BIOLOGICAL AND PHYSIOLOGICAL OBSERVATIONS ON THE INFLORESCENCE OF AMORPHOPHALLUS

by

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(With Tab. I and II).

Amorphophallus variabilis Bl. is a well known, though not very popular plant in Java. During the dry season when the leaves are gone the inflorescences appear everywhere in lightly shaded places (fig. 1). In the afternoons their fetid odour is wafted about.

The name given locally is *„Kembang Bangke"*, which means carrion-flower, but the smell is certainly not putrescent, though most people say so. There is no point, however, in discussing the smell of this and other fetid flowers here, though, personally, I find the smell of Amorphophallus variabilis more like that of the durian fruit.

In some other species the relations to carrions are more evident, as can be judged by the conduct of insects, which distinguish the different odours far better. In *Amorphophallus Titanum* a Sylphid, which has also been found on corpses, must be considered as the pollinator.

Aristolochia elegans Masters, and other species in Java attract only flies. *Arum nigrum* (6), however, attracts only dung-insects, no carrion-insects.

On *Amorphophallus variabilis* I have never observed Sylphidae or Coprinae nor flies of any kind, but exclusively Nitidulidae. In various places I found the same species as soon as the flowers began to give off odour. This is a small beetle of 2 mm long (c.f. Tab. I, A). The specific name cannot be given here as a systematic account of the Nitidulidae of Java is still lacking. Most representatives of this family live on flowers and in decaying vegetable substances.

In the course of my investigations I came upon the studies of C. A. Backer (1) on the genus *Amorphophallus*. Here (p. 178) almost the same beetles were found in the vicinity of Buitenzorg.

Fig. 1. Amorphophallus variabilis Bl. Complete flowering plant.

We may therefore assume that these Nitidulidae are not merely accidental visitors. The *Philanthus crassicornis* (a Staphylinid), which BACKER also mentions, I have never come across near Bandoeng.

The insects sit on the inferior part of the spatha. Here the inner surface is covered with yellow pimples over a distance of 1½—2 cm from the bottom and the beetles remain stationery for days together even when the spatha is cut off and put under the miscroscope (Tab. I A). When this is done one can clearly see the maxillae constantly gnawing the surface.

The upper part of the spatha is smooth and white inside, while the part with the pimples is tinted yellow. When examined microscopically the lower part shows, on and between the pimples, a superficial layer of cells of about 10 deep, entirely filled with starch grains and oil drops. The two outer cell layers contain oil almost exclusively while their walls are very delicate. In the upper part such a tissue is entirely lacking (Tab. I, B).

Here, no doubt, we meet with a new instance of a food-tissue where not nectar or pollen but a coherent tissue is offerred to attract pollinators. Up till now such structures have rarely been observed in ordinary entomophilous flowers. PORSCH (12) published a review of the occurrence of such „*Futtergewebe*" on the lips of many orchids. In many of these instances the nutritious substances are set free by disintegration of the cells, but in *A. variabilis* the tissue remains intact. When the beetles have been eating for some days, white spots indicate the places where the unterlying parenchym has been reached.

It is remarkable that in *Alocasia pubera* SCHOTT (11) the inflorescences have quite a different nutritious mass, namely the decaying male flowers. These, however, are not eaten by the pollinators themselves but by their larvae, that develop completely in the spatha around the ripening fruits [1]). BACKER (p. 168), though not aware of the significance of his findings, mentions larvae feeding on the spatha-bases of *A. variabilis*. I, too, found them, but as the spatha withers rather soon I doubt if, in this case, the insects can complete their life cycle.

I do not understand how BACKER (p. 168), an excellent observer, can say that the pimples produce a liquid, rather viscid secretion. In Bandoeng I have never seen any secretion.

As a rule the spatha opens early in the afternoon and from 16.30—19.30 during at least three days the odour spreads from the appendix. The ovaries with their very viscid stigma's are exposed all this time (Tab. I B). On the fourth afternoon pollen is emitted from the anthers just as toothpaste is pressed out of its tube. On this afternoon and mostly also on the fifth, when pollen again comes out, odour is still discharged. During the fifth, or eventually on the sixth day, the beetles have been walking in the pollen that has fallen into the spatha. Then,

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[1]) In this inflorescence I detected three ways of attraction: (1) Odour from far away, (2) Colour from about 50 cm. (3) The male flowers from quite near or after being touched. Perhaps the last attraction acts through organs (chemoreceptors) in the feet of *Atherigona*, the pollinating Anthomyid. Prof. Dr. E. HAZELHOFF suggested this possibility (c.f. 9 in the Literature).

when there is no food left, the spatha withers and the pollinators, entirely covered with pollen, escape and may visit other flowers. In one inflorescence I found on the fifth day still 20 beetles walking over the decaying, brown remainders of the foodtissue. The sixth day only 3 were left.

Though the visitors remain free to move all the time, we may classify the inflorescence of *A. variabilis* as a prison-flower or trap-flower, „*Fallenblume*" — (For the nomenclature of flower types, CAMMERLOHER (3), p. 72—88, may be consulted).

Perhaps *Amorphophallus variabilis* belongs to a special type of trap-flower which I might call a „food-trap-flower" (*Essfallenblume*). Other species like *Alocasia pubera* SCHOTT, (see p. 159) *Colocasia antiquorum, Philodendron* spec. might be added. In the spatha of *Colocasia,* MISS CLEGHORN (4) saw flies kept in prison for a day (without the attraction of food?) while the larvae developed on the decaying upper part of the spadix. KNUTH (7) (p. 89), mentions observations where the larvae of *Macrostola lutea* MURR. — a Nitidulid — were living in the spatha of *Philodendron* spec. They fed on the pollen till they escaped as full grown beetles.

The difference between this type and the other prison-flowers („*Gleitfallenblumen*" or „*Kesselfallenblumen*") where the insects are involuntary prisoners, is not quite distinct. *Aristolochia* has often „*Gleitfallenblumen*" but these are provided with nectaries [1]).

In *Colocasia antiquorum* there are also food and mechanical obstacles at the same time. Moreover the food is not always offerred to the pollinators themselves but sometimes to the succeeding generation of insects. In the latter case, however, there is not, as in *Arum,* merely a fraudulent trap, but a real feeding substratum for the larvae.

I cannot make out if it happens that the visitors of *Amorphophallus* rush down involuntarily into the spatha-kettle („*Gleitfalle*"). There is no distinct slippery zone. Probably they simply walk down over appendix and spatha. In doing this they will touch the stigma's.

The falling pollen sticks to the stigma's in great quantities but this seems to have no effect, as isolated inflorescences never

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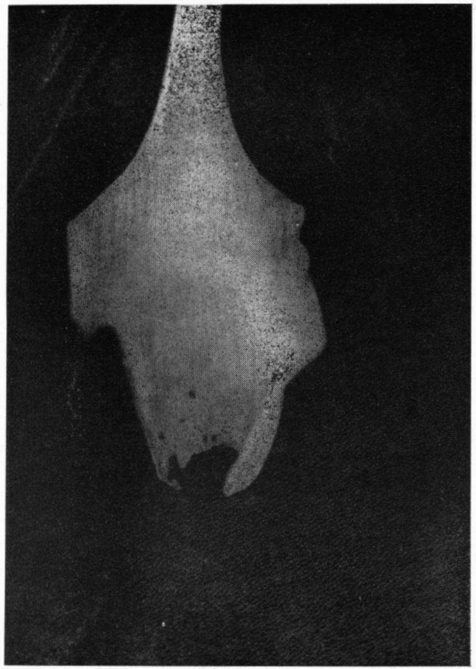
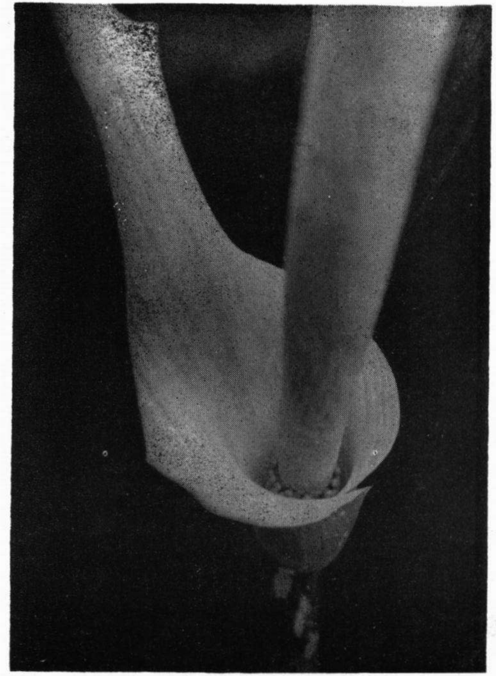
[1]) Though the secretion of nectar by these organs has often been described. I could not make certain that the insects have actually been observed feeding on them. Therefore I placed a fly from the kettle of *Aristolochia ringens* in a tube together with a cut-out nectary. Every time the fly trod on the nectary its proboscis was put into action. The experiment of MINNICK (9) gave no results in this case.

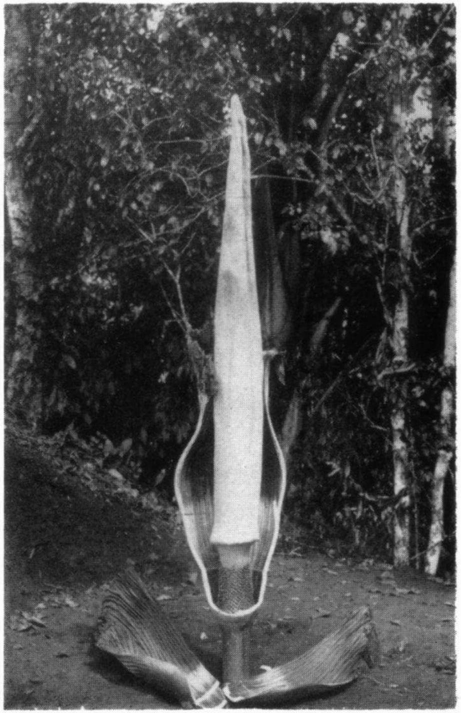
TAB. I



Tab. I A. A. variabilis Bl. Isolated spatha with eating Nitidulidae.



Tab. I B. A. variabilis Bl. Inflorescence seen from above. The female flowers and the food tissue are just visible.



Tab. II A. A. Titanum Becc. Inflor. recently closed. The spatha is partly removed and an incision made underneath the white zone.

Tab. II B. A. Titanum Becc. The foreside of the appendix has been cut off to show the interior. The incision in the spatha was made to bend it outwards.

result in fruits. Self-sterility must, therefore, be assumed.

It is remarkable that the development of odour is not accompanied by any important increase of temperature as it generally is (c.f. LEICK (8) p. 37, on *Arum italicum* MILL.).

In a paper I published some years ago (11) I suggested the possibility that, in *Alocasia,* the warmth might be useful for the evaporation of the odorous substances. Like so many suppositions to the significance of heat in Araceous flowers this one cannot be correct in all cases as the male flowers often produce heat but no odour (c.f. *Amorphophallus Titanum* on p. 165). Sometimes the two phenomena do not occur at the same time, (For further information about warmth in Araceous flowers I refer to LEICK's review (8).

The most conspicuous part of the inflorescence is the appendix. It is the sole origin of the odour and measures from 12 to 43 cms. In a young inflorescence the outer layers of the appendix are completely filled with starch. Though there is no increase of temperature perceptible by hand one might expect that all of this starch would be consumed during the flowering period. SACHS (cited from LEICK p. 34), proved this for *Arum maculatum* L., but an old appendix of *Amorphophallus* already wilting, still contained such a great quantity of starch that it seemed hardly diminished.

CAUSE OF RHYTHMIC ODOUR PRODUCTION.

SCHMUCKER found in *Cereus* (14) and, though doubtful, in *Arum* that a change from darkness to light caused the flowers to open. In many tropical plants, especially Malvaceae, I discovered independently another cause of the daily rhythm of flowers (10), namely, the change from light to darkness.

I now made an investigation of the daily occurrence of smell in *Amorphophallus,* based on the same idea, but without success. Artifical changes in the timing of darkness had no influence.

The change from darkness to light in the morning proved to be the determining stimulus for the production of odour. By altering the moment of this stimulus I could effect a *perfectly corresponding* alteration in the beginning of smelling and I could even reverse the rhythm so that flowers smelt early in the morning.

Apparently, the change to darkness induces the appendix to start a process that leads to the production of odour 10½ hours later. This is in striking conformity with SCHMUCKER's *Arum,* but the results are far more convincing. It would, of course, be most interesting to investigate chemically the subsequent phases of this process. I have not, however, the necessary time and equipment for this.

The following data may serve as illustration. (After the change three plants — always intact, — were left in constant light).

darkness-light	9.— A.M.	3.45 A.M.	18.—
weak smell	18.40	14.40	4.30
strong smell	19.—	15.10	4.50
weak smell	21.45	17.45	7.—
no smell	22.—	18.—	7.30

From these data we may conclude that, just as in *Cereus* and the Malvaceae the time of opening, in *Amorphophallus* the duration of odour production is autonomous and that it is not stopped by the darkness at night as one is apt to suppose.

In the above mentioned Malvaceous flowers the darkness had to be sustained for many hours after the stimulating change. In Amorphophallus it seems that the change acts exclusively as a stimulus; for when the inflorescences remained in the light for half an hour and were afterwards put back into darkness the smell started promptly after 10½ hours. In the Malvaceous flowers and *Cereus* a forced or natural rhythm stayed on for some days after the plants were put back into darkness for a period. In *Amorphophallus* the stimulus leaves no after effect.

Constant darkness produced no smell whatever.

Another point of interest was the question as to whether the appendix reacts as a whole or whether the separate parts act independently. That the first supposition is correct was shown by the following experiment: The upper half of an appendix was kept in darkness by means of paper for 6½ hours while the whole inflorescence was exposed to light. Though the odour in the upper part was somewhat retarded and weakened, the appendix reacted as a whole 10½ hours after the illumination of the inflorescence, while the partial illumination 6½ hours later, of the upper part, had no effect.

AMORPHOPHALLUS ONCOPHYLLUS PRAIN.

The inflorescences of this species are more conspicious. The inside of the spatha is pink dotted with white and the outside greenish with white dots. The inflorescences attain a length of

20—36 cm, from which the appendix takes 11—20 cm. The latter is oval on a transverse section, has a creamish-grey colour and shallow little pits on its surface. The numerous male flowers are bright yellow.

The appendix has a spongy pith, that partly disappears at ripeness. The peripheral part is almost cartilaginous and very consistent. It is just as in *A. variabilis* a starch-deposit, but is entirely exhausted during the flowering period. The whole rhythm is different from that in *Amorphophallus variabilis.* In closed inflorescences the spatha fits exactly around the appendix, that gradually grows out of it. One afternoon the spatha unfolds itself somewhat, but nothing further happens. On the following morning (1st day) smell is emitted from 5 a.m. till 8.30 or 9 a.m. In this period the appendix shows an increased temperature, easily perceptible to the hand. I measured it by boring a thermometer into the pith. In this way a decrease will become less marked than it really is, because the warm air cannot escape. This circumstance is also partly responsible for the fact that, even between the periods of intensive warmth production, the thermometer shows a slight excess inside.

The excess over the temperature of the outside air is about 6° C. at 5 a.m. and from 7° to 10° at 6 a.m. It diminishes to 3° at 8 a.m. From 9 a.m. to 3 p.m. the appendix produces neither warmth nor smell. As the temperature of the air increases during this time the curve of the absolute temperatures shows only a slight depression.

At 3 p.m. the appendix becomes active again, and by 3.20 p.m. it smells strongly. As a rule the temperature rises later in the afternoon, about 4.20 p.m., when there is an excess of 3°. It reaches 5° at 5 p.m. and diminishes slowly till at 7 p.m. it sinks below 4°. (See above for the influence of isolation).

After 6.30 p.m. the smell gradually decreases. At the end of this period the appendix apparently has lost its starch and never again produces warmth or smell. The male flowers never did this from the beginning.

In the Lyceum Garden at Bandoeng as well as in the original place from where I procured the plants for examination, the same beetles as in A. variabilis were found on the inflorescences. Once an animal, similar but twice as large, was found on the male flowers and once two individuals of the Melolonthid *Apogonia destructor* Bos. were found lying in the kettle. The latter are planteaters and the occurrence seems to be fortuitous.

The Nitidulids were always found on the male flowers. Many times I could observe them slighting directly on these. In contrast to those on *A. variabilis* they were in constant movement and I could not decide what they were looking for. When frightened the animals hid between the ovaries. In doing this they could rub off on to the stigma's the pollen which they eventually carried. A too close contact with the very viscid stigma's is more or less dangerous to the animals.

The inside of the spatha bears no food-tissue, only some small yellow papillae.

During the first day of flowering the anthers secrete drops of a clear liquid. DAUMANN (5) considers the secretion of nectar in *Arisaema* and *Anthurium* as more or less exceptional cases amongst the Araceae. TROLL (15), however, already found the same in *Spathicarpa*. One might suppose that the beetles consume this liquid or what remains of it after drying-out, but I could not observe this and the conduct of the insects is not in accordance to it. They walked the whole of the following night and day; disappearing for short periods between the female flowers. During the second day pollen comes out of the anthers. On odourless inflorescences in this period of flowering the beetles still walk in great numbers and become laden with pollen which apparently they do not consume. Especially the uncovered rear part of the abdomen, which is only well visible in living specimens, bears the masses of pollen.

If the beetles now change over to smelling younger inflorescences, pollination might be possible. In their own habitat I indeed observed many specimens flying around the inflorescences, suggesting the occurrence of such changes, but on the other hand I must say, that the old flowers still had much attraction. (c.f. *Alocasia* (11). What the real attraction is, in general, I hesitate to say; even two inflorescences that for unknown reasons gave no perceptible smell on the first afternoon attracted visitors.

Though I do not doubt that the Nitidulids really act as pollinators, there is another circumstance that makes the relations between *Amorphophallus* and these beetles less intelligible. The same beetles were observed on other *non-fetid* flowers, e.g. *Costus speciosus* where carpenter bees are the true pollinators. They walked on the inside of the leaf-like stamen among the scattered pollengrains.

One morning I observed three inflorescences, numbers 1 and 2 in their second day odourless and number 3 in its first day and smelling strongly. On 1 and 2 many visitors were present, on No. 3 none. Perhaps the insects fly only at night. Just as in *A. variabilis* self-pollination seems to have no effect.

Some few experiments gave me the conviction that the physiology of the flowering is also different from that in *A. variabilis*. As the smelling begins before sunrise this cannot be the stimulus. Just as in the Malvaceous flowers referred to on p. 161, the smelling could be delayed by changing the time of darkening on the previous afternoon. When this happened some hours after the usual time the whole process on the following day was delayed just as many hours. When the plant was illuminated the whole night there was, of course, no stimulus. In an inflorescence, treated thus, that had already opened and was no doubt ready to flower, none of the processes described appeared. This delay was but temporary, for put back into natural conditions the inflorescence showed at once the ordinary course of flowering.

Some morphological remarks about the nature of the appendix may beadded here. It is not a nude axis as in *Arum*, but it bears a thick mantle of staminodial origin. On the border of the appendix and the male flowers one often finds all kinds of transitions to fertile stamens. Sometimes a stamen is still fertile for one half (yellow and with a porus) and sterile for the other half (grey). It happens also that grey sterile stamens are situated amidst the upper male flowers.

AMORPHOPHALLUS TITANUM BECC.

As I have no observations of my own, I am indebted to Mr SPEE, of Fort de Kock, Sumatra, for allowing me to publish the following notes.

From the 12th to the 15th November 1931 a fetid odour escaped from a still closed inflorescence. On the 16th and 17th, when it had opened, the Sylphid *Diamesus osculans* VIGORS was observed in the spatha. On the 18th the spatha closed. The smell began every day at 6.— P.M. even the day after the closing. A curious phenomenon was that the male flowers showed a marked increase of temperature up to the second evening, when the pollen was emitted. The appendix never showed any increase of temperature.

DR. E. JACOBSON, formerly at Fort de Kock, who was able to observe quite a number of flowering specimens, communicates the following details:

Besides many specimens of *Diamesus* he regularly found some *Creophilus villipennis* KRAATZ (a Staphylinid) in the kettle.

The big *Diamesus*-beetles tried in vain to escape by climbing the spatha. There is on its lower part a broad zone (20—30 cms) covered by a white powder where walking is impossible (Tab. II B). The beetles then went upwards along the spadix between the ovaries and walked over the male flowers. Here they reached the appendix, but this part begins with an overhanging edge that makes such a sharp corner that the beetles cannot go farther and fall down every time they try. In Tab. II, A and B the situation is clearly visible.

The spatha started closing after less than 24 hours (sometimes after a period of almost 2 × 24 hours). It folded itself around the spadix but as, after the final closing, there remained open spaces and furrows the insects could escape.

Probably *A. Titanum* has a *„Gleitfalle"*, but the arrival of pollinators was not watched.

AMORPHOPHALLUS CAMPANULATUS BL.

Backer (2) mentions big papillae on the inside of the spatha that secrete some liquid. If this be true in all cases (see remarks on p. 159), this species may be biologically different, though it smells just as does *A. variabilis* and at the same time.

Ridley observed flies on the genera *Calliphora* and *Sarcophaga* on the inflorescences in Calcutta, but it is not certain that these were really pollinators. Knuth denies this.

Next year I hope to be able to investigate the above two species exhaustively.

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