

occurs, and even more rapidly, if the plants are brought back to Bogor after this period.

The possible interaction of growth-hormones in the processes involved is discussed.

Bogor, March 1952.

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ON THE FLOWER BIOLOGY OF SOME PLANTS FROM JAVA with general remarks on fly-traps (species of *Annona*, *Artocarpus*, *Typhonium*, *Gnetum*, *Arisaema* and *Abroma*)

by

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I. *Annona muricata* L.

The blooming of this well-known fruit plant (Sour Jack) deserves a special description as it is fit to become a standard example of self-pollination in the tropics.

Though the plant is not indigenous to Java (it was imported from the West Indies) its life-cycle appears natural there and the plant often fruits well. Some trees remain sterile.

BURCK² already pointed to the wide-spread autogamy in the family of the Annonaceae, where it is often correlated with non-opening flowers. The self-pollination generally takes place when the flower parts fall off at the end of anthesis.

WINKLER³ later on described the process of self-pollination in many other members of the family in South Africa. The phenomena described here for *A. muricata* agree more or less with WINKLER's finds in *Uvaria venklerei* DIELS and *Monodora preussii* ENGL. et DIELS. His data on *A. muricata* are less detailed than those on *A. polystriis*. Both show autogamy. No visitors are mentioned.

The flowers of *Annona muricata* hang down more or less vertically and are often cauliflorous. The very fleshy petals, yellowgreen, that scarcely open, give the flower such a peculiar shape that one expects a special pollinator, the more so since the flower gives out some sweet odour besides the peculiar smell that pervades the whole plant. I found, however, no visitors at all. While the three outer petals gradually open somewhat during the first three days of anthesis, the three inner petals never show any direct aperture, though they are not hermetically sealed.

There is a special reason why it would even be impracticable for possible visitors to act directly as pollinators in the next flower. The

anthers are closely packed together into one compact mass around the complex of pistils. In this way the pollen is entirely shut off from the exterior. The hard sterile heads of the anthers fit like stones in a wall. In fig. 1 the pollen is represented by dots in the thecae.

The number of pollen grains is strongly reduced. Each loculus contains only one row of tetrads, about twenty in length. Each tetrad of firmly connected pollen grains measures about 300 μ . The stigmas secrete a viscous slime that unites into a thick drop, dotted in fig. 1.

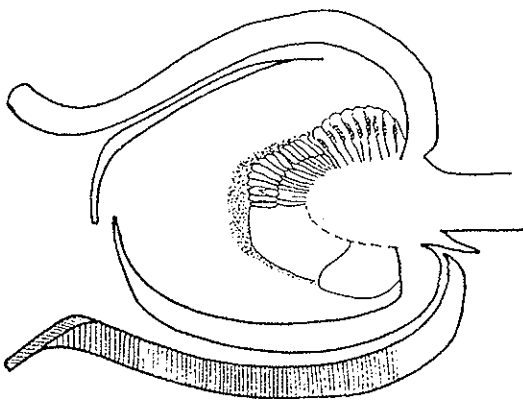


Fig. 1. Longitudinal section through flower of *Annona muricata* on its third day. The striped plane is not cut and lies slightly below the plane of design. Slime dotted.

that repeatedly gave rise to the belief of ghosts haunting the garden at night.

The sweet fruitish odour is perhaps a remnant of the primary condition, when beetles were the pollinators. BURCK² already suggested this possibility for the family. CORNER⁵ (p. 126) mentions small beetles as frequent visitors in other Annonaceae, as *Caramidium odoratum* BALD. In some of these cases (*Drepananthus*, *Xylopicia*, *Gonothalampus* and *Anacagorea*) he found that the flowers keep the visiting beetles in a trap for some days.

The exposition of the pollen shortly before the flower disintegrates does indeed fit in with what we know about trap flowers. As a consequence of extreme protogyny pollinators must be kept imprisoned till the pollen is ripe. Our *Annona* species has already evolved beyond this phase. I think the very large pollen tetrads would not be fit for transport by small beetles.

The antique way of pollination by beetles has been abolished entirely or partly by other beetle-flowers, like *Castanea*, as seen by FORSCH¹⁷.

In JULIANO's study¹ on *A. muricata* (and other species) in the Philippines this author says: "the flowers emit a fragrance which attracts visitors". As nothing further is said this makes the impression of being an assumption not based on actual observation.

JULIANO cites a study by WESTER, which was not accessible to me (Bull. Torrey Bot. Club 1910, 37: 529) and which describes beetles in flowers of *A. squamosa* in Florida.

JULIANO's data on the flowering of *A. muricata* differ in some respects from mine (e.g. dehiscence of anthers before anthesis). Perhaps he overlooked the protogyny and studied flowers during the last hours of anthesis only. This might explain his describing the opening of the flowers and the complete anthesis as taking place from 4.- till 10.- p.m. in one day. WESTER, however, seems to have described the protogyny as seen above.

2. *Arctocarpus heterophylla* LAMK.

The jackfruit or *nangka* is another common fruit-tree of which the flower biology should be better known.

Its green and fleshy flower-heads give the impression of being anemophilous like those of almost all members of the family.

CORNER⁵ (p. 650) already pointed to the fact that in the genus *Arctocarpus* there are anemophilous species with dry, dust-like pollen and odourless inflorescences, but that e.g. *A. heterophylla* has a sweet scent of honey and burnt sugar and that the flowers attract small flies and beetles.

In Java I also found our species to emit the odour of overripe fruit. The pollen is moreover not produced in large quantities and is sticky. On the thick male flowerheads a number of new anthers project from the matrix every day. The flowering of female heads also lasts for some days.

As visitors on male and female heads I found large numbers of small *Trigonabees* and small Drosophilid flies (genus *Deltosomyia*) together

with the common Phorid *Megaselia acclaris* LOEW. Small tjitjak-lizards (*Hemidactylus*) were obviously acquainted with the entomogamy, as they were regularly found waiting on the flowerheads. The same flies were present in great numbers on the fallen male flower heads that always cover the ground and decay when the atmosphere is sufficiently moist. As the insects lay eggs here, the improbably large flowerhead is not only a producer of pollen, but also a medium for the development of a new generation of pollinators.

When kept in a glass tube each male flower head of *A. heterophylla* produced a great number of the flies referred to.

In *Alouasia pubera* (notable by a temperature of 24.5°C. above air-temperature) I described¹¹ another instance of the pollinating flies (this time Anthomyids of the genus *Atherigona*) breeding on the decaying male flowers, but in this case there was a closer bond between flower and flies as the latter pupate inside the persisting spathe and escape just when the spathe-sealing of the apical opening disappears.

For the time being the bond is in *Artoctopus* only effective as a means to secure a constantly present population of flies near the plant but, far-fetched as it seems, it may perhaps be seen as the beginning of a symbiosis for the whole life-cycle. In a sense this would be comparable to the symbiosis between *Ficus* and *Blastophaga*.

The male flower heads of *Artoctopus heterophylla* are in a sense specially adapted to the breeding of their pollinators and are not just accidental media of development as any decaying vegetable matter. This is made clear by the following comparison to an anemophilous species.

When male flower heads of *Artoctopus elastica* REINW. (past anthesis) were placed in jars under diverse conditions as to moisture, a striking difference with *A. heterophylla* became evident. After two months hardly any insects had developed from them, merely some Nitidulid beetles and one single Drosophilid fly.

These flowerheads are anemophilous as indicated already by CORNER¹². Before the emergence of the anthers they are green. After this the general colour changes to light brown. At the time of opening a distinct smell is emitted, indicating the transitional nature of the anemophily. The smell is ester- or acetone-like. It (? still) attracts Drosophilids if placed in a room, viz., five flies to each one on neighbouring ripe bananas. After half a day the smell becomes musty and fades away. Perhaps a special compound inducing oviposition is lacking, compared to *A. heterophylla*, as I saw no signs of this process.

An analysis by an animal physiologist of the substances inducing the visit, sucking, mating and oviposition on flower parts might be valuable to flower biology.

The pollen is extremely fine and settles as a dusty layer on the table on which ripe flower-heads are placed. In newly opened anthers the grains still stick together.

3. *Typhonium trilobatum* SCHOTT.

In the month of August 1942 the curious spathe were found scattered between the grass along the fence of the prisoners' camp of Tjitjatap. For a good figure see BACKER, 1934. Onkruidflora Javasche Sukkerriet-Gronden (pl. 180).

The upper part of the spathe is almost flat and lies horizontally, touching the ground. The underside of the spathe is brownish green, but the upper side shows a most peculiar dark purple colour with a perfectly velvety surface, except for the basal part, which is green.

The lower, vertical part is greenish and encloses the female flowers. Later on it persists, enclosing the fruits. Between the lower and upper part we see a narrow throat.

The thread-like appendix of approximately 20 cm. in length is purple-coloured.

The yellow anthers are conspicuous above the throat.

Though experiments (cf. p. 97) seem to prove that in general the purple colour does not in the first place attract the flies in "*Ekelblaten*", it is curious that the purple colour and foetid smell usually coincide. The colour will perhaps prove to be of secondary importance in provoking the landing.

The same holds good for *Typhonium*. Its smell is musty, but difficult to define accurately. One observer compared it to stale, but not yet rotten meat. Another compared it to the smell of a stable. In my opinion the smell is comparable to that of old horse dung mixed with a sweetish smell of decaying fruit. After the productive period the smell still adheres to the appendix. Various inflorescences show the same rhythm in the course of the day.

The data are collected in the table of p. 82.

After the second day the upper part of the spathe withers and breaks off. The lower part remains succulent and even increases in size, giving the impression of a fruit. The plants produced many fruits.

At first no visiting insects were seen. It was peculiar that house flies did not show the least interest. A specimen of *Aphis indica* did, however, circle around the vertical appendix, many times even alighting for some

1st day	Spatha	Anthers	Appendix	
			Temp.	Smell
4.45 a.m.	splitting	closed	cold	none
5.30 a.m.	almost opened	"	"	"
6— a.m.	flat and horizontal	"	"	"
(sunrise)	flat and horizontal	"	"	"
7.15 a.m.	zonal	"	"	faint
7.30 a.m.	"	"	warm	increasing
8— a.m.	"	"	"	strong
9— a.m.	"	"	decreasing	decreasing
11.30 a.m.	throat closed	"	cold	none
13— p.m.	turning green	"	"	"
2nd day				
5.15 a.m.	green	incipient emission of pollen	"	"
5.45 a.m.	"	pollen on throat	"	"

moments. The throat underneath the male flowers is so narrow that it leaves a slit of less than 1 mm. so that small pollinators were to be expected. On closer observation very small beetles indeed appeared to be the pollinators. Against the dark spatha they were scarcely visible but I could sometimes observe their conduct. They landed on the spatha and immediately found their way via the throat into the ventricose lower part.

The inside of this kettle is not velvety but glossy. I am not certain that it acts as a "Gleitfalle" as some insects crawled back through the throat during the morning hours. Most visitors, however, remained in the kettle. When the throat was cut away the beetles were clearly seen to find it difficult to climb the wall of the spatha.

In the afternoon the aperture in the throat narrowed and became hermetically sealed so that the visitors were trapped inside. On an average they measured less than half a millimetre. I could recognize Staphylinidae (Athetinae), a Scydmaenid and a Nitidulid, so that the collection may provisionally be considered as carrion or dung insects. There must, however, be some narrower specialisation. No bigger carrion or dung insects tried to enter. The way in which some authors treat all carrion beetles and flies as one class of pollinators is certainly too simplistic.

Most of the captives were found between the yellow, hook-like projections above the female flowers. The ecological significance of these hooks

as bearers of nutritive tissue is obvious and I actually observed the beetles feeding on them. When eating they loosened a powder from the surface and became covered with it.

The subsequent stages of the flowering closely resemble those in *Amorphophallus* and other Araceae protogynic trap flowers.

The time of pollen emission in second-day flowers does not coincide with the time of attractiveness and receptivity in first-day flowers. At first this seemed strange but the following simple experiment made it clear that both stages nevertheless harmonize.

The pollen rests near the throat in the shallow pit of the spatha. It is pale violet and contrasts strangely with the greenish base of the spatha. I covered this part of the spatha, including a portion of the appendix, with a glass tube and sealed it at the bottom.

In numerous cases I found no beetles in the tube up till 7.15 a.m. of the second day, but at 7.50 a.m. a number of them had entered it from the throat. These insects must have waded through the very fine and dry pollen and carried it on their bodies. They would probably have been able to transport it to a young inflorescence.

The fact that the throat opened slightly during this period is partly due to the shrinking of the male flowers and of the axis between them. The axis also grows slightly upwards, but the opening and closing movements are principally governed by the thick throat of the spatha.

The data of the life history, given by BANERJI¹, do not primarily concern the flower biology. The flower biological details described differ in some points from those given above. His *T. trilobatum* var. *geminum* from India also shows a morphological difference, the spathae being erect and funnel-shaped.

BANERJI, however, also mentions small beetles as pollinators, and pollen lying at the neck of the constriction. He thinks that "the neuter flowers" are eaten away by the insects.

4. *Gnetum gnemon* L. var. *domesticum* Mgr.

Amongst the highest Gymnosperms (Chlamydospermae) the two families of the Ephedraceae and Welwitschiaceae are known to have developed flowers with insect pollination.

About the Gnetaceae, in so many respects evolved along the lines of the Angiosperms, we only have suppositions in this respect.

KARSTEN² thought he tasted sugar in the drop of fluid on top of the "style" and saw ants lick from it. He suggested the possibility of a secondary function as attractive material.

This "pollination drop" is in itself nothing new in Gymnosperms, but if it has indeed become nectar-like, it serves no longer only to capture the microspores, but has assumed a new function.

I could prove that the more or less slimy drop contains much sugar. It reduces strongly and without preceding hydrolysis an ammoniacal silver solution and a Fehling solution. Ants indeed gathered in great numbers around the fluid on glass slides.

There are other indications of entomogamy in *Gnetum*. Early in the morning male inflorescences emit a distinct, sweetish odour.

CORNER² (p. 725) also mentions a scent for the male flowers only. A visual attraction, as present in *Ephedra*, is probably unimportant here, certainly as far as the green female spikes are concerned. The male inflorescences in some *Gnetum* species, also in *G. gnemon*, are more showy because of the many white stamens.

The pollen is produced in small quantities and is sticky. It hangs together in Monilia-like strings.

Future observers should reckon with the right time of anthesis. The anthers open at about 7- a.m. and the stamens wither after 11- a.m. At about the same time or earlier one can find the nectar drops on fertile female flowers (cf. fig. 2) and on the sterile female flowers in the male inflorescences. Later in the day the drops often disappear again. This disappearance may be due to evaporation or to active processes. The secretion is decidedly dependent on atmospheric conditions. In a dry atmosphere no drops become visible, but when male or female inflorescences are placed under a moistened glass bell, secretion promptly starts at any time of the day. The drops then easily become bigger than under natural conditions. Many extrafloral nectarries in the tropics are for their activity bound to moist air in the same way. Obviously *Gnetum* is for its pollination adapted to humid forest conditions.

Under the glass bell not all female flowers reacted, only those of a certain dimension, viz., 3½-4 mm. (without style).

The flowers remain in this phase for a long time. Often the drops on female flowers do not disappear entirely but dry out to a viscous mass that turns again into a liquid during the night.

When I fixed a number of secreting flowers and cut them longitudinally I found that in all of them the embryo sac was in the phase of 32-64 free

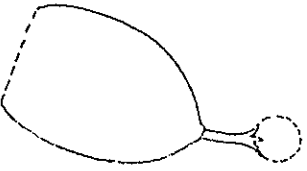


Fig. 2. Female flower of *Gnetum gnemon* with nectar drop on top of the inner integument.

nuclei. I found in these sections a distinct, though shallow, pollen chamber and none of the papillae FAGERLIND⁶ described. The place of origin of the fluid could be ascertained as the tip of the nucellus of which the cells had disintegrated and afterwards changed into an amorphous mass with remnants of nuclei. There was no other special secretory tissue. KARSTEN⁸ already arrived at the same conclusion.

The fast disappearance of the drop is different from what PORSCH¹² found in *Ephedra campylophoda*, where it remained throughout the heat of an August day in Dalmatia. The disappearance, even when the nectar is not taken by insects, is important for the fertilization. In this way, just as in most Conifers, the pollen is sucked into the very narrow style channel towards the nucellus. How it escapes being lapped up quantitatively together with the fluid remains to be studied.

Observations on the pollination of the tree in a cultivated condition are hampered by some circumstances, viz., firstly that around trees in gardens the atmosphere becomes too dry soon after sunrise and further that it is always doubtful whether the female flowers are in the right phase.

Once, however, early in the morning in a garden near Djakarta, I found that the nectar drops in male inflorescences were being lapped up by small flies. Small bees (*Trigona*) collected the pollen. As this observation was made in a Japanese prisoners' camp I could not make closer observations or collect insects. In the Bogor Botanic Garden, I found a good number of visitors of many kinds, mostly flies and mosquitoes. Female trees often produce some male inflorescences.

Later on I watched female inflorescences at all times of the day in Bandung, but could not find any visitors, so that the actual transport of pollen by insects is far from certain.

Of the female trees I watched in Bandung, the fruiting was decidedly poor. As said before female inflorescences never emit a smell and are inconspicuous. On the other hand there are no signs of anemophily.

The explanation of this absence of visitors can be sought in different directions:

- The visitors are specialized and not constantly present in city gardens (cf. *Abronia*).
- The visit to female flowers happens at other times and by insects other than those mentioned above.
- The attraction of female flowers differs from the attraction of male flowers. In this connection I may refer to cases as *Yucca* and some Cycadaceae, where one kind of flower is visited for pollen collecting and

the other for oviposition. PORSCH¹¹ compiled such data in his study on comparable phenomena in *Castanea*.⁹⁾

The observation of insects on male inflorescences of *Gnetum* might strengthen the idea that the spike of *Gnetum* is the fore-runner of entomogamous Angiospermous flowers in an ecological sense. PORSCH¹¹, however, already remarked for *Ephedra* that the nectar secretion through the micropyle is not a homologon to the nectar secretion of Angiosperms and that the whole contraption in *Gnetum* is a blind alley, only possible in bisexual inflorescences and with nude ovules. Angiosperms with covered ovules had to develop a new line, with other sources of nectar.

Although entomogamy as such in *Gnetales* still may be seen as an approach to conditions in Angiosperms, I must remark that in one other point the pollination of this group is more primitive than it is in some Conifers (*Taxus*, *Arucaria*) where the pollen germinates outside the micropyle and forms pollen tubes.

Angiospermy seems as a rule to have been preceded by siphonogamy. Though ungerminated pollen has been found inside the "closed carpels" of some Claytoniales, and though open styliar channels are not uncommon in Angiosperms, traces of the *Gnetum* method (sucking in of microspores) cannot be found as a primitive condition in Angiosperms. There are some cases of pollen being found in the styliar channel (*Batomopsis*, *Tribium*, *Pritchardia* etc., cited by MAHESWAR¹⁰ p. 423). These instances, however, do not give the impression of being transitions from the way in which pollination takes place in *Gnetum*.

5. LIGHT WINDOWS IN *Arisaema laminatum* Bl.

Of this *Arisaema* an excellent plate can be found in BLUME'S Rumphia I (Tafel 27). Whereas other *Arisaemas* grow in rain forests, this species prefers lighter forest on calcareous and other steep rocks.

Figure 3 shows the beautiful "light-window" in the spathe. Seen from the back this place in the knee of the spathe shows nothing peculiar except for a total absence of colour. Seen from the front (fig. 3) it is light, as if illuminated by a lamp. This feature is partly due to the transparency of this part of the spathe. The rest of the back of the spathe

⁹⁾ For *Cycas rumphii* Miq. I cannot confirm his general idea that the smell of the male cone of Cycadaceae has an attractive value and that the female sporophylls have no smell. When groups of female sporophylls arise on top of the stem they emit for many days on end the same strong and unpleasant smell as the male cones, but only in their youth. This takes place prior to the ripeness of the ovules as no pollination drops were visible and as ovules and sporophylls were not fully grown. In male cones the smell also precedes the dehiscence of the anthers by a long time. Perhaps the smell is primarily a result of metabolic processes during rapid growth.

is slightly more pigmented. Seen from the front the underside of the window is framed by a darker plane formed by the extra layer of the front of the spathe, though this side too is but slightly coloured. On the upper side the window is set off by the green horizontal part of the hood of the spathe. This contrast is especially emphasized by a dark-purple line — only on the inside — between white and green parts. (The same line is shown by the well-known window around the sexual organs in *Aristolochia* flowers). A comparable dark rim on the front edges of the spathe accentuates the contrast with the underside of the window.

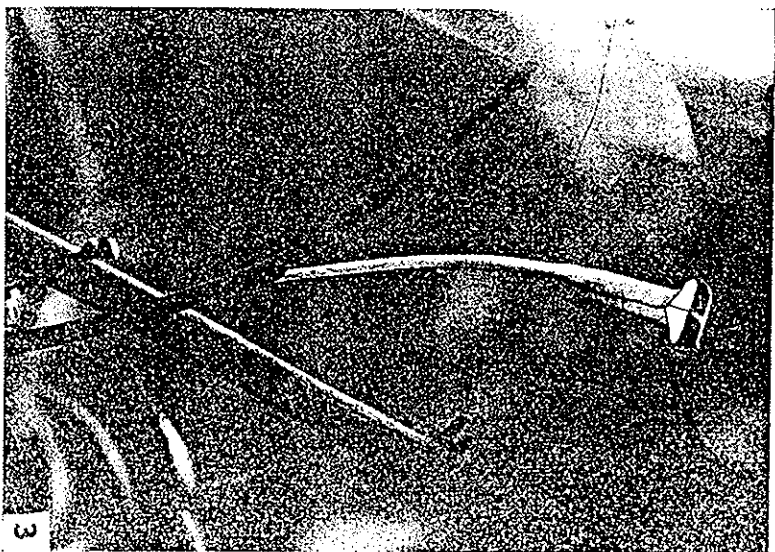


Fig. 3. *Arisaema laminatum*. Spathe seen from the front in its natural surroundings. $\frac{2}{3}$ nat. size.

The almost luminous spot does not simply let through light from back to front, as in that case it could never be lighter than the background,

which it often is (cf. fig. 3). It is brightest when light falls on it from the sides and from above. The tissue seems to reflect and refract the light, concentrating it towards the mouth of the spathe.

My notes on the find of this *Arisaema* (Mt Bongkok near Pleiad, Java) are lost and I do not remember finding insects in the spathe. Neither do I remember any special smell, but the absence of a smell might only be temporary—as we know from related Araceae trapflowers *Typhonium*, *Amorphophallus* etc. I am, however, certain that the window is a contrivance that acts on insects which have been lured into the neighbourhood by other means, tempting them to enter the trap or hindering them from leaving. The appendix, often so long in the genus, is short and inconspicuous in our species.

In *Aristolochia* the function of the window is perhaps more limited, viz., to that of keeping the insects near the sexual organs. The fact that light windows occur in other *Arisaema* species, either to trap insects or to keep them near the sexual organs, is clear from the figures in a study by BARNES². One of these Indian species (*A. tylophorum* FISHER) even looks identical with *A. laminatum* Bl. In *A. leschenaultiana* Bl. he figures dark and light longitudinal zones in the tube of the spathe, but apparently did not study them from the inner side. The name of an other species, *A. transluens*, is in itself significant.

BARNES describes the pollination of this species by small flies (Mycetophilidae) and mentions an unpleasant smell!

In the light of what we know about fly-flowers in general I want to draw attention to the remark about *A. convolutum* (a species with a curious shift of odour production from the appendix to the tail of the spathe limb), that "the tail serves as a setting place for the flies that are attracted". I am not sure whether this is a mere assumption or a reference to an actual observation.

In KIRCHNER's "Blumen und Insekten" we find (p. 207) that the small flies trapped in the spathe of *Arisarum vulgare* do not escape through the shaded mouth, but fly all the time against the transparent linear window in the kettle.

It is doubtful if this conduct of flies is sufficiently explained by their well-known phototaxy as demonstrated by flies on glass windows and *Drosophilas* in bottles. Perhaps it is a more intricate reflex connected with flight.

NEGER¹² (p. 613) already pointed to this supposed function of window-panes in flytraps.

KNOLL⁹ also noted this connection, when describing the remarkably bright interior of the kettle of *Arren* (pp. 426, 433). Here the mechanism can operate only on insects that have been trapped already.

In my inaugural address "Het ecologisch moment in de plantkunde" (Groningen, Batavia, 1948) I already pointed to the fact that light-windows in *Arisaema*, *Aristolochia* and *Darlingtonia* are not to be looked upon as mere expressions of a morphological type. From a review by TROLL²¹ that came to my knowledge after finishing this manuscript and that abstracted an unpublished study of his, I learned that he also had come to the conclusion that light windows may guide insects to the sexual organs of some flowers (*Aristolochia*, *Cyrtopetalum calceolus*, *Arisaema ringens* and *A. fargesii*) and into the traps of *Darlingtonia*.

A most convincing picture of a light-window in an insect-catching contraption is the one given by TROLL²², in his fig. 1611 of the pitcher of *Darlingtonia californica*.

TROLL says (p. 1825) that it has the form of the fly-catching glasses our grandparents used and that the window lures the insects into it. He remarks that the mesophyll in the translucent spots is absolutely free from intercellular cavities. Perhaps there is more than just transparency in the physics of this tissue.

In his latest publication TROLL²³ reverts to the subject of light-windows, describing them as "diaphane-Strukturen" to differentiate them from his *Fenster*, the slits in lantern flowers. In his fig. 24 the window pane of an *Aristolochia* appears lighter than the background. He also gives a clear photograph of the windows in *Arisaema fargesii* BUCH. and recognizes the ecologic significance of other details, such as the dark line surrounding the translucent parts.

MCCANN¹¹ described light windows in other fly-traps, viz., the flowers of *Ceropegia* and *Cryptocoryne* species. His explanation (illumination of the interior) is somewhat simplistic.

The windows in the hanging flowers of *Cyclamen* and *Fritillaria* have been described by STÄGER²⁰ as replacing nectar guides in flowers where the light from below might be insufficient to show coloured spots of the ordinary type. Here too the windows in the basal part do not only transmit light that enters vertically to the surface, but seem luminous when illuminated obliquely. There is, however, the difference that no dark frame surrounds the transparent area and that the surface seems equally bright from both sides. Perhaps these transparent areas belong to a different ecological class.

6. *Abroma augusta* L. f.

We possess an elaborate description of the flower biology of this Indonesian plant by WINKLER⁵⁷. It was made from a specimen cultivated in Camerun.

The main points agree with what I saw in Java. WINKLER pointed to the room formed by the queer and hard petal bases (cauculi) that have crystal-clear parts, whereas the upper parts of the petals above the constriction are thin and leaf-like and flutter to and fro (cf. fig. 4). The bases form the outer wall of a circular tunnel of which the inner wall consists of the five flat staminodes (between the anthers) that also have translucent parts (cf. fig. 5).

WINKLER admits that the ecological function of the flower construction is not clear, but supposes that the flower may be a *Phaegentäuschblume*, a fly flower with delusion of nectar. He saw numbers of small flies of the species *Oscinus alpinensis*, *O. virgosa*, *Desmometopa* spec. and *Mitichia vari-color*, all species described by DE MEYERE. Most of them were found walking round and round in the above-mentioned tunnel. Sometimes they went in and out through the outer entrances of this tunnel, viz., the slits in the side, where the five petal bases do not touch and leave pores of 2×3 mm.

We already know many instances of "kettle-trap flowers", that retain insects for a time in a kettle, but *Abroma* is the first with dialypetalous dicotyledonous flowers.

As the petal bases have strong purple bristles at their base and apex on the outside (see fig. 4) there is also an outside alley where flies can walk around the flower base. WINKLER saw flies walking here, coming in and out of the slits, covered with pollen. The fertile anthers shed inside the tunnel. The sense of this long stay not clear. There is certainly no direct, easy access to the pistil from the tunnel.

WINKLER saw flies enter the central, funnelshaped room around the pistil and inside the tunnel (see fig. 5). This must lead to pollination.

I could entirely corroborate WINKLER's description. In Java too the flies remained strongly attached to the tunnel and its outside alley, so much so that they even stayed in cut flowers carried home. The small flies were here also *Mitichia*s, probably *Phylomyza flavipennis* DE MEYERE,

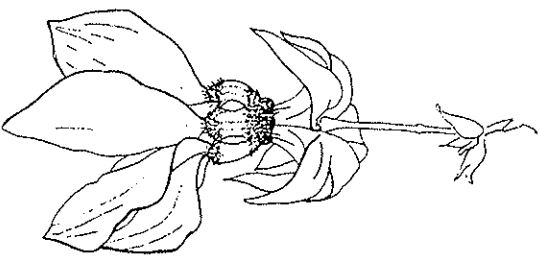


Fig. 4. Flower of *Abroma augusta*. $1/4$ nat. size.

which species nowadays is placed in the genus *Neophylomyza*. Their natural way of feeding is not known to me. Other flies or dung insects were obviously not interested.

The flies apparently breed on a special substrate, not always present near my garden. Sometimes during a period of some months not a single fly appeared on the flowers.

Like WINKLER I could not ascertain what the ultimate attraction might be, unless it were the odour itself, faint, more or less dung-like, somewhat disagreeable. The yellow discus inside the tunnel, regarded as a gland by WINKLER, showed no nectar in Java, as it did in Camerun. Neither has it the anatomical characteristics of a secretory tissue.

A stimulus of a more sexual character, leading to oviposition as in other fly flowers, was also absent or incomplete. I found neither eggs nor larvae, though the brown-purple colour and the smell characterize the flower as an *Ekelbüte*, a flower with a nauseating smell.

The curious flower reveals itself as an ingenious contraption for leading flies about in a predestined way, when we reconsider it in the light of "light windows" (diaphanous structures).

The petal bases as well as the staminodes are windows with translucent tissue framed by dark-purple rims, as familiar by this time. Only are the windows here divided into panes by secondary dark lines, recognizable as ridges in cross-section (cf. fig. 5).

The windows are luminous from one side only. They are of course equally transparent from both sides when held against the light, but they refract light and seem luminous against a dark background only when seen from one side.

The petal bases, when seen from the outside, are dull-coloured with light purple lines, not corresponding with the internal ridges. Their basal and apical parts, already described, make them from the outside resemble the head and thorax of a big fly. Seen from the inside of the tunnel—and of course also from the side entrances across the tunnel—the windows are bright, as visible in fig. 6.

From quite near, as seen with the eyes of flies on the outside wall, they are of course relatively larger and more conspicuous. A glance at fig. 5 will make this clear. The staminodes are luminous seen from the inner room, the pistil room.

In both windows the side with the dark ridges is the bright side. These windows are of course brightest when placed before gaps in the more peripheral whorl of the flower.

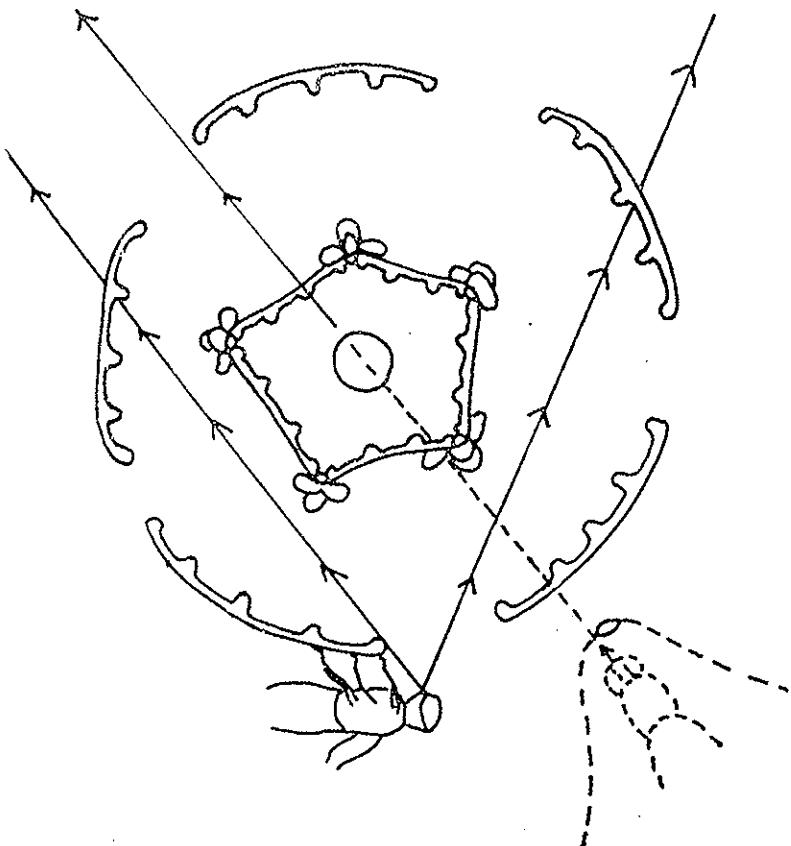


Fig. 5. Cross section through basal part of the flower (petal bases, stamens and staminodes) of *Abronia angustata*, with indication of the way flies can see the windows in the male and female regions. Interrupted lines indicate what lies below the plane of design. Magnified.

The stay of the flies in the tunnel is of course not the first phase after arrival. They could hardly land on the outside of the petal bases. Therefore it is necessary to reconstruct the whole process of the visit.

It is well known (cf. KNOLL) that visiting flies in *Abronia* first gather in the neighbourhood and only gradually come to the flowers proper. This is in accordance with the phobotactic nature of the stimulation. Only in a purely tropotactic stimulation the visitors make straight for the object. This may happen in the very last phase of the approach. The same is apparent in *Abronia*. As I saw personally, the visitors start on a nearby leaf and finally land on one of the hanging petals. Here they remain quiet for quite a time. Why this happens (it has been observed

in many fly-flowers), must be left to be studied by an animal physiologist, a sense-physiologist. In many studies on the smell-orientation of insects we find these stops, where the insects seem to elaborate the smell-excitation like dogs have a habit of doing (cf. OTTO 19). While this happens the tender petals often flutter to and fro. The petal blades, namely, are attached to their more solid bases with a very thin claw and the connection is built like a spring. These petal blades act as conductive organs that do not lead visitors straight away to the kettle but induce them to do so in a psychological way. When the visitors go upwards into the hanging flower (cf. fig. 4) they reach the narrow claws of the petals. The further way up is obstructed by the hard bristles on the base. Through the space between two neighbouring claws the insect looks obliquely upwards



Fig. 6. *Abronia angustata*, windows in petal bases seen through the pores against a dark background. (Visit to the male region).

Fig. 7. Flower viewed obliquely from below, window in a staminode as an incoming fly sees it. (Visit to the female region). $1\frac{1}{2} \times$ nat. size.

against the lighted window furnished by the staminode across the pistil room. (In fig. 5 the fly in this phase is drawn with an interrupted line and so is its line of sight, as long as it remains below the plane of the

section). In fig. 7 this window has been photographed obliquely from below, as the fly sees it on arrival. The fly now goes towards this window entering the pistil room, as described by WINKLER, and pollinates the flower. When a number of flies have arrived they jostle in the narrow room. *)

Between the spreading tips of the staminalodes are triangular openings through which the brighter outer windows of the petal bases are visible. Through these openings the flies can enter the outer circular room with the anthers. By their shape and lesser brightness, when seen from the tunnel, the openings act as one-way gates, so that flies can never go back from anther-room to pistil-room.

When the flies are in the outer tunnel they seem to be hindered from escaping immediately as described above.

As in most kettle-traps they now have come into the male sphere of the flower and are dusted with pollen. Even when going out through a side pore they go in through the next, perhaps constantly influenced by the windows and the smell.

In most kettle-traps the imprisonment of insects is necessary because of the strong proterogyny. In some other fly-flowers there is no detaining as the flower is not proterogynous or relies on repeated visits in male and female phases. In *Abronia* the differentiation between male and female sphere lies not so much in time as in space. The flower lasts but one morning.

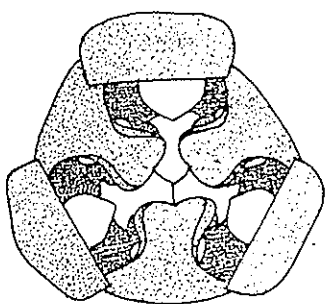


Fig. 8. *Tacca palmata*. Flower seen from above.

*) For the entrance proper I rely on WINKLER's observations.

This lantern-like type of flower with several slits in the sides seems to appeal to some instinct in the insects. The lantern-flower is consequently very typical of flowers visited by carrion or dung flies. *Ceropogon* is best known in this connection, but the type is present in many more example two drawings (figs. 8 and 9) of describe it in full detail I shall give as one more example two drawings (figs. 8 and 9) of *Tacca palmata* (*Tacca* is well known for its brown-purple flowers, visited by flies). Three recurved tepals give access to a circular tunnel as seen in fig. 9. Only in the places darkest in the drawing the six slits present opportunities to enter or to leave. The white stamens contrast strongly with the dark slits.

Though many other members of the Sterculiaceae, to which *Abronia* belongs, have purple, skatol-smelling flowers, only a few have the lantern type, as, for instance, *Agerium glabrescens*, described and pictured by SCHUMANN¹⁸ in his monograph on the curious cucullate Sterculiaceae. *Sterculia rubiginosa* also has lantern flowers. There, however, the lantern is formed by the calyx. The genus *Theobroma* is highly promising in this respect. The cocoa has some kind of special room between the petal bases, but this is not as secluded as it is in *Abronia* and windows are useless here. SOERJARDI¹⁹ described for Java how a midge (*Forcipomyia* spec.) enters this room and sucks from the tissues inside it.

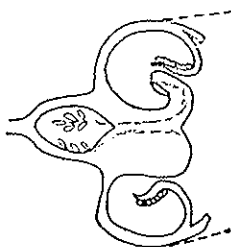


Fig. 9. Longitudinal section through basal part of flower to show the kettle-cavity. Tepals cut away.

7. Some general remarks about flowers with kettle-traps.

After having given some data about flowers which detain flies, we shall return to the kettle-trap flower as a constructional unity.

TROLL²⁰ did this in a brilliant, though in my opinion not satisfactory, way. He gave as characteristics of these *Kesselblumen*:

1. Ventricose lower part
2. Purple colour, sometimes with "panther-design"
3. Sometimes a hood or cover
4. Filiform appendages
5. Lantern flower with slits (The term *Fensterblüte* or window flower should not lead to confusion with my "light windows")
I might add (as TROLL did in later publications):
6. Light windows, which might be denoted as "diaphanous structures".

In this book TROLL sees the type as a purely morphological entity. He refuses to accept convergent adaptation as the cause of the similarity in flowers of such heterogeneous origin. We intend to show that it is not possible to avoid the ecological factor, though TROLL may be right in stating that the type ultimately develops beyond ecological wants.

Others too (and TROLL uses their sceptical remarks) have doubted the ecological value of many of the features as individual points. In most cases neither this criticism nor the positive assertions are backed by sense-physiological research of the insects.

Op point 4—threads that conduct flies to the centre—most doubt has been voiced. Nevertheless it is one of the most striking features of

fly-flowers, especially as these organs of ecological importance are produced by the most divergent morphological elements in the most different plants.

As instances (most of them have been illustrated by TROLL on pp. 378-393), I mention here in the first place a relative of *Abroma*, viz., *Theobroma Nariae* (see ENGLER-PRANTL, fig. 44) with filiform upper petal parts and further *Tacca* (sterile bracts), *Aristolochia* (tip of perigone lip or tips of separate lobes), *Masdevallia* (tips of outer tepals), *Cypripedium caudatum* (tips of inner tepals), *Himantoglossum* (labellum), many Araceae (appendix), *Strophantus* (petal tips). In *Arisaema* we find in one genus two different ways to obtain threads near the flower: in some species it is the filiform appendix, in others the thread-like tip of the spathe.

GOEBEL — as always allergic to assumed ecological adaptations — ridicules these conducting threads, the *organi conduttori* of DELPINO. Of course this is only justified in regard to simplistic ideas of insects marching right into the kettle.

NEGER¹² (p. 612) treated the matter more critically by looking for a connection with the habit of flies to sit for a while near the smelling bait. We already pointed to this possible relation on p. 93. Like NEGER other observers noted the preference of flies for alighting on hanging narrow objects. There must be some sense in the hanging of strips of fly-paper for domestic use.

That KNOLL, as cited by TROLL, found no preference of flies for the appendix of *Arum* is not decisive. This upright appendix has a different character. That CAMMERLOHER⁴ found no interest shown in the thread of *Aristolochia grandiflora* is also not to be wondered at as the giant flower itself covers quite a region around the sexual organs. His description nevertheless stresses the approach in steps, even when the visitors are already on the perianth.

When TROLL and KNOLL deny any ecological value of the threads in some *Arisaema* and *Aristolochia* species because other species manage without them, they in their turn are too simplistic. This method would enable us to deny the existence of TROLL's syndrome by pointing to the fact that each characteristic may be absent in some case. In every flower class some cases do without one of the characteristics and not all kettle-trap flowers have all the characteristics of points 1-6. The link with pollinators can in some cases even be based on only one of the many features of the syndrome.

Of course it is not necessary to recognize as alternatives only two viewpoints: a) of the purely morphological nature of the characteristics, b) of the selective value of each characteristic. The narrowing of the bonds with insects in general to one with a special animal can be ecologically understood, without thinking of selective advantage. TROLL is right in so far that adaptations of an originally ecological nature may become fixed as organizational characteristics, but I think he goes too far when concluding (p. 391) that threads near fly-flowers are neutral characters, just linked to other characteristics of the type.

Here too the last word rests with the animal physiologist.

The second point of which the ecological function has been criticized is the purple colour, though it is one of the most faithful companions of fetid smell. That it would be accidental is too improbable and to consider it as just linked up with other characteristics would be putting too much stress on correlation, the more so as in the end only the smell would remain as the 'vital characteristic' — and this characteristic is the one least common to fly-flowers in general and the point most specific to every individual plant and fly.

TROLL cites KNOLL¹⁰ as having proved that the purple colour is valueless — not of an ecological nature. Of course the old conception of a resemblance to blood or flesh is somewhat simplistic, the more so as it also occurs in flowers visited by dung insects.

Here too a renewed sense-physiological investigation including the "panther-design" might prove useful. From the study by STEINER²¹ we learn of an experimentally proved value of a black-and-white chequered design of certain dimensions to attract flies.

Point 5 - the lantern construction - TROLL (p. 371) considers he has explained sufficiently by assuming an arrest in development, which the *Gestaltungstypus* uses to express itself.

There must be something in the environment that lies at the base of the *Gestalt*. By the most different means a lantern flower is reached in species of the genera: *Masdevallia*, *Ceropegia*, *Abroma*, *Sarcobolus*, *Agave*, *Cryptophorum*, *Asarum* — all of them with fly-flowers. What the type means in the Burmanniaceae remains to be investigated.

In a recently received article by TROLL²³ this author maintains that the convergence *Ceropegia-Aristolochia* may be non-ecological as no use of the lantern construction can be detected.

About the ecology of light-windows I may refer to what I said in the foregoing in relation to *Arisaema*. Here I only want to stress that it may

be part of a syndrome and also an adaptive convergence, which should be studied experimentally.

To consider it only as a neutral part of a *Gestaltungstypus* would lead to the enormity, that in the leaf of *Duringtonia* the same blind "typus" works as in the flowers of *Ariseema*, *Ceropegia* etc. As stated before, TROLL in newer studies accepts the ecological function of these windows. Perhaps this may lead to the admission that also the points 1-5 are fundamentally ecological convergencies.

Bandung, November 1952.

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