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# ACTIVATION AND POSSIBLE ROLE OF THE "FOOD-BODIES" OF SAUROMATUM (ARACEAE)

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SUMMARY

In the inflorescence of the voodoo lily (*Sauromatum guttatum* Schot), the spectacular thermogenic respiration which manifests itself in the so-called appendix on the first day of flowering ("D-day") is coupled with unfolding of the spathe and is synchronized with a mild respiratory climacteric and fragrance-production in the yellow, club-shaped organs placed on the central floral axis just above the pistillate ("female") flowers. The agent (or mixture of agents) responsible for triggering these three coordinated events originates in the primordia (buds) of the staminate ("male") flowers, from which it begins to emigrate about one day before D-day. The present report is specifically concerned with the club-shaped organs, hitherto almost completely neglected: their structure, the fragrance they produce, the chemical nature and mobilization of the reserve material they contain, and the nature of the respiratory process to which they fall prey. The results, placed in the framework of certain literature-data, allow speculation as to their biological function, which may well be the stimulation of mating in visiting beetles, i.e., extension of the span of time these potential pollinators spend in the inflorescences. The possibility that in addition the club-shaped organs serve as food for the beetles cannot be excluded.

## 1. INTRODUCTION

The pioneer work on the biochemical changes taking place during anthesis in the inflorescence of *Sauromatum guttatum* Schott was done by VAN HERK (1937a, b and c), who continued and greatly expanded the experiments begun by WEEVERS (1911). VAN HERK (1937a) demonstrated that respiration in the so-called appendix is cyanide-insensitive. The present consensus (see MEEUSE 1975) is that this situation is based on the presence of a dual pathway for respiratory electron-transport: the "classical" one which is cyanide-sensitive and coupled with generation of ATP, and an alternative pathway which is cyanide-resistant and coupled with ATP-production to a limited extent only. Given the appropriate conditions, electrons can even in the natural situation be funneled through the alternative pathway as a result of saturation of the "classical" one, and the result will be thermogenicity rather than ATP-production. Biochemically senseless, this phenomenon has crucial biological significance. KNOLL (1926) has brought convincing evidence that the heat produced by the appendix of certain arum lily species has survival value in that it serves as a "volatilizer"

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for the pollinator-attracting odor which is also produced. Without heat there would thus be no sexual reproduction, i.e., no reshuffling of the genetical cards with its concomitant evolutionary advantages. Relevant for our present purposes is that in many instances the pollinators are beetles. In Costa Rica, *Cyclocephala*-species, e.g., are active in *Xanthosoma* (personal observation), *Dieffenbachia* (CROAT 1983) and *Syngonium* (RAY 1983). MEEUSE & HATCH (1960) found that in *Dracunculus vulgaris* the carrion- and dung-flies (*Calliphora, Lucilia* and *Sarcophage*) which are attracted by the stench of the appendix do not normally accumulate in the floral chamber. In stark contrast, 298 beetle-individuals belonging to 15 species accumulated precisely there in a group of *Dracunculus* inflorescences over a seven-day period. *Sauromatum* accumulated beetles along with flies in the floral chamber. Out of 6 species (47 individuals) of beetles collected in freely exposed *Sauromatum* over a period of 35 days, only one, *Glischrochilus 4-punctatus*, was found not to be a frequenter of carrion and dung. Not surprisingly, SMITH & MEEUSE (1966) found the odoriferous compounds of the *Sauromatum*-appendix to represent a mixture of at least a dozen different amines, plus ammonia. In 1971, CHEN & MEEUSE demonstrated that indole also is a major odor-component here. Paradoxical, at least at first sight, is the fact that the yellow, club-shaped organs found in the floral chamber on the central axis just above the pistillate flowers produce a fragrance which to the human nose is delicious, reminiscent of lemon and papaya but with spicy overtones. The pollen (*fig. 6*) has characteristics such as a tendency to clump, indicating dispersal by insects.

Another fundamental discovery made by VAN HERK (1937b, c) is that the thermogenic "metabolic explosion" in the *Sauromatum*-appendixis is triggered by an agent produced in the primordia of the staminate flowers. About 20 to 22 hours before D-day, it begins to migrate into the appendix where it appears to distribute itself evenly; at least, the heating-up on D-day does not manifest itself as a wave moving upwards from the appendix-base. In 1971, BUGGELN et al. could show that either the formation or the release of the agent is controlled by the particular light/dark regime on which developing inflorescences are kept; heat and smell will not be in evidence as long as a certain requirement for darkness has not been fulfilled. VAN HERK also succeeded in obtaining an extract from the buds of the staminate flowers which, when injected into isolated appendix-tissue obtained from "castrated" inflorescences, caused the heating-phenomenon to occur in a normal fashion. CHEN & MEEUSE (1975) have succeeded in purifying the responsible agent or agents, conveniently referred to as "calorigen", to a considerable extent; their procedure excludes compounds with a molecular weight exceeding 1,000. MCINTOSH & MEEUSE (1978), using the production of indole as a criterion for the action of purified calorigen on small appendix-sections under sterile conditions, could demonstrate that the compound induces the synthesis of new (enzymatic?) protein. The evidence is based on the observation that application of both calorigen and inhibitors of protein-synthesis at time zero prevented the production of indole and the boost in respiratory activity. Application of calorigen at time zero followed by that of inhibitors

after varying time-spans (up to 12 hours) demonstrated that after a few hours, "once the metabolic avalanche had started", escape from the inhibitory action is possible.

One aspect of *Sauromatum*-anthesis which initially was almost totally neglected was the possible involvement in the pollination-events of the club-shaped organs. It was not until 1961 that HESS made a very promising start with the study of these. Struck by the fact that their fragrance-production coincides in time with the generation of the carrion-like appendix-odor, he considered the possibility that the triggering substance in the appendix and in the appendages is the same. Since, as mentioned, the appendix activator begins to leave the primordia of the staminate flowers about 20 to 22 hours before D-day (unfolding of the spathe), it appeared plausible that the triggering of the club-shaped organs is also initiated about a day before they develop their fragrance and increased metabolic activity. Experimentally, such a postulate is easily verifiable, as follows. When the upper part of a pre-D-day *Sauromatum*-inflorescence is cut off just below the zone of the staminate flowers and put in water, the heating and the stench production of the appendix will occur in normal fashion, and it is therefore possible to determine, in retrospect, at what flowering stage the amputation took place: D-day-1, D-Day-2, etc. For each inflorescence, the respiration of the club-shaped organs is measured when the corresponding appendix reaches its metabolic peak.

If the "male" flower-primordia are not the site of origin of the triggering-substance for the club-shaped organs, the latter should always reach their metabolic peak at their normal time. If, however, the male flower primordia do represent the site of origin of the activating agent, the amputation should interfere with the normal sequence of events. An early separation between the "male" primordia and the lower portion of the inflorescence should completely block "peaking" in the clup-shaped organs, while one brought about less than one day before D-day would still permit the phenomenon, the activator having left the primordia already. Unfortunately, due to a lack of experimental material, only 4 separations of the type described could be carried out: one for D-day-3, one for D-day-2 and two for D-day-1. The results were highly suggestive but no conclusive.

In the present report, we will first of all consider the multiple role possibly played by "calorigen", In a war-time lecture, VAN HERK has provided evidence that it (or at least a product of the male primordia) is involved in the unfolding of the spathe, an event which is *not* just based on the activity of auxin (indole acetic acid). This raises to three the number of phenomena that are in all likelihood orchestrated and coordinated by one center of operations, the "male" flower primordia. There may even be four, since the possibility cannot by excluded that the receptivity of the pistillate flowers is regulated by calorigen; so far, however, conclusive proof for this is lacking.

Because of its size and the excellent spatial separation of the various organs it carries, the *Sauromatum*-inflorescence is an ideal subject for studying interactions and timing-events during anthesis. In general, these topics have been suffer-

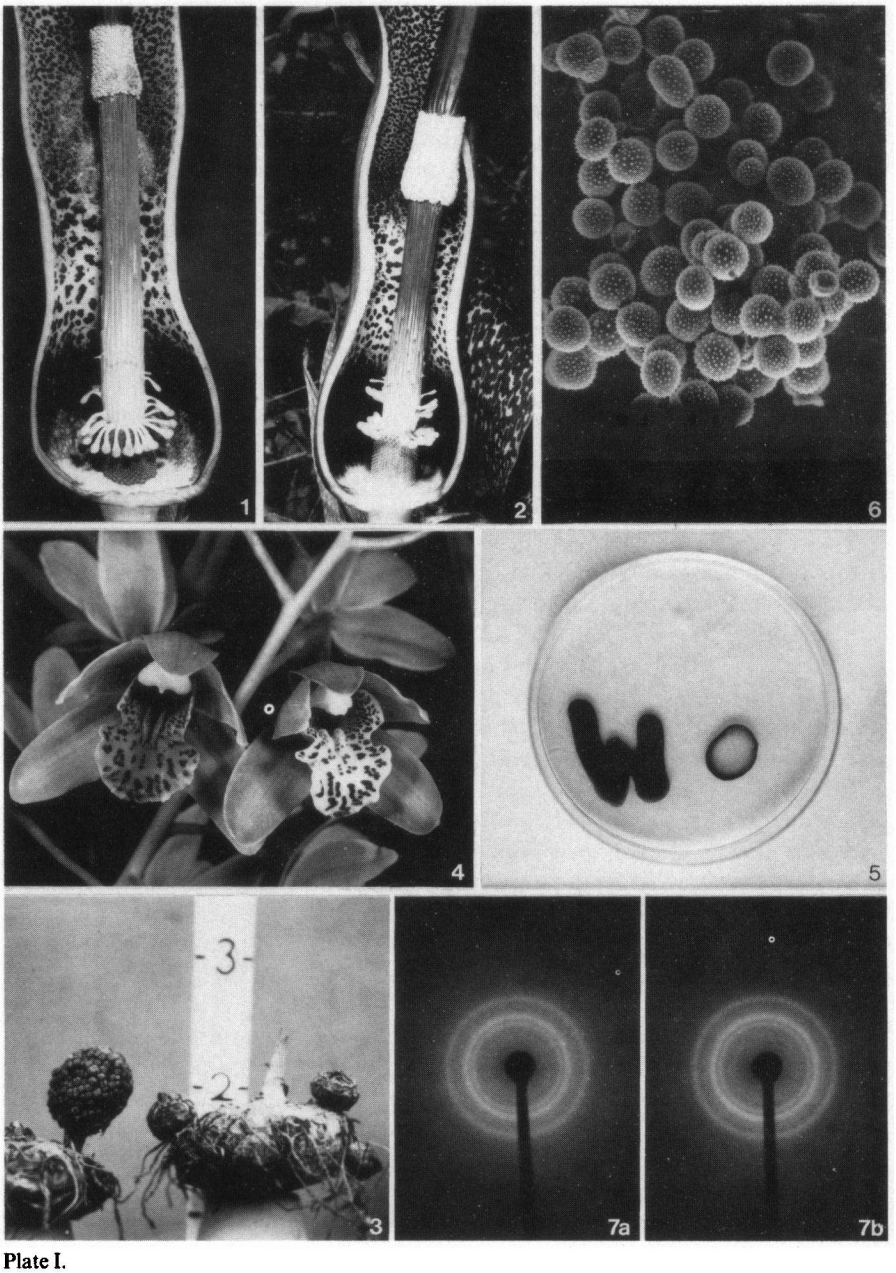


Plate I.

Fig. 1. Floral chamber of *Sauromatum* on D-day plus 1, showing shed pollen and club-shaped organs About half natural size.

Fig. 2. Floral chamber of *Sauromatum* on D-day. Staminate flowers still tightly closed. About half natural size.

ing from an astounding lack of attention, and for that reason our work can hardly fail to make at least some slight contribution. Secondly, we will concentrate on the characteristics of the clup-shaped organs and on the processes which on D-day are unleashed in them.

## 2. MATERIAL AND METHODS

*Plant material.* Plants were grown in the New Botany Greenhouse, University of Washington. Under normal conditions, *Sauromatum* displays a regular alternation of a vegetative and a sexual phase. At the end of the vegetative period, when the foliage had died off, the corms (tubers) were dug up immediately and left sitting on the soil surface to go through their dormancy-period. Thus far, we have not achieved much success in breaking the dormancy at will by artificial means, although there is some evidence that ethylene is slightly effective. The time of emergence of the inflorescences from corms varies a great deal from year to year, depending (among other things) on the planting-time of the corms that produced the vegetative phase, and also on the temperature. Thus, it is possible to have inflorescences available as early as October and as late as mid-May; a few may even emerge in mid-summer. In all this, however, there remains a great deal of unpredictability.

As in other arum lilies, sex expression in *Sauromatum* is labile; high temperatures in late spring may cause a sexual shoot to become vegetative. In two instances, we observed (*post facto*!) the formation of completely subterranean infructescences with viable seeds (*fig. 3*).

*Examination of the club-shaped organs.* For scanning electron microscopy, the organs were fixed in 50% ethanol, then dehydrated to 100% and gradually transferred to pentyl acetate. After having been critically point-dried, they were coat-

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Fig. 3. Infructescence with viable seed of *Sauromatum*, formed completely underground. This structure arose from a spot where, normally, a cormlet would have been formed asexually. Seeds produced normal offspring which was propagated normally.

Fig. 4. Typical "post-pollination" reaction of a *Cymbidium* orchid flower, following treatment of gynostemium with indole acetic acid or extract from staminate flowers of *Sauromatum* or extract from club-shaped organs.

Fig. 5. Synthesis of "starch" (amylose) from glucose-1-phosphate by phosporylase in an extract of club-shaped organs. The synthesized product is demonstrated with iodine. On the left (B, round spot): potato extract used as phosphorylase-source. The light spot provides evidence for amylase-action, which is totally absent in the extract from the club-shaped organs.

Fig. 6. Scanning electron photograph of *Sauromatum* pollen. This pollen has some tendency to clump.

Fig. 7a, b. X-ray diffraction diagrams of starch from club-shaped organs and from appendix of *Sauromatum*. The diagrams are identical, showing the pattern displayed by cereal starches.

ed with gold-palladium 60:40. The microscope was a Jeol SEM, model 25 S II. The material was examined at 25 kV. Paraffin sectioning and specific staining were done by conventional methods. Isolation of native starch from the club-shaped organs was achieved by homogenizing them in water and subjecting the resulting suspension to fractionnated centrifugation. For converting the native product into so-called soluble starch, the method of HASSID et al. (1950) was employed. In order to determine the starch-content of the club-shaped organs, those from one inflorescence, representing 250–350 mg wet weight, are divided into two equal batches. One of these is used for determining the percentage dry weight, while the other is thoroughly ground in water to give a 20-ml volume, which is then gelatinized by heat. After cooling, the gelatinized preparation is subjected to the action of an enzyme-mixture from the sugar-gland of *Cryptochiton stelleri* Middendorff which converts the starch quantitatively into glucose. The latter sugar is then estimated quantitatively by oxidizing it with the highly specific enzyme glucose oxidase (notatin), the oxygen-consumption being measured by the conventional (manometric) Warburg technique.

X-ray diffraction diagrams (powder diagrams) of the starch were obtained on flat pieces of film placed 40 mm from the purified starch specimens which were contained in 0.7 mm glass capillaries. An accelerating voltage of 40 kV was used. The X-rays from the Cu-source were Ni-filtered and collimated before passing through the specimens.

All exposures were for two hours. Contact prints of each of the negatives were made on ultra-hard (No. 5) paper. Measurements to determine the d-spacings were taken from these prints.

The beta-amylase breakdown limit of the starch was determined with crystalline beta-amylase obtained from the Sigma Chemical Company, with the aid of J. B. Sumner's 2, 4 dinitrosalicylic acid reagent (BERNFELD 1955; SUMNER 1924/1925). Phosphorylase activity in aqueous extracts of the club-shaped organs was demonstrated by allowing drops of these fluids to act for an hour, at room temperature, on an agar plate containing glucose-1-phosphate and some starter (commercial maltose, which normally is contaminated with traces of dextrin). At the end of the incubation-period, the plate was treated with an iodine-solution to reveal any synthesized amylose by its blue color-reaction.

Checks for the presence of alpha- and/or beta-amylase in the extracts were made with starch-gelatin plates according to WIJSMAN (1889). The presence of thiamin in the clup-shaped organs was demonstrated with the *Phycomyces*-method (SCHOPFER 1935; BONNER & ERICKSON 1938), that of auxin (indole acetic acid) by means of the color-change induced in the flowers of certain *Cymbidium*-orchids when a drop of aqueous extract from the bodies was left on the gynostemium. The presence of gibberellin in the primordia of staminate flowers of *Sauromatum* was demonstrated with the barley half-grain method. Respiratory gas-exchange of the club-shaped organs was measured in the conventional manner with Warburg equipment.

## 3. RESULTS

A number of criteria indicate that the starch which acts as the fuel in the respiration of *Sauromatum* cells is entirely normal. The X-ray diffraction diagrams produced by starch from the corm, the appendix and the club-shaped organs are identical and represent the so-called A-spectrum characteristic of cereal starches (*figs. 7a, b*). The light-absorption maximum of the starch-iodine complex prepared from solubilized *Sauromatum* starch lies around 570 nm, very close to that of solubilized corn starch.

Finally, the breakdown limit of *Sauromatum* starch achieved with beta amylase is close to 42%, indicating a degree of branching of the amylopectin molecules which is very close to that of corn starch.

As to the structure of the club-shaped organs, the SEM pictures allow the conclusion that there are no significant surface differences between the D-2, D-1, D-day and D+2 stages. Photos 8, 10 and 11 present a good overview of the change in character of the surface from the proximal to the distal region. The frequency of the intercellular spaces increases towards the distal ends, providing evidence that the club-shaped organs are involved in gaseous exchange or (more likely) in the release of volatile (odoriferous?) compounds. Light-microscopy of the paraffin-sections (not presented here) reveals that there is indeed a progressive disappearance of starch from D-day onwards. The respiratory quotient of the organs is close to 1, as expected.

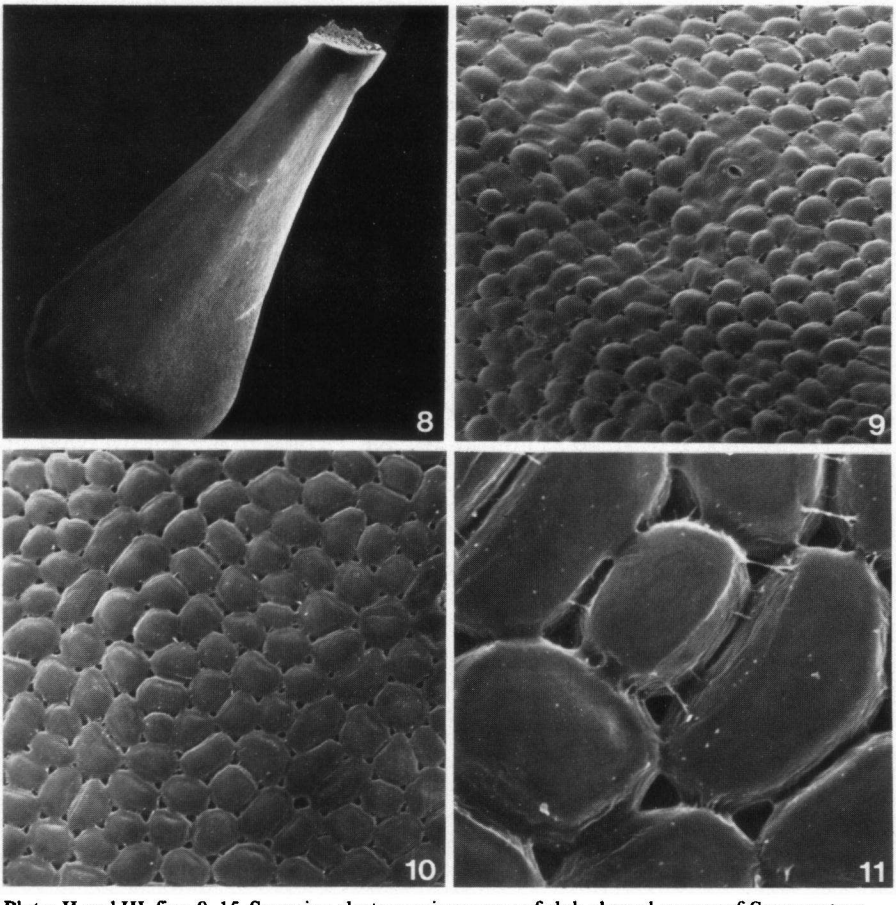
The result of the chemical analysis of the club-shaped organs reveals that about two thirds of their dry weight on D-day (which amounts to 30% or more!) is starch.

Amylose-phosphorylase is abundantly present (*fig. 5*), while amylase is absent. Roughly 10% of the dry weight is protein. Filter paper chromatography of aqueous extracts indicates that free sugar is present in very low concentration, in the form of glucose and fructose; sucrose appears to be entirely absent. The lipid content is extremely low. Thiamin, conceivably important if the organs do serve as food for visiting insects, could be demonstrated qualitatively. The club-shaped organs as well as the buds of the male flowers contain appreciable quantities of auxin, as revealed by the orchid test (*fig. 4*). They also contain gibberellin. Whether or not this has any significance for the activation of the club-shaped bodies is impossible to decide at this moment.

*Graph no. 1* reveals the important fact that, once the club-shaped organs have been activated, they follow their program even when separated from the rest of the inflorescence. Picked a few hours before the appendix reaches its metabolic peak, the club-shaped organs will initially show an increase in oxygen-consumption; picked at the appendix's peak-time, they show a decline. *Clearly, appendix and club-shaped organs are synchronized.*

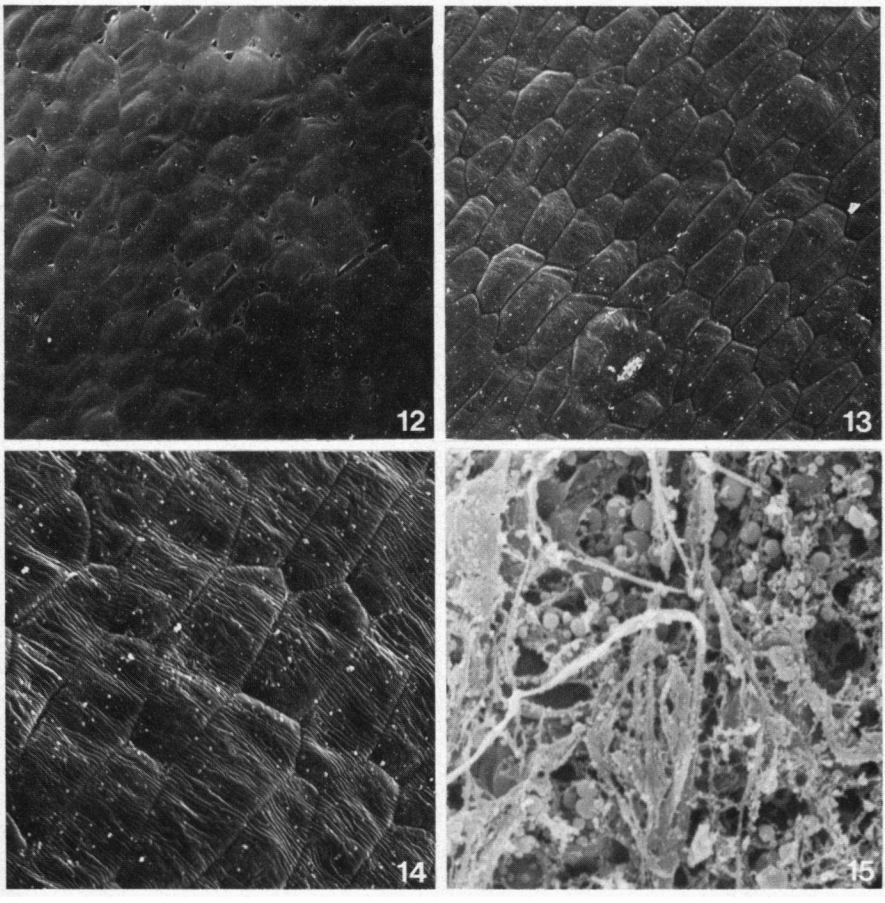
*Graph no. 2* illustrates the activity-increase in the club-shaped organs on D-day. *No such increase will manifest itself if the buds of the male flowers are separated from the bottom part of the inflorescence 2 days or more before D-day.*

*Graph no. 3* presents the change in dry weight of the club-shaped organs during




Plates II and III, figs. 8–15. Scanning electron microscopy of club-shaped organs of *Sauromatum*. Fig. 8: whole body, stage D+1, 10 ×; fig. 9: distal region, showing intercellular spaces and stoma (uncommon), D+1, 200 ×; fig. 10: distal end, note cell shape and presence of intercellular spaces, D−1, 200 ×; fig. 11: distal end, note intercellular space and pectin (?) strands, D+1, 1000 ×; fig. 12: mid-region; note disappearance of striations and appearance of intercellular spaces and also change in cellular orientation and shape; obviously a transition region, D−1, 200 ×; fig. 13: proximal end; note absence of intercellular space, stoma, D+1, 300 ×; fig. 14: proximal region, note cuticular (?) striations, absence of intercellular space and elongated (rectangular) cell shapes compared to high occurrence of dome-shaped cells at distal end, D, 700 ×; fig. 15: cross section through proximal end; note fibrous structure and abundance of spherical bodies, D−2, 700 ×.

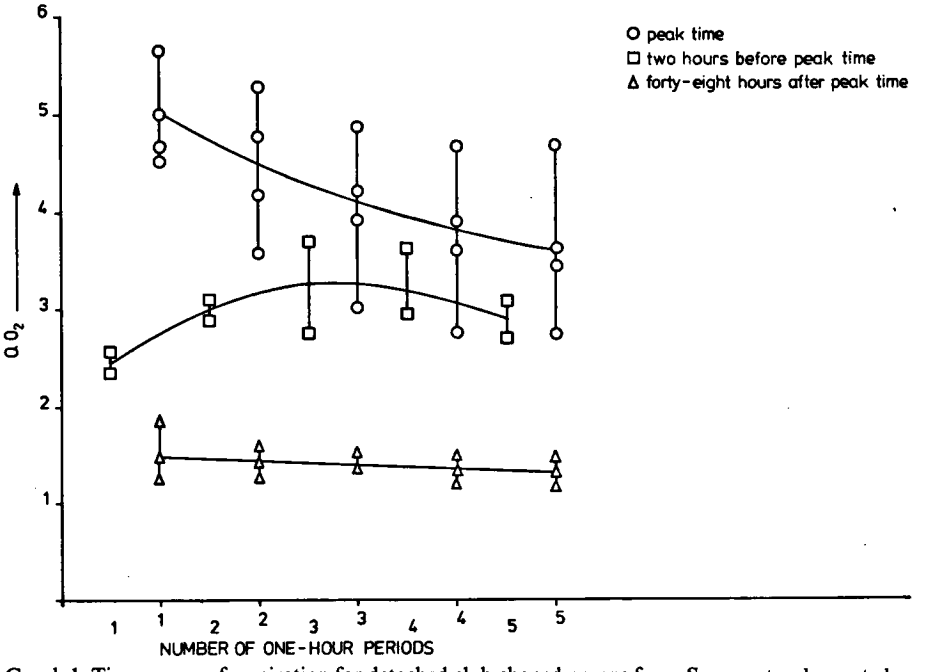
the natural course of events in the inflorescence. *No such change will occur if the influence of the buds of the male flowers is eliminated, as indicated for graph no. 2.*




## 4. DISCUSSION

A positive answer can now be given to the three main questions which have been addressed in our investigation:
1) Is the behavior of the club-shaped organs of *Sauromatum* synchronized with that of the thermogenic and odoriferous appendix?
2) Is it controlled by a hormonal factor originating in the buds of the staminate ("male") flowers?
3) Does scrutiny of the organs' structure permit conclusions as to their possible function?

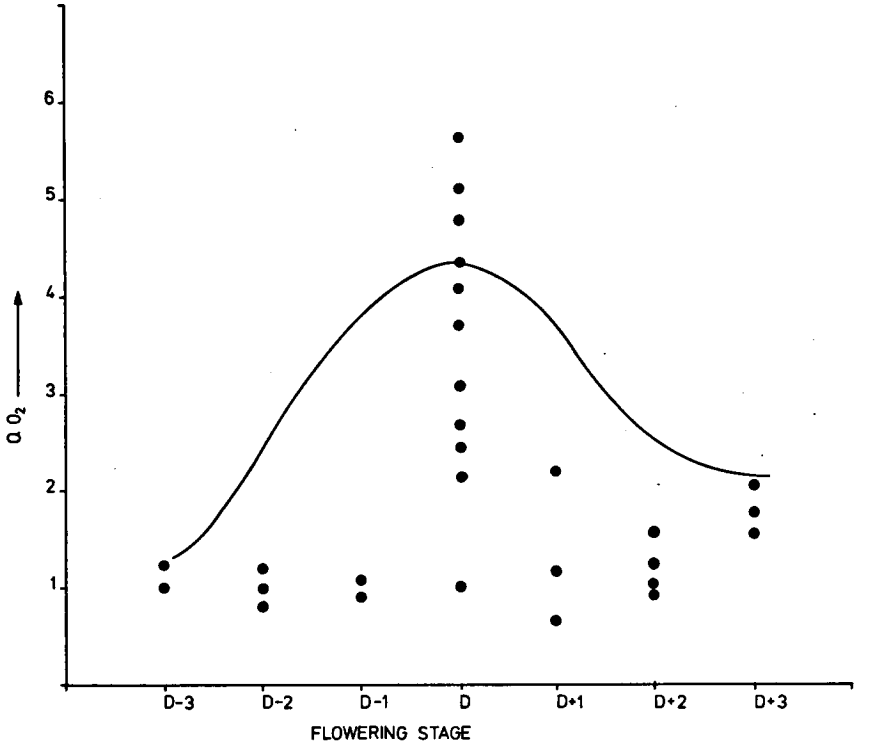
A cut through the spadix just below the "male" flower zone, made no later than a full 24 hours before normal opening-time of the inflorescence, eliminates exposure of the organs to the hormone and thus prevents them from behaving normally. We have used three criteria to judge and demonstrate this: the failure




Graph 1. Time course of respiration for detached club-shaped organs from *Sauromatum* harvested at various times.

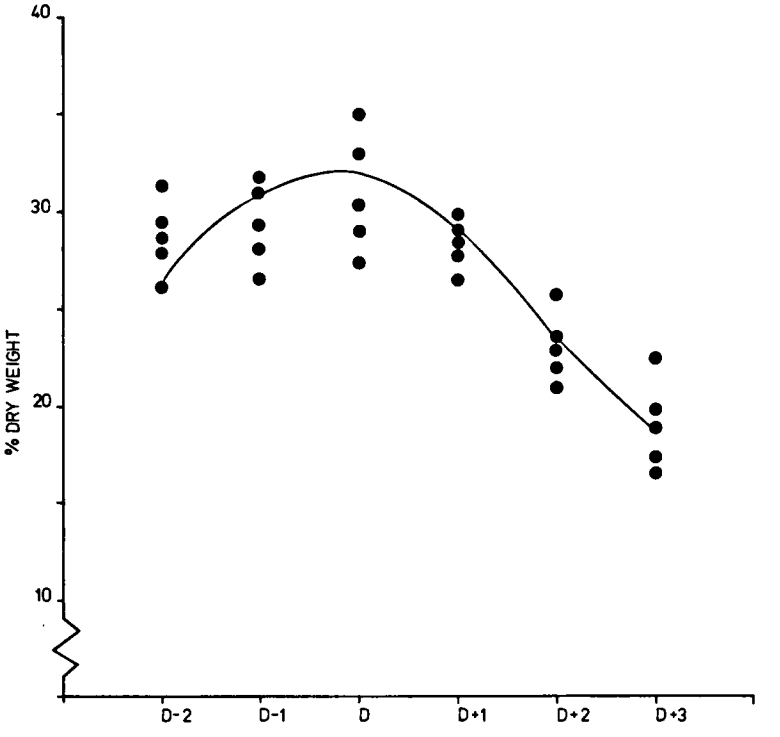
to develop fragrance, the non-appearance of the normal boost in respiratory activity, and the maintenance of a very high dry-weight level. A major question to which our research has led – as yet unanswered – is how the hormone finds its way from its site of origin to its target, and how it exerts its final action. It is plausible that the triggering factor is identical with the one activating the appendix which, as demonstrated by VAN HERK (1937b, c) can be obtained in aqueous solution and works in that form when injected into previously inactive appendix-segments. In two similar experiments, still in need of confirmation, we have obtained evidence that the factor triggering the club-shaped organs travels through the part of the spadix below the "male" flower zone. Development of fragrance was used as the criterion here. As already mentioned, VAN HERK's factor was purified to a large extent by CHEN & MEEUSE (1971), largely with the aid of thin-layer chromatography.

For this reason also, it cannot be assumed to be identical with ethylene. Nevertheless, admitting that at this juncture the evidence we have is entirely circumstantial, the possibility must be entertained that the action of the triggering factor is somehow connected with ethylene. SOLOMOS & LATIES (1976a, b) have argued in favor of a connection between cyanide-resistance (characteristic for *Sauromatum*!) and susceptibility to ethylene action. As early as 1969, MEEUSE & BUGGELN showed that inflicting a number of vertical razor slashes on the




Graph 2. Graph No. Q $O_2$ values for club-shaped organs from *Sauromatum* calculated over the first one-hour period.

floral chamber of a pre-D-day *Sauromatum* inflorescence led to anthesis even on a régime of constant light which had previously been shown to suppress it. It is well-known that in many instances the wounding of plant tissue leads to ethylene formation. It can also be argued that the events in the *Sauromatum*-inflorescence on D-day represent one of the most dramatic examples of a massive and rapid *senescence*, and the involvement of ethylene in the senescence of flowers and inflorescences has recently been supported vigorously by a number of investigators (see e.g. KENDE & BAUMGARTNER 1974; KENDE & HANSON 1976; MAYAK & HALEVY 1980). Thus far, we have not succeeded in demonstrating an appreciable level of ethylene in the floral chambers of pre-D-day and D-day *Sauromatum*-inflorescences. On the other hand, the air in a closed vessel in which fragrant club-shaped organs, collected on D-day, had been kept overnight, unmistakably contained some ethylene, as demonstrated by gas chromatography. Experiments now in progress are concerned with the effect on *Sauromatum* anthesis of air containing 4% $CO_2$ (a known competitive inhibitor of ethylene action). In others, we intend to study the influence of ethylene precursors such as ACC, and that of agents such as silver ions which eliminate ethylene as soon




Graph 3. Change in percentage dry weight in club-shaped organs of *Sauromatum*, as a function of flowering-stage.

as it is formed by plant cells. As to the biological function of the club-shaped organs: their structure appears to be eminently suited for the giving-off of gaseous substances (fragrance-compounds?) by their distal parts. Although their starch-content is very high and they also contain vitamin B1 (thiamin) and a fair amount of protein, their potential value as food-bodies for chewing beetles is debatable. Their level of lipids and free sugars is very low. The starch they contain can be seen as fuel for supporting the increased respiration (with slight temperature-increase and thus evaporation of fragrance!) on D-day. The bulk of the protein appears to be present in the form of mitochondria, which are likewise involved in cellular respiration. As a result of this process, the caloric value of these bodies drops rapidly. Promotion of mating-activities among and between visiting insects, as a means of keeping them "tied down" sufficiently long for the reception of pollen, appears plausible – the more so since such activities have frequently been observed in beetles pollinating other members of the arum lily family. The striking difference between the fragrance of the club-shaped bodies (which is due to α-pinene and limonene) and the odor of the ap-

pendix which to humans is so repulsive can probably be explained on this basis; the latter odor attracts visitors by appealing to the food-seeking instincts of the visitors.

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