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THRIPS POLLINATION IN *CALLUNA*

BY

O. HAGERUP

KØBENHAVN
I KOMMISSION HOS EJNAR MUNKSGAARD
1950

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1. Bee Pollination.

In Danish nature perhaps there is no plant the flowers of which may be pollinated in so many different ways as those of *Calluna*. Nearly all the commonest ways of pollination may be found realized in nature.

The heather flowers have both fragrance and honey and attract both man and insects. Hence they are nearly always surrounded by swarms of insects of many different species. The commonest visitors, however, are honey-bees and humble-bees, which with great industry collect the fine aromatic honey, which again is an article much desired by man.

The importance of the visit of the insects to the pollination appears so obvious that hardly anybody will think of doubting it. Still I came to doubt the necessity of the bees' visit during various stays in the Faroes (particularly in 1922—23 and 1947), where there are neither bees nor butterflies in so large a number that they can play any important part to the pollination of *Calluna*. In spite of careful investigation I did not succeed in seeing any large insects visiting the flowers. And still all flowers produced fruits with ripe seeds, and seedlings were of common occurrence in nature in the Faroes.

Visits by the usual large insects thus cannot be necessary to the pollination. But how, then, is the *Calluna* flower pollinated with the automatic certitude with which it takes place in nature? And is the visit by the bees more or less superfluous?

It is important for the pollination that the style should be so long that it projects outside the flower in a similar way as in many anemophilous flowers. This means that the stigma is easily touched by visiting insects. On the other hand the length of the style also makes it difficult for the insects to put their heads into the flowers, thus touching the anthers, which are short and nearly completely confined in the remarkably small corolla.

When bees and other insects with long proboscises visit the flowers they mostly keep at a suitable distance from it and extend

Fig. 1. *Calluna.* Flowering shoot from the Faroes. × 3.
Fig. 2. *Taeniothrips ericae* pollinating a flower (Denmark). × 12.
Fig. 3. *Erica cinerea* (the Faroes). Longitudinal section of flower-bud in self-pollination immediately before flowering × 12.

the proboscis to its full length. The proboscis is then inserted in the flower from its lower side (L in fig. 6), where there is the greatest space between the corolla and the stamens.

Hence the proboscis is often the only part of the insects which comes into direct contact with the anthers, but this smooth, thin organ is badly suited for receiving and retaining pollen and carrying it to other flowers.

On the other hand, the proboscises of the insects are rarely (or never?) inserted in the space (M, Q) between style and anthers. And at the bottom of this space a material part of the nectary (N) is hidden and thus inaccessible for the sucking of honey. In a cross-section of the flower (fig. 4) it appears that the nectary has a similar form as a cog-wheel, the anthers being placed in the spaces between the cogs. Only the tips of the cogs can be touched direct by the insects, and here some of the honey oozes out into the bottom of the corolla, which therefore is sticky, and there is always some pollen there.

The anthers split open along the side almost at the same time as the corolla opens; but as the anthers are placed very close together with the sides pressed against each other, very little pollen is liberated at a time. And during the whole flowering period there is constantly some pollen encased in the anthers, and almost everywhere in the interior of the flower some pollen may be found.

However, remarkably little pollen is seen on the insects that have visited *Calluna* only. And the proboscises that have touched the anthers as a rule do not get into contact with the stigmas.

Because of the mentioned structural feature of the flower the visit by the insects is hardly of any appreciable value to the pollination. *Calluna* may even completely do without visits by bees and butterflies (in the Faroes) and still be pollinated with automatic precision.

2. Wind Pollination.

If a person walks through a dense vegetation of flowering *Calluna*, his feet will be powdered with a fine layer of pollen. Also when it is windy, fine clouds of pollen are shaken out of the flowers.

Hence there is hardly any reason for doubting that the flower under certain circumstances can be pollinated by the wind.

But this way of pollination, too, may be uncertain, e. g. during a prolonged period of rain, for in this case the stigma will soon get wet, so that it can hardly receive pollen, and much pollen shaken into the air will be caught by the raindrops and beaten to the ground, where it perishes.

These drawbacks about wind pollination are particularly conspicuous in the Faroes, where there may at any time be protracted periods with violent rain. I have myself witnessed that it has been raining for five days in succession without any intervals. In such a case probably most of the pollen available will be shaken out of the flowers and be spoiled. And still the fructification is perfect also in the Faroes. Hence there must be securer ways of pollination of the flowers than by the aid of insects and the wind.

3. Self-Pollination.

In *Erica cinerea* (Fig. 3), which in the Faroes is growing together with *Calluna*, the flowers are self-pollinating: the anthers open immediately before the flowers come out, and pollen falls direct on to the stigma, which is also ripe at this early stage. When at length the beautiful hanging flower opens, it emits fragrance, and there is also plenty of honey present; but a possible visit by insects is without any importance to the flower at all, as it has already been pollinated.

In *Calluna* the anthers also open while the flower is in bud. But at this stage the stigma is not yet ripe for being pollinated. Only when the flower has opened (fig. 1), the stigma reaches its full length and then protrudes far out of the flower so that the stigma cannot get into direct contact with the anthers, from which a little pollen is constantly emitted into the air.

Some of the pollen thus liberated will probably be able to hit upon the flower in question itself or neighbouring flowers, i.e. provided that e.g. the very capricious weather of the Faroes does not prevent this somewhat uncertain way of pollination.

But as the flowers are placed so close together, wind-pollination is no doubt more effective than insect pollination, and many flowers inevitably receive pollen produced by themselves.

However, if the plant had exclusively to content itself with wind pollination, the consequence would undoubtedly be that many flowers were not pollinated, as is the case in e.g. *Empetrum*.

4. *Thrips* Pollination.

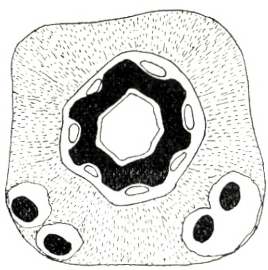
The above-mentioned three ways of pollination thus all involve a certain uncertainty. As, however, as mentioned, the pollination takes place with automatic certainty, the plant must dispose of other, more certain methods of pollination. But which? In order to obtain an answer to this question I examined the plant in the Faroes in 1947 throughout a flowering season and later supplemented the observations made by investigations in various places in Denmark.

Already Nordhagen discovered and described the curious way in which the corolla opens. This is pressed outwards because it grows very much in thickness at its base, where a circular pad ($A_1 - A_2$ in fig. 6) arises. The inspissation, however, is greatest on the lower side of the corolla (at A_1), the latter thus getting distinctly zygomorphic.

The filaments are just as curious as the corolla, being thin and band-shaped at their bases (figs. 4—6) so that a hinge is formed by which the filament may be moved towards or away from the style.

In the flower not yet full-blown the filament is of nearly the same thickness in its whole length (fig. 5); but when the corolla opens, this is to some degree due to a pressure from the bases of the filaments, these suddenly growing very fast in thickness as indicated by the dotted line in fig. 5. The inspissated part of the filament (U in fig. 6) is situated immediately above the thin hinge mentioned and opposite to the thick pad on the corolla. All these inspissations arise by the cells of the subepidermal layers of cells increasing their volume very considerably.

In a longitudinal section of the flower (fig. 6) it is seen that the inspissations in anthers and corolla are also situated nearly opposite to the thickest part of the ovary. The tensions arising mean that the lower parts of the filaments in the full-blown flower are squeezed very firmly into a definite position, viz. so that the anthers are closely united with their sides against each other. And as the anthers open at the sides (fig. 5) the tense position of the stamens causes that little pollen may be liberated at a time, the possibilities of pollination thus covering a comparatively prolonged period. The upper halves of the filaments, however, are both thin and S-shaped. Hence the anthers may be tilted to and fro so that the passage between style and anthers is not barred to small insects; but I have never seen large insects sticking their proboscises inside the stamina down to the part of the nectary concealed inside these (N in fig. 6), which is obviously reserved for particularly small insects.



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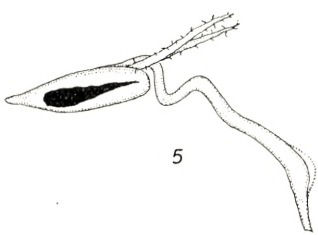

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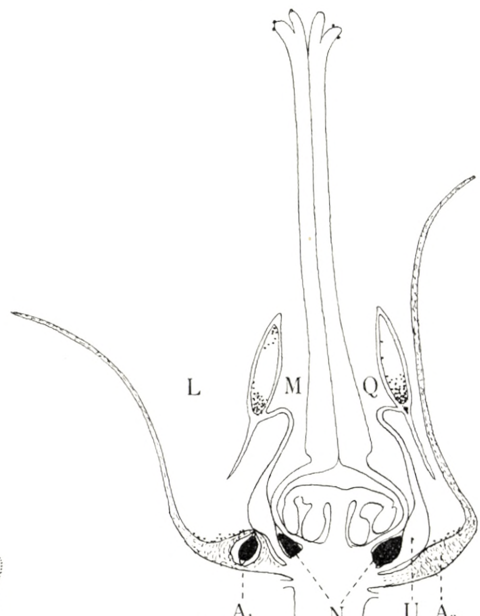

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Fig. 4. *Calluna.* Transverse section of old flower with four ova (black) of *Taeniothrips ericae* at the (hatched) base of the corolla. Nectary black. The Faroes. × 15.

Fig. 5. Stamen from bud. × 18.

Fig. 6. Longitudinal section of flower (the Faroes) with ova of *Thaeniothrips ericae* (at A_1) in the (hatched) base of the corolla. A_1—A_2: inspissated pad. N: nectary (black). The proboscis of a bee is inserted at L on the lower side of the flower. At M and Q *Taeniothrips* forces its way down to the nectary. × 15. For further details see text.

On the basis of experiences gained in Danish nature as regards pollination I searched during the flowering season in 1947 in the Faroes for large insects which might play a quantitatively significant part to the everywhere abundant fructification in *Calluna*; but all searching continued being in vain day by day. The riddle could not be solved by any of the usual channels.

The only insects which were common on the Faroese *Calluna* were some remarkably small *Thrips*; but these were only about

1 mm. in length and very slender. A priori it would seem impossible that such small creatures should be able to play the role of a large humble-bee; nor has such a view been advanced in the literature.

However, these small creatures constantly obtruded upon my attention when I examined the flowers; for they were always present, often several (up to 4—6) crawling in a single flower. In spite of their small size I was gradually forced to take the animals seriously and to subject their doings in the flowers to a more detailed examination.

It is not difficult to observe these *Thrips* closely in a magnifying-glass. They are unwilling to leave the flowers even if these are shaken in a collecting box on a long excursion in the mountains. Likewise they are particularly stationary during rain and gales when they have a really good hiding-place at the bottom of the bell-shaped corollas, which because of their position, small size and narrow entrance are not filled with rain-water. I have had flowers of *Calluna* steeped in water (to which was added a little formalin) for three years without any water entering the corollas and the (dead) *Thrips* lying in there.

The corollas do not only offer an ideal hiding-place to these insects during the frequent Faroese storms, but there the *Thrips* may constantly and undisturbed perform their other life functions, both—as we shall see below—eating, copulating, and laying ova at a time when the other types of pollination fail.

Thrips are lively animals, which are constantly moving about the inner parts of the flower, and because of their small size they can even easily crawl into the narrow space between style and stamina (M and Q in fig. 6), where the proboscises of larger insects, as said above, will not go. In this room at the base of the style the animals thus may be sitting quite unmolested, sucking off the whole surface of the nectary (black in figs. 4 and 6), which cannot be touched by bigger insects. Bees can only collect the honey which through the spaces between the bases of the stamens seeps into the bottom of the corolla, but as regards bees a direct contact with the nectary can only take place on the fine tips of the cogwheel-shaped nectary (fig. 4).

However, what is of special interest in this connexion is the fact that *Thrips* cannot reach down to their favourite haunts on the nectary without touching the anthers, which are just giving off pollen at the same time as the nectary secretes honey. As mentioned above, the anthers open at the sides (fig. 5), but these are set together so closely that very little pollen may be given off at a time, and this particularly takes place when the anthers are pressed apart, as is just the case when a *Thrips* squeezes down into the narrow space between style and stamina. A direct examination actually shows that pollen may be found everywhere on the visiting *Thrips*. The small insects transport few pollen grains at a time, it is true, but then only a small number of ovules (about 20) are found in the ovary, and hence about 5—6 tetrads will be sufficient to fertilize a flower, a quantity of pollen small enough for being easily transported by one *Thrips* at one visit only.

What particularly causes the insects periodically to be restless and to move about not only between the sexual leaves of a single flower, but also to fly about from flower to flower, is the fact that the individuals of one sex—the males—are apterous and comparatively rare, so that the females have to roam about to seek out the males.

Hence it is quite a normal thing to observe a female which has stayed so long on the nectary that it has eaten its fill in its hiding-place inside the filaments. It is now sexually mature, and if it has not been fertilized it will leave the nectary to search for a male, which takes place in the following characteristic way: (1) It leaves its place on the nectary (N in fig. 6), and from here there is generally only one beaten path, which the insect mostly follows slavishly by (2) crawling along the tubular channel (M, Q) between stamens and style. By squeezing through this narrow passage the insect cannot avoid touching the anthers and receiving pollen.

(3) The insect now naturally continues its way along the style, like so many other insects wanting to seek out as spacious a starting-place as possible, where it can freely unfold its wings without these striking against neighbouring objects.

(4) As a matter of fact it is difficult for *Thrips* to get the four wings clear of each other and have them unfolded, because along their edges they are densely set with a fringe of long stiff hairs which clutch each other so that the wings function as if

they were glued together. Hence the insect often sits on the stigma, bending its abdomen up and down in order thus to disengage the pair of wings. During these efforts the insect trips to and fro above the stigma in order to find the most favourable position for its start (Fig. 2). These manœuvres to make the wings ready to start take some time and offer rich opportunities for the pollen which the insect carries with it to be shaken off on the stigma or even be pressed direct on to its sticky surface.

In short, the *Thrips* uses the style in the very same way as the starling utilizes the perch of a starling-box. And exactly in the most spacious place of the flower is the stigma. It has not been possible to see whether arriving insects land on the stigma, too; but during the roaming of the insects both in the flower and from flower to flower, they must be able to transport pollen from the flower in question itself as well as pollen from other flowers and pollinate the stigma with it.

(5) After the vegetative period of the insect on the hidden parts of the nectary the copulation follows, and soon the time approaches when the *Thrips* is to deposit its ova. In these last phases of the insect's life it generally stays outside the stamens at the bottom of the corolla. Here it again takes nourishment, both by sucking honey from the same sources as are utilized by possible bees, but also by gnawing at the juicy tissue which is particularly well developed in the lower parts of the corolla. This tissue formerly served to open the corolla. Now it has been smeared with nectar. Further there are still numerous pollen grains which have stuck in the viscous nectar, and the viscous pollen sticks to the insects when they move about this favourite haunt of theirs and occasionally creep over the anthers on to the stigma in order, perhaps, to attempt a fresh start to another flower.

The juicy tissue which is eaten by the *Thrips* is found not only in the above-mentioned pad (A_1 and A_2 in fig. 6), but also at the base of the stamens (see fig. 5—6). Hence it is often seen that the insects simply fell the stamens by gnawing through the bases of them, which are particularly attractive by being smeared with honey. These overturned stamens particularly easily give off pollen, part of which is caught in the honey, from where it thus may be transported to the stigma.

(6) The *Thrips* does not even leave the flower when it is

going to deposit its ova. But the symbiosis between the insect and *Calluna* is so thorough that the insect sticks its short and sharp ovipositor into the thickest, soft tissue of the corolla, immediately into the above-mentioned pad (A_1 and A_2 in fig. 6), which is the only place in the corolla that affords room for the comparatively large ova.

Calluna is one of the few plants indigenous to Scandinavia the corollas of which generally remain on the plant until the next year. These withered flowers thus contain the ova of the insects that may pollinate the flowers of the coming season. It is true that some of the withered flowers fall to the ground during the following winter, but mostly they remain under the plants in the dense vegetation so that the hidden ova are not removed very far. As regards the flowers which remain on the plants until next year, the tender larvae thus are hatched close to the place where they may spend the rest of their life until oviposition and death.

A series of longitudinal sections through an insect which has stayed inside the stamens showed that the abdomen contained four ova only. And series of transverse-sections through flowers (fig. 4) which had begun withering, further showed that the ova are deposited in pairs in small chambers in front at the base of the corolla, where there is most space. Here the insects remain, safe and independent of storms. They cannot be chased away by an obtrusive proboscis of a bee, and the oviposition may be observed direct through a magnifying-glass. Perhaps the individual insect may lay more than one hatch of ova.

The development of the insect from ovum to imago is not known in detail. The larvae, however, are found in the flowers (together with the imagos), where they move about and also transport pollen so that they may contribute their share to the pollination. Preisner (1926) assumes that the pupation takes place on the ground under the plants, from where the imagos of the *Thrips* after hibernation emerge next summer, when the flowering season approaches. In the Faroes the imagos were already found in the flowers which had come out first. Preisner found the first females as early as May and the last in November. This late occurrence only indicates that *Calluna* is in bloom much later in Southern Europe than in Scandinavia.

It would be interesting to investigate to how high a degree the curious conditions of symbosis between *Calluna* and *Thrips* may be generalized. J. Maltbæk states that all the Faroese *Thrips* belonged to the species *Taeniothrips ericae* Holiday. It is also this species which dominates in the Danish *Calluna*, but here we may also find interspersion of other species (e. g. *Frankliniella intonsa* Trybom). *T. ericae* is "common in West Jutland, but also elsewhere in Jutland and North Zealand in regions with heath and bog". Its existence is closely connected with

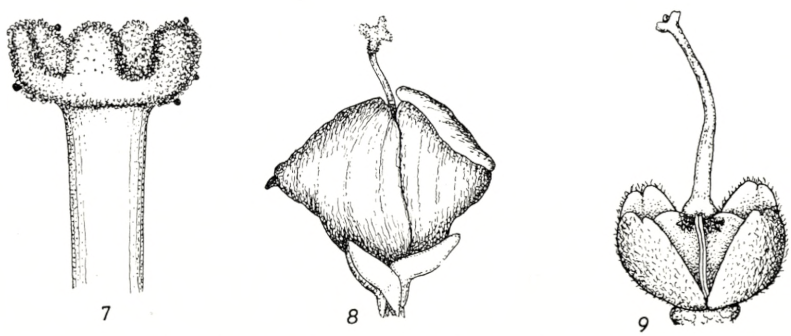

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Fig. 7. Stigma with few tetrads pollinated by *Taeniothrips*. The Faroes. × 50.
Fig. 8. Hibernated flower. The Faroes. × 7.
Fig. 9. Hibernated, empty fruit. The Faroes. × 7.

Calluna, even though it also may be found on other plants, particularly such, however, as belong to the *Ericaceae*.

T. ericae is distributed from Northern Iceland to the Mediterranean and from Russia to England (Preisner), thus with a similar distribution as *Calluna* (Nordhagen).

In other species of *Thrips* parthenogenesis is common, and in some species males are even completely unknown.

The fact that *Thrips* are of importance as dispersers of pollen is both recorded in the literature and easy to observe in many different flowers.

Dr. A. Löve has found *T. ericae* in abundance in Iceland, where bigger pollinating insects are absent. Both here and in the Faroes this small insect obviously is one of the conditions that *Calluna* is found at all in the place in question, as both wind- and self-pollination will fail in most normal years because of the climate. Further, if there were no *Calluna* in the Faroes the sheep would starve to death in unfavourable winters, which again would mean a catastrophe to the population. The Faroes (literally 'the Sheep Islands') would not either have been given this name about a thousand years ago.

The fact that the insect may also occasionally be observed on other plants only indicates the vagabondizing tendencies of this lively animal, which again are due to its search for food and for the other, wingless sex (the males). I have myself found *Thrips* on *Erica*. It should be investigated whether the insect may also deposit its ova in the hibernating corollas of this plant.

Altogether the importance of the various species of *Thrips* to pollination ought to be investigated in more detail. As an illustration of this wish *Silene acaulis* may be mentioned. In the Faroes, where this species is generally distributed, single tufts are often found removed from other individuals. Even when such individuals are purely female, they do set abundant fruit although there are no pollinating insects upon them other than *Thrips*. In a number of *Compositae*, *Armeria* and many others as well, it seems that the flowers may be pollinated by *Thrips*. J. Grøntved further has found many *Thrips* in regions in Greenland poor in insects, where the flowers generally seem to be thrown upon self-pollination.

Hence, continued investigations of the doings of the other *Thysanoptera* in other flowers might open a new chapter in the biology of pollination.

A generalization from morphological points of view seems particularly natural within *Bicornes*, most species of which have stamens reminding of those of *Calluna* by forming a narrow tube encircling both style and nectary, which is accessible just to such small insects as *Thrips*. Hence it should be investigated whether e.g. our native species may occasionally or mostly be pollinated by *Thrips* and, if so, where these insects deposit their ova in the case of the species the corollas of which are dropped immediately after the flowering season. Similarly the flowers of many *Compositae* seem to be adapted to *Thrips* pollination because the nectary in these, too, is hidden at the bottom of a very narrow tube into which only very small insects may squeeze.

It should, however, be emphasized that the way in which a plant is pollinated may change greatly from place to place and from year to year. *Calluna* is a particularly fine illustration showing how cautious one should be as regards generalizing within floral biology.

The winter of 1946—47 was so unfavourable to the hibernation of *Calluna* that a considerable number of the old plants died in the greater part of Scandinavia. In the few flowers which developed the next summer (1947) there was a nearly normal number of *Thrips*, as some of the ova obviously had been destroyed with the plants killed.

The following summer (1948) the heather had already succeeded in regenerating because the youngest individuals had been able to stand the unfavourable winter. Hence there was a rich flowering in 1948; but now there was a deficiency of *Thrips* because these deposit comparatively few ova and no doubt require several years to reach a normal number of individuals again, which may be of importance to the pollination. However, there were (1948) abundant visits by bees, and hence the stigmata were densely filled with pollen (in Denmark); but at the same time *Calluna* is referred to *Thrips*- or wind-pollination in other regions where larger insects are missing or are rare.

For the further understanding of the value of the various methods of pollination I isolated a flowering plant under glass so that neither wind nor insects might cause pollination. None of the numerous flowers then set fruit.

Other individuals were planted in the open, but 1 km. from the nearest *Thrips* locality. These were pollinated by wind and bees and set abundant fruit.

Hence it follows that *Calluna* cannot fructify without pollination and that according to external conditions pollination may take place either by (1) wind, (2) bees, (3) butterflies, or (4) *Thrips*. According to circumstances the flowers are pollinated by pollen originating from the same flower or from other flowers; but a direct contact between anthers and stigma is unknown. From a genetic point of view, however, the pollination of *Calluna* in many cases must be designated as autogamy.

Summary.

Calluna may be pollinated in many different ways. The one which may be observed most easily is bee-pollination; but this method of pollination fails completely in some regions, e. g. in the Faroes, where large pollinating insects are absent.

In (probably the whole of) the area of distribution of *Calluna* the flowers, however, may be pollinated by a very small insect (*Taeniothrips ericae*), which even deposits its ova in the swollen base of the corolla (figs. 4—6). The stamens form a tube at the bottom of which the greater part of the nectary is hidden in so narrow a room that only very small insects may squeeze in there.

In the corolla the insect seeks shelter (from storms), food, and a breeding-ground. In return it pollinates the flower by creeping on to the stigma (fig. 2), from where the winged females mostly start when flying away from the flower, e. g. in search of the wingless and rarer males.

Without this curious symbiosis there would hardly be any *Calluna* and hence hardly any sheep in the Faroes and other northern regions.

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