

## NOTES AND COMMENTS

### THE EVOLUTION OF FLORAL HETEROMORPHISM AND GYNODIOECISM IN *SILENE MARITIMA*

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#### 1. INTRODUCTION

In a thought-provoking article Crowe (1964) has put forward an evolutionary scheme in which she derives the various outbreeding systems known in flowering plants by stages from a single pre-angiosperm incompatibility system. One of these stages involves the evolution of gynodioecism (where outcrossing is assisted by some of the plants in any population being pistillate while the remainder bear hermaphrodite flowers) from heteromorphic self-incompatibility (heterostyly). For illustration she uses *Silene maritima*, With. This note points out that such an evolutionary derivation is not appropriate for this species and comments on some related statements made in Crowe's article.

Crowe writes (*op. cit.*, pp. 443-4), "It . . . comes as no surprise to find relic heteromorphy in the gynodioecious species *Silene maritima*. . . . The styles of the two sexes are equal in length although they are thicker in the flowers of the females. The stamens, however, differ in height. Anthers in the hermaphrodite flowers are on a level with the stigmata when mature while the barren anthers of the female are situated half-way down the corolla tube. Thus the hermaphrodites correspond to long homostyles and as is to be expected they are self-compatible. The females on the other hand correspond to pin plants. The pronounced pollen dimorphism in the hermaphrodites of *S. maritima* confirms this interpretation since it has been shown that some heterostyled plants of *Primula* are heterozygous for the alleles which govern pollen size in their heterostyled ancestors. A slight delay in the activity of these alleles in *Silene* would cause them to act directly on individual pollen grains so that those carrying the S allele would be large and those with the s allele small."

#### 2. FLORAL VARIATION IN *SILENE MARITIMA*

In the first place, it would be quite surprising to find "relic heteromorphy" in *Silene maritima* for heteromorphic incompatibility systems are completely unknown from the whole of the large family Caryophyllaceæ and, indeed, no incompatibility system of any sort has been found in this family (East, 1940; Fryxell, 1957; Baker, 1959). The self-compatibility of the hermaphrodite flowers of *S. maritima* is typical of the family and does not constitute evidence that these flowers are "long homostyles" from a self-incompatible heterostylous ancestor. The stamens of pistillate flowers reached half-way up the corolla tube in Crowe's material; other observers, including myself, have seen a complete spectrum of filament lengths in pistillate flowers from shorter than the ovary to longer than the full length of

the corolla tube, although with contabescent anthers (*cf.* Marsden-Jones and Turrill, 1957, p. 321). This is because the stamens in pistillate flowers are *aborted* to various degrees. It is surprising that Crowe does not recognise the distinction between short, aborted stamens (as these are) and the fully vital, pollen-producing short ones which are part of a regular heterostylous out-breeding system.

However, the theory of derivation of the floral condition in *S. maritima* from a heterostylous ancestor becomes untenable when it is remembered that some plants in almost every population of this species are *gynomonoecious* (*i.e.*, bear hermaphrodite and pistillate flowers on the same plant). These

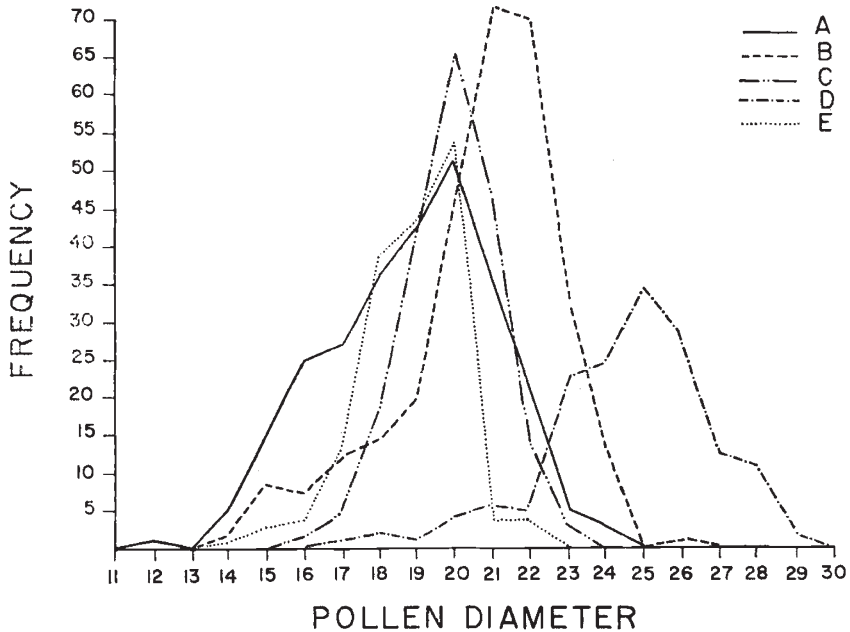


FIG. 1.—Frequencies of pollen grains of various diameters (micrometer eyepiece units, each equivalent to  $3\mu$ ) in anthers of five separate plants of *Silene maritima*. Plant A is gynomonoecious; plants B-E are fully hermaphrodite. Despite variability within and between plants, none of these graphs is bimodal.

gynomonoecious plants have appeared repeatedly in my cultures and in those grown by Marsden-Jones and Turrill (1957, pp. 319, 321) who found that approximately 5 per cent. of all plants fell into this category. The proportions of the flowers which are pistillate varies from year to year on the same plant. These pistillate flowers are comparable in every way with those which appear on purely pistillate plants and there is no way in which they can be formed except by simple abortion of the stamens in the hermaphrodite flowers. They are in no sense the flowers of "pin plants".

Pollen dimorphism within individual anthers of hermaphrodite flowers of *Silene maritima* could be explained in several other ways than the one postulated by Crowe, which involves several assumptions. However, in my cultures (derived from seed collected at Worm's Head, Glamorgan and Rhandir-mwyn, Carmarthenshire, both in Wales, in 1964) there is no sign of such pollen dimorphism within the anthers of hermaphrodite flowers (fig. 1).

There is considerable variability in pollen size *between* anthers in the same flower and between plants, but there is no suggestion of bimodality in any of the curves obtained. Marsden-Jones and Turrill (*op. cit.*) who observed the pollen of *S. maritima* incidentally in their detailed studies of the bladder champions do not report any such dimorphism, neither does their photograph of the pollen show it. Consequently, pollen dimorphism can hardly be used as evidence of heterostylous ancestry for *S. maritima*.

### 3. ORIGINS OF GYNODIOECISM

In her discussion, Crowe implies that gynodioecism may often arise from heterostyly. If this should be so, and the pistillate plants in gynodioecious species should regularly be derived from "pin" ancestors, they would be expected to be homozygous for their version of the heterostyly supergene (because almost always in heterostylous species "pin" is homozygous recessive—*cf.* Baker, 1966). Crowe (p. 443) has provided other reasons for believing that the pistillate plants will be homozygous. However, in *Limnanthes douglasii* R. Br. var. *rosea* (Hartw.) Mason (Limnanthaceæ), where I have strong evidence that gynodioecism is recently evolved (from purely homomorphic, self-compatible ancestors in northern California), the pistillate plants are heterozygous and it is the hermaphrodite ones which are homozygous recessive (*i.e.*, it is a dominant allele which produces male-sterility). Heterostyly is unknown in the Limnanthaceæ.

Crowe (*op. cit.*, p. 438) states that "Apart from one case in *Fuchsia*, gynodioecious species are confined to the more advanced herbaceous orders". However, there are records of gynodioecious populations in *Ranunculus acris* L., (Marsden-Jones and Turrill, 1957), other species of *Ranunculus* (Ranunculaceæ), *Cardamine amara* L. (Cruciferae), and many members of the Caryophyllaceæ (Baker, 1948). None of these is generally considered an "advanced" order (nor is the Limnanthaceæ) and they are not known to have had any heterostyly in their histories.

Gynodioecism is not unknown in homomorphic derivatives from heteromorphic systems. Thus, *Armeria maritima* (Mill.) Willd. var. *californica* (Boiss.) Lawr. (Plumbaginaceæ) is a self-compatible homomorphic derivative from a dimorphic self-incompatible plexus (Baker, 1953). Its Californian populations contain a number of male-sterile individuals (Baker, 1966), so that they are gynodioecious, but the male-sterility bears no relation to any ancestral "pin" type of flower because, in fact, the well-known dimorphism in the ancestral self-incompatible *Armerias* does *not* include variation in style and stamen lengths.

There is no denying that gynodioecism *could* evolve from a heteromorphic incompatibility system. What is missing is any evidence that it has done so. The closest approach that I know about is the isolated example of functional true dioecism arising from heterostyly which I have shown from West African species of *Mussaenda*, in the Rubiaceæ (Baker, 1958, 1959). Here the narrow corolla-tube tends to be more or less choked with scaly hairs so that pollen can be picked up from low anthers or reach low styles only with difficulty. In those species with the most extreme choking of the corolla-tube, the only effective pollination is from the high anthers of short-styled plants on to the stigmas of long-styled plants. In such species the low anthers in long-styled plants may become abortive and it is only these plants (functionally pistillate) which set seed. The short-styled plants function only as staminate plants

However, this is not gynodioecism (where all plants in a population are seed fertile), but functional true dioecism.

In the case of *Mussaenda* the heterostylous and dioecious species occur in the same genus and there is no difficulty in tracing the evolutionary connection. This is a very different matter from a gynodioecious species in a family where heterostyly and self-incompatibility are both unknown—as in *Silene maritima* and the Caryophyllaceæ. The evolutionary story in the *Silene* case remains to be worked out and no generalisations can be made from it at this moment.

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#### THE CO-ORIENTATION OF NON-HOMOLOGOUS CENTROMERES

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MULTIPLE and multivalent associations can orient in various ways though the possibilities are limited somewhat by the form of the association as determined by chromosome morphology and the frequency and distribution of chiasmata. The factors influencing the orientation of structurally similar associations have been discussed frequently and generally in relation to simple rings of four chromosomes.

The discordant arrangement depends on the co-orientation of only two centromeres which are at opposite sides of the ring. In multiple associations these are non-homologous and neither in them nor in multivalent associations is this orientation expected to give numerically equal separation. This can be achieved, however, when only two pairs of centromeres co-orient. In