

A BRIEF REVIEW OF STIGMA AND POLLEN TYPES IN ACANTHOLIMON AND LIMONIUM

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ABSTRACT. Stigma and pollen types are reviewed in *Acantholimon* and *Limonium*. A careful examination of all Turkish species of *Acantholimon* reveals that this genus is distinctly dimorphic in stigma and pollen types and is heterostylous. The reported occurrence of hammer-headed stigmas in *Limonium griffithii* and capitate stigmas in *L. macrorhabdon* (Baker, 1953) is not confirmed by the present examination of these species. The loss of stigma and stylar inhibition in *L. gmelinii* (Sect. *Limonium* subsect. *Genuinae*) is reported for the first time, and there is no doubt that the usual incompatibility system prevalent in this subsection has been relaxed in the papillate stigma of this species.

Stigma and pollen types in Plumbaginaceae have been extensively investigated (Erdtman, 1940; Iversen, 1940; Baker 1948, 1953). Baker besides surveying the distribution of pollen and stigma dimorphism among the genera of Plumbaginaceae also demonstrated the relationship between such dimorphism and the well-known phenomenon of heterostyly. The present work is restricted to the examination of herbarium material and no crossing experiments have been done. Besides briefly reviewing the general pattern in *Acantholimon* and *Limonium*, some of the findings which do not agree with Baker's work are also discussed.

OBSERVATIONS AND DISCUSSION

In *Acantholimon*, Baker (1948, 1966) reported dimorphism of pollen as the only visible evidence of heteromorphism, the stigmas being said to be capitate and uniform. In the present investigation, however, examination of all the Turkish species has shown that the genus has distinctly dimorphic pollen and stigmas, and is heterostylous. In *Acantholimon*, as in the dimorphic species of *Limonium*, the "cob" stigmas are found in flowers producing type A pollen and "papillate" stigmas in flowers producing type B pollen (fig. 1). In type A pollen there is a complex ornamentation consisting of polygonal or irregular areoles surrounded by rods with swollen ends. These rods are sufficiently closely packed together to form complete rows. In type B pollen, the ornamentation of the grain consists of fine spines disposed at random or more or less arranged in small polygons.

The "hammer-headed" stigmas of *L. griffithii* reported by Baker (1953, p. 443) and the capitate stigmas of *L. cabulicum* (l.c.) are not confirmed by my own observations. In *L. griffithii* (and *L. macrorhabdon*), the stigmas are asymmetrically oblong-capitate (plate 1, b) and in *L. cabulicum* the stigmas were found to be broadly linear and agree with the figure drawn on a herbarium sheet at Kew (a specimen collected by Griffith, from near Karabagh, Afghanistan). The fact that the broadly linear structure is a stigma, and not a terminal part of the style after the capitate stigma has been lost (as supposed by Baker), is confirmed by the germinating pollen grains seen throughout its entire length (plate 1, c from Hb. Griffith. No. 4171 at Kew). As the

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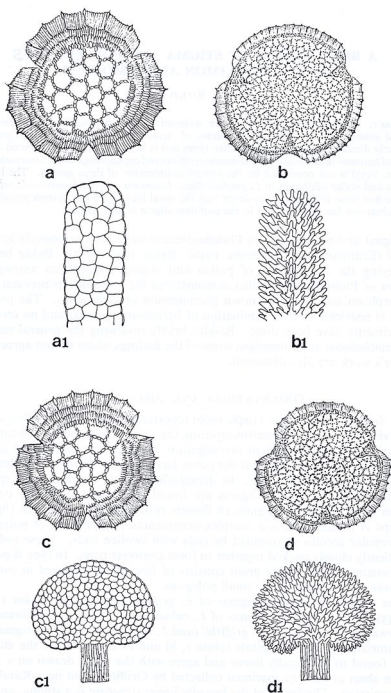


FIG. 1. Stigma and pollen types in: a-b1, *Limonium vulgare*—a, type A pollen; b, type B pollen; a1, portion of cob stigma; b1, portion of papillate stigma (adapted from Baker, 1953). c-d1, *Acantholimon acerosum*—c, type A pollen; d, type B pollen ($\times 800$); c1, cob stigma, d1, papillate stigma ($\times 80$).

genus *Acantholimon* has dimorphic pollen and stigmas, and the above-mentioned *Limonium* species do not possess typical capitate stigmas, Baker's fig. 5 (1966, p. 353) showing the postulated sequence in the build-up of a heteromorphic incompatibility system needs alteration.

Limonium shows three situations with regard to stigma and pollen types. In the first, exemplified by *L. vulgare*, populations consist of two strikingly different types of plants. One has long styles bearing stigmas with a "cob" pattern, the stamens are shorter than or as long as the styles, and have type A pollen. The other plants have short styles with strikingly papillate stigmas, while the stamens are long and produce type B pollen.

The second type is found within the usually dimorphic sections such as Sect. *Limonium* and others. Here there are a few monomorphic species (Baker 1953, 1966) which are characterised by the possession of either type A pollen and papillate stigmas or type B pollen and cob stigmas. In each case, however, the pollen type is associated with the stigma type opposite to that with which it usually occurs in dimorphic species. This produces a combination suitable for successful pollen tube growth, even with self pollination.

The third type occurs in some species belonging to Subsect. *Densiflorae*, *Dissitiflorae* and *Steirocladae* (Sect. *Limonium*). Here although populations are monomorphic, the pollen and stigma combinations are either A/cob or B/papillose, or in some cases pollen is not produced. In all such cases there is a high proportion of small mis-shapen pollen grains. Some of these species have been proved to be apomicts (Baker 1953, 1954) and in *L. virgatum* apomixis has been cytologically demonstrated (Amato, 1949).

The suggestion that monomorphism of these taxa of *Limonium* is of secondary nature is supported by their geographical distributions, which are noticeably peripheral or otherwise of types probably representing the end of a migratory trail involving some kind of 'long distance dispersal' (Baker, 1966).

It has been assumed that the incompatibility system linked with pollen and stigma dimorphism is similar to that of *L. vulgare* in all the dimorphic taxa of Subsect. *Genuinae* (Sect. *Limonium*). But a different picture is given by examination of *L. gmelinii* from Turkey. This species is dimorphic and heterostylous, but as is vividly clear on plate 1a both types of pollen grains germinate on the papillate stigma. In spite of recent extensive work on *Limonium*, this situation has not been recorded elsewhere in the genus. The cited photograph was sent to H. G. Baker for his comments and he agreed 'that there is no doubt that the papillate stigma of the plant of *L. gmelinii* has relaxed the usual incompatibility system' (written communication). He also suggests that this occurrence in *L. gmelinii* seems to be directly comparable with the situation in *Armeria maritima* var. *maritima* population of sea-cliffs on the mainland of Shetland at Hillswick Ness, where in a usually dimorphic population, self-compatibility has been produced by loss of power of inhibition of pollen tube growth in stigmas and styles without the occurrence of any morphological rearrangement.

Experimental results obtained by Baker (1966) support the following genetical scheme which he put forward. The various morphological and physiological features of a heteromorphic incompatibility system are due to separate genes which are so closely linked together that they may be recognised as co-operating together in a unit—a "supergene". The gene

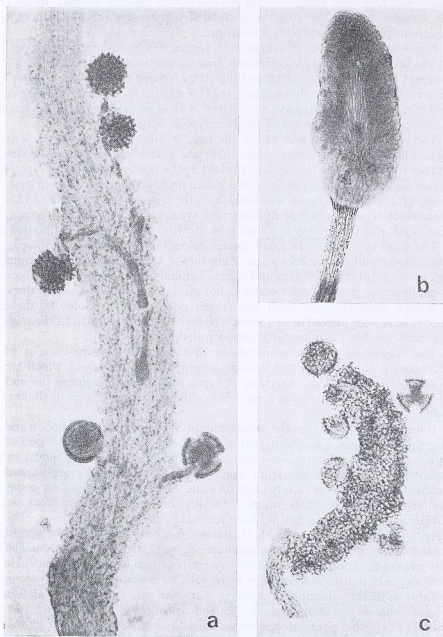


PLATE 1. Stigmas and pollen types of: a, *Limonium gmelinii* showing pollen types A and B, and pollen tubes within the papillate stigma; b, *L. griffithii* showing its oblong-capitate stigma; c, stigma of *L. cabulicum* with germinating pollen grains. a $\times 250$, b and c $\times 150$.

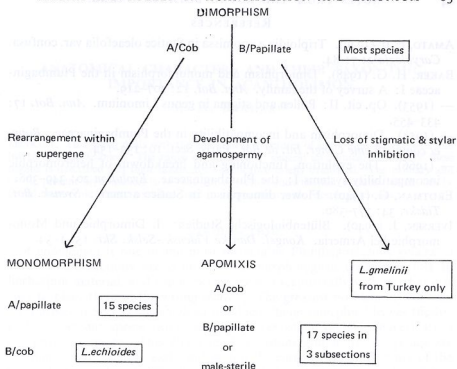


FIG. 2. Pathways in the breakdown of heteromorphic incompatibility system in *Limonium*. (Adapted from Baker 1966).

controlling the pollen form also controls the incompatibility reaction of the pollen tube, while the gene controlling stigma form also controls its incompatibility reaction. In a dimorphic taxon, A/cob plants are heterozygous for the supergene, while B/papillate plants are homozygous for it. In the production of secondary monomorphic taxa in which usually the A/papillate combination is characteristic, there must have been two separate events: (1) cross-over or mutation within the supergene which produced the A/papillate combination; (2) a loss in the stigmas and styles of the power of inhibiting pollen tubes, since even grains of type B are capable of bringing about fertilization, even when they are derived from grains of type B. If self-compatibility is favoured in particular ecological circumstances prevailing at that time, the monomorphic condition which is the result of the first event (1) would very likely become established as a characteristic of the population (Baker, 1966).

In *Armeria maritima* from Hillswick Ness and *Limonium gmelinii* from Turkey, only the second event (2) has taken place: the loss of inhibitory power in stigmas and styles, but this has not been followed by morphological rearrangement in pollen and stigma types. In Hillswick Ness *Armeria*, the dependence to a greater extent on self-pollination is supposed to be due to scarcity of potential insect pollination owing to the strong and more or less incessant wind. The conditions which have led to the loss of self-incompatibility system in *L. gmelinii* are not known, but with the discovery of loss of stigmas and styles inhibition power in this species, Baker's fig. 9 (1966, p. 364) has to be slightly altered.

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