

962

POLLINATION AND SEED PRODUCTION  
IN ALPINE PLANTS.

A Thesis

Submitted to the Faculty of the Graduate School  
in partial fulfillment of the requirements for  
the degree of Master of Arts.

by

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Table of Contents.

Method of procedure.

Index of flower records.

Flower records.

Table showing maturity of anthers and stigmas.

Time of insect visits.

List of flowers and insect visitors.

List of insects found pollinating flowers.

Summary.

Conclusions.

Bibliography.

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During the summer of 1912 observations were made to find out

- (1) How pollination took place;
- (2) What attracted the insect to that particular type of flower;
- (3) Flower adaptations having special relation to the visitor;
- (4) Relation between the amount of pollen, the number of seeds produced, and the visitors.

The work from June 15 to August 1 was done in the Pike's Peak region at the Alpine Laboratory, near Half Way, Colo.; from August 1 to September 15, at the foot of Long's Peak in Estes Park. Much of the work was done at an elevation of 9000 feet, but a range of from 7000 to 14000 feet was accessible.

#### Method of Procedure

##### I. Floral Mechanisms.

Plants in unmolested places were selected and flower clusters on these marked with card labels written

in indelible ink. Sketches were made of the cluster, and each flower numbered in the order of its maturity, so that records for each flower might be kept as it developed.

Thin waxed paper bags were tied with yarn about buds ready to open, to find whether fruit could be produced and to what extent without the agency of insects. Rather large bags were used to allow the unrestricted development of parts. Buds in inconspicuous places were chosen so they would not be molested.

The following points were noted daily, sometimes several times a day:

- A. Positional changes of the flower as a whole, from bud to maturing fruit;
- B. Time of anthesis, withering, falling of parts;
- C. Changes in reproductive organs,
  - (a) Stamens
    - (1) position
    - (2) length
    - (3) condition, time and period of dehiscence of anthers.

(b) Style

- (1) position as a whole and of outer end,
- (2) length
- (3) time of development of stigmatic surface
- (4) length of time stigmatic surface is receptive.

II. Flower Visitors.

The insects were captured either by a net or by holding a wide-mouthed jar beneath the flower and suddenly putting the lid in place enclosing the insect. Chloroform was used for killing them. They were later labeled and recorded. Before taking the insects the following observations were made:

A. Insect visitors

- (1) kinds of insects visiting each flower species,
- (2) types of flowers preferred by each insect,

- (3) peculiarities of the flower having special relation to the particular visitor,
- (4) the insects choice of flowers studied to find whether they were specialized or universal with regard to the flowers visited,

B. Insect methods,

- (1) Pollen collecting
- (2) Nectar gathering
- (3) Pollen deposit on stigma

C. Insect efficiency,

- (1) Number of flowers visited in unit time

III. Relation Between Amount of Pollen and Number of Seeds produced.

Anthers nearly mature, and pistils were preserved and later prepared slides made to find the number of pollen grains per anther and ovules per pistil. Longi and cross sections were made. Those cut .025 mm. thick were most useable in this work. The tendency of the pollen grains to fall out as the slides were washed made the work unsatis-

factory. The actual number of pollen grains in the cross sections were counted and averaged, and that number multiplied by the average number in a lengthwise row. A more accurate method would be counting the number of cross sections per anther having pollen grains and multiplying this number by the average number in cross section .

In the following plant descriptions, the location of the nectaries is in most cases quoted from Knuth, since original observations were not made. The date given is the time at which observations were begun and the first day mentioned means the first day after that date.

Many of the flower records are incomplete. In some cases the daily records were interrupted by accidents to the plant. Where no daily record was possible, the positions taken by floral organs at different times were noted in the several flowers on the plant. Insect visitors were convenient for study at some times and the floral mechanisms not carefully observed.



FLOWER	I N D E X	DESCRIBED SPECIES
Ranunculaceae		P
<i>Clematis alpina</i>		13.
<i>Aquilegia coerulea</i>		14.
Brassicaceae		
<i>Stanleya pinnatifida</i>		15
<i>Cléome serrulata</i>		16
Fumariaceae		
<i>Capnoides aureum</i>		17
Solonaceae		
<i>Quincula lobata</i>		18
Geraniaceae		
<i>Geranium Fremontii</i>		19
Fabaceae		
<i>Petalostemon candidus</i>		20
<i>Lupinus luteus</i>		21
Rosaceae		
<i>Sieversia ciliata</i>		22-23
<i>Drymacollis fissa</i> ( <i>Potentilla?</i> ) <sup>24</sup>		
<i>Potentilla pulcherrima</i>		25

	Edwinia americana	P 26
	Prunus demissa	27
	Rubus deliciosus	28-29
	Rubus strigosus	30
	Rosa Engelmannii	31
	Fragaria americana	32
<b>Saxifragaceae</b>		
	Ribes lacustre	33
	Hemlock Hallii	34
<b>Onagraceae</b>		
	Chamaenerion angustifolium	35-36
	Pachylophus speciosa	37
<b>Asteraceae</b>		
	Helianthus petiolaris	38
<b>Campanulaceae</b>		
	Campanula rotundifolia	39
<b>Primulaceae</b>		
	Dodocatheon Meadii	40-41
<b>Asclepiadaceae</b>		
	Asclepias speciosa	42

**Gentianaceae**

<i>Frasera speciosa</i>	43
<i>Gentiana Parryi</i>	44-45
<i>Gentiana elegans</i>	46
<i>Gentiana affinis</i>	47
<i>Gentiana frigidis</i>	48

**Polemoniaceae**

<i>Gilia aggregata</i>	49
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**Hydrophyllaceae**

<i>Phacelia heterophylla</i>	50-51
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**Boraginaceae**

<i>Mertensia pratensis</i>	52
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**Scrophulariaceae**

<i>Pentstemon unilateralis</i>	53
<i>Pentstemon humilis</i>	54
<i>Pentstemon glaucus</i>	55
<i>Pentstemon secundiflorus</i>	56
<i>Pentstemon glaber</i>	57
<i>Castelleia miniata</i>	58
<i>Pedicularis canadensis</i>	59

Lamiaceae

Scutellaria resinosa 60

Liliaceae

Allium recurvatum 61-62

Wagnera stellata 63

Zygadenus elegans 64

Calochortus Gunnisonii 65

Ranunculaceae

*Clematis alpina*

Flowers solitary. Buds and flowers pendulous. Insect attraction, large, blue violet, sepals. Petals small, stamen-like. Anthers, filaments and styles somewhat hairy. Anthers dehiscing, closely crowded about receptive stigmas, at anthesis. Filaments longer than styles preventing autogamy. Nectar secreted at the grooved inner surface of basal half of filament.

Pollen from mouth parts of bombus rubbed onto stigmas, as it pushes down among the filaments for nectar, producing allo-autogamy.

*Aquilegia coerulea*

July 5, 11 a.m. Bud drooping, reaching an angle of sixty degrees first day 1.30 p.m. and beginning to open. Stigma receptive. Second day, stamens 1 mm. longer than style. 8 a.m. third day, corolla fully open, anthers unequal in length, smaller anthers grouped about stigmas, larger anthers on filaments curved out away from stigmas. On fourth day, few anthers dehiscing, stamens 2 mm. shorter than style. Horizontal position of peduncles reaching angle 180 degrees, many anthers dehiscing, fifth day. Styles elongating and curving outward until they are 7 mm. beyond stamens, sixth day. Corolla drops off twelfth day.

Nectar secreted and concealed at bottom of petal spurs.

*Bombus proximus* lands on stamens. Head pushed into nectary, two front legs on forward projecting part of spur, hind legs on styles and anthers. Pollen collects on under side of abdomen. Allogamy or autogamy produced in older flowers as spreading receptive stigmas come in contact with abdomen of bee.

Brassicaceae

*Stanleya pinnatifida*.

Tall raceme. Flowers yellow. Petals and sepals, long and narrow. Stamens six, equal in length, filaments twice length of style. Young anthers straight. Mature anthers roll inward as filaments elongate, spreading away from style, aiding allogamy.

*Apis mellifica* most frequent visitor. Alights on lower petal and sucks nectar.

*Cleome serrulata*.

Filaments long, coiled in bud. At anthesis, filaments extend anthers beyond petals and short style, thus avoiding autogamy. Stipe elongates, bearing capsule in air, projecting whole length beyond anthers.



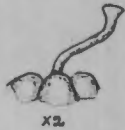
Fumariaceae

*Capnoides aureum*.

Buds point upward. Open flowers horizontal, corolla mouth toward sun. Hood formed from upper and two inner petals. Lop-sided spur formed from outer petal. Other outer petal spoon shaped, fitting into depressed front part of spur petal. Honey secreted by common prolongation of upper stamens. Nectar protected by hood, made accessible by flowing down to tip of spoon-shaped corolla.

*Bombus proximus* lands on hood, with hind legs on lower petal, pushes head into hood. In young flower style straight, same length as dehiscing anthers. Head and under parts of *bombus* receive pollen.

In older flowers, receptive stigma bent sharply upward, projects above anthers, receives pollen from head and abdomen of *bombus*.



x2

Fig. 1



x2

Fig. 2



x2

Fig. 3



x2

Fig. 4



x2

Fig. 5



Fig. 6



Fig. 7



Fig. 8

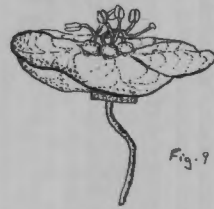


Fig. 9



Fig. 10

Quincula lobata

- Fig. I, II, III, - Style somewhat erect
- Fig. IV - Style U - shaped
- Fig. V - Style looped
- Fig. VI - Style erect - bud
- Fig. VII, VIII, - Style bending down
- Fig. IX - Style bent out of the way - Stamens  
dehiscing
- Fig. X - Style looped, erect, stamens spread-  
ing, nearly through dehiscing.

Solonaceae

*Quincula lobata.*

Disc shaped, blue corolla serves as landing platform. Fleshy nectaries at base of filaments white, direct insects to nectar.

Style twice as long as filaments, in bud, shortened by looping. At anthesis, style bends from vertical to horizontal, thus moving away from dehiscing anthers. Anthers mature at separate times. Bend in style increases until it forms a loop, places stigma in upright position on level with anthers. Filaments curve outward at dehiscence.

Mustideae sp. holds filaments between front legs eating pollen and moving abdomen constantly.



Fig. X2.



Fig. X3.

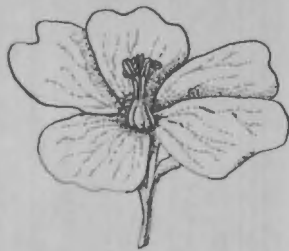


Fig. X4.



Fig. X5.



Fig. X6.

Geranium Fremontii

- Fig. I - Unopen bud O style tip bent at right angles.
- Fig. II - Stamens bending outward away from styles.
- Fig. III - Stamens grouped closely about stigmas.
- Fig. IV - Styles outcurved. Filaments straight, grouped closely at center.
- Fig. V - Petals fallen - styles recurved.

Geraniaceae

Geranium Fremontii.

Bud pendant, starting to elevate at 6 a.m.

July 4. Peduncle angle 100 degrees. Corolla opening, filaments vertical, styles tightly grouped together at center, first day, 2 p.m. Peduncle angle 160 degrees, corolla fully open, plane turning toward sun, filaments curving outward 2 p.m. second day. Five inner stamens grouped closely about styles, dehiscing, styles outcurved receptive 10.30 a.m. third day. Second set stamens vertical, dehiscing, first set stamens fallen 8 a.m. fourth day. Petals fallen 9 a.m. fifth day. Upper edges of petals hairy at narrower end to protect nectar from rain. Red stripes on petals, insect guides.

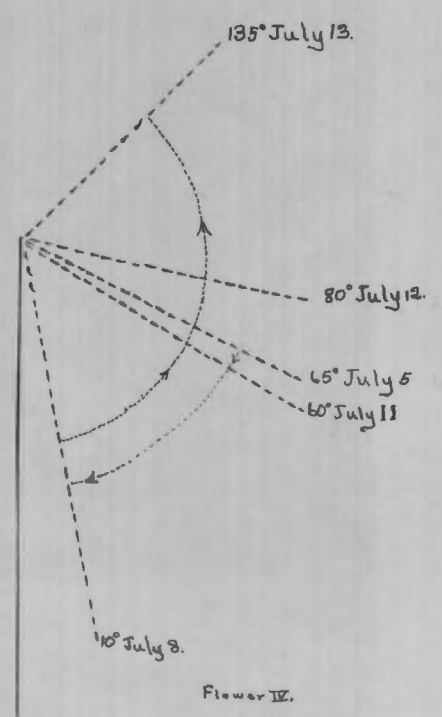
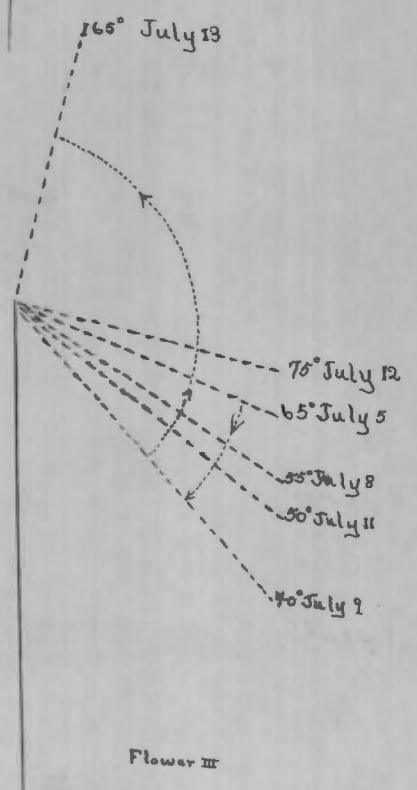
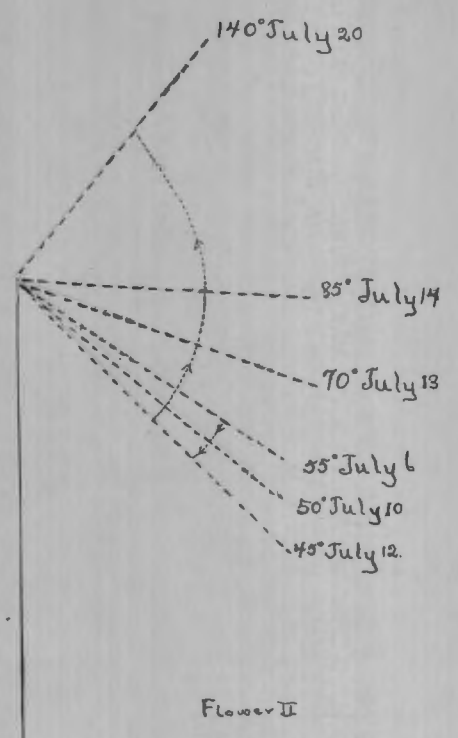
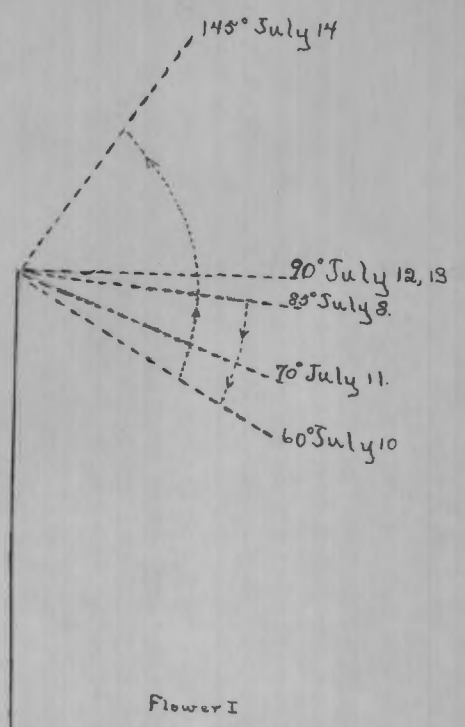
Nectar secreted by glands on outer side of bases of five inner stamens. Autogamy may occur when styles are bent outward and come in contact with anthers.

*Lupinus luteus*.

Flowers on raceme. Conspicuous because of abundance and bright blue color. Buds erect, open flowers hang downward.

In young flowers, stigma straight, shorter than filaments. As anthers dehisce, drying filaments carry them away from stigma. Style, meanwhile, elongated and bent sharply upward for one third of its length. Receptive stigma in position where insects can hardly avoid brushing against it, producing allogamy. In the first stage visitors collect pollen from the anthers. Flowers fading to pale blue after pollination enables insects to distinguish flowers to visit.





*Sieversia ciliata*

Diagram showing rate of changes in position of flowers.

Rosaceae

*Sieversia ciliata*.

Bud oblique, peduncle bending downward, July 5, 9.30 a.m. Sepals bending back. Stamens and styles equal in length, first day. Corolla mouth, hairy, opening second day, 1 p.m. Anthers and receptive stigmas grouped at corolla mouth. Corolla fully open third day, 8.30 a.m., anther dehiscence commencing. Pendant position of flower causes pollen to collect at corolla mouth, styles 2 mm. longer than stamens.

Fourth day, 9 a.m. declination of peduncle reached angle 40 degrees and begins to curve upward. Anthers half fallen fifth day. Sixth day, styles have become plumose and elongated 8 mm. in past four days. Peduncle makes angle 165 degrees eighth day. Plume of fruit spirally coiled and ready to disseminate ninth day.

Nectar secreted in numerous drops in receptacle.

*Bombus Edwardsii* lands on a flower, just opening. Second pair of legs rest on petals, hind legs in air, head and first pair of legs pushing into corolla tube, while

sucking nectar. Goes to all open flowers in cluster.

Halictus (sp.) lands at point of attachment of calyx lobes. Projects ligule 6 mm., explores between calyx and corolla for entrance and steals nectar.

*Drymocallis fissa.*

Buds and flowers in almost vertical position, turning toward sun. Stamens in three rows. As each row matures, filament is incurved so that anthers are above receptive stigmas while dehiscing, then bend away from stigmas. As petals drop off, calyx closes about ovary, to protect maturing fruit.

Half concealed nectar secreted only as a thin annular shining layer on inner wall of the receptacle and not forming actual drops.

*Potentilla pulcherrima*

Corolla expands horizontally in bright sunlight, but closes at night and on cloudy days. Corolla opening, stamens in three rows, two outer rows with long filaments, inner row with short ones, anthers not dehiscing, stigmas receptive, July 9, 9.30 a.m. Inner row of anthers dehiscing second day. Third day, petals fallen. Fourth day, sepals closed about few anthers still remaining, seeming to press pollen into stigmas. Protandry aids allogamy while anthers are covered by petals in half open flowers. Nectar formed in thin shiny layer at base of outer row of pistils and inner row of filaments, partly concealing it, except in bright light.

*Bombus proximus* lands on petal, then moves to center of flower where it tramps about collecting pollen on its legs and abdomen as in *Rubus*. From this flower to *Taraxacum*, another bee of same species. Goes to all open flowers on one plant, then to next plant of same species. *Campanula*, *geranium*, *galium*, *mertensia*, which are in the same vicinity are all passed over by this *Bombus*.

Edwinia americana.

Bud erect, petals loosening, stamens of uneven length, July 4, 6 a.m. Corolla fully open petals expanding in horizontal position, serve as attraction and landing platform for insects. Three stamens withered, stigmas receptive, projecting 5 mm. beyond anthers, first day, 2.30 p.m. Anthers mature separately, all but five anthers dehiscing then bending away from stigmas, second day. Petals withered, two styles close together, third one bending away, fourth day. Petals gone, fifth day.

27

*Prunus demissa*.

In bud, filaments so bent that anthers are under stigma. As bud opens, receptive stigma projects, petals covering stamens. In open flower, filaments elongate and straighten out in three sets, outer row first, each set bending above stigma at dehiscence, then away.

*Rubus deliciosus*

July 4, 6 a.m., sepals separating, petals unfolding. Second day, 2.30 p.m., corolla opening; expanding in vertical plane, small opening into corolla mouth. Third day, central stamens dehiscing. Fourth day, 10 a.m., corolla about half open. Petals of upper edge extended, those of lower edge slower to spread apart. Stamens at center withered, upper edge dehiscing, lower edge not dehiscing; 5 p.m. all but a few of shorter stamens withered, corolla half closed. Fifth day, 6 a.m., corolla wide open, withered stamens covering stigma. Seventh day, petals gone, sepals turned back tightly about pedicel, stamens withered and held tightly about styles, nectar secreted in circle around base of pistils.

Insect attraction, pleasant odor, conspicuous large white petals.

*Bombus proximus* revisits the same flower several times, other flowers in meantime. Buzzes as it alights and works. Since pollen is very abundant and ex-



posed, *Bombus* collects large pollen masses on its hind legs and body becomes well dusted. As *Bombus* tramps around, stigmas may receive pollen from under side of body or autogamy may result as the stamens are spread apart so that the stigmas come in contact with the anthers.

*Bombus flavifrons* tramps around among the anthers. Does not enter flowers with dried anthers.

*Vespa germanica* pushes head among stigmas, sucking nectar from various positions. Goes to flowers in which stamens are quite dry.

Rubus strigosus.

Petals small, inconspicuous because of erect position. Stamens maturing by rows, bending inward above styles at dehiscence, then outward.

Honey secreted by fleshy ring upon border of receptacular tube, internal to attachment of stamens.

Visitors alight in center of flower, mouth parts become dusted with pollen as proboscis extends for nectar, anthers and stigmas are brushed against one another at same time.

*Rosa Engelmannii*

Bud erect, petals loosening, stamens grouped at center, July 4, 6 a.m. Corolla expanded, plane turning to sun, petals not entirely folded back, stigmas receptive, stamens dehiscing and spreading away from pistils, 1 p.m., first day. The oblique position of the open flower places the anthers in such a position that pollen may fall on receptive stigmas. Two petals gone, filaments inflexed placing anthers above stigmas, eight anthers gone, second day. Three petals gone, two remaining curved over stamens to protect from rain, third day.

*Bombus Edwardsii* tramps about among the stamens as in *Rubus*. *Bombus* goes from *Rosato Rosa* or *Rosa* to *Rubus*. If stamens and pistils are covered by unfolding petals, *Bombus* goes on to open flower without stopping.

A *Bombus flavifrons* tried to enter a half open flower. Landed on lower petal, then tried to push its head into flower. Made several unsuccessful attempts.

*Fragaria americana.*

Bracts half spread out, sepals separating from petals at 11 a.m., June 20. Corolla fully open, stamens in three rows of five each, filaments of various rows different lengths first day, 11 a.m. Stigmas receptive second day. Anthers dehiscing, two petals withering third day. Petals gone, stamens withered, fourth day.

Nectar secreted by narrow fleshy ring at base of receptacular tube, sheltered between stamens and outer carpels.

Horizontal corolla, convenient landing place for insects. Different rows of stamens make it almost impossible to secure nectar without distributing pollen.

Saxifragaceae

*Ribes lacustre*.

Calyx beginning to open 9 a.m. June 20. Calyx opening, anthers visible, filaments inflexed crowded about stigmas first day. Anthers maturing separately, second day. Two dehiscent anthers bending outward, away from mature stigma, which is on level with anthers, third day. Sepals withering, fourth day. Autogamy easily possible because of proximity of parts, especially in flowers in horizontal position.

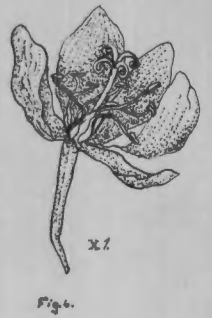
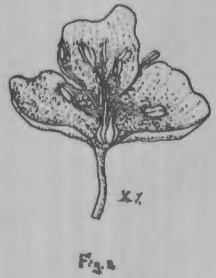
*Heuchera Hallii*

Bud erect, starting to hang down, June 21.

Reaching the horizontal and opening, receptive stigmas close together dusted with orange pollen from the one mature anther, showing at corolla mouth, first day.

Petals straight out, corolla pointing somewhat downward, three anthers mature, second day. Petals recurved, stigmas separating, outcurved, anthers withered, third day.

Many small, black, pointed-bodied beetles collect pollen on antennae and rub against the pistils while eating pollen. Beetles only visitors observed.



*Chamaenerion angustifolium*

- Fig. I - Unopen bud - stamens and style equal in length - style straight.
- Fig. II - Open flower - style beginning to bend down - stamens somewhat spreading.
- Fig. III - Style decurved between sepal and petal - anthers dehiscing.
- Fig. IV - Flowering stem showing changes in position from bud to mature flower.
- Fig. V - Style ascending - stylar branches recurving - stamens spreading.
- Fig. IV - Style erect - stylar branches much recurved.



Onagraceae

*Chamaenerion augustifolium*.

Flowers conspicuous because of tall magenta racemes. Bud pendant but pointing angle 45 degrees upward, style straight, equal in length to stamens, July 28. Upper petals opening, lower three sepals held together at tip including lower petals, style bending downward, stigmas close together, first day. Corolla expanded, style bent down between lower petal and sepal, angle 160 degrees, stylar branches recurving, stamens of two lengths, four longer filaments curving somewhat outward, shorter filaments more nearly erect, one anther mature, second day.

Style parallel to petals, stigmas widely recurved, filaments diverging, four anthers mature, third day.

Style elongated, erect, stylar branches much enlarged, recurved, all anthers mature, fourth day.

The concealed nectar secreted by upper surface of ovary about base of style, filaments form protective ring above nectar. Hairs at top of ring prevent entrance of water, but allow insects to reach nectar. In first stage, insects alighting on central part of flower touch

36

only dehiscing stamens. On older flowers the stylar branches form the alighting place.

Pollen is green, making it conspicuous and held together by viscin threads.

*Bombus Edwardsii* stands on erect style and pushes ligule into cone, formed from base of stamens, and secures nectar, goes only to flowers with recurved stylar branches.



Fig. I.

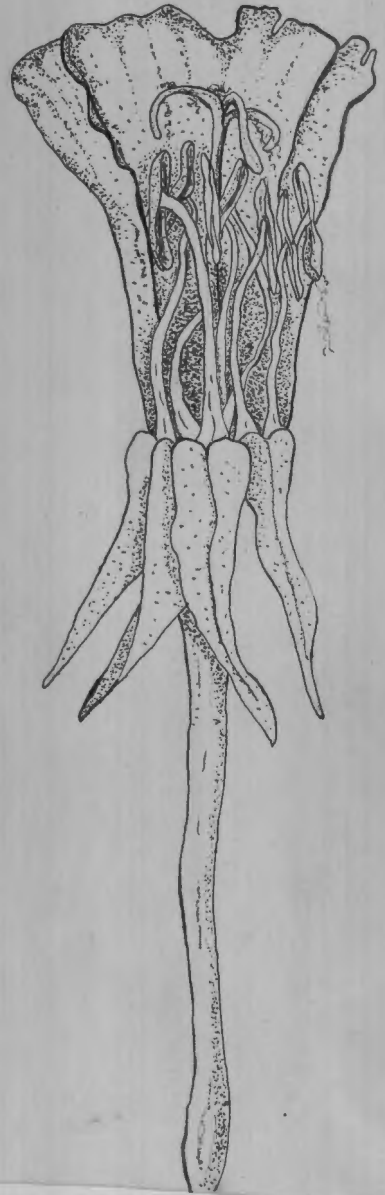


Fig. II.

*Pachylophus speciosa*

Fig. I. - Flower just open - Stylar  
branches opposed.

Fig. II. - Anthers dehiscing - Stylar  
branches recurved - Stigma  
receptive.

*Pachylophus speciosa*.

Flowers solitary. Calyx tube 9 - 10 cm. long extending beyond the ovary. Petals white, turning rose colored the second day, attached to calyx at the point where sepals separate. Stamens attached where petals join calyx. Anthers grouped closely about style in young flowers. Style 13-14 cm. long to branches. Styler branches opposed, closely held together, first day. Anthers dehisce at anthesis, pollen grains held together by threads of viscin. The second day when dehiscence is nearly over the style bends downward and the styler branches separate exposing stigmatic surfaces. Styler branches are so long that some of them come in contact with anthers making autogamy possible, if insects have not produced allogamy. The extremely long calyx tube with nectar secreted at the base limits the visitors to those insects with very long suctorial discs as moths or <sup>to</sup> humming birds.

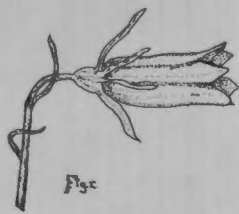
Asteraceae

*Helianthus petiolaris*.

Flowers form head, ray flowers neuter, central disc flowers mature first, later those at edge.

Stamens form cylindrical collar about style, stigmas opposed in young flowers, later diverging widely. As styles, which are covered with bristles, elongate, they collect pollen from inner sides of anthers.

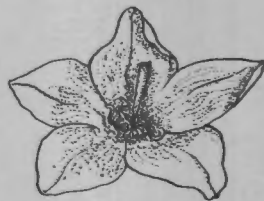
Insects landing on flower disc collect pollen on bodies from stylar bristles. Pollen from insect brushed onto stigmatic surface.



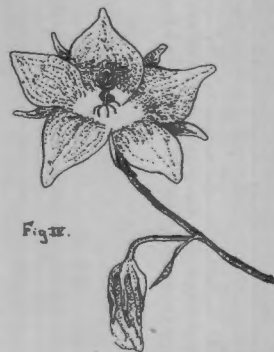
Figc



Figz.



Figze



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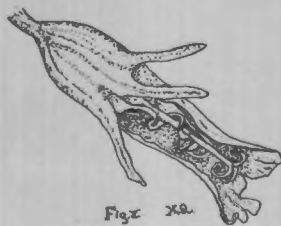


Figze.

X1



Figze.



Figze Xa.

*Campanula rotundifolia*

Fig. I - Opening bud in lateral position

Fig. II, Fig. III, - Anthers dehiscing and spread apart. Stylar branches opposed.

Fig. IV, Fig. V, - Receptive stigma exposed on recurved stylar branches. Anthers dried about style.

Fig. VI - Corolla dried tightly about style.

Fig. VII - Group of flowers showing changes of position.

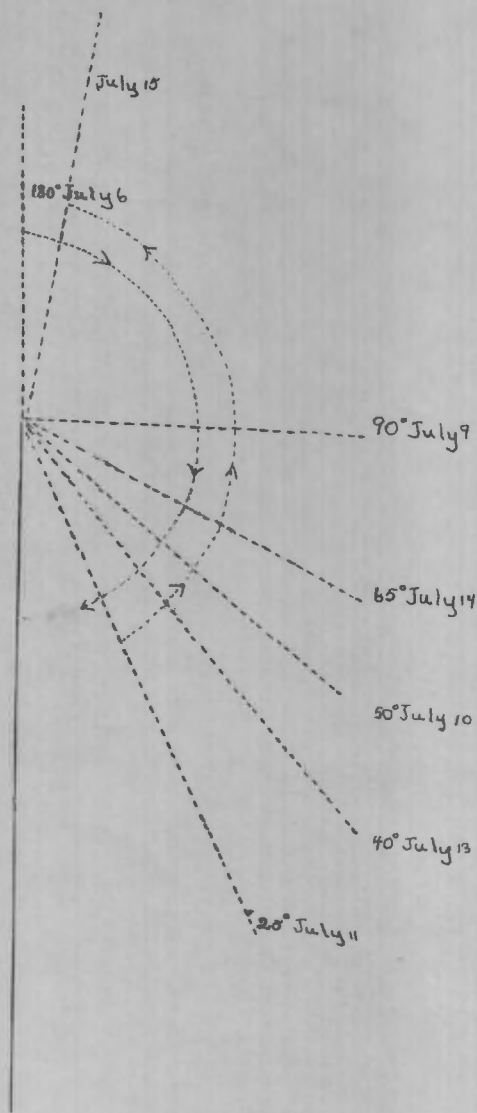


## Campanulaceae

### *Campanula rotundifolia*.

Corolla blue, campanulate, attractive. Bud pointing upward, making angle 50 degrees with pedicel, five stamens forming sheath about style, styles forming cylindrical column closely covered with hairs, July 26. Bending down, reaching angle 150 degrees, corolla open, anthers dehiscing introrsely, stamen sheath splitting, styler branches opposed first day. Style elongating, styler branches diverging widely, gray pollen collecting on styler brush, second day. Autogamy may now occur by contact of stigma with decurved styler brush, if allogamy has not taken place. Corolla withering, dried filaments, coiled about base of style, third day. Corolla dried tightly about style, aiding contact between stigma and styler brush, fifty day. Honey secreted and born by yellow epigynous disk, surrounding base of style.

*Megachile wootoni* lands on petal, sways flower stem and shakes pollen onto its body as it works. *Bombus Edwardsii* pushes head down to nectary while abdomen is in contact with stigma, producing allogamy.



### Dodocatheon Meadia

Diagram showing rate of changes in positions of flower.

40  
Primulaceae

*Dodocatheon Meadii*

Bud erect July 6. Starting to hang down reaching the horizontal third day, angle 25 degrees fifth day. Flower ascending angle 35 degrees, upper petal perpendicular to bud slightly exposing anther. Anthers flat, elongated, triangular, grouped closely about style sixth day. Petals all turned back, pistil projecting 2 mm. anthers dehiscing seventh day. Petals twisting transversely, stigma receptive eighth day. Flower angle 90 degrees anthers separating ninth day. Petals fading, stamens diverging, flower almost vertical tenth day. Petals gone, fruit erect eleventh day.

Nectar hidden at base of inner surface of anthers. Upward inclination of peduncle places stigma in position to receive pollen falling from anthers above.

Insects dislodge stamen and push proboscis between style and anther to reach nectar, thus covering mouth parts with pollen.

*Bombus Edwardsii* lands on pistil and stamens,

head up. Rubs lower edge of anther vigorously with hind legs as it sucks nectar.

*Bombus flavifrons* rests on anthers, collects pollen with front and hind legs, abdomen bent about stigma.

Asclepiadaceae

*Asclepias speciosa*

Flowers in spherical umbel. As fruit begins to develop, flowers hang downward. Sweet honey odor, attraction. Only few flowers produce fruit. Petals folded along edges over stamens.

*Apis mellifica* stands with body across central anther disk, dipping ligule into nectar at base of each of petals. Occasionally the humble bee stops at only three or four of petals for nectar. Sometimes instead of reaching across anther disc, it stands on one petal and secures nectar from adjoining nectary. In reaching for nectar, hind legs which are flattened, catch in stamen slit. In trying to free itself, the bee pulls and buzzes until claw withdraws pollonia with it.



Fig. 1 X20.



Fig. 2 X22.



Fig. 3 X21.

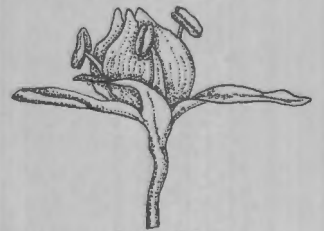


Fig. 4 X21.



Fig. 5.



Fig. 6.

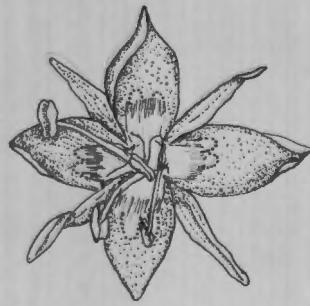


Fig. 7.



Fig. 8.

*Frasera speciosa*

- Fig. I - Unopen bud - Petals removed.
- Fig. II - Flower just open
- Fig. III - Stamens oblique, bending away from styles.
- Fig. V - Corolla closed as at night
- Fig. VI - Corolla and filaments withered.
- Fig. VII - View of corolla from above.
- Fig. VIII - Petals closed pressing stamens against  
pistils.

Gentianaceae

*Frasera speciosa*.

Flowers on tall, loosely flowered, pyramidal panicle, conspicuous because of its height.

Color, greenish yellow, marked with small, brown, purple dots. Four petals form flat expanded disc which is landing platform for visitors. Fringed glandular spot on each lobe of corolla, serves as protection for nectar. Anthers versatile, pointing toward ovary in young flowers. At dehiscence they balance on the other side and point away from the stigma. Mature filaments bend away from stigma.

Anthers dehisce separately. As anthers wither, the protective sheath over the nectar gland hairs, rolls back.

Corolla closes at night and anthers protrude at corners. Corolla closes about maturing fruit.

*Bombus bifarius* stands on nectar hairs, sucks nectar, then flies away, rubbing against stigma as it passes, and pollinating it.



### *Gentiana Parryi*

In bud, style bent, 3 mm. shorter than stamens. Anthers grouped closely together above stigma.

At dehiscence, anthers spread apart from style, filaments becoming vertical, anthers balancing at tip. When anthers are nearly thru dehiscing, style straightens, pushes its way between anther tips and projects beyond them. Two stigmas then separate, exposing the stigmatic surfaces.

*Bombus Nevadens* and *Bombus juxtus* go head first into corolla, extract nectar from each nectary. While doing this, the outer edge of stamens and tip of under part of abdomen, rub stigmas of older flowers. In younger flowers, where stamens are longest, anthers brush against under side of abdomen. The *Bombus* turns around in the corolla and leaves the flower head first i.e. comes out of bell shaped corolla head first even though head is down while getting nectar.

*Bombus juxtus* goes to buds just beginning to loosen at corolla mouth, but does not succeed in entering. Flowers with withering corollas, nearly closed are entered. Buds open 2-3 mm. at corolla mouth, *Bombus juxtus* can open

them enough to enter and find nectar. Dips into each nectary in each flower. Goes from flower to flower in a cluster. One *Bombus juxtus* observed went from *Gentiana Parry* to *Campanula* near by.

During an hours observation *Bombus juxtus* was the only visitor.



Fig. 1.



Fig. 2.



Fig. 3.



Fig. 4.



Fig. 5.

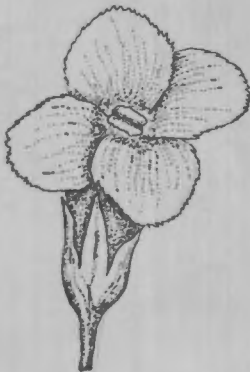


Fig. 6.



Fig. 7.

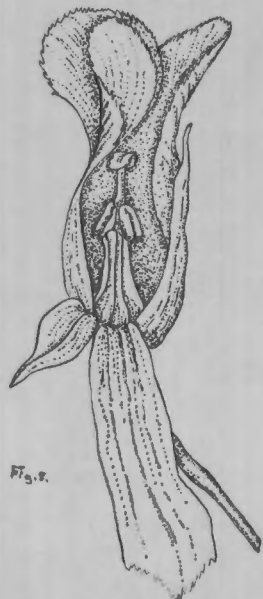


Fig. 8.

*Gentiana elegans*

- Fig. I - External view of bud
- Fig. II - Petals torn away to show position of stamens in unopen bud. Bud green.
- Fig. III - Tip of bud blue, but still tightly closed - anthers straight - stigmatic lobes spreading.
- Fig. IV - External view closed flower.
- Fig. V - Internal view of Fig. IV.
- Fig. VI - Top view of flower showing exposed stigmatic lobes at corolla mouth.
- Fig. VII - Longi view of Fig. VI - stamens spreading somewhat.
- Fig. VIII - Longi view - stamens grouped closely about style.

*Gentiana elegans.*

Bright blue color attracts insects, pale yellow stigma and flower center direct insects to nectary.

In unopen buds, stamens are 1/2 - 1/3 length of pistil, anthers pointed inward.

Stigmatic surface, is two lobed, somewhat fringed and flattened. When fringed corolla limb first expands, receptive stigma fills opening into corolla tube. As anthers mature, they point away from stigma.

Insects to reach nectar secreted at base of the filaments, must push stigma aside and reach down to nectaries. In so doing, pollen is rubbed on to the stigma and the bee from the anthers.

*Gentiana affinis.*

Flowers, pale lavender, borne on short peduncles arising from main axis of inflorescence.

Corolla tube long, equal width thruout its length. Anthers exposed at corolla mouth at dehiscence, mature anthers pointing away from stigmas. Fringe of hairs at corolla mouth where limb bends outward, acts as distributing agent for pollen, rubbing it off from insect, and then when hairs shrivel, coming in contact with stigma. Insects cannot reach nectar without rubbing against the anthers.



Fig. 1



Fig. 2



Fig. 3



Fig. 4

*Gentiana frigida*

- Fig. I - Open flower
- Fig. II - Open flower - corolla opened to show position of stamens - stylar branches opposed.
- Fig. III - Corolla opened to show stamens dehiscing - stylar lobes spreading apart.
- Fig. IV - Corolla withering, beginning to close - stylar branches recurved.



*Gentiana frigida.*

Flower bell shaped, pale green in color, with dark purple spots and lines. Grows close to ground in rocky places at about 12,000 feet elevation and is conspicuous because other forms of vegetation are not crowded closely about it.

Stamens much shorter than pistils. Anthers opposed and curve outward instead of simply separating as in other described gentiana.

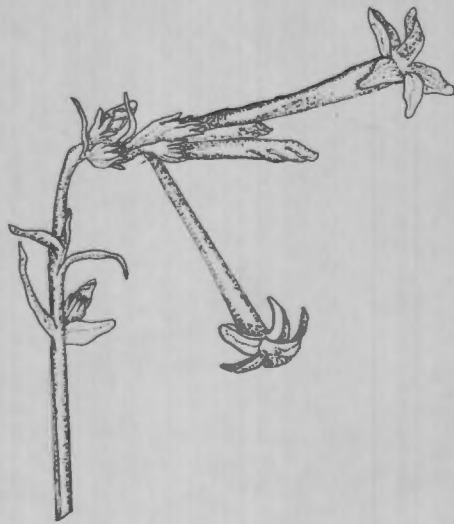


Fig. 1



Fig. 2



Fig. 3



Fig. 4

*Gilia aggregata.*

- Fig. I - Flowering stem showing changes of position of flowers.
- Fig. II - Unopen bud - style extending to anthers.
- Fig. III - Corolla elongated - anthers beyond style.
- Fig. IV - Corolla descending in oblique position - style elongated, stylar branches opposed - anthers dehiscing.

Polemoniaceae

*Gilia aggregata*.

Bud erect, making angle 30 degrees with vertical  
July 26. Corolla tube horizontal, deep pink colored,  
opening at tip, dehiscing anthers projecting from sides of  
corolla tube toward center, style only half as long as  
corolla tube, stigmas closely held together at tip, first  
day.

Corolla descending, oblique, petals inflexed  
toward midrib, style extending almost to dehiscing anthers,  
second day.

Style reaching to corolla mouth, stylar branches  
curved outward exposing stigmatic surface, pollen nearly  
gone, third day. Corolla falling off fourth day.

When the stigmatic surface is exposed, the pendant  
position of the corolla allows some pollen to reach stigma.  
Corolla in falling off carries dried anthers with it and some  
pollen may rub against stigma.

Hydrophyllaceae

Phacelia heterophylla.

Corolla, pale bluish lavender color, campanulate in form. Calyx densely covered with white hairs, giving it a fuzzy appearance, which together with the close grouping of flowers in scorpioid cyme makes it conspicuous.

Hairy corolla and stem prevent undesirable creeping insects from ascending.

Filaments coiled and anthers bend inward, stylar branches bend down and outward in bud. At anthesis, filaments straighten and extend anthers vertically 4-5 mm. beyond corolla mouth. Anthers mature separately, filaments bending outward as they wither. In young flower, style extends just beyond corolla and stylar branches are bent at right angles to filaments. Stylar branches then take vertical position. "Style has terminal stigmas which are receptive thru the flowering stage, but are better developed in the later stage".

In the young stage the insect entering the flower from above brushes against the anthers, but the stigmatic surface is bent away and will only be touched by insects

entering from the side.

In the second stage, the straightened stylar branches are elongated and almost in contact with the anthers so that insects may produce autogamy or it may take place by pollen falling on the stigma.



Fig. 1. X2.



Fig. 2. X2.

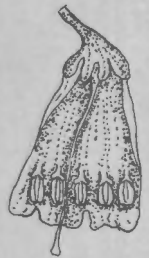


Fig. 3. X2.



Fig. 4. X2.



Fig. 5. X2.



Fig. 6. X2.

*Mertensia pratensis*

Fig. I - Unopen bud - part of corolla cut off

Fig. II - III - Unopen bud - corolla split and  
flattened out to show stages in  
elongation of style.

Fig. IV - Open flower - part of corolla cut off.

Fig. V - Fruit - corolla just dropped off.

Fig. IV - Corolla dried about style.



Boraginaceae

*Mertensia pratensis*.

Flowers formed in loose, short panicles. Pinkish flowers become light blue as they open.

Bud pendant, style shorter than anthers July 5. Corolla open, style receptive, 2.5 mm. longer than stamens, reaching to corolla mouth, stamens grouped closely about style, first day. Stamens dehiscent, spreading away from style, second day. Corolla gone, third day.

The nectar glands are alternate with the carpels.

Corolla dries about stigma and in falling off anthers rub against stigma making autogamy possible.

*Bombus Edwardsii* enters flower, resting on lower lobe of corolla, while its head is in the tube and proboscis sucking nectar. Stigma comes in contact with abdomen by pollen collected there. Head parts brush against dehiscent anthers and collect pollen.

Scrophulariaceae.

*Pentstemon unilateralis.*

At anthesis stigma lies in ridge between two upper petals, is straight and slightly shorter than longer stamens. Stigma elongates and bends downward when outer pair stamens mature. Staminode covered for greater part of its length, with long rather stiff hairs.

As mustidae (sp.) enters flower, pollen is rubbed from under side of its body onto staminode. Pollen collected from staminode as it leaves flower. Weight of insect in leaving flower pushes style down and stigma comes in contact with pollen from previous flowers on dorsal surface of Bombus. Four anthers pushed down by staminode fit dorsal surface of Bombus closely. Autogamy may take place as withered corolla with attached stamens drops off.

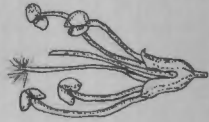


Fig. 1



Fig. 2



Fig. 3

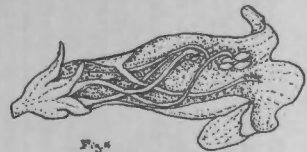


Fig. 4

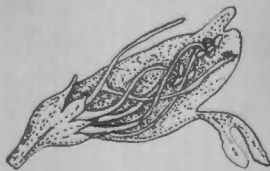


Fig. 5



Fig. 6

*Pentstemon humilis.*

- Fig. I    — Dorsal view., stamens not dehiscing.  
Fig. II   -- Dorsal view, two anthers dehiscing,  
          grouped about style.

*Pentstemon secundiflorus,*

- Fig. III   -- Bud / .  
Fig. IV    -- Style tip pointing down among anthers.  
Fig. V     -- Tip of style straight / .  
Fig. VI    -- Corolla gone .

*Pentstemon humilis*.

Staminode tip covered with long hairs. Shorter hairs cover the surface for a short distance from the tip.

Behavior of reproductive parts same as in *Pentstemon unilateralis*, except that staminode rolls under at tip, when all anthers have dehisced. This places hairs from staminode, which have received pollen from bodies of visitors in contact with style and insures pollination.



Fig. 1.



Fig. 2.



Fig. 3.



Fig. 4.



Fig. 5.

Pentstemon glaucus.

Fig. I \_ External view. Staminode at corolla mouth.

Fig. II \_ Portion of corolla removed, showing staminode.

Fig. III \_

Pentstemon glaber.

Fig. III \_ Newly opened flower. Staminode tip slightl  
coiled.

Fig. IV \_ Staminode as seen from above.

Fig. V \_ Withered flower. Staminode tip coiled so  
that hairs come in contact with stigma.

*Pentstemon glaucus*..

Staminode slightly hairy at tip and although straight when young, bends downward when older. Corolla tube expands at mouth much less than in other forms. Very distinct, purple and white or dark violet and white lines extend lengthwise on corolla. Stripes on lower lip, together with hairs 2.5 mm. long serve as nectar guides.

Young buds point upward, as flowers open, they take horizontal position and then hang downward. At dehiscence of the second pair of anthers, first pair crowd closely about stigma.

*Bombus Edwardsii* lands on lower corolla lobe and following guide lines, walks in - goes into flower just far enough for pollen loads on hind legs to be visible at edge of upper corolla lip. *Bombus* buzzes as it flies from flower to flower.

One *Bombus Edwardsii* found bud not quite open at corolla mouth. Tried to turn around and walk in upside down but without success.

*Bombus proximus* enters all flowers by landing on top of upper corolla lobes, then around the tip and walks

incomplete



*Pentstemon secundiflorus.*

Flowers large, conspicuous and bright blue. Tip of staminode slightly spatulate, has but few hairs and these very short. Hairs 2 mm. long on lower part of corolla where limb expands. Filaments slightly hairy on lower surface.

Bud opening, long stamens beginning to dehisce, style straight at tip, July 6. Corolla open, anthers nearly thru dehiscing, tip of style with receptive stigma bent sharply downward, staminode rolling under at tip, first day. Corolla withered second day. Corolla gone third day.

*Bombus proximus* lands on lower lip of corolla, then turns around and onto upper lip, standing there upside down while working. The *Bombus* works from open flower to open flower in a cluster, then flies to next cluster.

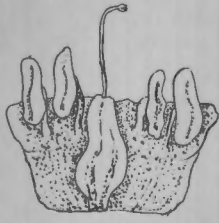
*Vespa germanica* stands on lower lobe of corolla and pushes its head far into the flower to the nectar. Standing on lower petal, it transfers pollen collected by head parts, onto its hind legs, with front legs. After visiting numerous flowers, it rests on the ground, then to more flowers.

*Pentstemon glaber*.

Large brightly colored flower. Staminode broadly spatulate, covered for nearly half its length with long hairs, in two rows, with path between. Young stigma straight, extending to just behind front pair of anthers. Later stigma elongates and bends downward, almost touching the staminode. In older flower, staminode coils inward coming in contact with stigmatic surface.

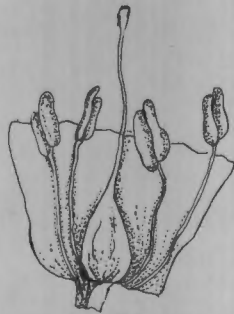
*Bombus Edwardsii* enters flower, guided to staminode by corolla hairs, and to nectar guided by line, between two rows of hairs on staminode.

*Bombus proximus* lands on lower lip of corolla, climbs over upper lip and onto the outside of the tube. A lengthwise depression on this upper side of the corolla tube directs the bee to the nectar end. It then extends its ligule and pierces a hole in the corolla tube where it joins the calyx and sucks nectar thru this. Many flowers were pierced in more than one point. Perhaps all the nectar was not accessible from one point.



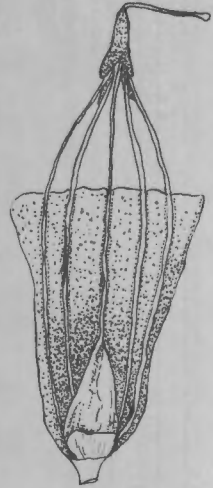
X2

Fig. I



X2

Fig. II



X2

Fig. III.



Fig. IV



Fig. V



Fig. VI

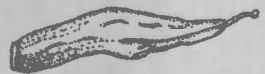


Fig. VII.

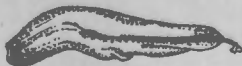


Fig. VIII.

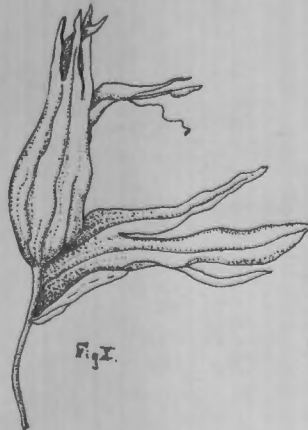


Fig. IX.

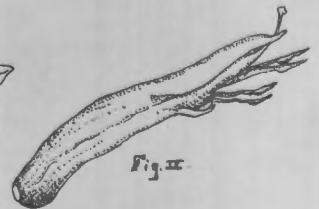


Fig. X.

*Castelleia miniata*

- Fig. I - Unopen bud. Corolla spread out to show short filaments.
- Fig. II - Corolla flattened to show relation of stamens and pistil. Style straight.
- Fig. III - Style tip bent at right angle. Stamens of two lengths. Anthers on shorter filaments crowded into anthers on longer filaments.
- Fig. IV - IX - Stages in development of flower, showing changes in position of style tip.
- Fig. X - Flower drying. Dehiscing and dried anther projecting at the side. Corolla split.

*Castelleia miniata.*

Flowers showy, because of scarlet bracts which surround flower. These with the reddish calyx serve as insect attractions. Calyx slender and tubular in shape, completely enveloping the corolla. Calyx cleft almost half its length and two small lobes on lower edge serve as an alighting place for insects. Nectar flows from nectary to these small calyx lobes, is exposed there and attracts visitors to that part of the flower. As insects alight on these projections or the humming birds bill is inserted, the upper calyx and corolla lobes spread apart laterally, exposing the anthers.

Bud 2.3 cm. long unopen, filaments short as anthers, style straight, extending to calyx tips July 7. Flower 3.5 cm. long, stigma projecting 2 mm. beyond tip of calyx, 2 anthers mature, style straight, first day. Flowers 3.7 cm. long, anthers all dehiscing, sepals spreading apart exposing to view small lip of corolla, style bending down angle 90 degrees at tip, second day. Style straight, third day. Style bending upward, anthers projecting beyond calyx, sepals more widely spread at lower edge, fourth day.

*Pedicularis canadensis.*

Corolla tubular, two lipped, upper lip forming a laterally flattened hood, lower lip being three lobed and spreading. Stamens in pairs, anthers edges so close together that they appear united. Longer filaments hairy near upper end and place their anthers directly in front of shorter stamens. Style formed in lateral ridge of the hood, bends sharply down at tip extending the knob shaped stigma beyond the corolla. Honey secreted by the green fleshy base of the ovary and lies at bottom of tube. Lower lip of corolla bent obliquely to left, making right edge lower than left.

*Bombus Edwardsii* enters flower from right and lands on lower lip, which is probably cause of oblique position of lower lip. As *Bombus Edwardsii* pushes its head into corolla tube, back of its head touches stigma. As it goes farther into the corolla, the sides of the hood are pushed apart, releasing the stamens, so that anthers come in contact with bombus head. Hairs on the longer filaments, below the dehiscing anthers collect pollen that does not fall on the bombus and it is brushed onto the next

Bombus as it enters.

Bombus proximus enters corolla from the side, abdomen bent at the place where the upper and lower corolla lobes meet, so that hind legs rest on outside of corolla tube, while head is obliquely directed toward nectar on inside. Corolla dries in place about the flower parts making contact between stigma and anthers.

Lamiaceae

*Scutellaria resinosa*.

Corolla tubular, divided into an upper and lower lip. Upper lip hood shaped, edged by three scallops and has two longitudinal depressions.

Bud horizontal July 25. Hood ascending to a vertical position, lower lip spread sharply downward forming a convex upper surface, the two long stamens projecting beyond the corolla mouth, stigma tip curved downward angle 90 degrees, 3.5 mm. shorter than long stamens, first day. Corolla vertical, filaments arching in 2 longest stamens anthers dehiscing, two younger stamens straight and reaching to corolla tip. Tip of receptive stigma slightly bent forward and placed between stamens, second day. Two anthers gone, 2 dehiscing, style bent angle 90 degrees third day.

Insect lands on lower lip of corolla, guided to nectar by whitish color at petal center. As it pushes its head into the corolla throat, the anthers and stigma are pushed downward and rub against the dorsal surface of the *Bombus*. Since the stigma is receptive, this may either produce autogamy or allogamy.





Fig. 1 X2



Fig. 2 X2



Fig. 3 X2



Fig. 4 X2

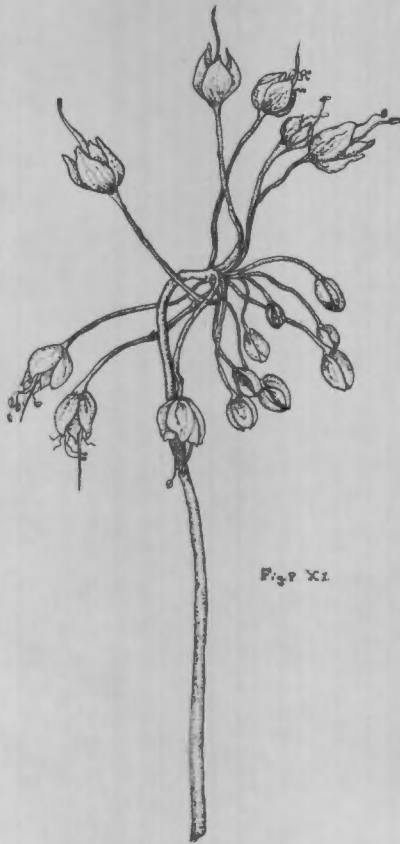


Fig. 8 X1



Fig. 5 X2

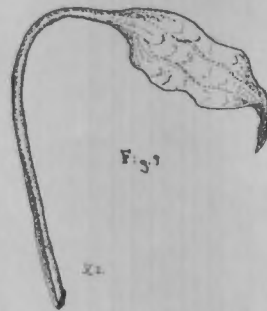


Fig. 9

X1



Fig. 6 X2



Fig. 7 X2

*Allium recurvatum.*

Fig. I -Unopen bud.

Fig. II -One stamen visible.

Fig. III -One filament elongated.

Fig. IV- Second and third stamens visible.

Fig. V -Style visible at corolla tip.

Fig. VI -Two anthers dry remaining anthers dry,  
remaining anthers visible.

Fig. VII -Style projecting beyond dried anthers.

Fig. VIII -Umbel showing changes in position of flowers

Liliaceae

*Allium recurvatum*.

Flowers with long pedicels forming an umbel.

Bud pendant, style three fourths as long as stamens July 27. Corolla open, 3 anthers projecting beyond the corolla, 2 dehiscent, three anthers and style not visible at the corolla mouth first day. Pedicel ascending, two anthers gone, two stamens with straight filaments and dehiscent anthers, one stamen reaching corolla tip, one not visible. Style extending 1 mm. beyond the corolla, the second day. Corolla mouth horizontal, filament outcurved, pollen nearly gone in 2 anthers, filament straight, anther dehiscent in 2 stamens, style projecting 4 mm. receptive, third day.

Corolla mouth vertical, anthers all gone, style projecting 5 mm. fourth day. Corolla mouth closed, style tip curving forward angle 30 degrees fifth day.

The honey is secreted by the ovary in the three notches between the carpels and fills the space between these notches and the bases of the three inner stamens. The petals have a lengthwise ridge which serves as a nectar guide. When the corolla reaches the upward oblique

position autogamy may take place, before this the protandry indicates an adaptation for allogamy.

*Bombus Edwardsii* hangs downward, with its front feet on the edge of the petals while getting nectar. The hind feet are on the filaments and styles in such a position that the anthers rub against the tip of the abdomen in young flowers or stigma in older ones.

*Vagnera stellata.*

Flowers grouped on upper surface of a horizontal drooping raceme. Bud opening June 20. Calyx and corolla half open, style and stamens of equal length, stigma receptive, one anther dehiscing, first day. Corolla open, three anthers of outer row dehiscing second day. All anthers of outer row, two of inner row mature third day. Calyx, corolla, style, stigma, withered sixth day.

Since this flower has few and simple parts, nectar and pollen are exposed, it is accessible to all kinds of insects.

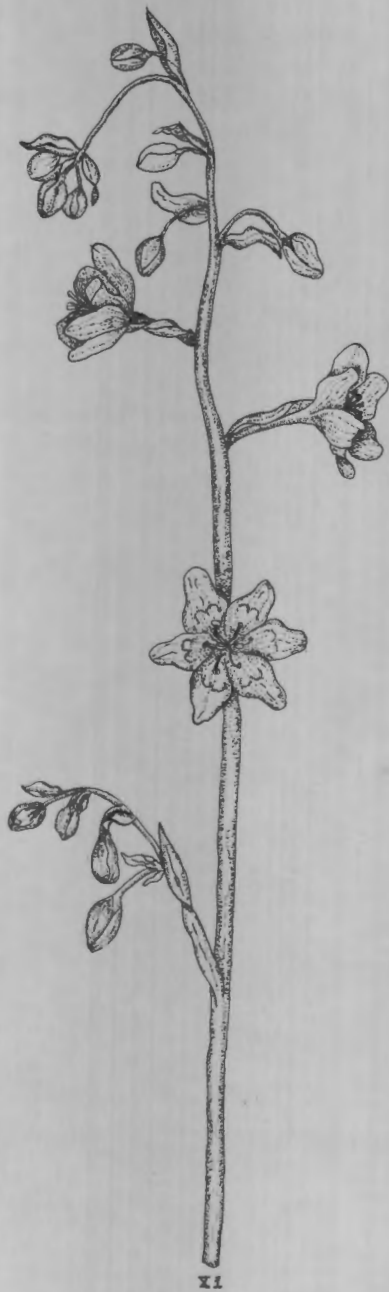


Fig. III.

*Zygadenus elegans*

- Fig. I - Styles and anthers grouped closely together at center.
- Fig. II - Three anthers mature - bending away from styles. Three immature anthers grouped at flower center.
- Fig. III - Flower stem showing changes of position during development.
- Fig. IV - All anthers bending away from styles
- Fig. V - Anthers dried. Mature styles curved outward.

*Zygadenus elegans.*

Buds point slightly below the horizontal, but at anthesis, flowers point somewhat obliquely upward. Floral envelopes greenish white, pair of glandular spots at the center of each sepal and petal. Immature anthers grouped closely about stigmas. At dehiscence, filaments curve outward consecutively, from the flower center. Later the styles curve outward and drying stamens group closely about them making autogamy possible.



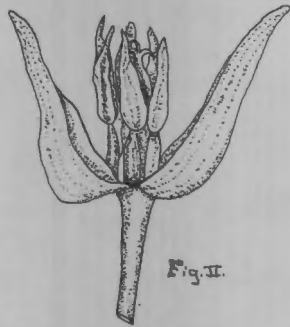


Fig. II.

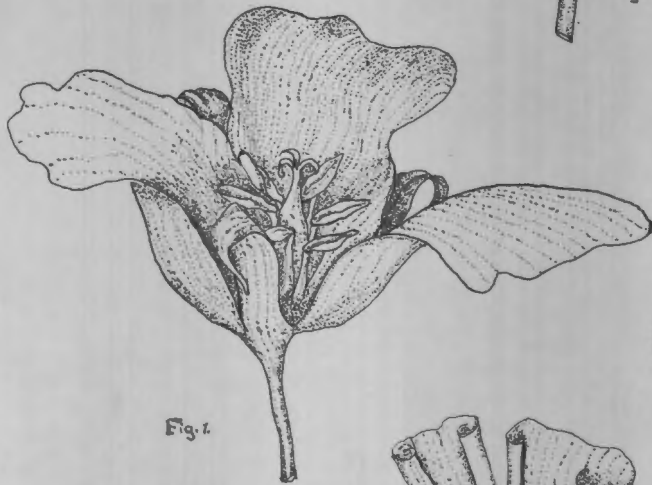


Fig. I.

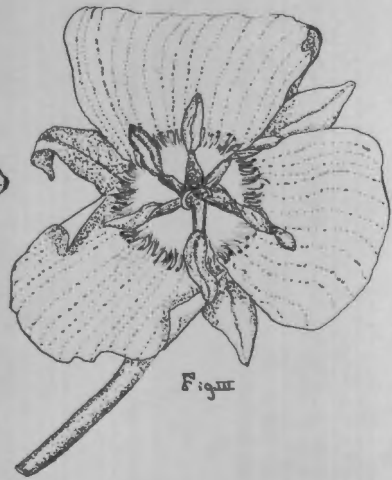


Fig. III.

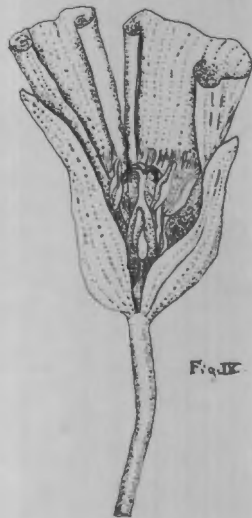


Fig. IV.

*Calochortus Gunnisonii*

- Fig. I - Newly open flower. Anthers horizontal, filaments bending away from stigma.
- Fig. II - Unopen bud. Anthers vertical.
- Fig. III - Stamens spreading, anthers twisted spirally.
- Fig. IV - Withering flower. Petal edges rolled inward. Stamens vertical. Anthers in contact with recurved stigmas.

*Calochortus Gunnisoni*.

Flowers solitary, large and showy. Corolla, delicate lilac color, shallow, spreading and campanulate form. At point where petals bend outward, there is a band of very dark blue extending around the corolla. Hairs 1-2 mm. long, knobbed at the top and producing a sticky secretion are found at the lower edge of the dark band.

When the flower opens, the three styles diverge, exposing the stigmatic surfaces. Anthers vertical and grouped closely about the stigmas. Filaments attached at the inner end of the anthers, diverge at dehiscence, soon after anthesis. Filaments are broad and flat, and together with the anthers twine spirally, horizontally as the anthers dry. The horizontal position of the dehiscing stamens places the pollen some distance from the stigmatic surface and pollen visitors will touch anthers and stigmas at separate times. The hairs in the corolla base become dusted with pollen as insects move from anther to anther.

Petals inflexed horizontally at each edge as they wither and hairs of the corolla which have received pollen from these anthers or insects bodies, come in contact with the stigmatic surface.

TABLE SHOWING MATURITY OF ANTHERS AND STIGMAS.

<u>Protandrous</u>	<u>Protogynous</u>	<u>Homogamous</u>
Aquilegia coerulea	Castelleia confusa	
Allium recurvatum	Calochortus gunnisonii	Clematis alpina
Capnoides aureum	Dodocatheon Meadia	
Cleome serrulata	Drymochollis fissa	Heuchera Hallii
Chamaenerion augustifolia	Edwinia americana	Scutellaria resinosa **
Campanula rotundifolia	Fragaria americana	Sieversia ciliata
Frasera speciosa	Gentiana elgans	
Geranium Fremontii	Gentiana frigida	
Gentiana Parryi	Helianthus petiolaris	
Gentiana affinis	Mertensia pratensis	
Gilia aggregata	Pedicularis canadensis	
Lupinus luteus	Potentilla pulcherrima	
Pachylophus hirsutus	Prunus demissa	
Petalostemon candidus	Quincula lobata	
Pentstemon unilateralis	Rubus deliciosus*	
Pentstemon humilis	Rubus strigosus	

\* slightly  
 \*\* perhaps protandrous

TABLE SHOWING MATURITY OF ANTHERS  
AND STIGMAS (continued)

<u>Protandrous</u>	<u>Protogynous</u>	<u>Homogamous</u>
Pentstemon glaucus	Rosa Engelmannii	
Pentstemon glaber	Wagnera stellata	
Pentstemon secundi- florus		
Phacelia heterophylla		
Ribes lacustre		

TIME OF VISITS.

	<u>heads</u>	<u>seconds</u>	<u>heads</u>	<u>seconds</u>
<i>Petalostemum candidus</i>				
<i>Apis mellifica</i>	12	70	1	5.8
	17	80	1	4.7
<i>Potentilla pulcherrima</i>	<u>Flowers</u>		<u>Flowers</u>	
<i>Bombus proximus</i>	23	90	1	4
	20	70	1	3.5
<i>Rubus deliciosus</i>				
<i>Bombus proximus</i>	38	35	1	1
<i>Rubus strigosus</i>				
<i>Bombus proximus</i>	10	70	1	7
<i>Bombus Edwardsii</i>	8	60	1	7.5
<i>Rosa Engelmannii</i>				
<i>Bombus Edwardsii</i>	5	20	1	4
<i>Campanula rotundifolia</i>				
<i>Bombus Edwardsii</i>	5	30	1	6
<i>Asclepias speciosa</i>				
<i>Apis mellifica</i>	10	60	1	6
	6	50	1	8.3
* Did not enter the five nectaries in nearly all	11	60	1	5.5
* Entered only two or three nectaries in each flower	14	60	1	4.3

## TIME OF VISITS

<i>Gentiana Parryi</i>	<u>Flowers</u>	<u>Seconds</u>	<u>Flowers</u>	<u>Seconds</u>
<i>Bombus juxtus</i>	4	30	1	7.5
	1	12	1	12
	7	80	1	11.5
<i>Mertensia pratensis</i>				
<i>Bombus Edwardsii</i>	26	110	1	4.2
	7	40	1	6
<i>Pentstemon glaucus</i>				
<i>Bombus Edwardsii</i>	24	60	1	2.5
	17	40	1	2.3
<i>Bombus proximus</i>	27	60	1	2.2
	22	60	1	2.7
<i>Pentstemon glaber</i>				
<i>Bombus proximus</i>	5	25	1	5
<i>Vespa germanica</i>	14	75	1	5.3
<i>Quincula lobata</i>				
Muscidae sp.	4	200	1	50

LIST OF FLOWERS AND INSECT VISITORS.

The following abbreviations prefixed to the scientific names of the visitors indicate the insect order to which they belong:

Hymenoptera	-	Hym.
Diptera	-	Dip.
Coleoptera	-	Col.
Hemiptera	-	Hem.
Lepidoptera	-	Lep.

Numbers after scientific names indicate length of proboscis in mm. (from Knuth)

The nomenclature of the flowers is that adopted in "Flora of Colorado" by Dr. Edith Schwartz Clements and Dr. Frederic Clements.



Achillea millefolium

Lep.

Chrysophanus helioides

Synanthedon albicornis

Hym.

Halictoides mamus

Aconitum columbianum

Hym.

Bombus Edwardsii var. bifarius

Allium recurvatum

Hym.

Bombus Edwardsii var. bifarius

Lep.

Parnassius smintheus

Aquilegia coerulea

Hym.

Bombus proximus

Arclostaphalus Uva - Ursi

Hym.

Bombus Edwardsii, var. bifarius

*Asclepias speciosa*

Hym.

*Apis mellifica*

*Astragalus* sp.

Lep.

*Monumetha albifrons*

*Aster foliaceus*

Hym.

*Bombus flavifrons*

*Bombus Edwardsii* var. *bifarius*

*Calochortus Gunnisonii*

Dip.

*Cyrtopogon leucozona*

Col.

*Trichinis affinis*

*Caltha leptosepala*

Hem.

*Irbisia brachycerus*

Hym.

*Ophion* sp.

*Campanula rotundifolia*

Hym.

*Bombus Edwardsii* var. *bifarius*

*Megachile wootonii*

*Odynerus* sp.

Lep.

*Chrysophanus rubidus*

*Capnoides aureum*

Hym.

*Bombus proximus*

*Carduus Traceyi*

Hym.

*Bombus proximus*

*Bombus Edwardsii* var. *bifarius*

Lep.

*Euxoa olivalis*

*Grapta hylas*

*Satyrus charon*

*Chrysophanus rubidus*

*Pieris sisymbri*

Colias Edwardsii  
Colias Scudderi  
Parnassius clarius

Castelleia minfata

Hym.

Bombus proximus

Lep.

Colias Keewaydinus

Humming Bird

Chamaenerion angustifolium

Hym.

Bombus nevadeus

Bombus proximus

Bombus vagans

Bombus Edwardsii var. bifarius

Megachile wootoni

Lep.

Monumetha argentifrons

Basilarchia Weidenmeyerii

Chrysopsis foliosa

Hym.

Bombus juxtus

Bombus Edwardsii var. bifarius

Panurginus Cressonickus

Dip.

Echinomyia algens

Cleome serrulata

Hym.

Bombus Edwardsii var. bifarius

Dip.

Eliphilus latifrons

Clementsia rhodantha

Dip.

Anthomyidae sp.

Dasiphora fruticosa

Hym.

Bombus flavifrons

Lep.

Erebia epipsodes

Brenthis ericlaris

Coenonympha pamphiloides

Delphinium scrophularum

Hym.

Bombus appositus

Dodocatheon Meadii

Hym.

Bombus flavifrons

Bombus Edwardsii, var. bifarius

Draba sp.

Lep.

Chionobos macounii

Drymocallis fissa

Hym.

Bombus Edwardsii

Hem.

Irbisia brachycerus

Lep.

Parnassius Smintheus

Edwinia americana

Hym.

Bombus bifarius

Vespa germanica

Hem.

Irbisia brachycerus

Erigeron macranthus

Hym.

Bombus rufosuffusus

Bombus Edwardsii var. bifarius

Andrena apacheorum

Panurginus Cressonickus

Vespula sp.

Tenthredo uncinclutus

Lep.

Satyrus charon

Chrysophanus helloides

Brenthis helena

Coenonympha pamphiloides

Parnassius clarius

*Erysimum asperimum*

Hym.

*Bombus proximus*

*Frasera speciosa*

Hym.

*Bombus Edwardsii* var. *bifarius*

*Bombus flavifrons*

Hem.

*Thyreocoris anthracina*

*Fragaria praeata*

Hym.

*Bombus Edwardsii* var. *bifarius*

*Gallium borealis*

Hym.

*Lycaena glaucon*

*Geum rivale*

Dip.

*Archytas* or *Peleteria* sp.



*Gentiana parryi*

Hym.

*Bombus juxtus*

*Bombus nevadensis*

*Bombus appositus*

Dip.

*Syrphus opinator*

*Geranium Fremontii*

Dip.

Stratiomyidae sp.

*Tabanus rhombicus*

Hem.

*Irbisia brachycerus*

Hym.

*Panurginus Gressonickus*

Lep.

*Parnassius Smintheus*

*Erebia epipsodes*

*Genis uhleri*

*Lycaena pseudargiolus*

*Helianthus petiolaris*

Lep.

*Argynis eurynome*

*Lemonias nubrigena* var. *wheeleri*

*Heracleum conatum*

Hym.

*Bombus proximus*

*Tenthredella* sp.

Dip.

*Hammerschmidia ferruginosa*

*Henchera parva*

Col.

Small beetles only

*Henchera Hallii*

Col.

Small beetles

*Ibidum strictum*

Hym.

*Bombus Morrisoni*

Bombus appositus

Panurginus Cressonickus

Halictus sp.

Hem.

Lygus pratensis

Iris missouriensis

Lep.

Parnassius Smintheus

Chionobos macounii

Green humming bird.

Lathyrus ornatus

Hym.

Bombus Edwardsii var. bifarius

Lupinus luteus

Lep.

Monumetha albifrons

Malvastrum coccineum

Hem.

Irbisia brachycerus

82.  
Mertensia pratensis

Hym.

Bombus flavifrons

Bombus Edwardsii var. bifarius

Dip.

Scaba opinator

Opuntia sp.

Hym.

Anthophora sp.

Oreochrysum Parryi

Lep.

Chrysophanus heloides

Pedicularis racemosa

Hym.

Bombus proximus

Bombus Edwardsii var. bifarius

Petalostemon candidus

Hym.

Apis mellifica

Bombus proximus

Sterictiphora sp.

Phacelia heterophylla

Lep.

Chrysophanus rubidus

Physaria didymocarpa

Hym.

Halictus sp.

Hem.

Thyreocoris anthracina

Polygonum buxiforme

Lep.

Gnophoela vermiculata

Potentilla pulcherrima

Hym.

Bombus proximus

Panurginus Cressonickus

Halictus sp.

Hem.

Geocoris bullatus

Dip.

Chrysotoxum ventricosum

Lep.

Colias Alexandra

Chionobos macouni

Parnassius Smintheus

Erebia epipsodes

Nathalias Iole

Gnophoela vermiculata

Prunus demissa

Hym.

Bombus proximus

Bombus flavifrons

Andrena sp.

Vespa germanica

Lep.

Coenonympha pamphiloides

Erebia epipsodes

Brenthis ericlarius

Pentstemon glaucus

Hym.

Bombus Edwardsii var. bifarius

Bombus proximus

Pentstemon glaber

Hym.

Bombus Edwardsii var. bifarius

Bombus proximus

Vespa germanica

Anthophora bomboides

Pentstemon unilateralis

Hym.

Mustidae sp.

Vespa germanica

Pentstemon humilis

Hym.

Bombus Edwardsii var. bifarius

Pentstemon secundiflorus

Hym.

Bombus Edwardsii var. bifarius

Bombus proximus

vespa germanica

Rosa Engelmannii

Hym.

Bombus Edwardsii var. bifarius

Bombus flavifrons

Bombus proximus

Rubus strigosus

Hym.

Bombus Edwardsii var. bifarius

Bombus flavifrons

Bombus proximus

Andrena Lewisii

Lep.

Synanthedon albicornis

Gnophoela vermiculata

Rubus deliciosus

Hym.

Bombus proximus

Bombus flavifrons

Vespa germanica

Vespa maculata

Rydbergia grandiflora

Hym.

Bombus Edwardsii var. bifarius



Bombus flavifrons

Bombus appositus

Osmia megacephala

Dip.

Eristalis temporalis

Lep.

Lemonais nubigena var. wheeleri

Melitaea Whitneyi

Argynis eurynome

Sambucus racemosa

Col.

Leptura chrysocoma

Scuttelaria Brittoni

Hym.

Bombus Morrisoni

Sieversia ciliata

Hym.

Bombus Edwardsii var. bifarius

Bombus proximus

Halictus sp.

Stanleya pinnatifida

Hym.

Bombus Morrisonii

Mustidae sp.

Apis mellifica

Vespa germanica

Lithargus apicalie opuntiae

Dip.

Volucella satur

Sedum stenopetalum

Lep.

Argynnis eurynome

Satyrus charon

Phycodes camillus

Pieris protodice

Solidago sp.

Hym.

Bombus proximus

Bombus flavifrons

Bombus Edwardsii var. bifarius

Prosopis

Col.

*Mordella maleana*

Lep.

*Gnophoela vermiculata*

*Taraxacum dumetorum*

Hym.

*Apis mellifica*

*Osmia propinqua*

*Valeriana* sp.

Hym.

*Bombus Edwardsii* var. *bifarius*

*Osmia propinqua*

Lep.

*Chionobos macouni*

The Insects found visiting flowers.

The Lepidoptera were identified largely from Edwards "Butterflies of North America" Hollands "Moth Book".

The identifications of the other orders were made or checked by the following:

Diptera - Bureau of Entomology, Washington, D. C.

Hymenoptera - T. D. A. Cockrell, University,  
Boulder, Colorado.

Coleoptera and Hemiptera - Professor Oesterlund,  
University of Minnesota.

Order Hymenoptera

Family Apidae (Long tongued bees)

Social bees.

*Apis mellifica* Linn (5.5 - 6.5 mm.)

*Asclepias speciosus*

*Petalostemon candidus*

*Stanleya pinnatifida*

*Taraxacum dumentorum*

*Apis mellifica ligustica*

*Asclepias speciosa*

*Petalostemon candidus*

*Bombus* (Humble bees) (9-21 mm.)

*Bombus Edwardsii* var. *bifarius* Franklin

*Allium recurvatum*

*Arctostophalus uva-urci*

*Aster foliaceus*

*Agoseris glauca*

*Companula rotundifolia*

*Chrysopsis foliosa*

*Dodocatheon Meadia*

*Edwinia Americana*

72

Erigeron macranthus  
Fragaria bracteata  
Fraseria speciosa  
Mertensia pratensis  
Potentilla pulcherrima  
Pentstemon humilis  
Pentstemon glaucus  
Pentstemon glaber  
Pentstemon secundiflorus  
Pedicularis racemosa  
Rosa Engelmannii  
Rubus strigosus  
Rydbergia grandiflora  
Sieversia ciliata  
Solidago sp.  
Valeriana sp.

*Bombus proximus* Cresson

*Aquilegia coerulea*

*Carduus Traceyi*

*Capnoides aureum*

*Chamaenerion angustifolium*

*Erysimum asperrimum*

*Heracleum conatum*

*Pedicularis racemosa*

*Petalostemon candidus*

*Potentilla pulcherrima*

*Pentstemon glaucus*

*Pentstemon glaber*

*Pentstemon secundiflorus*

*Prunus demissa*

*Rosa Engelmannii*

*Rubus deliciosus*

*Rubus strigosus*

*Solidago* sp.

*Sieversia ciliata*

Bombus flavifrons Cr.

Aster foliaceus

Dodocatheon Meadia

Dasiphora fruticosa

Frasera speciosa

Mertensia pratensis

Rosa Engelmannii

Rubus deliciosus

Rubus strigosus

Rydbergia grandiflora

Solidago sp.

Bombus appositus Cr.

Aconitum columbianum

Delphinium scrophularum

Gentiana parryi

Ibidum strictum

Rydbergia grandiflora

Bombus juxtus cr.

Chrysopsis foliosa

Edwinia americana

Gentiana parryi

Mertensia pratensis



85  
Bombus Morrisoni Cress.

Ibidum strictum

Scuttelaria Brittoni

Stanleya pinnatifida

Bombus Nevadens cr.

Chamaenerion angustifolium

Gentiana parryi

Bombus vagans

Chamaenerion angustifolium

Bombus rufosuffusus ck ll.

Erigeron Macranthus.

Anthophora bomboides Kirby (15-17 mm.)

Pentstemon glaber.

Mellisodes confusa Cresson

Stanleya pinnatifidae.

95.  
Osmia hypoleuca Ck. 11

Silene Hallii

Osmia propinqua

Valeriana sp.

Potentilla pulcherrima

Taraxacum dumetorum

Osmia megacephala CN.

Rydbergia grandiflora

Panurginus Cressonickus Ck 11.

Chrysopsis foliosa

Erigeron macranthus

Geranium Fremontii

Ibidum strictum

Potentilla pulcherrima

Mustidae sp.

Frasera speciosa

Mega chile (Leaf cutters, solitary long tongued)

Megachile Wootonii ck 11

Chamaenerion angustifolium

Campanula rotundifolia

Lithurgus apicalis opuntiae Ck 11

Stanleya pinnatifida.

Family Andrenidae (short tongued bees).

*Andrena apacheorum* Ckll. G.

*Erigeron macranthus*

*Dasiphora fruticosa*

*Sieversia ciliata*

*Andrena Lewisii* Ckll.

*Rubus strigosus*

*Halictus* sp. (15 - 6 mm.)

*Potentilla pulcherrima*

*Sieversia ciliata*

*Ibidum strictum*

*Halictoides manus* Cr. F.

*Achillea mellifolium*

*Prosopis* sp. (1 - 1.25 mm.)

*Solidago* sp.

Family Ichneumonidae

*Ophion* sp.

*Caltha leptosepala*.

Family Vespidae (Social Wasps)

Vespa maculata

Rubus deliciosus

Vespa Germanica

Rubus deliciosus

Pentstemon glaber

Pentstemon unilateralis

Prunus virginiana

Edwinia americana

Polybia flavitarsis Sanss

Stanleya pinnatifida

Vespula (sp.)

Erigeron macranthus

Odynerus

Campanula rotundifolia

Family Tenthredinidae (Saw flies).

Tenthredella (sp.)

Heracleum conatum

Tenthredo uncinclutus D. T.

Erigeron Macranthus

Sterictiphora (sp.)

Petalostemon candidus

Cimbx americana

Taraxacunn dumetorum.

100

Order Lepidoptera

Argynis egleis

Carduus Traceyi

Dasiphora fruticosa

Argynis eurynome (9 - 10 mm.)

Rydbergia grandiflora

Helianthus petiolaris

Sedum stenopetalum

Basilarchia Weidemeyeri

Chamaenerion angustifolium

Brenthis ericlaris Hubner

Dasiphora fruticosa

Prunus ericlarius

Brenthis helena

Erigeron macranthus

Cenis Uhleri

Geranium Fremontii.

Coenonympha pamphiloides (7 mm.)

Erigeron macranthus

Dasiphora fruticosa

Prunus demissa

Chionobas macounii

Draba sp.

Valeriana sp.

Potentiella pulcherrima

Iris missouriensis

Chrysophanus helloides

Achillea mellifolium

Erigeron macranthus

Oreochrysum parryi

Chrysophanus rubidus

Carduus Traceyi

Companula rotundifolia

Phacelia heterophylla

Colias Keewaydinus

Castelleia miniata

Colias Alexandra

Potentilla pulcherrima

*Colias Scudderi*

*Carduus Traceyi*

*Colias Edwardsii*

*Carduus Traceyii*

*Erebia epipsodes*

*Dasiphora fruticosa*

*Geranium Fremontii*

*Potentilla pulcherrima*

*Prunus demissa*

*Euxoa oldvalis*

*Carduus Traceyi*

*Grapta hylas*

*Carduus Traceyi*

*Gnophoela vermiculata*

*Polygonum buxiforme*

*Potentilla pulcherrima*

*Rubus strigosus*

*Solidago sp.*

*Lemonias nubigena var. wheeleri*

*Helianthus petiolaris*

*Rydbergia grandiflora*



Lycaena pseudargiolus  
Geranium Fremontii  
Lycaena glauca (7 - 8 mm.)  
Gallium borealis  
Melitia Whitneyi  
Rydbergia grandiflora  
Monumetha albifrons Kby.  
Lupinus luteus  
Astragalus sp.  
Monumetha argentifrons  
Chamaenerion augustifolium  
Nathalias Iole  
Potentilla pulcherrima  
Parnassius Smintheus (12 - 13 mm.)  
Drymocallis fissa  
Erigeron Macranthus  
Geranium Fremontii  
Potentilla pulcherrima  
Allium recurvatum  
Iris missouriensis

Parnassius clarius

Carduus Traceyi

Erigeron Macranthus

Phycodes camillus

Sedum stenopetalum

Pontia prodite

Draba sp.

Petalostemon Candidus

Potentilla pulcherrima

Iris Missouriensis

Pieris sisymbri

Carduus Traceyi

Pieris prodite (13 - 18 mm.)

Sedum stenopetalum

Synanthedon albicornus

Achillea mellifolium

Rubus strigosus

Satyrus charon

Erigeron macranthus

Sedum stenopetalum

Carduus Traceyi

Order Diptera

Family Syrphidae (syrphys flies)

Syrphus opinator O. S.

Gentiana Parryi

Scaba opinator

Mertensia pratensis

Eliphilus latifrons L. W.

Cleome serrulata

Chrysotoxum ventricosum L. W.

Potentilla pulcherima

Eristalis temporalis Thoms.

Rydbergia grandiflora

Volucella satur O. S.

Stanleya pinnatifida

Cyrtopagon leucozona L. W.

Calochortus Gunnisonii

Hammerschmidtia ferrugimosa Fallen

Heracleum conatum

Family Asilidae (Robber flies)

Tabanus rhombicus O. S.

Geranium Fremontii.

Family Muscidae

*Peleteria prompta* Mg.

*Peleteria* or *Archytas* (sp)

*Geum rivale*

*Echinomyia algens* Wied.

*Chrysopsis foliosa*

Family Tachininae (Tachina Fly)

Family Anthomyiidae

*Clementsia rhodantha*

Family Stratiomyidae

*Geranium Fremontii*

Order Hemiptera

*Thyreoeoris anthracina* Uhl.

*Physaria didymocarpa*

*Frasera speciosa*

*Geocoris bullatis* A. H.; Say. Mont.

*Potentilla pulcherrima*

*Irbisia brachycerus* Uhl.

*Geranium Fremontii*

*Caltha leptosepala*

*Malvastrum coccineum*

*Edwinia americana*  
*Lygus pratensis* Linn.  
*Ibidum Strictum*.

Order Coleoptera

*Clerus abruptus* Lec.  
*Stanleya pinnatifida*  
*Mordella melaena*  
*Solidago* sp.  
*Frichins affinis*  
*Calochortus Gunnisonii*  
*Leptura chrysocoma*  
*Sambucus racemosa*

## SUMMARY

### I. Flower Factors in Pollination

#### A. Movement

(a) Of flowers as a whole: This movement is continuous throughout the development from the bud to the mature fruit. It aids autogamy by placing the stigma in line with the falling pollen or allogamy by removing the stigma from the pollen path. Three general types of movement were noted.

- (1) Flower ascending from pendant position of bud - *Aquilegia coerulea*; *Sieversia ciliata*; *Dodocatheon Meadia*.
- (2) Flower declining from erect position of bud, - *Campanula rotundifolia*; *Gilia aggregata*.
- (3) No movement from bud to fruit - *Clematis alpina*; *Rubus strigosus*; *Gentiana Parryi*.

(b) Of floral envelopes: This movement shields the dehiscing anthers and receptive stigma from dews or rain - noted particularly in flowers with a broad disc-shaped corolla, horizontally placed, where stamens and style are exposed. The two kinds are:

(1) closing of the corolla - *Rosa Engelmannii* (partial); *Potentilla pulcherrima* (complete);

(2) temporary drooping of pedicel - *Geranium Fremontii*.

(c) Of reproductive parts as they develop: These movements are arrangements for preventing autogamy until the flower is almost ready to wither.

Stamens:

(1) Filaments vertical then deflexed - *Geranium Fremontii*; *Gentiana Parryi*.

(2) Filaments inflexed till contact

with stigma, then afterwards straightened -  
*Prunus demissa*.

- (3) Filaments deflexed, then spirally  
twisting - *Calochortus Gunnisonii*

Styles:

Young style is usually straight - in  
a few cases as in *Quincula* it is bent.

- (1) Tip of style bent at maturity so that  
it will come in contact with insect  
visitors as they enter or leave the  
flower - *Penstemon glaucus* (bent  
down); *Castilleja confusa* (bent up).
- (2) Styles deflexed at maturity so that  
they may come in contact with the  
anthers or insect visitors - *Geranium  
Fremontii*.
- (3) Stylar branches recurved at maturity,  
expose greater surface to insect vis-  
itors and finally touch anthers -  
*Campanula rotundifolia*.
- (4) Style bending horizontally during



anthers dehiscence, then by forming a loop, standing vertical when anthers deflex - *Quincula lobata*.

B. Maturing of the reproductive parts at separate times are adaptatious for allogamy. Autogamy may often take place just before the pollen is gone. The insect must visit two flowers to produce one fertilization. Protandrous, protogynous and homogamous flowers are the three groups. In some cases they are not sharply separated, some flowers of the species developing the one way, some the other. In homogamous flowers the chance for allogamy and autogamy are about equal for the insect may be dusted with pollen from the previous flower.

Comparatively few flowers of the list were homogamous, seeming to indicate that flowers adapted for allogamy had the best chance of producing seed. Protandry is supposed to occur much more frequently than protogyny. The list of flowers observed included about an equal number of each.

The apparent difference may be explained by the fact that the flora as a whole in one vicinity was not studied throughout the season, but interesting forms were selected in the region.

Protandry is the more economical device for the plant since each anther, the pollen of which is not utilized, by an insect visit at the time of dehiscence, simply reduces the chance of pollination. If a stigma is mature before pollen of this species has developed there is no chance for the fertilization of any of the ovules.

The amount of pollen available depends on the method of dehiscence,

- (1) consecutive dehiscence of the individual anthers or of stamen cycle extends the available pollen over a long period.
- (2) Simultaneous dehiscence makes the collection of pollen by insects very sure if the visitor is present at the proper time and stigmas are receptive then.

### C. Attraction

Insects are attracted to flowers by odor, if there is one, and later by color and form. Lepidoptera and flies particularly are guided chiefly to plants by sense of smell; Hymenoptera mainly guided by sight. Attraction may be due to;

(1) the flower grouping, as the spherical umbel of allium or asclepias; the tall panicle of Fraxinea; Chamaenerion or a head of Helianthus;

(2) The individual flowers: The more intense color is usually in the part first seen by the insect, the paler portions direct the way to the interior.

The most efficient flowers for insect pollination are those we call the higher flowering plants which have adapted themselves for attraction by reducing the number and perfecting the parts.

The same result has been attained by three methods:

(a) Among the lower monocotyledons the sur-

face for attraction is increased by colored sepals, as in *Zyadenus elegans*.

- (b) The higher monocotyledons and many dicotyledons have elevated the corolla to make it seen more easily, as in *Iris missouriensis*; *Ibidum strictum*; *Chamaenerion angustifolium*.
- (c) Union (which also elevates the parts) and zygomorphy, which limits the convenient landing place, as in *Campanula rotundifolia* (regular); *Pentstemon secundiflorus* (zygomorphic).

Once landed color markings of dots or lines (*gentiana parryi*), lighter color interior (*campanula rotundifolia*) ridges or hairs (*Pentstemon glaber*) serve as a guidance to the nectar.

- D. Numerous flowers were bagged to find out to what extent autogamy would take place in the absence of visitors, but storms, burros, and chipmonks molested them to such an extent that no results were obtained.

In most of the flowers adapted for allogamy

provision is apparently made at the end for autogamy. Although the first method is preferable, the plant may be fertilized in many cases if allogamy fail. Methods used for final autogamy are:

- (a) Drying of corolla tightly about style and stamens - *Campanula rotundifolia*.
- (b) Shriveling of the anthers so that they come in contact with stigmas - *Allium recurvatum*.
- (c) Closure of corolla - *Potentilla pulcherri-*  
*ma*.
- (d) Corolla falling off carrying stamens so that anthers come in contact with stigma as it falls - *Gilia scariosa*; *Pentstemon secundiflorus*.
- (e) Recurving of stylar branches so they touch anthers - *Pachylophys speciosa*.

## II. Insect relations to flowers.

### A. Purpose of visit.

Insects visit flowers in search of nectar, pollen or shelter.

(1) Nectar may be found in exposed places as in the simple, open, regular flowers of *Wagnera stellata*, *Sedum stenopetalum*.

Nectar partly concealed by petals or crowded stamens and pistils is found in such flowers as *Potentilla pulcherrima*.

Nectar is found concealed at the end of a long tubular corolla as in *Pentstemon glaucus*, or in an irregular-shaped pocket as in *Capnoides aureum*.

Pollen is produced in abundance in many of these flowers and in securing nectar the pollen collects on the hairs on the various parts of the insect's body.

There should be this cooperation between the insect and flower so that the plant receives pollen transfer in return for the nectar it produces for insect food. Some insects, as *Bombus*, which have a proboscis too short to reach the nectar or the body too large to enter the particular corolla tube conveniently, steal nectar by sucking it through holes which they make at the base of the corolla tube. This means no pollen transfer and is a disadvantage to the flower.

- (2) Pollen: In pollen flowers there is no nectar, but the pollen is produced in abundance in accessible places, as in *Rosa Engelmannii*. Insect visitors come for pollen only and belong to those genera with special collecting apparatus as *Bombus*.

(3) Shelter: The campanulate corolla of Campanula and Gentiana, and the tubular corolla of Pentstemon furnish shelter for insects. Incidental to this protection is the collecting of pollen by parts which come in contact with the anthers or the pollinating of the stigma as the insect touches it.



Tabular summary showing comparison of insect groups as pollinating agents:

	Insects		Number of flower species visited	Number of flower visits	Per cent of total number flowers observed visited
	Number of genera	Number of species			
Order Hymenoptera	24	35	52	114	78
Family Apidae	9	20	45	91	68
Genus Bombus		9	40	69	60
Genus Apis		2	4	6	6
Genus Osmia		3	5	5	
Genus Panurginus		1	5	5	
5 remaining genera		5	6	6	
Family Andrenidae	4	5	8	9	12
Family Ichneumonidae	1	1	1	1	
Family Vespidae	4	5	8	9	
Family Tenthredinidae	4	4	4	4	
Order Lepidoptera	23	33	25	57	38

	Insects		Number of flower species visited	Number of flower visits*	Per cent of total number flowers observed visited
	Number of Genera	Number of species			
Order Diptera	13	13	13	13	19
Family Syr- phidae	8	8	8	8	12
Total 5 other families	5	5	5	5	
Order Coleop- tera	4	4	4	4	6
Order Hemip- tera	4	4	7	7	10

\* Each flower species was only visited once by each insect but this number represents the total number of visits by each group (Order, Family, or Genus)

Total number flower species observed 66  
 Total number insect species observed 89

## B. Insect Types.

The insects studied were representatives of five orders:

- (1) Hymenoptera were the most frequent visitors and the genus *Bombus* appeared to be the most common. This may have been due to the fact that this genus was present in larger numbers at that time of year than other genera or that they are conspicuous and easily captured. However, the following characteristics show it particularly well adapted to securing pollen or nectar from most types of flowers and this seems to be the explanation: Proboscis 9 - 21 mm. long, whole body covered with long, feathered hairs, pollen basket on hind legs in which pollen moistened with honey is packed. In many of the Scrophulariales and Lamiales the visitors are limited to those having a body size which is no larger than the narrowed part of the corolla mouth. The anthers are

so placed that they fit closely to the insects back. Smaller insects would not come in contact with these and larger ones are prevented from entrance to the nectar. Genus *Bombus* fulfills the requirements of being intelligent enough to know where to find the nectar and various species are of the proper size to fit the corolla mouth. The unsuccessful attempts, because of size, of some *Bombus* species to enter particular flowers, and their success in other flowers, shows the specialization. *Apis* has a more highly developed pollen apparatus but was not common because of the altitude.

In the other genera of Hymenoptera represented, the proboscis is shorter, varying from 1 mm. in *Prosopis* to 6 mm. in *Halictus*. The pollen is not moistened but entangled in the hairs of the leg as in a brush. The principal collecting apparatus is the ventral surface of the abdomen which is covered with

a brush of stiff bristles pointed backwards.

- (2) Lepidoptera visited the more highly developed flowers. They all have a long, slender proboscis, able to reach nectar concealed in very deep tubes and because of this have an advantage over the other orders. Pollen collects on the proboscis, which is moistened with nectar, as it leaves the flower.
- (3) The order Diptera was represented by a number of families. Syrphidae, Muscidae, and Stratiomyidae obtain both pollen and nectar. The Syrphidae were the most common. The proboscis in these can be extended 4 - 8 mm. which limits the flower choice largely to those with exposed or partly concealed nectar. Flaps, the surface of which is covered with parallel ridges of chitin, grasp the pollen mass and pass it backward into the groove on the lower lip. The moistened pollen which collects about the mouth parts is very likely to come in contact with the stigmatic surface of the next flower

on which it works and produce pollination. The complicated process of feeding on pollen by collecting it on the proboscis, grinding it down, passing it backwards to the lips and into the mouth account for the comparatively long time each insect spends at one flower.

- (4) Many Coleoptera are carnivorous and some of these were found simply resting on flower parts. Those listed had to do with pollination and were adapted for a floral diet. The pollen collecting apparatus consists of a development of hairs on the lobes of the maxillae.
- (5) The Hemiptera are unimportant in connection with pollination since they have no particular adaptations for pollen collecting. In sucking nectar for food pollen becomes dusted on the under side of the body and legs and some reaches the stigma in this way.

#### C. Time of Visits.

The number of flowers which an insect can visit in

a unit time depends on the proximity of the flowers of a given species which are open and exposing nectar or pollen. The ease or difficulty of gaining entrance to the corolla, and then to the nectar when entrance is gained, all are related to the time element. In flowers which have numerous nectaries, each nectary is sometimes visited. This makes the chance of pollination much more sure, for the same reproductive parts are touched as the insect reaches into each nectary. Humble bees which enter flowers of the rose type for pollen, collecting it by tramping about on the anthers, can visit many more flowers in a unit of time than the *Bombus* seeking nectar.

The flower from which pollen was collected most rapidly was *Rubus deliciosus*. This was due to the abundance of pollen present and the wide open corolla. *Bombus proximus* and *Bombus Edwardsii* collected pollen from *Potentilla pulcherrima* and *Rosa Engelmannii* by tramping about spending four seconds in each flower. These flowers are of the same simple type as *Rubus deliciosus*.

Pentstemon glaber has a staminode covered with long hairs, while Pentstemon glaucus has a narrow, slightly hairy staminode. The hairs hinder the entrance to the corolla, and that, or a difference in the amount of nectar obtainable, accounts for the fact that *Bombus proximus* spends twice as long at *Pentstemon glaber* as at *Pentstemon glaucus*.

### III. Number of Pollen Grains per Ovule.

Species	'Average 'number of 'pollen 'grains in 'cross sec- 'tion of 'anthers	'Average 'number 'of pol- 'grains 'in row 'longi	Average number of pollen grains per anther	Number of anthers per flower	Total num- ber pollen grains per flower
<i>Chamaenerion angustifolium</i>	35	21	735	8	
<i>Potentilla pulcherrima</i>	48	30	1440	many	numerous
<i>Pachylophus speciosa</i>	22	80	1760	8	14080
<i>Silene Halii</i>	69	40	2760	10	27600
<i>Rosa Engelmanii</i>	100	41	4100	numer- ous	



Species	Average number of pollen grains in cross section of anthers	Average number of pollen grains in row longi	Average number of pollen grains per anther	Number of anthers per flower	Total number pollen grains per flower
Rubus deliciosus	94	45	4140	many	
Castelleia confusa	103	71	7313	4	29,252
Aquilegia coerulea	202	76	16352	many	
Pentstemon secundiflorus	346	76	26296	4	105,184
Gentiana Parryi	229	175	40075	5	200375
Mertensia pratensis	462	400	184800	5	924,000
Dodocatheon Meadia	482	595	286790	5	1433,950

Since the number of ovules per pistil and number of pistils per flower in many cases are not available, further study will be necessary before this part of the work is completed.

## Conclusions

- I. Autogamy is avoided in most flowers by flower movements or the successive development of reproductive parts. Usually there is a contrivance for making autogamy possible at the end, before the stigmatic surface dries.
  
- II. Flowering plants are classified according to the degree of adaptation for pollination. Flowers with the most highly specialized corolla attract the most specialized intelligent insects. These higher, insect-pollinated plants need few stamens and pistils because of the certainty of pollination.
  
- III. Hymenoptera is the most important order of pollinating insects.

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