THE TRUTH ABOUT POLLINATION IN *ARUM*

By K. J. DORMER

Botany Department, University of Manchester

(*Received* 20 *January* 1960)

An elementary textbook of botany commonly includes an account of the pollination of *Arum*. The story which is generally told of the relationships between the inflorescence and its insect visitors is highly standardized. It has an established place in formal teaching and frequently appears also in expositions of a more popular character.

There can of course be no dispute regarding the arrangement of the principal parts of the inflorescence, but the usual explanation of the biology of pollination is quite incorrect. It suffers from the further disadvantage of being much less interesting than the real facts of the case.

English textbooks lay stress upon the pronounced heating of the inflorescence by its exceptionally rapid respiration, and also upon the presence of those curious bristles or tentacles which are usually regarded as sterile flowers. The resulting pollination story has three characteristic features. Insects come to the plant largely in search of shelter and warmth. They crawl into the basal bulb of the spathe, forcing the tentacles aside in the process. Insects are retained in the bulb by a mechanism similar to that of a lobster-pot, being unable to deflect the tentacles upwards.

These three assertions were completely disproved by the brilliant work of Fritz Knoll, an Austrian whose investigations seem to be unknown to most British botanists. Working in Dalmatia with *Arum nigrum* Knoll (1926) discovered a fascinating system of biological relationships. He made few observations upon *A. maculatum*, but his general principles evidently apply to that species also. The present short note may be useful in bringing Knoll's results before a wider public, but I hope that no interested person will think it unnecessary to look at his hundred pages of illustrated text.

The epidermis of the spathe plays a vital part in pollination. Whereas the outer epidermis is quite conventional, with a distinct cuticle and many stomata, the inner epidermis is highly specialized. Stomata are rare and cuticular development is so slight that a grain of sugar on the surface promptly plasmolyses the cells. From the tip of the hood down to the middle of the bulb every epidermal cell has a large papilla. These papillae are turgid and springy, and they all point downwards. The papillate epidermis carries numerous drops of oil. These are easily washed off with water; their natural state is seen only in dry preparations. When 'printed' on to a glass plate the drops remain unchanged for days. In the bulb, especially in its upper part, the inner epidermis has intercellular spaces communicating through the mesophyll and outer stomata with the external atmosphere. The lower part of the bulb has a non-papillate epidermis without oil.

The smell is produced by the tip of the spadix, and in *A. nigrum* resembles the smell of human excreta. The odour is strongest early on the first day of anthesis. Cut specimens standing in water never develop it properly.

Observations on wild plants at sunrise show that as soon as the air temperature begins to rise insects congregate in the vicinity, alighting in the first place on stones and vegetation within a radius of about 20 cm. The congregation consists of insects which normally feed on dung, but includes some species which will never get into the bulb. Presently some of the insects fly to the inflorescence and alight on it. They can walk freely over the outer surface, but any insect which ventures on the inner surface of the hood falls off, either immediately or after taking a few paces. One might expect that a winged insect which lost its foothold would fly away. In reality only the larger ones (the size of a housefly) can do so. Smaller insects take too long to get their wings into operation, and therefore fall into the bulb, passing between the tentacles, which are at this stage smooth and oily. The plant thus catches only the smaller insects attracted by the smell. Large ones often make an inspection and fly away. If they alight and fall off they generally become airborne very promptly. In the last resort the stiff tentacles will always save them from falling through into the bulb. No insect ever significantly deflects the tentacles and no insect ever walks into the bulb. Individual inflorescences vary considerably in the development and spacing of the tentacles, and the size of the largest insects trapped varies accordingly.

A comparison between the epidermal papillae and the claws of insects' feet reveals the impossibility of any firm grip by the claws upon a vertical or steeply sloping portion of spathe. It can be shown experimentally that the adhesive lobes which some insects also possess are quickly put out of action by minute quantities of oil. Insects placed on a piece of spathe at the critical angle are obviously aware of the insecurity of their position, moving their feet with unusual care and often also attempting to clean off the oil. At the edge of the spathe is a transitional zone across which the special properties of the epidermis become gradually more apparent; this is perhaps more effective, because more insidious, than a sharp boundary would be.

When an inflorescence which has caught insects is transferred in the early afternoon to an insect-proof chamber it is found that no insect escapes before nightfall. The behaviour of the prisoners can be studied by fitting a window in the side of the bulb. The amount of activity depends on the density of the population. The more crowded the bulb, the more the insects disturb each other; in average conditions they are always distinctly agitated. They can walk freely on the lower surface of the bulb, and can climb over the female flowers. Above that level there is no foothold, either on the walls or on the central column. Removal of the spadix and tentacles does not allow the insects to escape, but if the bulb wall itself be inverted, so that the papillae point upwards, then some insects can walk up the wall. In a crowded bulb there is enough traffic to remove most of the oil from the lower margin of the papillate surface, so that some insects find their range of movement increasing a little as time passes, but this process is never fast enough to liberate insects on the first day.

Two optical considerations contribute to the retention of insects within the bulb. Experiments in chambers with opaque or translucent walls show that insects do not attempt to use their wings unless a certain minimum volume of open space is visible to them. The bulb is below the critical size and is further obstructed by the organs inside it, while the hood makes it impossible for the captives to see the sky. Insects enclosed in a glass tube with a central rod, reproducing the essential dimensions of the bulb, distribute themselves uniformly, even under unilateral illumination, so long as they are calm. But if the insects are agitated, by shaking the tube, or by over-crowding them, they become positively phototactic. In *A. nigrum* actinometric tests show that illumination in the bulb comes predominantly from below.

Conditions in the bulb are favourable to the survival of the insects. The humidity is high, the system of intercellular spaces provides for ventilation, and the female flowers supply water and some organic solutes. These conditions are important, because many of the flies are very delicate. In dry air some of them will not live 12 hours; to be effective pollinators they must remain active much longer than that. Congenial though conditions may appear, however, the behaviour of the insects clearly indicates that they would escape if they could. Usually there are some deaths in the bulb.

On the morning of the second day the appearance of the inflorescence is not much altered. There is no conspicuous wilting, but the scent is much weaker. The surfaces of bulb and hood remain unclimbable, but the whole inflorescence axis, from the floor of the bulb to the tip of the spadix, now offers a good foothold because the epidermal cells have crumpled. The insects walk up the column and usually take flight from the spadix. Sometimes they can cross over to the spathe where it is in contact with the spadix and where there has been enough friction between the two organs to damage the papillae and create a safe standing-place.

The attraction of insects to the plant was investigated by using artificial inflorescences made of glass. Each model had a hood approximating to the natural shape, but instead of a bulb there was only a pair of concentric tubes. Retention of the catch depended upon two things: the dusting of the glass with talcum powder to produce an unclimbable surface, and the use of a black paper sleeve to ensure that in the base-tube the main lighting should come from below. The models had no tentacles, nor any constriction at the base of the hood. In a position corresponding with that of the natural spadix various objects could be placed to act as allurements.

A model fitted with a roll of filter-paper dipped in a mixture of glycerine and stale blood catches an assortment of corpse-feeding insects. A model fitted with a natural first-day spadix catches the same dung-feeding species as a real plant, and in about the same proportions. Prior to capture these insects behave just as they would in the presence of an inflorescence. The model is less malodorous than the real thing, and takes a smaller catch. Having no tentacles it sometimes captures an insect too large to enter a natural bulb.

A model with an older, scentless, spadix catches nothing. Two scented models close together catch more than they would separately; two non-scented ones close together catch nothing. A non-scented model will catch insects if it stands close beside a scented one. The hoods of the models being interchangeable, experiments can be made with hoods of the natural dark purple or with white hoods. The purple spadix can be left visible or it can be masked with a white sheath. These colour differences have no perceptible effect upon the nature or size of the catch.

To test the hypothesis that insects enter in search of warmth and shelter a model can be fitted with an electric heater. Heated models make no significant catch, though scented controls prove that suitable insects are abundant in the vicinity. In nature insects which approach a plant late in the day and are overtaken by darkness while they are still sitting on surrounding objects do not make any special effort to enter the bulb. They often pass the night in the open, even though the spadix is still scented and even though their presence in that place is obviously a response to the presence of the plant.

The conclusion must therefore be that the attraction of insects from a distance is entirely due to the scent of the spadix. The subsequent behaviour of the insect is certainly influenced by visual factors, because with models most insects alight on the unscented glass hood, not on the scented spadix. Colour, however, seems to be unimportant.

A census of dung-feeding insects in the locality shows that almost all species which are small enough to pass the tentacles are actually found as prisoners in the spathe-bulbs. The trapping mechanism is quite unselective; nor is it highly efficient, for many of the eligible insects attracted by the smell of an inflorescence go away again. As, however, inflorescences which are deprived of insect visits set no seed, it follows that in nature, where seed is abundant, many insects are caught more than once. Where there is one inflorescence an insect has a good chance of avoiding incarceration. Where there are hundreds the average period of liberty is likely to be significantly shorter.

REFERENCE

KNOLL, F. (1926). Die *Arum*-Blütenstände und ihre Besucher. *Abh. zool.-bot. Ges. Wien*, **12**, 381.