

# Noncarpellary pollination and 'hyperstigma' in an angiosperm (*Tambourissa religiosa*, Monimiaceae)

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**Summary.** In *Tambourissa religiosa* (Monimiaceae), the flowers are pollinated at a 'hyperstigma' formed by the mouth of the floral cup, and not at the carpels. This is an extraordinary feature in angiosperms.

One of the most characteristic and exclusive features of the angiosperms which is used to separate them from the gymnosperms, is the enclosure of the ovules and seeds by the carpels. Pollination takes place not directly at the ovular micropyle but at the stigma, i.e. on the outer surface of the carpel. At this site, the pollen grains germinate and from here the pollen tubes grow through the carpel towards and into the ovule and the embryo sac.

A different receptive site for pollen grains, which is unique in angiosperms, has been discovered in *Tambourissa religiosa* (Tul.) A. DC. (Monimiaceae) from Madagascar, belonging to the otherwise relatively conservative group of the woody Ranales (Laurales). As in many other genera of the Monimiaceae, the unisexual flowers consist mainly of an urceolate floral cup and a number of carpels or stamens inside the cup, the perianth lobes are extremely reduced. There is only a narrow pore at the top of the floral cup. Anthers and stigmas never protrude out of the pore. Therefore, the gross appearance of such a flower resembles the inflorescence of *Ficus*. Generally, such Monimiaceae apparently show a normal carpellary pollination by small insects (e.g. Thysanoptera) which may creep into the flowers. In old flower buds, larvae have been found inside the cup near the poral region (*Mollinedia*<sup>2</sup> and unpublished personal observations in *Steganthra* and *Wilkia*).

Unlike these genera, the female flowers of *Tambourissa religiosa* (figure) at anthesis surprisingly produce a mucilaginous plug of disintegrating cells in the apical pore.

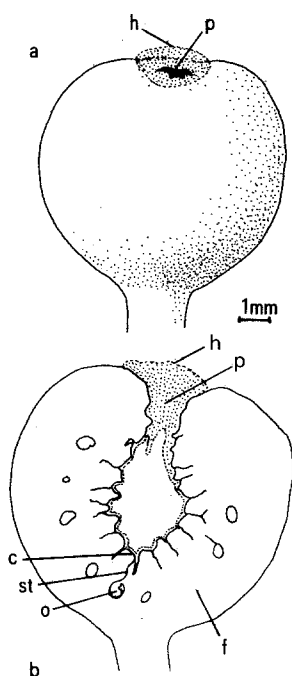
Possibly the mucilage mainly consists of pectic substances from the cell walls. Also the whole inner surface of the cup is covered by a mucilaginous film, apparently produced by the outer walls of the epidermis cells of the carpels. This film is continuous with the pollen transmitting tissue of the carpels. In contrast, the male flowers do not produce any mucilage.

The pollen grains deposited on the outer surface of the mucilaginous plug germinate at this site and the pollen tubes grow through the mucilage to the inner surface of the floral cup, where they reach the carpels. The ovaries are deeply immersed in the wall of the cup, the free apical parts of the carpels being very short. In a morphological sense, the gynoeceum is syncarpous and inferior, but in a pollination-biological sense it is apocarpous, as there is no interconnection between the pollen tube transmitting tissues of the individual carpels below their apical parts. Instead, the transmitting sites communicate above the carpels.

By this behaviour, *Tambourissa religiosa* has reached a new level of organization, which is unique in flowering plants: not only angiospermy, but 'angiocarpy'. The step from angiospermy to angiocarpy has the same dimension in a comparative morphological sense as the step from gymnospermy to angiospermy: The receptive site for the pollen grains has not only shifted from the micropyle to the stigma, but furthermore from the stigma to the mouth of the floral cup, which, hence, represents a 'hyperstigma'. The only difference is that, from this new evolutionary level, apparently no successful adaptive radiation has taken place. Angiocarpy sinks into insignificance by the side of the great diversity of the recent seed plants with normal gymnospermy or angiospermy. Earlier, the occurrence of noncarpellary pollination in angiosperms has been supposed only for *Hennecartia* (Monimiaceae) and only from herbarium material<sup>3</sup>.

In contrast, in most angiosperms of more derived groups than the Ranales, syncarpy has been successfully developed. Certainly, syncarpy is an evolutionary trend into a similar direction, as it also works towards the more economical uniting of the receptive site for all carpels and ovules of one flower. However, it is somewhat less different from the apocarpous angiospermous starting point than angiocarpy, in so far as the receptive site, the stigma, has remained on the carpels themselves and has not been transferred to any other floral organ outside.

The evolution of this hyperstigma in *Tambourissa religiosa* could be understood as an advantageous protection against predating damage of the carpels by pollinating insects, which may only visit the inner side of the male flowers but not the female ones because of the mucilage barrier. It would be interesting to look for the existence and the eventual site of an incompatibility-recognition system in these plants, which might give some relevance for the rare occurrence of this floral type.



Female flower of *Tambourissa religiosa*. a Surface view. b Longitudinal section. f, Floral cup; h, hyperstigma; p, floral pore with mucilaginous plug; c, apex of one of the carpels; st, styler canal; o, ovary and ovule.

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2 G. Gottsberger, Plant Syst. Evol., suppl. 1, 217 (1977).

3 Janet Perkins and E. Gilg, Pflanzenreich 4, 9 (1901).