

# Heterostyly and pollinators in *Plumbago auriculata* (Plumbaginaceae)

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## Abstract

Plants with hermaphrodite flowers risk conflict between male and female sexual function due to close proximity of sexual organs. Heterostyly, a genetic floral polymorphism characterized mainly by reciprocal herkogamy, may reduce this sexual conflict by increasing the precision of pollen transfer between morphs. This sexual organ reciprocity is often associated with various ancillary characters and a heteromorphic incompatibility system. Here we describe the morphometrics associated with heterostyly and ancillary characters in *Plumbago auriculata*. Using controlled pollination experiments, we show that this species has a heteromorphic incompatibility system. We also document the fauna of long-proboscid fly and butterfly pollinators in a *P. auriculata* population in KwaZulu-Natal, South Africa.

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## 1. Introduction

Conflict between the male and female sex functions due to lack of precision in pollen transfer or through stigma interference in hermaphrodite flowers can be alleviated by various adaptations that promote cross-pollination (Barrett, 2002). One of these adaptive ‘strategies’ is heterostyly, a floral polymorphism primarily characterized by reciprocity in sex-organ levels (reciprocal herkogamy) between a “Pin” (Long-style) morph, with stigma above anthers, and a “Thrum” (Short-style) morph, with the reverse positioning (hereinafter termed L and S-morphs). Reciprocal herkogamy is usually accompanied by a sporophytic heteromorphic incompatibility system that prevents self- and intra-morph fertilizations, and a set of ancillary characters that differ between morphs, mainly related to pollen or stigma features (Ganders, 1979; Barrett, 1992; Dulberger, 1992).

Two different mechanisms are involved in the reduction of interference between reproductive functions of female and male organs in heterostylous plants. One is reciprocal sex-organ positions in the style morphs, whose function is apparently to increase male fertility by promoting more precise pollen dispersal among plants and thus reduce male gamete wastage through self-pollination (promotes male fitness). The second is self-incompatibility, which safeguards against self-fertilization and inbreeding depression (promotes female fitness) (Barrett, 2002).

Discrete sexual polymorphisms (i.e. dioecy and heterostyly) have been used as models for the evolution of reproductive strategies and in particular, sexual systems ever since Darwin (1877) first drew attention to their adaptive significance. To date, heterostyly is known to occur in at least 28 families of flowering plants (Barrett et al., 2000), including the family Plumbaginaceae, which provides one of the best examples of the complexity that heterostyly can attain.

Phylogenetic studies of the Plumbaginaceae have confirmed the monophyly of the two subfamilies Plumbaginoideae and Statioideae, which are well differentiated by morphological, chemical, and molecular characters (Lledó et al., 1998, 2001). Plumbaginoideae comprise four genera, of which *Plumbago*,

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with approximately 20 species, is the largest. Heterostyly is known to occur in several different genera of both subfamilies (*Acantholimon*, *Armeria*, *Goniolimon*, *Limonium* and *Limonium* in subfamily Staticeae; and *Ceratostigma*, *Dyerophytum* and *Plumbago* in Plumbaginaceae) (Ganders, 1979 for heterostyly description). Three genera are found in southern Africa, *Dyerophytum* Kuntze, *Limonium* Mill. and *Plumbago* L. Dimorphisms in pollen size, pollen sculpturing and stigmatic surface occur throughout the family (Baker, 1948, 1953, 1966; Vuilleumier, 1967; Dulberger, 1975; Nowicke and Skvarla, 1977), accompanied in some cases by reciprocal herkogamy (e.g., some species of *Limonium*) but not in others (*Armeria*, *Limonium*). Due to such a range of variation, Plumbaginaceae provides an ideal system in which to test hypotheses on the evolution of heterostyly. One of the most notable propositions to emerge from such studies in the family is that of Charlesworth and Charlesworth (1979), who hypothesized that heterostyly would have originated in an ancestor with strong inbreeding depression. The proposed evolutionary sequence starts with a change in pollen and a consecutive change in stigma types bringing about a heteromorphic incompatibility system and finally, only after incompatibility is established, does reciprocal herkogamy evolve. On the other hand, Lloyd and Webb (1992), following Darwin (1877) ideas, emphasized the initial evolution of reverse herkogamy as a mechanism promoting pollen transfer.

In view of these conflicting hypotheses and in order to provide the baseline data necessary to study the evolutionary steps leading to heterostyly occurring in the family, (evident by the wide variation in stylar polymorphism), it is useful to further describe heterostyly in the members of Plumbaginaceae. To this end, we investigated various aspects of the floral biology of *Plumbago auriculata* in a natural population in KwaZulu-Natal, South Africa. In particular, we characterized the morphometrics of the stylar polymorphism and compared pollen and nectar features between morphs. We also investigated the incompatibility system and the pollinator spectrum in this population.

## 2. Materials and methods

### 2.1. Study species

*P. auriculata* is a shrub, 0.3–1.39 m high, with leaves thin in texture and with minute glandular dots; the petiole is winged at the base and auriculate. The leaves are weakly discolored, greyish green beneath and sometimes with whitish scales apparently for light reflection. The species is a common constituent of lowland scrub in eastern South Africa up to 1623 m altitude, and blooms mostly between November and May, although there are often flowers at other times of the year. The salver-shaped (hypocrateriform) flowers are pale blue, actinomorphic, and grouped in terminal inflorescences (Pooley, 1998; Aubrey, 2001).

Our study was carried in a natural population on the eastern edge of the Umkomaas Valley between Richmond and Ixopo in South Africa (S29° 58.946 E030° 14.918).

### 2.2. Stylar polymorphism and proportion of morphs

One flower per plant from a total of 52 shrubs (24 L-morph and 26 S-morph) was collected and kept in 70% ethanol until measurement. The number of flowers and inflorescences in 24 random plants of both morphs was counted. Flowers were slit longitudinally and various morphological parameters measured with a caliper to the nearest 1 mm. The following measurements were recorded: (1) corolla tube length; (2) style length, up to the stigmatic surface; (3) stamen height, up to the midpoint of every anther (one stamen measured per plant) (Fig. 1). Differences between the two morphs were tested by applying a *t*-test for independent samples. Additionally, with the flowers collected we estimated the morph ratio in the population and calculated the reciprocity between sexual whorls following Sánchez et al. (2008).

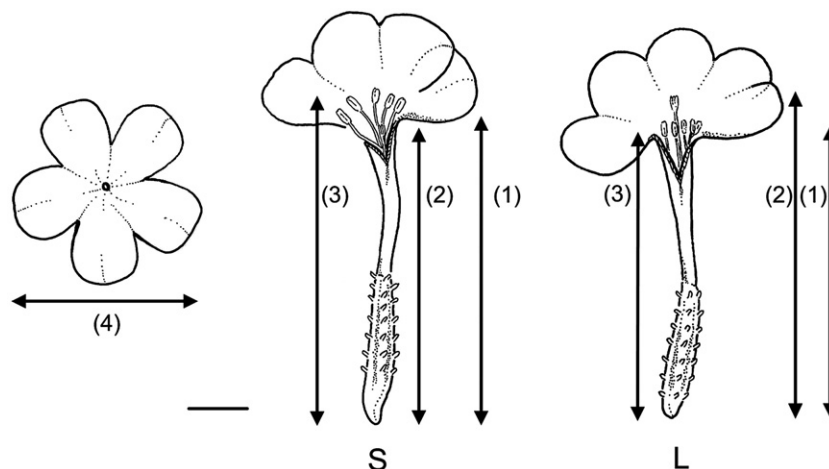


Fig. 1. Short-morph (S) and Long-morph (L) flowers of *Plumbago auriculata*. Numbers correspond to the morphometric measurements recorded for each flower: side view: (1) corolla length; (2) style length; (3) stamen height; front view: (4) corolla width. The top of the corolla tube was slit longitudinally to facilitate measurements. Scale bar = 10 mm.

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