

## NECTAR AND THE POLLINATION OF BREAD FRUIT, *ARTOCARPUS ALTILIS* (MORACEAE)

N. B. M. BRANTJES

Biologisch Centrum, Afdeling Plantensystematiek, postbus, 9750 AA Haren (Gn)\*

### SUMMARY

In Cametá, PA, Brasil, *Trigona (Trigona) fulviventris* var. *guianae* Cock. bees collect pollen and presumably also nectar from staminate inflorescences of *Artocarpus altilis* (Park.) Fosberg (= *A. communis* = *A. incisa*). In this tree the production of staminate inflorescences alternates with that of pistillate ones (second-order dichogamy). Pistillate inflorescences do not produce any nectar.

Microtechnical and anatomical studies confirmed the nectar production from morphologically unspecialized cells in the perianth bases. The nectar is secreted through stomata into the interfloral spaces.

This primitive mode of secretion might be an indication of a novel development rather than a rudimentary character. Its adaptive value remains uncertain.

The relevance of this nectar production is discussed in the light of conflicting views about the evolutionarily oldest mode of pollination in the Moraceae: anemophily or zoophily?

### 1. INTRODUCTION

Bread fruit, *Artocarpus altilis* (Park.) Fosberg (= *A. communis* = *A. incisa*), once the staple food of the Polynesians, is now grown and consumed throughout the tropics. Pollination in this genus, as in many other genera in the Moraceae (OSMASTON 1965; BERG 1977a), is not well understood, e.g. *A. altilis* is regarded as secondarily anemophilous (FRANKEL & GALUN 1977), and *A. heterophylla* as entomophilous (VAN DER PIJL 1953; JARRETT 1959).

In northern Brasil the trees of *A. altilis* are cultivated on a small scale in gardens near the houses. There, we studied the pollination system in order to try to contribute to the solution of the controversy existing in literature (BERG 1977a, VAN DER PIJL 1978 versus FRANKEL & GALUN 1977) about the question whether anemophily or entomophily is the basic mode of pollination in the Moraceae.

### 2. MATERIALS AND METHODS

From 14 December 1979 till 18 January 1980 and from 6 April 1980 till 19 April 1980 insect visitors were observed on five trees of *A. altilis* in orchards in Cametá, in Pará, Brazil.

In the field nectar was made apparent with Clinistic®, of Ames Comp., Elkhart, Indiana 46514 USA, which strips react positively at concentrations exceeding 0.25 % glucose (= 14 mMol/l).

On 14 December 1979, 11.00 a.m., part of a male inflorescence, at the first day

\*Present address: Transferbureau van de Universiteit, postbus 72, 9700 AB Groningen.

of anthesis, was collected. Fixation: Alcohol 70%. Anatomical sections were made one month later; embedding medium: Paraplast; microtome sections: 10 µm thick; stain: several sections with aqueous JKJ solution; other sections with astra blue, auramine and safranin (MAÁ CZ & VÁ GÁ S 1963).

Bee specimens, collection numbers 70710303 till 70710308, are deposited in the Rijksmuseum voor Natuurlijke Historie, P.O. Box 9717, 2300 RA Leiden, The Netherlands.

### 3. RESULTS

#### 3.1. Phenology

The flowers are arranged in condensed inflorescences. Within each inflorescence the flowers function as one unit: pseudanthium = blossom (FAEGRI & VAN DER PIJL 1979). Each pseudanthium contains only staminate or only pistillate flowers, which can be seen as a second-order dicliny. In this way *A. altilis* is monoecious.

By 16 December 1979, each of the seven main branches of one tree (A) had at the end one pistillate inflorescence, which had been in flower recently, as the wilted stigmas showed. In the second next axil each branch had a staminate inflorescence which flowered during the period between 16 and 20 December 1979. No new inflorescences had formed by 15 January or by 6 till 19 April 1980. In between 6 and 19 April three other trees showed developing synfructescences with, at the same branches, staminate inflorescences each of which had an anthesis duration of about four days. Most of the male inflorescences started anthesis simultaneously. However, on two trees there were a few that flowered one week later. A fifth tree produced many staminate inflorescences by 6 April and started by 19 April anthesis of a few pistillate inflorescences on the same branches.

Thus, flowering seems highly synchronised between the branches of one tree. The tree as a whole alternates anthesis of the pistillate and staminate inflorescences. This second-order dichogamy (FAEGRI & VAN DER PIJL 1979) produces a second-order dioecy, which makes self-pollination, of geitonogamy, impossible. And, because the trees seemed not synchronised with each other, mutual cross-pollination remains possible, with alternation in the direction of the pollen-flow. The second-order dichogamy provides in this way a better use of the reproductive capacity than is the case in other Moraceae like *Chlorophora excelsa*, with subdioecy, and *Musanga cecropioides*, with dioecy (OSMASTON 1965).

#### 3.2. Staminate inflorescence and visitors

The staminate and the pistillate inflorescences were odourless. When a staminate

Fig. 1. Staminate inflorescence of *A. altilis*.

A. Pollen collecting *Trigona fulviventrís* var. *guianae*.

B. Nectar probing *Trigona* at the morning of the first day of anthesis. Not all flowers are open. The bees neglected the outside raindrops.



inflorescence is shaken the powdery pollen grains sink slowly through the air. This suggests anemophily. This pollen was collected by black stingless bees, *Trigona* (*Trigona*) *fulviventr*is var. *guianae* Cock. (fig. 1A). After hovering in front of an inflorescence the bees landed and brushed the front legs over the protruding anthers, towards the middle legs, working the anthers with their mandibles. After several seconds of brushing the bees took wing and hovered in front of the inflorescence scraping the middle legs along first the front legs and then the hind legs. The hind legs were also rubbed together. These movements transported the pollen grains to the corbiculae, where a large mass of pollen accumulated. This behaviour sequence was repeated several times. Pollen collection lasted from about 12.00 hours till sunset (18.00 hours). A mean number of four bees were active on each inflorescence at one time. The anthers remained firmly attached to the flowers even after the inflorescence had dropped from the tree. This contrasts with the situation in other Moraceae (CARAUTA 1972; BERG 1977b). At the location only *Trigona* bees showed interest in the nectar or in the pollen. On a neighbouring tree of *Bixa orellana* L. several other insects (*Xylocopa* sp., *Euglossa* sp., *Melipona* sp. and Syrphidae) were collecting pollen and neglected that of *A. alt*ilis, which, presumably, was of low attractive value to these insects.

The pollinating value of the pollen-collecting *Trigona* bees would seem to be low, because the pistillate inflorescence, lacking pollen, will not attract pollen collectors. However, there appeared to exist another floral attractant. In the morning, starting at sunrise, the staminate inflorescences were visited by the same species of *Trigona* bees (fig. 1B), which now behaved differently from the afternoon visitors. After landing the bees walked over the inflorescences and probed them, also on the area with unopened flowers (see two upper bees in figure 1b). This indicates that the proboscis was inserted *between* the flowers. Often the bees remained for tens of seconds with their proboscis in the inflorescence. They were probably drinking nectar: captured bees regurgitated a large quantity of sweet liquid when they were killed.

The volume of nectar in the inflorescence was too small to be collected with a 1 µl. capillary. Glucose test strips gave a positive reaction when touched against the base of the flowers, but gave no positive reaction with latex from the inflorescence, or with fluids pressed from parts of the leaf, stem and the receptacle of the inflorescence. Therefore we concluded that there exists a glucose containing fluid (nectar) only at the bases of the flowers. The exact position was studied by making anatomical sections of the staminate inflorescence.

### 3.3. Staminate flower

The individual flower consists of one anther, surrounded by a perianth (fig. 2.2). At anthesis the filament elongates and pushes the anther out of the tube, whereafter the theca opens. The perianth tube consists of multilayered parenchymatic cells. The tip of the perianth seems to be inflated by several parenchymatic cells with a wide lumen (fig. 2.5). Of the epidermis cells only those on the top of the perianth tube have thick cell walls. The perianth contains longitudinally oriented vascular bundles.

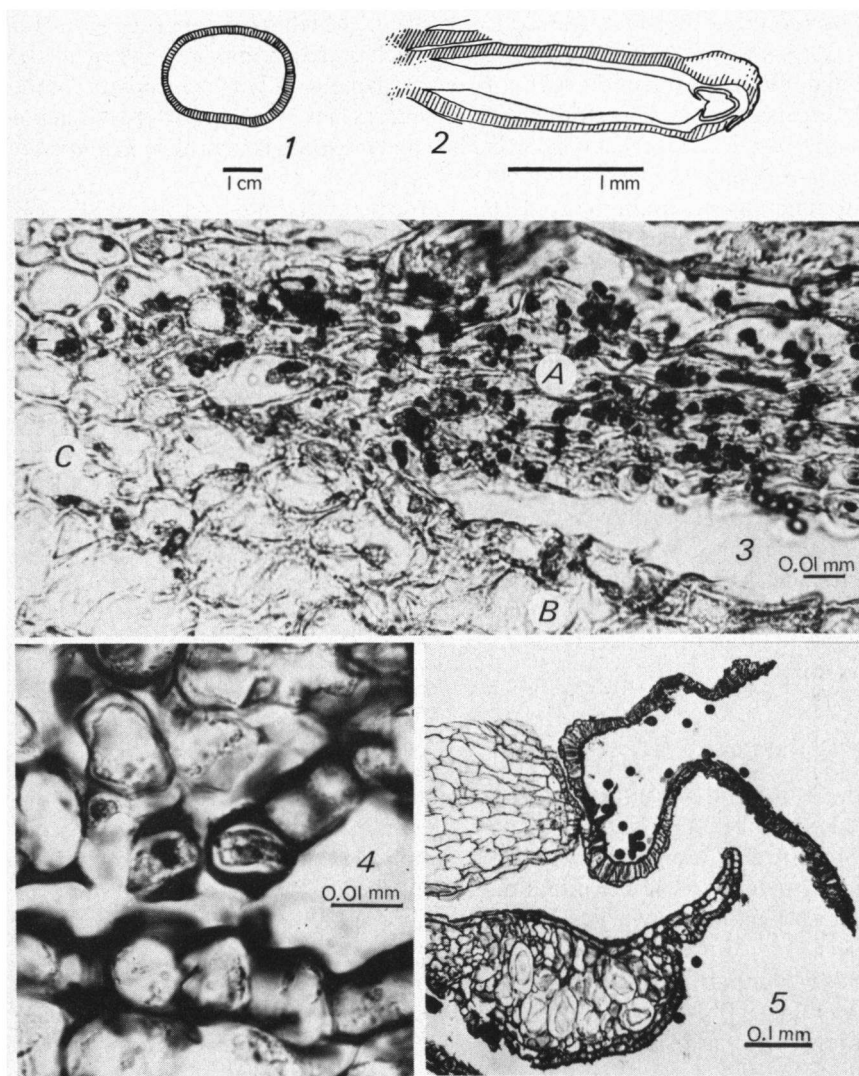


Fig. 2.

1. Cross section of the staminate inflorescence of *A. altilis*.
2. Staminate flower in bud. The area with starch deposits in hatched.
3. Detail of the flower base; A. perianth; B. filament; C. inflorescence stalk. The starch grains are stained black with JKJ.
4. Cross section through stoma at the base of the perianth. The left cell is dislocated during preparation.
5. Top parts of anther and perianth.

The perianth cell contains several leukoplasts, which stain dark blue with JKJ (fig. 2.3), which is indicative for starch. Such starch grains are absent in the inflated cells in the top of the perianth, in the filament and in the receptacle of the inflorescence (fig. 3). Therefore, the starch occurs in well localized deposits in the perianth (fig. 2.2). Starch has also been located in young nectaries of *Pedilanthus* and *Vinca* (FAHN 1979).

Stomata are present in the epidermis of the perianth, in the basal, middle and top region, always on the outside of the perianth only. Many stomata were localized in the basal region (fig. 2.4).

Morphologically specialized secretion cells are absent. Presumably the nectar will be produced from all perianth cells into the intercellular spaces and, thereafter, will be secreted through the stomata into the lumen in between the flowers: extrafloral, but really nuptial (FAEGRI & VAN DER PIJL 1979). This confirms the evidence which was obtained by microchemical tests, made in the field, and by the observations of the insect behaviour.

FAHN (1979) regards the mode of secretion from morphologically unspecialised gland cells through stomata as primitive. This can be a motive to see the observed nectar production in *A. altilis* as a novel development in the genus or in the species, which, because of its recent appearance, still is far from perfection. The secretion of the nectar seems to be restricted to the morning hours, because between 12.00 and 13.00 the *Trigona* bees changed from nectar drinking to pollen collection.

#### 4. DISCUSSION

Nectar is a floral attractant, which, in contrast to pollen as attractant, can be produced in both staminate and in pistillate unisexual flowers. In this way nectar enables the evolution of dicliny in entomophilous flowers. In the genus *Artocarpus* the top parts of the perianths of the adjacent pistillate flowers are continuous (or fused), leaving no outside opening in between the flowers (JARRETT 1977).

This will impair access to the nectar if production occurs in a similar way as in the staminate flowers. Therefore, no nectar can be expected in the pistillate inflorescences, and in fact there were never bees observed on any of these inflorescences.

The absence of visitors and the morphological impossibility of nectar secretion on pistillate inflorescences make entomophily improbable, and anemophily seems probable, also from other evidence, which has been mentioned before.

Then, the nectar in the staminate inflorescences cannot be interpreted as an attractant for pollinators. Moreover, nectar seems redundant, because the pollen itself acted as attractant for visiting bees. The primitive mode of secretion might indicate a novel development in the species.

What might be its adaptive value? A possibility might be to have "insect assisted wind pollination". That means that the bees' activities promote the

release of the pollen from the protruding anthers, which pollen grains thereafter are borne by the wind.

Such an insect-assisted pollen release might be a compensation for the absence of versatile anthers, or of explosive pollen ejection like it occurs in *Chlorophora excelsa* and some other Moraceae (OSMASTON 1965). The suggested functional explanation of insect assisted wind pollination has an equivalent in the wind assisted insect pollination in *Bulbophyllum warminghianum* (SAZIMA 1978). However, there remain two contra-indications for this explanation: 1. the pollen itself was sufficient to stimulate the bees to walking and scratching on the inflorescence; 2. evolution of nectar production might be expected on the pistillate inflorescence to open the way to, at least additional, insect pollination.

An alternative opinion might be that the nectar is not a novel evolution in *Artocarpus altilis* but a residual character which remained after an evolution from entomophily to anemophily. Such an interpretation cannot be rejected as long as the principle mode of pollination in the Moraceae family remains unclear. Both modes of pollination occur, e.g. *Cecropia* spp. (BERG 1977b) and *Antiaris* spp. (OSMASTON 1965) seem to be anemophilous, whereas in *Dorstenia* spp. the inflorescences show many features indicative for myiophily. HEIDE (1927) observed bird visits to *Conocephalus pectoralis*. VAN DER PIJL (1978) regards the Moraceae as secondary insect-flowers (*pollen-flowers* is a misprint). Entomophily in *Ficus* evolved as a kind of balanced parasitism. A more primitive parallel of this is provided by *Artocarpus heterophylla*, where pollinators breed in the fallen male inflorescences (VAN DER PIJL 1953). *Artocarpus* pollen has been found in the guano of bats (SOEPADMO & EOW 1977), which suggests a possibility of chiropterophily.

Another evidence for zoophily gives JARRETT (1959), by citing records made by Corner of odour production in staminate inflorescences of *A. heterophyllus*, *A. integer* and *A. dadah*, whereas Jarrett regards *A. rigidus*, *A. communis* and *A. elasticus* as anemophiles. St. Vogel (pers. comm.) found on Borneo *Artocarpus* inflorescences with an odour reminiscent of *Alocasia*. This is indicative for fly pollination. Yet the evidence seems too scarce for a decision on the primacy of anemophily or zoophily in the genus *Artocarpus*. Therefore, the explanation of the nectary as residual cannot be supported nor rejected.

As a consequence of this, the question whether or not entomophily is basic in the Moraceae family cannot be solved by using the evidence of nectar in staminate inflorescences of *A. altilis*. It would be of interest to examine the occurrence of nectar production in other genera of the Moraceae.

#### ACKNOWLEDGEMENTS

I thank the Prelazie of Cametá, for hospitality, Prof. Dr. B. M. Moeliono for research facilities, and Prof. Dr. L. van der Pijl, Dr. C. C. Berg, and Dr. S. A. Corbet for their valuable suggestions.

## REFERENCES

- BERG, C. C. (1977a): Revision of African Moraceae (excluding *Dorstenia*, *Ficus*, *Musanga* and *Myrianthus*). *Bull. Jard. Bot. Natn. Belg.* **47**: 267–407.
- (1977b): Abscission of anthers in *Cecropia*. *Acta Bot. Neerl.* **26**: 417–419.
- CARAUTA, J. J. P. (1972): *Dorstenia hirta* Desvaux (Moraceae) Figueirilha; estudo de sua biologia floral. *Atas. da Soc. Biol., Rio de Janeiro* **16**: 7–11.
- FAEGRI, K. & L. VAN DER PIJL (1979): *The principles of pollination ecology*. Pergamon Press, Oxford (3d. ed.).
- FAHN, A. (1979): *Secretory tissues in plants*. Acad. Press, London.
- FRANKEL, R. & E. GALUN (1977): *Pollination mechanisms, reproduction and plant breeding*. Springer Verl., Berlin.
- HEIDE, F. (1927): Observations on the pollination of some flowers in the Dutch East Indies. *Dansk Bot. Ark.* **5**: 1–42.
- JARRETT, F. M. (1959): Studies in *Artocarpus* and allied genera, III, a revision of *Artocarpus* subgenus *Artocarpus*. *Arnold Arbor.* **40**: 113–155.
- (1977): The syncarp of *Artocarpus* – a unique phenomenon. *Gard. Bull., Singapore* **29**: 35–39.
- MAÁ CZ, G. J. & E. VÁ GÁS (1963): Untersuchung des Lugholzes mit dreifacher Färbung. *Acta Biol. Hung.* **13**: 341–346.
- OSMASTON, H. A. (1965): Pollen and seed dispersal in *Chlorophora excelsa* and other Moraceae, and in *Parkia filicoidea* (Mimosaceae), with special reference to the role of the fruit bat, *Eidolon helvum*. *Commonw. forestry rev.* **44**: 96–104.
- PIJL, L. VAN DER (1953): On the flower biology of some plants from Java with general remarks on fly-traps. *Annls. Bogor.* **1**: 77–99.
- (1978): Reproductive integration and sexual disharmony in floral functions. In: A. J. RICHARDS (ed.). *The pollination of flowers by insects*. Acad. Press, London, 79–88.
- SAZIMA, M. (1978): Polinização por moscas em *Bulbophyllum warmingianum* Cogn. (Orchidaceae), na Serra do Cipó, Minas Gerais, Brasil. *Rev. Bras. Bot.* **1**: 133–138.
- SOEPADMO, E. & B. K. EOW (1977): The reproductive biology of *Durio zibethinus* Murr. *Gard. Bull., Singapore* **29**: 25–33.