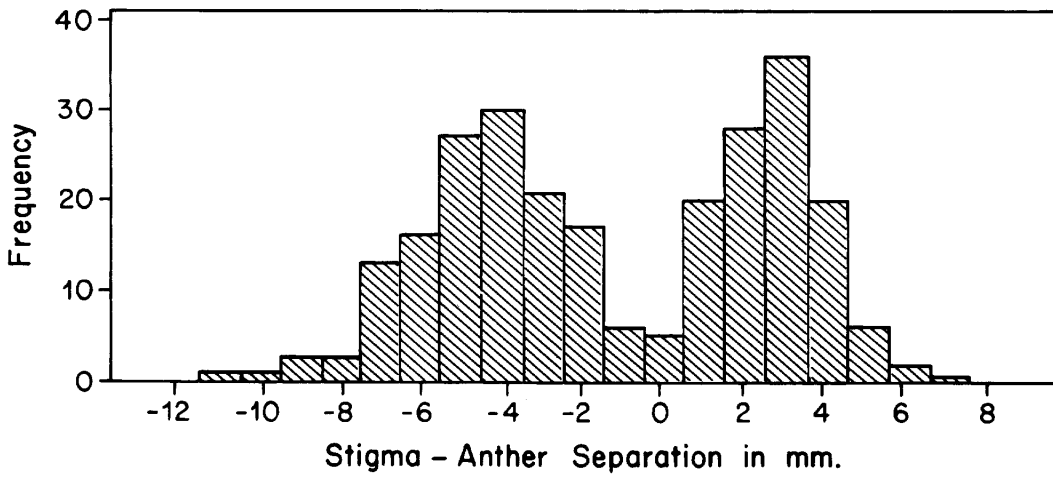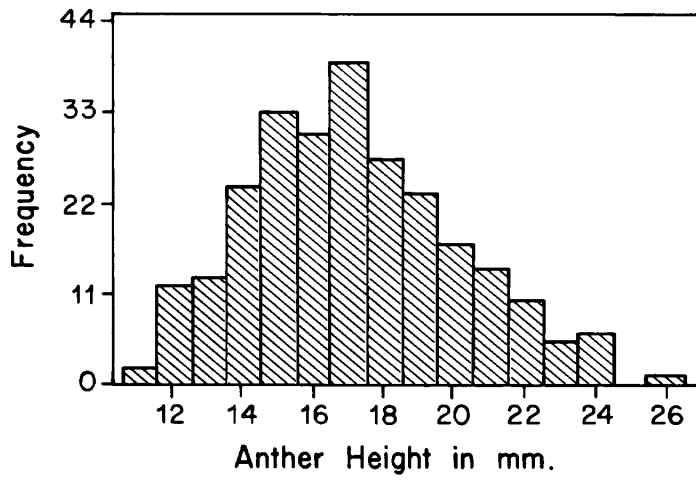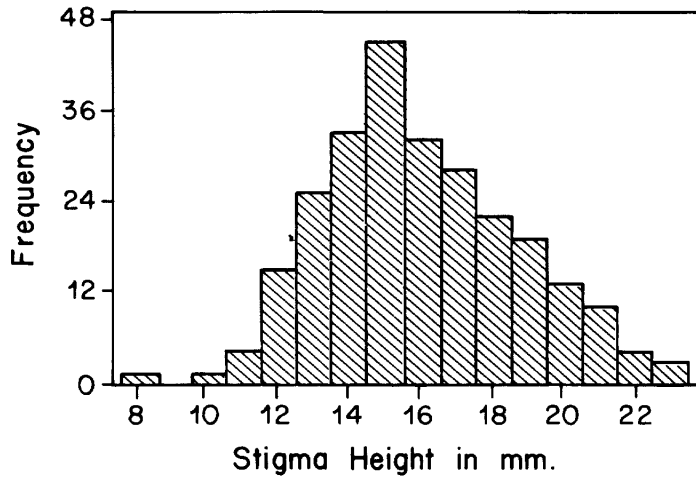
The diverse expression of reproductive characters among species which have been classified as having "anomalous" heterostyly indicates that they do not form a cohesive syndrome. For this reason we suggest that these species be simply referred to as possessing floral heteromorphisms not as heterostylous species. The effect of these heteromorphisms on the mating systems and population structure of species in which they occur deserves detailed study.

Future Studies

Researchers grounded in temperate botany may be reluctant to consider studying the breeding systems of tropical plants, particularly those that are woody in nature. While often posing certain logistical difficulties, tropical studies also provide many obvious advantages, including the extended season, greater opportunities for comparative work owing to the frequent co-occurrence of related species, and the possibility of examining populations in relatively undisturbed communities. Biosystematic and genetic studies of tropical species can also be conducted under glasshouse conditions in the temperate zone. Many herbaceous tropical plants, particularly those with weedy tendencies, are well-behaved under controlled conditions and can prove to be excellent experimental material because of their rapid growth rates and, often, day length insensitivity.

While the basic features of heterostyly are similar in both tropical and temperate regions, many unresolved problems and fertile areas for future research that involve tropical heterostylous groups remain. Below we offer suggestions for field studies of heterostyly, review several issues relevant to current research in reproductive biology, and suggest various taxonomic groups that would repay intensive study. As mentioned above, a large number of tropical species, re-

ported as heterostylous in taxonomic treatments, are essentially unstudied and confirmation of the occurrence and nature of heterostyly in these groups awaits future field studies. These need not be particularly sophisticated or time-consuming, since a considerable amount of basic observational information and quantitative data can be obtained in a short interval.

Field studies of heterostylous plants should at a minimum involve the collection and fixation in preservative of flower buds, mature flowers and developing fruits from a random sample of individuals from several populations. These can be used for measurements of a range of floral traits and fertility estimates, such as style length, anther height, pollen size, pollen production, stigmatic pollen loads, ovule number and percentage seed set (e.g., Glover & Barrett, 1983). Counts of the relative frequency and spatial distribution of floral morphs at a site can provide valuable information on population structure, as well as on the possibilities of deviations from disassortative mating (e.g., Opler et al., 1975; Barrett, 1978). Field pollinations involving hand selfs and crosses followed by bagging can be used to determine whether floral heteromorphism is accompanied by a diallelic self-incompatibility system and where inhibition of illegitimate pollen tubes occurs (e.g., Barrett, 1980; Bawa & Beach, 1983). Finally, if plants in populations are bearing mature seed, collections from individual maternal parents (families) are valuable to examine the segregation of floral morphs, and if electrophoretic techniques are available, to estimate mating system parameters, heterozygosity and levels of genetic diversity in populations (e.g., Shore & Barrett, 1985a; Glover & Barrett, 1986a, 1987; Barrett et al., 1987). These approaches do not involve extended periods in the field and can provide critical information on the breeding systems of heterostylous plants.

Although heterostyly depends on the establishment of two or three distinctive developmental pathways within a single species, few studies of these developmental changes exist. Recent work on the developmental basis of tristyly

in *Eichhornia paniculata* (Richards & Barrett, 1984) has provided a context in which to understand the evolution of semi-homostyly in populations of the species. Similarly, developmental studies of floral trimorphism in *Pontederia cordata* (Richards & Barrett, 1987) suggest that tristyly in the Pontederiaceae is developmentally distinct from that in either the Lythraceae or Oxalidaceae. Comparative developmental studies of additional heterostylous and related homostylous species will reveal the developmental modifications necessary for the evolution of this syndrome. Such studies may also identify the developmental basis of convergences among heterostylous species.

Ecological studies of tropical heterostylous plants provide opportunities to investigate a wide range of problems concerned with plant-pollinator interactions, pollen transport processes, gene flow and neighborhood sizes. We know very little about the fine scale details of the pollination process in most heterostylous plants (but see Barrett & Wolfe, 1986; Weller, 1981), let alone those that occur in tropical areas. Information is required on pollen deposition patterns on pollinators, the extent of pollen carryover, and the effectiveness of different pollinators at mediating legitimate and illegitimate pollination. Because of the small number of mating groups in heterostylous plants, the extent of pollen flow in populations is a critical aspect of the mating structure of populations. In woody species with small effective population sizes, considerable inbreeding may occur, despite self-incompatibility. Detailed studies of fruit and seed production, with special attention to early abortion phenomena (Seavey & Bawa, 1986) would be of particular interest in tropical woody species that occur at low density.

Several taxonomic groups deserve special attention, either because some controversy surrounds the nature of their breeding systems or because they offer unusually good opportunities for in-depth evolutionary studies. In the former category are *Bauhinia, Agelaea* and *Hugonia*; in the latter are *Averrhoa* and *Nesaea*. Several species of *Bauhinia* are reported as distylous (e.g., *B.*

←

Fig. 9. Distribution of reproductive organ size in a population of *Guettarda scabra* (Rubiaceae) from S. Florida (J. H. Richards & S. Koptur, unpublished data).

esculenta), and, as such, represent the only taxa in the large family Fabaceae in which heterostyly is reported. There are no experimental studies of these species, and, since other species in the genus exhibit variable sex expression, the precise nature of the floral variation needs careful checking. Similarly, reports of tristyly in *Agelaea* and *Hugonia* should be treated with caution, despite the occurrence of distyly elsewhere in their families. Several genera that were once reported to be heterostylous (e.g., *Cleome, Aneilema, Gilia, Aegiphila*) have on further study proven not to be so.

There are several hypotheses in the literature that attempt to explain the evolution of distyly from tristyly in the genus *Oxalis* (Charlesworth, 1979; Heuch, 1979; Mulcahy, 1964; Ornduff, 1972; Weller, 1986). Studies of the related genera *Averrhoa* and *Biophytum* would be valuable, since in both taxa distylous and tristylous populations are reported. In *Oxalis* the evolution of distyly commonly involves loss of the M morph, and it would therefore be of particular interest to determine whether the same pattern is evident in natural populations of *Averrhoa* and *Biophytum*. If this is the case, it could shed light on the processes involved and may suggest a common selective mechanism for the Oxalidaceae. Similar contrasts could also be made between *Lythrum, Nesaea* and *Pemphis* of the Lythraceae, since these genera also possess distylous and tristylous breeding systems.

Finally, outstanding opportunities for studies of floral evolution are provided by the large family Rubiaceae. Bir Bahadur (1968) reports distyly from 416 species in 91 genera and, while these specific figures need confirmation, it has been recognized since Darwin (1877) that the family contains the largest number of heterostylous species of any angiosperm family. Distyly in this family occurs in both temperate and tropical taxa and in herbaceous and woody species. Since the species are distributed among 21 tribes, it is quite possible that the polymorphism has had multiple origins within the family. If this is the case, it raises the interesting question of what special attributes taxa of Rubiaceae possess that have facilitated the repeated origin of distyly within its members. Anderson (1973) suggested that a predisposition for the evolution of distyly in the family is the occurrence of well-developed protandry in many taxa. While his model of the

genetic modifications of protandry that could give rise to heterostyly is unconvincing, it is possible that the developmental systems that regulate style length and stamen maturation in protandrous Rubiaceae might be simply modified, as he suggests. Studies of floral organogenesis in selected tribes of Rubiaceae both with and without heterostyly would be valuable for assessing these ideas, as well as in shedding light on whether the polymorphism is of polyphyletic origin within the family.

Acknowledgments

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Appendix

Families with tropical genera in which heterostyly has been reported. References given are the most recent and where possible involve experimental work. For a complete list of heterostylous taxa see Ganders (1979a).

Acanthaceae
    Oplonia   Ornduff, 1979b

Boraginaceae
    Cordia   Opler et al., 1975

Clusiaceae
    Cratoxylum   Lewis, 1982
    Eliaea, Vismia   not studied

Connaraceae
    Byrsocarpus   Baker, 1962
    Agelaea, Burttia   not studied, tristyly reported
    Cnestis, Connarus
    Ellipanthus, Jaundea
    Santaloïdes

Erythroxylaceae
    Erythroxylum   Ganders, 1979b

Fabaceae
    Bauhinia   not studied, see Vogel, 1955; Ornduff, 1974; Arroyo, 1981

Gentianaceae
    Sebaea   not studied, see Vogel, 1955; Ornduff, 1974

Linaceae
    Hugonia   not studied, tristyly reported, see Robson, 1963

Loganiaceae
    Gelsemium   Ornduff, 1970
    Mostuea   not studied

Lythaceae
    Pemphis   Lewis, 1975
    Nesaea   not studied, see Ornduff, 1979c

Menyanthaceae
    Nymphoides   Barrett, 1980

Olacaceae
    Schoepfia   not studied, see Tomlinson, 1980

Oleaceae
    Jasminum   not studied, see Ornduff, 1974
    Schrebera   not studied, see Verdoorn, 1963

Oxalidaceae

Biophytum	Mayura Devi, 1964
Oxalis	Ornduff, 1974
Sarcotheca	Lack & Kevan, 1987
Averrhoa, Dapania	not studied

Plumbaginaceae

Limonium	Baker, 1953
Ceratostigma, Plumbago	not studied
Vogelia	

Pontederiaceae

Eichhornia	Barrett, 1985a
Pontederia	Barrett, 1977b

Rubiaceae

Cephaelis	Bawa & Beach, 1983
Coussarea	Bawa & Beach, 1983
Faramea	Bawa & Beach, 1983
Guettarda	Richards & Koptur, 1987
Hedyotis	Bir Bahadur, 1970a
Morinda	Pratap Reddy & Bir Bahadur, 1978
Mussaenda	Baker, 1958
Oldenlandia	Bir Bahadur, 1968
Palicourea	Sobrevila et al., 1983
Pentas	Bir Bahadur, 1970b
Psychotria	Baker, 1958
Rudgea	Baker, 1956
Uragoga	Baker, 1958

Many additional genera are listed as distylous by Bir Bahadur, 1968. These are unstudied and need confirmation

Santalaceae

Quinchamalium	Riveros et al., 1987
Arjona	not studied, see Skottsberg, 1940

Sterculiaceae

Melochia	Martin, 1967
Waltheria	Bir Bahadur & Reddy, 1977

Turneraceae

Piriqueta	Ornduff & Perry, 1964
Turnera	Barrett & Shore, 1985
Hyalocalyx, Loewia	not studied, see Vogel, 1955
Streptopetalum, Wormskioldia	