OBSERVATIONS ON
THE POLLINATION OF THE PRIMROSE,

By F. E. WEISS, D.Sc.

A considerable amount of uncertainty exists as to the manner in which the pollination of the primrose is effected. Darwin¹ has recorded how rarely insects can be seen during the day visiting the flowers of the primrose, and he came to the conclusion that they were commonly fertilized by nocturnal Lepidoptera. Writing in 1897 on the fertilization of spring flowers on the Yorkshire coast Mr. Burkill² says with regard to the primrose: "the fertilization of this plant is yet unexplained. None of the insects seen on it through many hours of watching are sufficient for its fertilization." He was consequently inclined to accept Darwin's conclusion as the correct one. In a more recent publication entitled "The Primrose and Darwinism" the author, "A Field Naturalist" states it as his belief "that the primrose gives unimpeachable evidence that self fertilization of heterostyled plants is the natural and legitimate fertilization as being fully productive." This conclusion so directly at variance with Darwin's explanations of the importance of heterostyly as ensuring cross pollination was largely based on the absence of insect visitors to the primrose, of such insects at least as could effect the pollination of the flowers. Only four such visitors were observed by "Field Naturalist," "after seeing and examining thousand and thousands, we might say millions of the flowers."

Other British botanists³, it is true, have recorded the visits of various insects to the flowers of the primrose, but their observations do not seem to have been regarded as conclusive by Darwin, Burkill, or "Field Naturalist." Knuth⁴ has given a complete summary of the observations made upon this subject up to the year 1899 both by himself and others, yet one cannot help feeling that there is a considerable amount of conflicting evidence, for while Knuth and Scott Elliot look upon *Bombus hortorum* as one of the most important agents of pollination, Darwin states definitely⁵ that

¹ Darwin, C. *Forms of Flowers*, p. 36.

² Burkill, I. H. *Journal of Botany*, 1897.

³ (i.) Briggs. T. R. Archer. *Journal of the Plymouth Institution*, 1871-72.

(ii.) Miller-Christy. *Trans. Essex Field Club*, 1884.

(iii.) Scott-Elliot. *Flora of Dumfriesshire*, 1896.

⁴ Knuth, P. *Blüthenbiologie*, 1899, vol. II., p. 313.

⁵ Darwin, l.c. page 56.

"the primrose is never visited (and I speak after many years' observation) by the larger humble bees and rarely by the smaller kinds."

These conflicting views do not of course imply inaccurate observations, but may be readily explained by the fact that the latter were made in different localities and, probably, under varying conditions. As I had an opportunity during the Easter vacation of observing large quantities of primroses near Church Stretton in Shropshire, it seemed to me important to make some more observations on the visits of insects to these plants with a view of helping to settle this somewhat vexed question. I confined my observations mainly to two large patches of primroses, on the east and west of a narrow lane, a portion of Watling Street. Both positions were sheltered from the prevalent north-westerly winds, which were often strong and sometimes bitterly cold. I visited one or both of these places on eight successive days between 11 a.m. and 1 p.m., staying from half-an-hour to an hour on each occasion, and each time I was able to observe some insects visiting the flowers. Taking the eight occasions together the flowers at these two places were visited by

- 17 *Bombylius major* L.,
- 3 *Bombus terrestris* L.,
- 7 *Anthophora furcata* P._z (6 ♀ and 1 ♂),
- 1 *Apis mellifica* L.,

and by numerous (more than 20) *Andrena Gwynana* K.

On two occasions observations were made on two other stations and yielded

- 3 *Bombylius*,
- 4 *Bombus*,
- 5 *Anthophora*,
- 2 *Apis*,
- numerous *Andrenas*.

The number of insects varied greatly on different days, owing to considerable differences in the temperature, and to different amounts of sunshine.

It will be noted that *Bombylius* was the most frequent of the long tongued insects, and was a far more regular visitor than the *Andrenae*, which, though present in considerable numbers on the 19th and 20th of April when the sun was powerful and the wind less strong, were absent during the earlier days, when there was less sun and a stronger wind. *Bombylius*, indeed, was the most

regular of all the visitors, having been observed on seven days out of the eight, and on the occasion when he was not observed I think this was due to my visit being earlier than usual, *i.e.* before 11 a.m. A fresh wind from the north-west was blowing at the time and very few insects of any kind were to be seen, so that in all probability *Bombylius* would have made its appearance a little later in the morning.

Bombylius, as has been noticed by other observers, hovers about the flowers in the graceful manner of a humming bird or humming bird hawk-moth and is said by some not to settle on the flower. Though this may be the case with certain flowers, yet in almost every instance when it visited the primrose, I saw this graceful insect ultimately settle on the flower, and, after its wings had come to rest, push its head as far as possible down the corolla-tube and remain in that position for some time, evidently sucking nectar. This is no doubt necessitated by the very long corolla-tube of the primrose, and it is an important fact, as the tuft of hairs on the top of the head thereby comes in contact with the pollen of the short-styled forms, and becomes a means of pollinating the long-styled flowers.

After visiting a few primroses (three or four) on the earlier colder days, and as many as eighteen or twenty in warmer weather, *Bombylius* rested on a dead leaf, well protected by its colouring, and cleaned off the pollen grains that were adhering to its head and proboscis. Considering the regularity of the visits of *Bombylius* and the relatively large number observed in really fine weather, eight in an hour and a half on April 19th, I have no doubt that this insect is an active agent in the pollination of the primrose. It seems admirably suited to obtain nectar from the depths of the tubular corolla with its long proboscis, and it seemed at this time of the year to confine its attention to the primrose. Only on one occasion did I observe a *Bombylius* sucking nectar from the celandine which is so largely visited by the ordinary bees.

Various species of *Bombylius* are known to visit other species of *Primula*, as for instance the Bardfield Oxlip, and even on the primrose Archer Briggs¹ observed *Bombylius medius*, a slightly smaller species, as did also Cobelli,² 1892.

As stated above there is a considerable difference of opinion

¹ Briggs, A. l.c.

² Cobelli, R. Zool. Bot. Ver. Wien. Abhandl.

as to whether the larger humble bees visit the primrose or not. On five different occasions I have observed *Bombus*, chiefly, I think, *Bombus terrestris* visiting primroses, and generally in such a manner as to ensure the pollination of the flowers. In two cases, however, I noticed the humble bee not sucking at the flower but moving all over the corolla, both at the front and the back of the flower, apparently endeavouring to obtain the honey by illegitimate means, just as Darwin observed them at times biting through the corolla in the case of the cowslip, of which they are regular visitors. I ought to state clearly that *Bombus* was a more frequent and regular visitor of other flowers than the primrose, and was more commonly seen on the willow, the dandelion, the violet, and the barren strawberry.

A smaller humble bee however, *Anthophora furcata*, though less plentiful in the district, was more often seen on the primrose to which it seemed to confine its attention. There can be no doubt that this insect is both able to gather honey from the primrose flower and also to effect its pollination. The female insects were more frequent visitors than the males, from which they differ greatly in appearance, and they seemed to be also more efficient as pollinating agents, as they remained longer at the flowers.

Apis mellifica L appeared to be less hardy than the humble bee or *Bombus*, for it only gathered honey on warm days and was not observed at all on several days, when *Bombus*, *Bombus* and *Anthophora* were about.

The bees visited chiefly the celandine, barren strawberry, wood anemone, violet and dandelion. Occasionally a stray one would visit a number of primroses, but did not spend much time on each. They were evidently endeavouring to obtain the nectar, which however, they were unable to reach. They stayed a little longer on the short-styled flowers from which they collected a little pollen. They were obviously not the regular visitors of the flowers though they could no doubt bring about cross fertilization of the long-styled forms.

The crossing of the long-styled flowers would also be effected by the visits of *Andrena Gwynana* ; but this insect must be placed in a different category from the bee, for it is a regular and busy visitor of the primrose and more commonly seen by me on its flowers than on those of other plants. It was only observed towards the close of my visit when the weather was much milder, but then it was present in considerable numbers. It gathered the pollen greedily, and in

getting at it poked its head deep into the mouth of the corolla. It naturally stayed longer in the short-styled flowers, but its movements in the long-styled forms were sufficient to pollinate the protruding stigma. There would seem to be no doubt that in the Church Stretton district these are very active agents of cross-pollination of the primrose, just as Briggs found them to be at Plymouth. They can however only bring about the pollination of the long-styled flowers.

From the instances given above, therefore, there is no doubt in my mind that primroses are efficiently cross-pollinated in the district under observation by *Bombylius*, *Anthophora* and *Andrena* with the addition of occasional, though by no means isolated visits of *Bombus*, the same genera indeed to which Briggs attributes the pollination of the primrose around Plymouth. The absence of these insects during the observations made by Darwin and Burkill must I think be due to their observations having been made in somewhat exposed situations, at all events this seems very probable in the case of Burkill.

On the days on which I observed insects in the sheltered spots which I had selected, I looked in vain for such visitors in large primrose covered areas at the foot of Caer Caradoc, which were exposed to the west winds which prevailed during my visit.

In normal Spring weather the slopes sheltered from the east wind would probably have yielded positive results, and indeed, on one somewhat less windy day several specimens of *Bombus* were noted visiting the primroses here. On that day *Apis* was also in evidence visiting the celandines and wood anemones with which the primroses were associated.

There is no doubt that unfavourable weather is prejudicial to the cross pollination in many places owing to the absence of insects in those localities. That however, cross-pollination in the district under observation must be a pretty general phenomenon is I think borne out by the fact that in most of the patches of primroses I examined I met with one or more specimens of the so-called oxlip, the hybrid between *Primula acaulis* and *P. officinalis*. Both parents were pretty plentiful in the district and generally specimens of both were found near the hybrids. There can, I think, be no doubt that these hybrids owe their origin to cross-pollination by insects, and as the chances of such hybridisation must be somewhat limited in species which differ slightly in their time of flowering, the occurrence of a fair number of hybrids argues a considerable frequency of insect visitors to both parents.

I did not come across any of the beetles *Meligethes picipes*, (Sturm) which Christy found so frequently on the primroses in Essex; nor was I able to observe any butterflies alighting on primroses, but that may have been due to the scarcity of Lepidoptera owing to the cold weather. No observations were made at night as the severe night frosts seemed to preclude the possibility of nocturnal visitors to the flowers.

SELF POLLINATION.

That self-pollination may occur fairly often in the primrose cannot be denied, and indeed, Darwin observed the frequent presence in both the cowslip and the primrose of Thrips which he considered aided the self fertilization of both forms.¹ In many primroses which I examined numbers of Thrips were present and in these flowers it was very common to find pollen grains scattered throughout the tube of the corolla and it seemed likely that it had been carried about there by these small insects.

Another agency for self-pollination is no doubt the wind taken in conjunction with alterations in the position of the flower. I agree with "Field Naturalist" in thinking that too little importance was attached by Darwin to the effect of the wind. At all events in the absence of cross-pollination which must frequently happen in flowering plants, in early spring the strong winds of that season are probably of considerable use. Watching the primroses on the hill-side, much exposed to the wind and in which the absence of insects as stated above was very marked, the violent shaking of the flowers was a noticeable feature.

This must however be considered in conjunction with the singular adaptation for self pollination which I think is shown in both the primrose and the cowslip, in the changes in position of the flower. In the primrose the flowers open at first in a vertical position and if the flower is short-styled the pollen from the opening anthers can readily be shaken by the wind on to the lower standing stigma. But towards the end of the flowering the flower stalk has grown considerably in length and the flower passes into a horizontal and often a pendant position so that the long-styled forms have a chance of self pollination too, when the flowers are agitated by the wind. It may be thought that this movement is mainly for the concealment of the fruits which in the primrose are ripened beneath the foliage, but though this may be to a certain extent the case, I cannot but believe that the self-pollination is also a

¹ Darwin., l.c., p. 37.

determining factor in this movement. For in the cowslip the very opposite occurs. The flowers, at first pendant, offer greater facilities as far as self-pollination is concerned to the long-styled forms, but later on the flowers become erect and thus in the absence of cross-pollination the short-styled forms will have ample opportunity to be self-pollinated.

From the observations I have made on the primrose I feel convinced that it is both regularly visited and cross-pollinated by insects under favourable climatic conditions, but that like most flowers adapted to the visits of insects, it is provided with efficient means for self-pollination and these are important to a plant flowering at so early a period of the year when the visits of insects may be precarious.

ON A NEW METHOD FOR FACILITATING THE STAINING OF MICROSCOPICALLY SMALL OBJECTS,

BY V. H. BLACKMAN, M.A.

THERE is a great need for a really satisfactory method of dealing with microscopically small objects so that they can be stained by the most modern methods and handled as easily as are microtome sections fixed to a slide.

The obvious method, by *decantation*, in which the objects (small unicellular organisms, etc.) are fixed, washed and stained by successive quantities of fluid which are decanted off from the sediment of material, is objectionable, not only from its tediousness and difficulty of thorough washing, but also from the fact that it prohibits the use of the more delicate cytological stains. With these stains it is very generally necessary that a given fluid, after producing the right degree of differentiation, should be quickly and completely removed; such a rapid change of fluid is however impossible by the decantation method.

The difficulty in question could clearly be got over by fixing the objects to a slide in the manner of sections. For this purpose two methods have been devised, but both have considerable objections. One method is that of Overton (*Zeit f. wiss. Mikroskopie* Bd. vii. 1890, p. 9), in which the objects, after being brought up to absolute alcohol (if necessary, by placing them in dilute alcohol

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