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THESIS

Fertilization of Flowers

C. Fay Wheeler

1899

THESIS

A Thesis  
on the  
FERTILIZATION OF FLOWERS,  
by  
C. Fay Wheeler,  
Agricultural College, Michigan.  
Class of '99.

THESE

## FERTILIZATION OF FLOWERS.

It is only a comparatively short time ago that the real significance of the flowers began to be perceived, that their beautifully tinted corollas, sweet perfume and singular forms were known to have some purpose, viz., to attract the bees, other insects, birds and snails. The whole object of the flower's life is to secure the production of seeds, and the production of seeds is the chief end of the act of fertilization. Everywhere about us, during the summer months, are examples of the ways in which this life work is being accomplished. Some flowers are adapted for self-fertilization, while others have their pollen carried by the wind, but the flowers of most kinds of plants are so constructed as to be occasionally or habitually cross-fertilized by pollen, each from another flower, insects being the chief fertilizing agents. As plants are adapted by such diversified and effective means for cross-fertilization, it seems that some great advantage must be derived from the process. Indeed, Darwin and others have proved by investigation and experiment that in case of cross-fertilization the flowers bear much better seed than when self-fertilized, though it often happens that in default of insect visits the same flower is capable of self-fertilization.

On the 23rd. of June, 1898, I began to study certain plants of Scrophulariaceae, to "find how the flowers were fertilized, and if

cross-fertilized, to determine by what insects they were visited, how these insects acted and to study the structure of the flowers. Paper bags were placed over a few of the buds on each plant to see if the flowers were capable of self-fertilization in the absence of insect-visitors.

Seriphularia agnatica is of European origin. When I first began to study the plant it was visited by honey bees, in great numbers, with now and then a wasp or a yellow jacket, but after some time the honey bees left and the yellow jackets took complete possession. The bees are very busy about the plant all day long, which shows that the flowers secrete an abundance of honey. The two large drops of honey at the base of the wide, globular corolla near the superior side may be plainly seen. The bees cling to the outside of the flower and insert their heads between the upper and lateral lobes of the corolla and reach the honey very easily. The pistil and the four stamens (there were originally five stamens, but the fifth has become abortive and is now simply a little, black scale-like appendage on the upper wall of the corolla) are so arranged that the ventral surface of the insect comes in contact with them. The flowers are protogynous. As the bud unfolds, the pistil is seen, always on the right side of the lower lobe, extending beyond the corolla and leaning towards the lower lobe, with the receptive stigma pointing slightly upward. A bee which has just visited an older flower and has the underside of the head and the pro-

*SCROPHULARIA AQUATICA.*

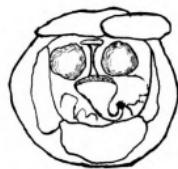
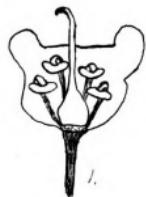


Diagram 5 showing position of 5... the bud.

Looking down into the flower, showing position of honey glands.  
Diagram 6 position of 6... stem.  
Diagram 7-8-9 show the order in which the stamens are

and meso-thorax dusted with pollen, comes to this newly opened flower and, while getting the honey, leaves a portion of the pollen on the stigma, which it necessarily touches. A short time after the stigma has received the pollen, the style bows down close over the lower lobe of the corolla, and the stamens, which until now, have been unfolded close to the style below the opening, begin to appear, the one to the left of the pistil always appearing first and beginning to shed its pollen before the second one appears at the right, and so on. Thus, the younger flowers are fertilized by pollen from the old. The inflorescence is a cymose panicle and I had difficulty in determining whether the bees as a rule begin at the lower flowers and go upward, or at the upper flowers and proceed downward. They appear to work both ways. Some of the buds on a branch that had been brought into the house opened, and the pistils instead of drooping as in the flowers out of doors, remained erect until the stamens had appeared and the anthers dehisced. In some way, pollen got onto the stigmae. Thus, it would seem that the flowers were capable of self-fertilization in the absence of insect visits, for some of the flowers that were covered by paper bags, produced seeds.

#### DIGITALIS PURPUREA.

The structure and size of the flowers of this plant suggest that they are adapted for bumble bees. The corollas are tubular, with wide mouths and with the lower and inner sides of them sticky

and covered with hairs to keep out the smaller insects. The bumble bee can crawl into the pendant flowers with ease, using these hairs as foot-holds. The flowers are protandrous, the two upper and longer stamens shedding their pollen before the two lower and shorter ones, and these before the lobes of the stigma separate to expose the surface that is sensitive to pollen. The anthers are large, and at first stand transversely with respect to the corolla tube, but twist around and place themselves longitudinally before shedding their pollen. As the anthers begin to wither, the lobes of the stigma separate and droop slightly so as to receive the pollen from the back of the bee, as it enters the flower. The inflorescence is a raceme, and as a rule, the bees visit the lower flowers first and go on up to the younger ones, where they become dusted with pollen, then go to the lower flowers of the next raceme and brush the pollen off on the receptive stigmas, and so on. I found slits in the sides of nearly all of the flowers, made there, I should judge, by the carpenter bees which, together with the honey bees, were very busy stealing honey from them. The bumble bees paid no attention to these slits, but continued to get their honey in the honorable way.

#### DIGITALIS LUTEA.

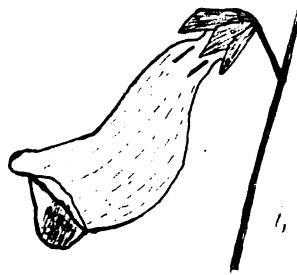
The flowers of this plant, though smaller, are very much like those of the *Digitalis purpurea* in form and structure. The lower lip of the corolla is very pubescent, and with the four anthers in

a row at the top of the corolla, the opening is made very small. Bumble bees visit the flowers and can only insert their heads into the corolla, getting the pollen on the back of their heads. The two longer stamens appear first as in the *Digitalis purpurea*, and after shedding their pollen, move to the sides of the flowers to make room for the next pair. Then the style becomes longer and the stigmatic lobes separate. The honey bees and the carpenter bees were very busy at the slits in the sides of the flowers of this plant also. Occasionally a honey bee would make a mistake and go to the mouth of the flower, and several times I noticed humming birds about the flowers. They would begin at the lower flowers and go on up the stalk, never missing a flower. Their bills were white with pollen. The honey is secreted by a ridge surrounding the base of the ovary.

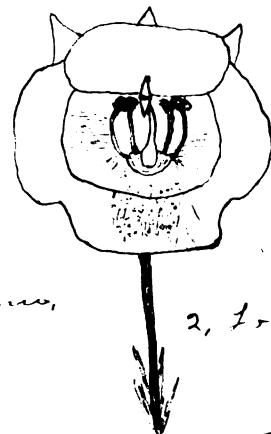
#### VERBASCUM SPECIES.

This plant has open flowers with freely exposed reproductive organs, the flowers taking an almost vertical position. The flat corolla is five lobed, the interior lobe being the longest and the two superior lobes shorter than the lateral lobes, so the insect lights most naturally upon the inferior lobe. The five stamens are arranged alternately with the lobes of the corolla, and project almost horizontally, diverging slightly from one another. The three upper ones are covered with hairs and the filaments are rather short, while the two inferior are longer and smooth. The pollen which is

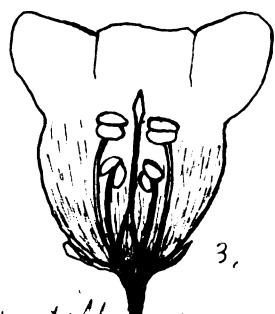
DIGITALIS PURPUREA.



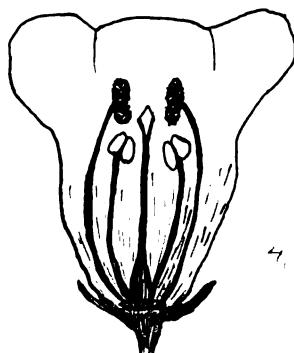
1. Shows the position of  
the flower on the stem.



2. Looking into the flower.



3.



4.



5.

3-4-5 show different stages  
in the development and growth  
of the stamens and pistil.

DIGITALIS LUTEA.

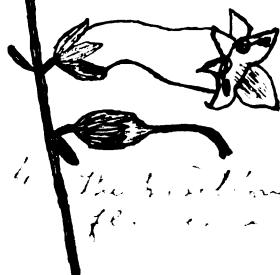


Looking into  
the flower.

2.



Shows  
longer  
4. The  
stamens  
and  
pistil.



5. The  
position  
of the  
flower  
on the  
stem.



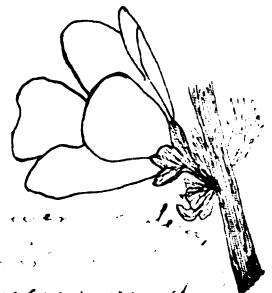
6. The  
position  
of the  
flower  
on the  
stem.



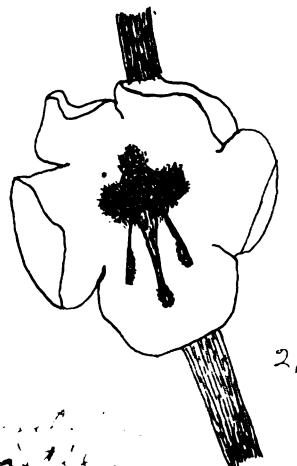
7. The  
position  
of the  
flower  
on the  
stem.

very abundant, is shot along the outer edges of the anthers and is of an orange-red color. The pistil, which is shorter than the two inferior stamens, takes its position just between them and is bent down slightly below them. An insect lighting on the inferior lobe would touch the stigma first. Bumble bees and honey bees, which occasionally visited the flowers, would light on this lobe, crawl up over the pistil to the stamens, grasp them with their legs and circle around as if seeking honey at the base of the corolla, thus becoming covered with pollen. As far as I could make out, the flowers secret no honey, whatever, but are visited mostly by pollen collecting insects, the most frequent visitors being the Syrphus flies. They usually have great balls of pollen attached to their hind legs. As a rule, these insects do not light on the lower petal, but being small, either light on the anthers and begin to collect the pollen immediately, or light on the edge of the corolla and crawl along to the stamens. I would watch a certain flower for some time and a great many of these insects would visit it, but perhaps none of them would go near the pistil during that time. Then at other times, they would either light on the stigma "first or crawl up to it in search of pollen. The bees then, seem to be the most certain means of carrying the pollen from one flower to another. The stigmatic surface is along the edges of the stigma and the pollen on it can be plainly seen. As soon as the stigma has been fertilized and the pollen collected from the anthers, the superior stamens curl down

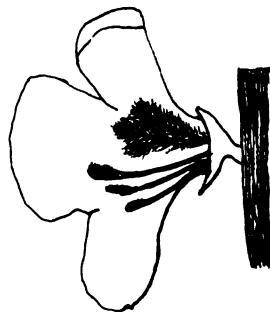
VERBASCUM SPECIOSUM.



Flower on a stem  
and stamens in it.

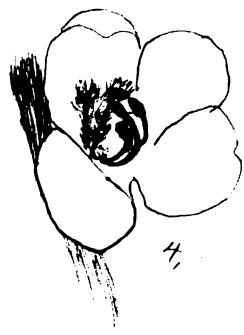


2.



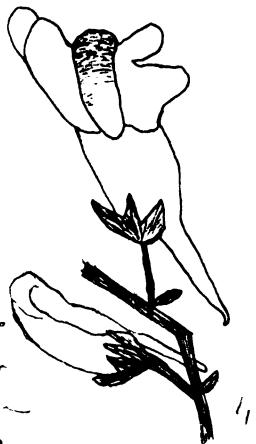
3.

The flower on the stem is  
about 1 1/2 inches long.  
Also shows the two lower stamens  
and the upper one which holds pollen  
and has the style. This style does the same  
after being fertilized.



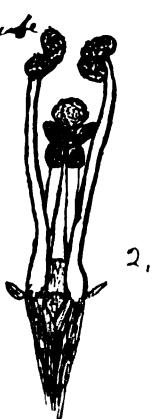
4.

LINARIA VULGARIS.

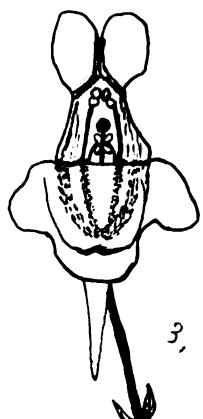


Flowers on a stem of flower

on a stem.  
The arrangement of stamens  
and pistil. The two upper  
stamens shed their pollen  
into the two lower. Also  
shows the round ligulate  
anthers & style of the upper  
and pistil of the lower  
upper part of the anthers.



2.



3.

and the pistil and inferior stamens curl up to meet them.

#### LINARIA VULGARIS.

Both the position and the arrangement of the flowers of this plant are very peculiar. The corollas are tubular, with long spurs at the lower extremities which contain the honey, and with very peculiarly shaped lower lips, which meet the upper lobes of the corollas in such a way as to completely close the tube. The flowers point directly upward. A bee lights upon the lower lip and its weight partially opens the tube so as to enable it to creep into the flower and thrust its head into the wide entrance of the spur. In doing this, the back of the bee comes in contact with the anthers and the stigma which mature simultaneously, the stigma lying between the shorter and longer pairs of stamens. The insect visitors are chiefly hive bees and bumble bees. The bumble bee can only insert its head, thorax and fore legs into the flower, getting the pollen on the back of its head. I noticed several of the smaller bees lighting on the upper lips of the corolla and going into the flower, head downwards, so as to get the pollen on the front part of its body instead of on the back.

#### CAMPANULA PERSICIFOLIA.

This is the only plant of the family Campanulaceae that I studied. The flowers are bell-shaped, the corolla five lobed. In the bud, the three stigmas(sometimes four) lie closely pressed together, forming a cylinder whose outer surface is thickly covered with hairs, and

the anthers are placed close around this cylinder. They discharge on the inner side and shed their pollen on these hairs. When this has taken place, the stamens wither and fall to the base of the corolla. The flower now opens and the stigmas are seen standing erect and thickly covered with pollen which is soon rubbed off on the bodies of the insect-visitors. The hairs wither; the divisions of the style separate and curve backwards to expose the inner surfaces, which are the stigmatic surfaces, to the bees. Bumble bees are the most frequent visitors. As they light on the flower, they grasp the lobes of the stigmas of the younger flowers with their legs, and in searching for the honey, which is secreted by a yellow disk around the base of the ovary, they circle around the base of the corolla, thus getting a great deal of pollen on the front part of their bodies; then, grasping in the same manner, the stigmas of the next flower, which is perhaps older and has the stigma lobes separated, the pollen is rubbed off on the receptive stigmas. If the flowers are kept where the insects cannot reach them, the stigmas bend back further still, till they touch the pollen which remains attached to the hairs. Thus self-fertilization is normally effected. Upon removing the paper bag that had been placed over a number of the buds, I found, however, that none of the flowers had produced seed.

#### GRATICIA OFFICINALIS.

The flowers are small and tubular, with the stellate stamens

CAMPANULA PERSICIFOLIA.

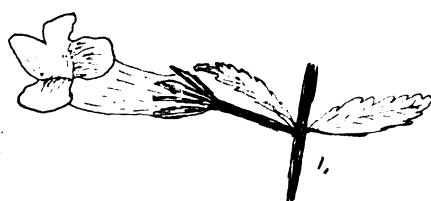


1. The older flower with its  
calyx removed to expose the stamens.  
2. The newest flower showing the divisions of the calyx  
others shed during pollination, the stamens not yet separated,  
3. same, in a still younger flower, the hairs on the back of  
the calyx petals may be seen,  
4. a small portion of the stem and leaves.

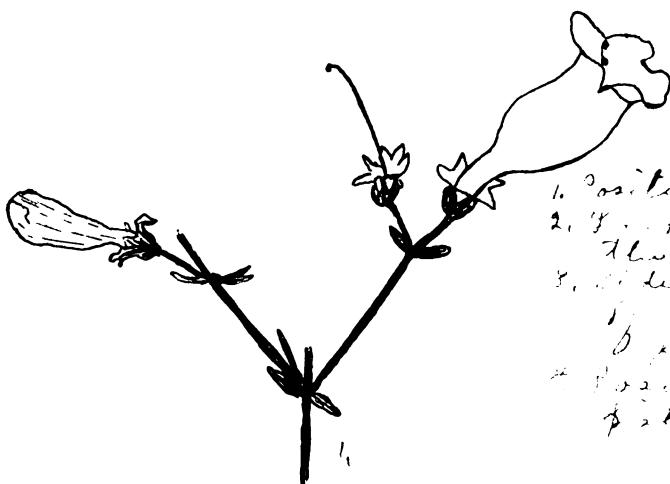
*GRATIO LA*      *OFFICINALIS.*



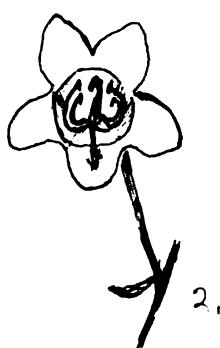
position of flower on stem,  
the appearance of the flower-  
ing branches than from its  
twigs, showing position of  
leaf and stamens,  
a call tube to a.  
is the attachment of  
twigs,



PENTSTEMON GLABRA.



1. Position of flowers on a  
2. Type of flower stalks  
3. Attachment of stamens  
4. The few stamens are  
5. In pairs and distal  
6. Position of stamens on a  
part of the plant



so arranged that the back of the insect touches them as it enters the flower. Two of the stamens are attached to the upper part of the corolla tube, and two to the lower part. The latter ~~start~~ warm so that the anthers of these come just below the anthers of the first pair. The filaments are very slender and the anthers small, containing but little pollen. The anthers and the stigma mature simultaneously. The most frequent visitors are the Ceratinae, which creep down into the flower for the honey. Upon removing the paper bag the plant was found to have developed no seed.

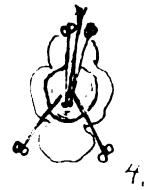
#### PRISTIMON CHABRA.

The flowers of this plant are protandrous. The corollas are long and tubular with the stamens and pistil near the upper side, the insects getting the pollen on their backs. The fifth stamen is abortive and lies along the lower part of the tube. The stamens are in pairs, the longer pair shedding their pollen before the shorter. The flowers point directly out to the side. Bumble bees occasionally visit them, but the most frequent visitors are Megachile.

#### BALLOTA ITALICA. (LABIATÆ).

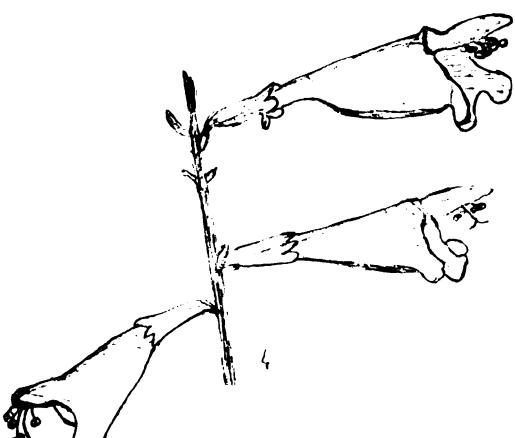
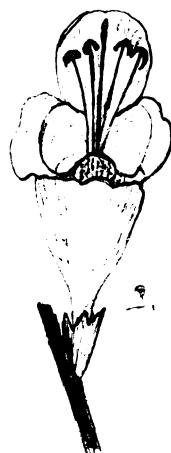
The tubes of the flowers of Ballota Italica are comparatively short, but the upper and lower lobes of the corolla are quite long, making a narrow opening. The upper lobe is slightly domed-shaped, and protects the stamens and pistil. The lower lobe is a little longer and broader than the upper and forms a landing place for the insects.

*LOPHATHUS NEPETOIDES.*



1. Shows position of flowers.
2. Shows arrangement of stamens in the flower.
3. Shows the attachment of stamens to the corolla.

*PHYSOSTEGIA VIRGINIANA.*



1. Shows position of flowers.
2. Points to the flower, to the stem, and against the calyx.
3. Shows by the form of the corolla tube and of the stigmas and anthers.
4. Shows hairy gland at the style.
5. Shows the attachment of the stamens and anthers.

There are two long and two short stamens, the anthers all shedding pollen at the same time. The pistil is between those two pairs of stamens and after the pollen is shed, it bends down and the stigmatic lobes separate. The flowers are visited mostly by Megachile, *Bombylius*, *Bombus*, *Bombus fervidus*. They alight to the lower lobe and insert their heads between the two lobes, getting the pollen on the back of their heads in the younger flowers and rubbing it off on the stigmas of the older flowers. The honey is secreted by a fleshy, yellow disk, at the base of the ovary.

#### *SAVIA GRANDIFLORA.*

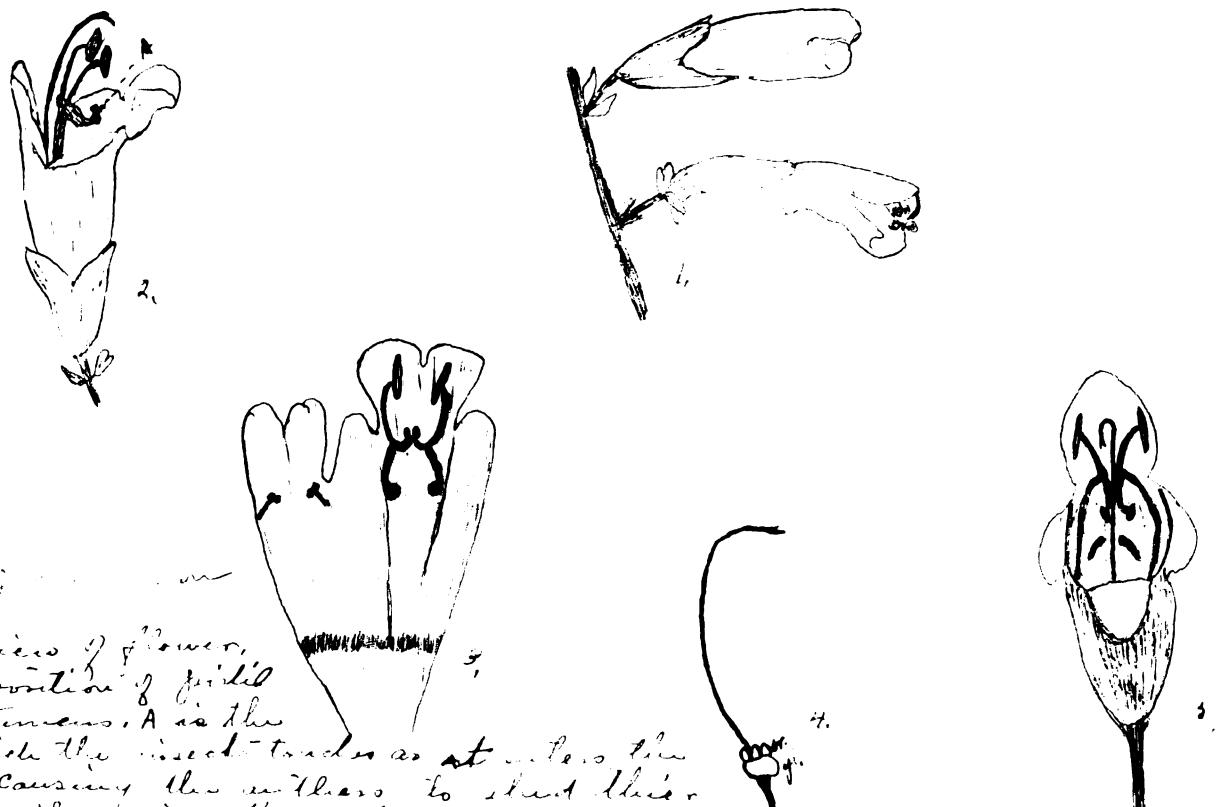
The flowers of this plant are large with wide-mouthed, tubular corollas. The upper lobes are dome-shaped and protect the stamens and pistil, and the two lateral and the long, broad, lower lobe form a landing place for the bees. The flowers are characterized by the peculiar lever-like action of the stamens. The two filaments start at the base of the lower lobe of the corolla, one at each side, and remain close to the lateral lobes till at the base of the upper lobe, then there are two divisions of each, or rather two arms, and at the end of each arm is an anther-lobe. The two longer arms of the filaments round upward into the dome-shaped, upper lobe of the corolla and the two shorter bend downward and stand in the mouth of the flower, so that the two upper anther-lobes are slightly above and in front of the lower ones. The upper lobes are larger and contain much more pollen than the lower. The two lower arms touch each other

BALLOTA ITALICA.



1. Shows position of flower on stem.  
 2. Shows leaves of plant.  
 3. Shows position of stamens.  
 4. Shows fruit of plant.  
 5. Shows tube of flower.

SALVIA GRANDIFLORA.



1. Shows flower on stem.  
 2. Side view of flower.  
 3. Position of filaments  
over lobes. A is the  
place which the insect touches at after the  
tube, causing the anthers to shed their  
pollen on that insect's back.  
 4. Development of flower to ovule tube.  
 5. Leaf of plant.  
 6. Seed of plant.

and as a bee enters the flower, it first contacts its head against the two inferior anther-lobes which block the entrance, and these arms rotate in such a way that the two upper anther-lobes fly down and strike on the back of the bee, leaving their pollen there. This pollen is then rubbed off in older flowers upon the downward bent stigmas. At each side of the base of the upper corolla lobe is attached a small body which may be an abortive stamen. Insects which visit these flowers are *Bombus ferrugineus*.

#### *LUPHAGUS NEPHOTILES.*

The inflorescence is a spike, with small flowers pointing out to the sides and with the four stamens and the pistil projecting beyond the corolla tube; the pistil and two shorter stamens near the superior side, while the two longer stamens are attached to the superior side, about half way up the tube from the base, but slant so that they appear to be fastened to the base of the corolla on the lower side of the tube. In the bud, they are all bent down and held by the lobes of the corolla, but as soon as these unfold, they spring up. The stigmatic lobes are separate in the bud.

The flowers are visited by small bumble bees. They begin at the lower flowers and crawl around and around the spike, dipping their proboscides into every flower and in so doing, the front part of the head comes in contact with the two superior stamens and the pistil, while the pollen of the inferior anthers is brushed off by the legs of the bees as they crawl along, and pollen may be

conveyed to the stigma either way, by the head or by the legs of the bee. The stigmas and anthers mature at the same time. Insects, *Bombus fervidus*, *Bombus scutellatus*.

*PHYSOSTEGIA VIRGINIANA*.

In the early stage, the flowers of this plant occupy a horizontal position as regards the main stem, but are inclining to droop as they become older. They are protandrous, the stigmas coming to occupy the place of the anthers. The pistil and the four stamens are near the upper wall of the corolla, so the bee receives the pollen on its back. The anthers are so arranged that the pollen is completely removed by the first insect-visitor. Very soon after the flowers open, the anthers will be found to be entirely empty. The pistil lies close against the upper wall of the corolla tube at first, with the stigmatic lobes slightly separated. When the anthers are empty, the style becomes longer and bends forward, and the lobes of the stigma are more widely separated. The visitors consist of bumble bees which rest on the lower lip of the corolla and insert their heads far enough so that the stigma touches the thorax. The inflorescence is a spike, and as a rule, the bees visit the lower flowers first, which are the older ones, and as they go on up the stalk, they become dusted with pollen from the younger flowers, then fly to the lower flowers of the next cluster, and the stigma there get the benefit of the pollen just collected, and so on. The honey is secreted partly by the base of the ovary and partly by a little

bract-like projection, which is attached to the stem on the lower side. The insects are *Bombyx farinosa*, *Bombyx separatus* and *Bombyx pennsylvanicus*.

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