INSECT FERTILIZATION OF AN AROID PLANT.

By Henry G. Hubbard.

In the dense forests of the West Indian Islands a very characteristic feature of the luxuriant vegetation is afforded by the abundance of aroid plants. The giants of the family, Anthurium, Monstera, and their allies, are everywhere present, ascending the tree-trunks, or climbing along the outstretched branches and sending down their cord-like roots in a tangle of llanas; others less arboreal overhanging the

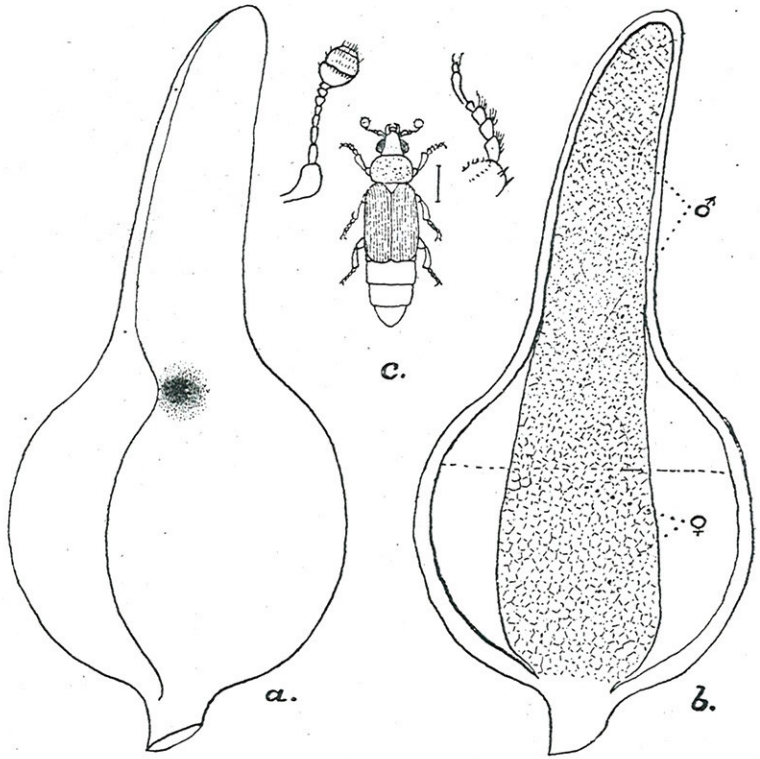

Fig. 33.—Inflorescence of *Philodendron* sp.: *a*, exterior of spathe, showing fungus spot; *b*, section of spathe, showing spadix one-half natural size; *c*, *Macrostola lutea* enlarged—front leg and antenna do.—more enlarged. (From diagrammatic drawing by the author.)

rocky ledges and spreading over the path their huge caladium-like leaves to intercept any ray of sunlight that may chance to penetrate the arboreal shield overhead. Among the varied forms, one of the largest is a species of Philodendron. This plant is nearly terrestrial, growing among rocks or upon fallen tree trunks. It is an indifferent climber and its root-stalk, although six or eight inches in diameter, does not, as a rule, exceed four feet in length. Being a very accessible and at the same time a very common plant, no wanderer in the mountain forests can fail to observe its inflorescence. This consists of greenish or purplish flask-shaped organs, resembling huge unopened buds, growing upright in groups upon the rhizome, at the bases of the leaf-stalks.

The flower case has about the size and very much the shape of a sixteen-ounce Florence flask. When cut open and examined it is found to consist of a thick and leathery spathe wrapped in a spiral about an upright, cylindrical spadix. The enveloping spathe tightly clasps in its embrace the upper, pollen-producing portion of the spadix, but expanding below, leaves the fruiting portion free, in a cavity which is partially filled with a mucilaginous liquid. All evaporation is prevented by the overlapping of the spathe, and the floral organs thus hermetically sealed within the flask would seem to be destined to self-fertilization most rigidly enforced. Indeed it is difficult to conceive how any fertilization could be accomplished by the plant itself, since the pollen tubes of the spadix, being tightly enrolled by the inner folds of the spathe, are unable to give forth their fertilizing grains.

During a recent visit to the island of Montserrat, one of the Leeward group of the Lesser Antilles, I had occasion to observe that the maturing flowers of this plant are infested with numerous larvæ of sap-loving beetles and flies, which swarm in the flower-cases, feeding upon the envelope and breaking it down, until at last the ripening fruits surrounding the base of the spadix are stripped of their covering and stand exposed, to be carried away by birds and other agencies which aid in the dissemination of the seed. The immature inflorescence, however, contained at first no insects, but in every case, sooner or later, a brownish spot, caused apparently by a rot-fungus, made its appearance upon the exterior of the flower-case (spathe). It was remarked that the fungus spot invariably occupied the same position, occurring always at the extreme outer edge of the overlapping spathe, opposite a deep sinus which cuts into the margin. The accompanying diagrams, although they do not attempt to reproduce exactly the structure of the floral organs, will serve to illustrate the general features of the inflorescence. Fig. 33 *a* represents the flask-like spathe upon which the fungus spot will be seen in process of development. Fig. 33 *b* gives a section of the same, showing the internal cavity, and the spadix with its base immersed in liquid, the surface of which is indicated by a horizontal line.*

* Fig. 33 *b* is reproduced from rough field notes, and does not present an actual section of the spathe, in which the upper male portion of the spadix is enrolled within the inner flap of the spathe. The upper portion of the inflexed spathe goes more than once around the spadix, which does not come in contact with the outer walls as shown in the figure. Of the double envelope thus formed, the inner walls should descend around the spadix very nearly to the surface of the liquid.

As the result of the examination of numerous flower-cases, the fungus-spot was found to increase in area until it reached the size of a shilling piece. Its growth then ceased. In the meantime the tissues affected by the fungus shrink and finally split, leaving an opening into the cavity of the spathe through which saprophagous insects can enter at will.

In examining flowers not yet attacked by the fungus, or in which its presence is barely indicated by a slight discoloration, the author of the contrivance is frequently disclosed. This is no other than a sap-beetle of the family Nitidulidæ, a pair of which, male and female, are invariably found together, forcing their thin bodies under the overlapping fold of the spathe. Mr. E. A. Schwarz has identified this beetle with *Macrostola lutea* Murray, described from Cumana, Venezuela.

Fig. 33, *c* gives an outline of the beetle, with its antenna and front leg more enlarged. The hair line at the side of the figure shows the natural size.

The Macrostolas evidently consume some days in gaining an entrance into the flower-case. In this laborious effort they are materially assisted, first by the plant, which has accommodatingly reduced the distance to be traversed by the beetle by means of the sinus in the edge of the spathe, without, however, in the least degree breaking the seal of the flower-case. The instinct of the beetle in selecting this weakest point for its attack appears to be unerring. Secondly, I believe that the aid afforded by the rot-fungus, which promptly attacks the surface gnawed by the beetles in their effort to cut a passage onward, is most material in causing the tissues of the thick and leathery spathe to soften and perhaps to warp slightly in shrinking Thus the beetles are enabled to accomplish that which without this assistance would be impossible to their feeble powers. At any rate, the passage of the pair of insects is made without, for the time being, breaking the closely guarded seal of the plant, and they enter into undisturbed possession of their new home. The point of entrance lies just above the surface of the liquid in the cavity. Once inside, the beetles make their way to the spadix, and force a passage upward along its polleniferous portion. The female, as she proceeds, deposits eggs, which soon produce a numerous colony of larvæ. By the time their progeny are half grown, the parent beetles, having fulfilled the measure of their existence, perish. Their dead bodies will invariably be found together at the upper end of the spadix, firmly wedged beneath the fold of the spathe, and incased in a thick paste of pollen grains agglutinated by the mucilage of the plant.*

The brood of larvæ live and complete their growth within the flower-case, feeding upon the pollen, in search of which they burrow and mine

*A similar life-long attachment and association of a single pair of adult beetles has been noticed by me in the case of *Epuræa monogama* Crotch, another member of the family Nitidulidæ. Compare, "Inhabitants of a Fungus." (Can. Ent., vol. XXIV, 1892, pp. 250 ff.)

along the spadix, thus detaching the inner coils of the spathe from their grasp upon the anther cells. A copious discharge of mucus from the walls of the spathe causes the released pollen to stream down into the cavity below, converting the limpid liquid into a turbid, soup-like mixture. Every portion of the interior is soon bedaubed with a farinaceous paste, upon which the swarming larvæ live and feed riotously. They finally pupate and transform to perfect beetles. In the meantime the diseased spot in the spathe completes its growth and drops away, leaving a yawning orifice, through which other saprophagous insects gain an entrance and add their increase to the swarming population of the flower. Prominent among these is a fly maggot, similar to those which infest fungi. This maggot feeds upon the ripening parenchyma of the floral envelope and destroys it. The liquid within the cavity becomes putrid, and finally escapes through the breaking down of the containing walls.

The brood of Macrostola beetles, by this demolition of their domicile, are driven forth to mate and betake themselves to neighboring flowers, where they repeat the process just described. They bear with them in the pollen paste with which their bodies are plentifully bedaubed, the material necessary for the fructification of the new inflorescences into which they enter.

The part played by the rot-fungus is an important one, equally advantageous to the beetles and to the plant. It aids the former by first softening the tissues of the spathe, thus allowing the beetles to advance in their passage into the flower-case, and afterwards hardening and for the time being effectually closing the entrance against other intruders. After the Macrostolas, in undisturbed possession of the flower-case, have accomplished the fertilization of the stigmas and released the pollen, the fungus in maturing breaks the seal of the plant and admits destructive insects. The aroid thus secures the expulsion of its pollenizers as well as the proper ripening and disseminating of its seed.

Observations upon the fertilization of aroids are not often met with in botanical literature. The flowers of the more common northern species have been studied by various authors, but the tropical forms have been seldom examined in their native habitats, and most of the observations upon their methods of fertilization have been made in European greenhouses.

The flower-cases of many species exhale powerful, often foul and putrescent, odors, which attract scavenger insects of various kinds, and slugs, also, being particularly abundant in greenhouses, have often been observed creeping about the flowers. Not a few of the records made under these unnatural conditions add but little to our knowledge of the manner in which the fertilization of these plants is accomplished in the tropical forests where they are at home.

The treatise of A. Engler upon the arrangement of the sexual organs

and methods of pollenization in the Araceæ (Botan. Jahrb., IV, pp. 341–352, 1883), in which, in addition to his own profound researches, those of all previous writers on this subject are summed up, shows that the disposition of the sexes and the modifications in form of the inflorescence in this family are exceedingly varied and complex. Contrivances adapted to insure cross-fertilization abound. A great number, perhaps the majority of the species that have been noted, are proterogynous, i. e., the female element of the flowers or flower-spike precedes the male in time of blooming. To this class most, if not all, of the Philodendrons belong.

Among those aroids in which the upper portion of the spadix bears male and the lower part female flowers, Engler notes eleven distinct arrangements of the sexes upon the spadix, or modifications of the spathe with respect to these arrangements. Those species in which the spathe is open and the entire spadix free, may be fertilized by insects of many kinds and even by snails. The odors given off by aroids having an inflorescence of this character are often fragrant, or at least not offensive to man, and are such as attract most insects, and the list of species which have been observed to enter the spathes is a very extended one. Some aroids of this class on the other hand exhale the odor of carrion and are visited by carrion insects, such as *Lucilia cæsar*, the common blow fly, or carrion beetles, *Saprinus nitidulus*, etc.

Many aroids, as noted by Engler, have the spathe constricted in various ways so as to partly inclose the spadix and divide more or less completely the portion bearing male from that bearing female flowers. The fertilization of the inflorescence in such cases must be effected by those insects which are adapted to creep through narrow apertures or to live in dark quarters, and the majority of insects which frequent ordinary flowers are excluded. The pollen in aroid flowers of this class is usually given off in vermiform masses, and is more or less glutinous and not dry as in open flowers. The odors in the few cases in which they have been noticed are said to be disagreeable or peculiar.

In *Pinellia tuberifera* Ten. the spathe is constricted, so that an aperture only one square millimeter in dimensions connects the male with the female chambers. Breitenbach and Engler also observed that swarms of small gnats passed freely through the minute opening, and that they were able to carry off pollen adhering to their bodies. It is probable, however, that in the tropics aroids, in which the spadix is wholly inclosed or difficult of access, are fertilized for the most part by sap-beetles. And when the life-histories of the numerous tropical species of Cillæus, Macrostola, Brachypeplus, Conotelus, and their near allies, shall have been made known, many of them will no doubt be found to be connected with the economy of some aroid, the plant and the beetle being mutually dependent the one upon the other.

No entomologist, as far as I am aware, has given any attention to the fertilization of West Indian aroids by insects, but Sallé and Fleutiaux (Ann. Soc. Ent. de France, 1889) record *Cillæus linearis* Er. as occurring in decaying aroid flowers in the island of Guadeloupe.

In the Montserrat aroid, having the spadix entirely within a flask-shaped spathe,* the inflorescence is proterogynous. Whether or not some of the female flowers remain receptive at the time the pollen is released by the Macrostola beetles, I am unable to say. Even were this the case, it seems likely that, as in *Dracunculus vulgaris* Schott and some other aroids in which the fact has been ascertained, the pollen is not potent to effect fertilization within the inflorescence, and setting of the fruit follows only upon the introduction of foreign pollen from without. Upon this assumption, taken in connection with the observed facts, the following summary may be given of the successive stages in the flowering of this plant:

1. Female flowers at base of spadix receptive, and immersed in liquid; upper portion of spadix male; flowers immature, and tightly enrolled by inner fold of spathe.
2. Entrance of a single pair of Macrostola beetles, bringing with them upon their bodies the pollen from an older inflorescence; fertilization of the receptive female flowers by the foreign pollen, aided by the mucus of the plant.
3. Maturing of the anther cells in upper portion of the spadix, and pollen released by the Macrostolas and their offspring.
4. Seal of the inflorescence broken by the ripening of the rot-fungus; entrance of saprophagous insects and destruction of the spathe; Macrostolas ejected, bearing pollen upon their bodies to enter and fertilize other flower cases.
5. Ripening of the fruiting portion of the spadix in open air, and dissemination of the exposed seed.

NOTES AND OBSERVATIONS ON THE TWIG GIRDLER.

(*Oncideres cingulata* Say.)

By Theo. H. Scheffer, *Lawrence, Kans.*

The beetle usually known as the hickory twig girdler, injurious also to the persimmon among forest trees and the apple and pear in orchards, has appeared in eastern Kansas, as a depredator upon the white elm (*Ulmus americana*). So far has it departed from its known and recorded preference† that hickory groves and orchards in this vicinity show no signs of its work, while elms, both in natural groves and in yards and parks, are more or less affected.

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*The material at hand is unfortunately insufficient for the proper classification of the plant, and the species can not be determined. It is apparently a Philodendron belonging to Engler's section IV of this genus, as given in his classification of aroids (Die natürlichen Pflanzen-Familien, Endlicher u. Prantl; Araceæ von A. Engler, p. 134).

†Note.—Since writing the above my attention has been called to a short article in the Kansas Horticultural Report for 1882, in which this insect is spoken of in connection with its work upon elms.—T. H. S.

It is also mentioned as attacking elm by Professor Riley, in the third volume of the *American Entomologist* (p. 297, December, 1880). See also First Report South Carolina Agr. Exp. St. 1888-'89, pp. 40, 41.—Ed.