

DET KGL. DANSKE VIDENSKABERNES SELSKAB  
BIOLOGISKE MEDDELELSER, BIND XVIII, NR. 5

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# RAIN-POLLINATION

BY

O. HAGERUP



KØBENHAVN

I KOMMISSION HOS EJNAR MUNKSGAARD

1950



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## 1. The Problems.

It is a well-known fact that rainy weather may have a very injurious effect on many flowers. The fructification becomes poor and many flowers may be completely ruined during showers of rain because petals are beaten off, stamens and styles rot, and pollen is spoilt and washed away while at the same time visits by insects are prevented.

In nature finer flowers (e. g. those of grasses) may be injured by rain in a similar way as flowers in gardens. In the literature there is plenty of information about such structural features as serve to protect flowers from the injurious influence of rain.

All these questions forced themselves upon me during a year's stay in the Faroes (1922—23), where it is raining—little or much—on most of the days of the year. I have even witnessed that it has been raining incessantly there for five days running. Thus the flowers of the wild plants must be able to stand the rain without the fructification being prevented. In 1947 the Carlsberg Foundation again enabled me to study in the Faroes, where conditions of pollination are much simpler than in Denmark, because the usual big pollinating insects (bees, butterflies) are practically absent. Further the abundance of rain gives good occasion to investigate how the flowers behave in the kind of weather which tempts the floral biologist to keep indoors. Later the observations made in the Faroes were supplemented by studies in Denmark.

The available information of the injuriousness of the rain perhaps might even seem to be in too good agreement; for indeed it is fact that numerous wild flowers are completely open even during the heaviest showers of rain, so that one may ask about the usual injurious effects on e. g. the beautiful abundance

of *Caltha* on Danish meadows when a violent thunder-shower sheds so much water that the open flowers may be filled with water several times. When the storm is over the flowers still appear to have got unhurt through this event, which e. g. to the blossoms of apples and cherries has proved a catastrophe.

Thus there must be some way in which certain flowers may hold their own through showers of rain. But how, then, are these protected from destruction, e. g. in other climates where it is raining much more frequently than in this country? Indeed, some aquatic plants (e. g. *Zostera*) are normally pollinated by

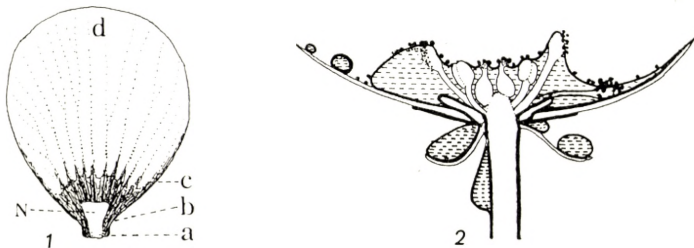


Fig. 1. *Ranunculus repens*. Corolla from the upper surface. N: nectary; a—c: area binding water; in the curve, b, part of the outlet is found; c—d: nonabsorbent area.  $\times 3$ . Denmark.

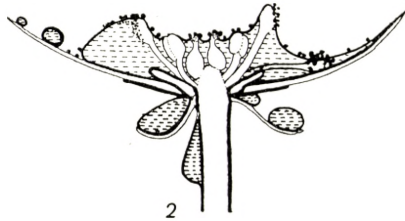


Fig. 2. *Ranunculus flammula*. Longitudinal section of flower. Rain-water dotted and with fat contour. On the surface of the water pollen is floating to the stigmas. Surplus water is drained off through the outlet at the bottom. The Faroes.  $\times 5$ . See further the text.

means of the water. Might it be possible, after all, that some of the terrestrial plants were able to be pollinated by means of rain?

If on a normal spring day one approaches a Faroese settlement, the problems of the rain often arise at once, because the small brooks are bordered by a vivid yellow fringe of *Caltha* on which the rain is pouring down. Later it appears that all the flowers have still been normally pollinated and numerous seeds float on the violently rushing water. The pastures round the houses, too, have a yellowish tinge, originating from the numerous *Ranunculus* flowers, which are not either injured by the rain. And on the untilled parts of the mountains yellow spots of *Narthecium* are seen, the flowers of which are wide open and turned towards the rain. This species, too, fructifies abundantly.

In what follows a few examples will be adduced which go to show how flowers can manage all right in the rain without

having their pollen washed away and spoilt. But beyond having this purely defensive and passive task to perform, some flowers also prove to have a positive faculty of utilizing the rain in the service of pollination.

## 2. *Ranunculus.*

Among most European peoples the buttercups enjoy a remarkably great popularity, which is reflected in numerous picturesque vulgar names. In the Faroes the flowers thus are called "Sun-eye", which name does not only refer to the colour of the corolla, but also to the bright and glossy surface of the latter, a special quality which is not found to such a pronounced degree in any others of our wild plants. Hence the question naturally arises whether the glossiness of the corolla should somehow be of use to the flower. If one tries to drip water into fresh flowers, it appears at once that the petals are markedly nonabsorbent. The water gathers in nearly spherical drops, which soon trickle down the more or less obliquely upward turned glossy petals until they come to rest at the bases of these.

If one takes a fresh petal and dips it into water, it proves that it is not equally nonabsorbent on the whole of its surface. On the upper side there is at the base a scale which covers a nectary. Here the water is bound very strongly, while the rest of the upper side is the most nonabsorbent part of the corolla.

On its lower side the corolla is also distinctly nonabsorbent on the whole of its outermost broad part; but at the base a darker part is seen (fig. 1), which has a dull surface that binds the water. This curious base is situated immediately above the sepals, for which reason a small room thus forms between calyx and corolla where rain-water may be kept by capillary action.

A stamen is nonabsorbent except at its base and in the places where the anther has opened. Hence pollen is easily washed away from the stamen when it is raining, and water and pollen are distributed among the numerous stamens at the bottom of the flower.

Further, ripe stamens may bend outward and downward when the petals are moist on the upper side. Then they generally lie down right on the surface of the water, which is soon filled



with floating pollen, this being rapidly distributed everywhere in the interior of the flower where there is any water, e. g. between the bases of the stamens and on the petals. At new supplies of rain-water the stranded pollen is again whirled round in the interior of the flower.

In the young flowers the carpels are nonabsorbent at their tips. The flower is then particularly susceptible to insect pollination. But at that time there is little chance of self-pollination, because the youngest stamens, which are closest to the gynaecium, are not yet open, and hence cannot place their pollen direct on the stigmas.

In the fully developed flowers the gynaecium, however, easily gets moist in rainy weather. If a small drop of water is placed on one side of a gynaecium, it is in few minutes sucked down between the carpels, and the water then may be observed direct between these. This absorption of water thus does not take place momentarily as in filter paper. If the water is placed at the base of the gynaecium, where the stamens are situated, it is particularly easily absorbed, as the axis of the flower binds it just at the bases of the stamens. The normal direction of the water in the gynaecium thus is from below upwards; but below we just find pollen floating on the surface of the absorbed water.

If a drop of water is placed on the tip of the gynaecium, it is absorbed slowly between the carpels. This water will not be of any great value to the pollination, either, because it carries no pollen.

The drops of rain which hit the tip of the gynaecium are soon thrown towards the sides by the shakings produced by both wind and rain. Thus pollen may come to float on the water, which is rapidly absorbed between the stamens and soon ends at the bottom of the flower, where it is united with the pollen-bearing water already found there, which is drawn up between the bases of the carpels and further up to the stigmas by capillary action.

The curious capillary absorption of water in the gynaecium is conditioned by the form of the carpels and their mutual position, as illustrated in figs. 2, 3, 4, and 8 (where the paths of the water are indicated by dots). The carpels are placed close together; but still there are quite small channels between their

edges (figs. 4 and 8). Particularly wide are the spaces at the bases of the carpels, where the water may rise along the axis of the flower. From these mains the water flows out through the narrow passage along the inward turned edges of the carpels (fig. 4), but exactly here is the lowest part of the stigma (figs. 3 and 8).

The adhesion of the water to the carpels is facilitated by small fixed glands in the surface of the carpels. These are particularly conspicuous in *R. sardous*.

If this curious flower is exposed to a heavy rain which hits all the parts of the flowers, the open anthers are nearly completely

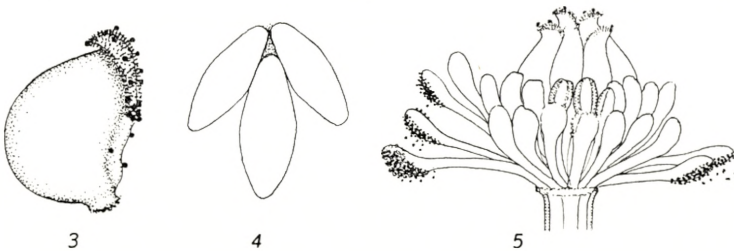


Fig. 3. *Ranunculus bulbosus*. Carpel.  $\times 12$ . Denmark.

Fig. 4. *Ranunculus bulbosus*. Cross-section of three carpels; path of the water dotted.  $\times 17$ . Denmark.

Fig. 5. *Caltha palustris*. Flower without petals.  $\times 4$ . The Faroes.

opened and pollen is flung aside and on to the water at the bottom of the flower, where it floats on the surface, which rises more and more. If the water could fill the flower completely so that it overflowed, the pollen would get lost by being washed away. The flower must have some protection from this catastrophe to the pollination; for during continued rain the amount of water may be so great that all the buttercups in the region in question may even be filled several times and hence are washed out completely. In nature we do not find that the flowers may be brimful of water, either, nor that the water overflows. The amount of water is rarely greater than indicated in fig. 2. In the flowers which have been exposed to rain for a prolonged time we only observe the very thin coat of water which has been bound by capillary action.

The greatest amounts of water are found in the flowers at the beginning of the rain, because the faculty of shedding water is greatest as long as the flower is still dry and young. This

faculty, however, is lost completely or in part during continued rain. Even the upper surface of the petals, which are the most nonabsorbent parts of the flowers, may in time come to bind water (fig. 2 on the left).

Fig. 2 illustrates the first filling of rain-water in *R. flammula*. As described in more detail above, the drops trickle down along the insides of the hollow petals, where they may wash off the pollen which is nearly always futilely sticking here. Other drops wash out nearly all pollen from the open anthers and accumulate at the bottom of the flower to form a connected body of water with abundant pollen on the surface. During continued rain the water rises between the carpels, where the moving grains of pollen soon hit the stigmas and these are pollinated.

Not only the interior of the flower is moistened during heavy rain. The stalk of the flower is moistened as well, even immediately below the flower where no drops fall direct.

If one holds a cut flower of e. g. *R. repens* or *R. bulbosus* vertically between one's thumb and fingers and drips 5 to 10 drops into it, it soon appears that the water can run through the bottom of the flower, which thus must have some outlet of a suitable size.

If the water passed rapidly through the flower, the pollen would be carried away by the stream and be lost; but the outlet at the bottom of the flower is so narrow that most of the pollen on the surface of the water gets stranded on the large number of obstacles at the bottom of the flower or rises again to the surface of the arriving rain-water, from where it has again a chance of getting up to the stigmas.

There is nearly always a little pollen in the water that runs out of the bottom of the flower. This water, however, is comparatively poor in pollen (or completely without it) as compared with the surface water. It is of course of great importance for the pollination that no great quantities of pollen are lost through the outlet.

The narrower and the more sinuous the outlet, the more slowly the water will pass and the less pollen will be lost.

Exactly according to these principles the passage through the bottom of the flower is arranged. Further, the water naturally flows first over the surfaces which bind the water to the highest degree.



In fig. 2 the paths of the streams of water are indicated by water-surfaces being drawn with a fat, black line, while the rest of the water is dotted.

The petals are placed so close together that there is only a narrow fissure between each two. And the passage between them is further made difficult by the fact their edges are nonabsorbent except along the small part where the nectary is situated, and, as appears from fig. 1, there is also here a slight bend (b) of the edge. In this place the first and most difficult passage in the outlet is found, and exactly off and under this place the sepals are situated in the hollow surface of which the water oozing through is collected, often as a big drop that above is bound to the lower surfaces of the petals, which exactly in this place bind the water.

If more rain comes down, some of it may drop down from the tips of the sepals. In most species, however, the water is slowly drained off through the fissures between the sepals. It is then collected at the bases of the sepals, from where it further trickles down the stalk. This passing stream is easy to point out when one holds a flower in one's hand and drops water into it. The water will then soon drop into one's hand.

During natural rain the water which passes through the bottom of the flower generally does not gather into drops, but flows evenly down the stalk. Thus it is avoided that the water by sudden and violent movements tears pollen with it.

This important fact, that the stream is even, has in certain species been secured by various contrivances in the structure of the stalk. The regulating faculty of the stalk is particularly clearly observed in *R. bulbosus* (and *R. repens*), the stalks of which are provided with deep grooves, which are highly conductive to water, as can easily be seen by direct observation.

The capillary action of these grooves may also be demonstrated by placing a gynaecium which has been relieved of all the leaves placed under it, in a glass of water. The water then rises through the grooves where it is kept as a fine stream under numerous hairs along the sides of the grooves which bind the water. By way of the grooves the water is carried right up to the gynaecium the carpels of which the next day prove to have been moistened by water that has been transported through the grooves of the stalk.

One more form of stream regulator is found in the sepals in *R. bulbosus* (figs. 6 and 7), which have a sharp transversal bend so that the outermost and longest parts of the sepals are directed downwards, the tip thus being situated close to the stalk of the flower.

If any water enters this flower, it runs out between the bases of the petals—as in other species—and collects in the space between the bases of petals and sepals. From here the water passes out between the sepals; but then it collects in the large

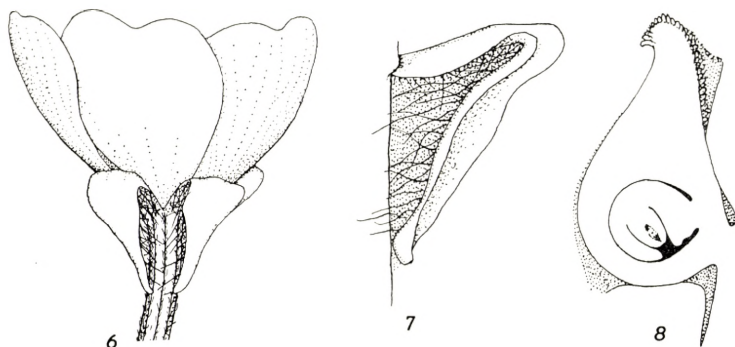


Fig. 6. *Ranunculus bulbosus*. Flower. From the lower surface of the pilose and retroflex sepals surplus water is drained off by the grooves on the stalk. Denmark.  $\times 2$ .

Fig. 7. *Ranunculus bulbosus*. Sepal with rain-water (dotted) confined under it. Denmark.  $\times 6$ .

Fig. 8. *Ranunculus acer*. Longitudinal section of carpel in rainy weather. The surrounding water dotted. The Faroes.  $\times 40$ .

space between the stalk and the lower side of the retroflex part of the sepals, where it is retained between remarkably long and stiff hairs which are found exclusively in this place.

From this curious reservoir under the sepals (fig. 7) the water is carried downwards to the tips of the sepals and from there farther on to the grooves on the stalk. This transport takes place slowly and evenly and in a way which reminds of that in which ink flows from the tip of a fountain pen, where the fluid is bound in a similar way as under the sepal of *R. bulbosus* and is given out in a corresponding continuous manner.

There are considerable differences in the ways of pollination in the various species of *Ranunculus*. Thus they are all visited

by insects, as has been exactly recorded in the literature, which is amply summarized by e. g. Knuth.

*R. acer* is the species which is visited by most insects. In the Faroes the species particularly grows near inhabited places, where there is a particularly large number of flies, and in most flowers some insect is constantly observed. During rain the thin stalks are bent so that the flower nods and turns the lower side towards the rain. In the dry interior of the flower the insects then find an excellent shelter and food.

The flies generally sit on the petals and thrust their proboscises down to the nectary under the stamens. Often they also creep over the interior of the flower and transfer pollen to the stigmas.

*R. acer* thus is a typical insect-pollinated flower; but self-pollination may also take place in older flowers by the pollen of the innermost stamens dropping direct on to the stigmas.

During rain and gales the flies remain in their shelters, where they creep about in order to suck all the five nectaries; but at the same time the stigmas are pollinated with the flower's own pollen. Often *Thrips* are also found in the flowers and like the flies give rise to autogamy. Rain-pollination has not been observed in *R. acer*.

In *R. flammula* the pollination (in the Faroes) is quite different from that in *R. acer*. Thus the flowers in *R. flammula* are not bell-shaped, but are formed like a low bowl, because the petals have been spread out nearly horizontally, in which position they can catch the greatest possible quantity of water (figs. 9—10). The thin flexible stalk always bends so that the open flowers are all spread out nearly horizontally. In *R. acer* the flowers in many cases are held in a more or less oblique position and forming a deeper bowl. These differences in the position and form of the flowers is not particularly conspicuous when the two species are growing together.

In Denmark *R. lingua* behaves in a similar manner as *R. flammula*.

The flies have a predilection for *R. acer*, whereas visits by insects are remarkably few in *R. flammula* when the two species are growing together, and when the rain comes, it is the flowers of *R. flammula* which dominate the picture.



The farther one gets away from the Faroese settlements, the fewer pollinating insects are found. *R. acer* disappears with the flies. In remote localities where there are no insects at all, *R. acer* often is completely absent, whereas *R. flammula* may very well be common along the streams. This difference in distribution is no doubt in part conditioned by the fact that *R. flammula* fructifies excellently after rain-pollination.

A third type within the genus is represented by *R. bulbosus*, which is a typical self-pollinator. The chance of insect pollina-



Figs. 9—10. *Ranunculus flammula*. After rain grains of pollen (big dots) may be found everywhere in the flower, also on the stigma. The Faroes.  $\times 5$ .

tion is small, as the gynaecium is hidden between the remarkably long stamens. As in the other species, however, pollinating *Thrips* often creep about the flower, but they particularly transport the flower's own pollen.

In *R. bulbosus*, too, the outermost stamens open first, while the innermost ones unopened cover the gynaecium. At this stage the flower may be pollinated by rain.

Only when the flower begins withering, the innermost anthers open, and their pollen now falls direct on to the stigmas. But this latter method of pollination is only a last resort, as the flower generally has been pollinated before.

This last-mentioned form of self-pollination may also occur in the other species, but not so conspicuously and functioning so unerringly as in *R. bulbosus*.

In order to investigate the effectivity of rain-pollination a number of large flower-buds of *R. repens* were placed at the same time in two different glasses, where they burst without

being pollinated by insects. One glass with fresh flowers then for an hour was moved out into natural rain, after which it was again placed beside the other so that no insects had admission to the flowers.

In the glass which had been exposed to rain all the flowers fructified; but in the glass which had been isolated from both insects, shakings, and rain it proved that pollination had taken place only exceptionally in a few flowers where a little pollen had dropped from the innermost stamens on to the stigmas.

In order to test the viability of the pollen after rain I collected some flowers of *R. bulbosus* which had been exposed to heavy natural rain in the open for three hours. Both styles and stamens were drenched. The outermost stamens in the usual way had bent down towards the petals, which had plenty of pollen sticking to their insides. Some of this pollen, which was also drenched by rain-water, was placed in ordinary water in a microscopical preparation without addition of sugar or other nourishing substances, and the next day the germination was in full swing.

Another portion of the pollen wetted by the rain was smeared on the stigmas of one side of a flower, while the other side of the flower was not pollinated. Some days after this local pollination it was easy to see that only those carpels which had received the wet pollen had been pollinated and developed seeds.

Thus there is no reason to believe that *Ranunculus* pollen should lose its faculty of fertilizing by being moistened by rain.

### 3. *Caltha palustris*.

Conditions of pollination in *Caltha* (fig. 5) remind of those observed in the *Ranunculus* species (figs. 1—10).

The remarkably large flowers are highly attractive to flies, a great number of which, in many different sizes, creep about the flowers. As the carpels in the Faroese form are considerably longer than the stamens nearest to them, a pollination as a consequence of direct contact between anthers and stigmas is impossible during the first part of the flowering season. Only towards the period of withering the inmost stamens stretch so

far that they can touch the stigmas; but at that time the stigmas have nearly always been pollinated by insects long ago, and the fructification is always plentiful.

The typical insect pollination is one of the reasons why *Caltha* in the Faroes is especially found near places where the offal and droppings of man and birds are favourable breeding places to flies.

During rain the flowers are wide open and collect a large amount of water. The perianth leaves then are moistened along their insides, as they are not glossy and nonabsorbent like the petals of *Ranunculus*. But the large quantities of water are drained off faster than in the insect-pollinated *R. acer*, because sepals are missing so that the water can easily run out through the base of the perianth, from where it is rapidly transported away through the grooves of the stalk.

Both carpels and stamens also get wet in rainy weather, and pollen is distributed all over the interior of the wet flower so that pollination may also take place if prolonged rain keeps the insects away.

The stalk is so stiff that the flower cannot bend aside a little such as that of *R. acer*, for which reason the flies do not seek shelter in the flowers of *Caltha* during rain.

This species thus can be pollinated in at least three different ways just as the buttercups.

#### 4. *Narthecium ossifragum* (Figs. 11–16).

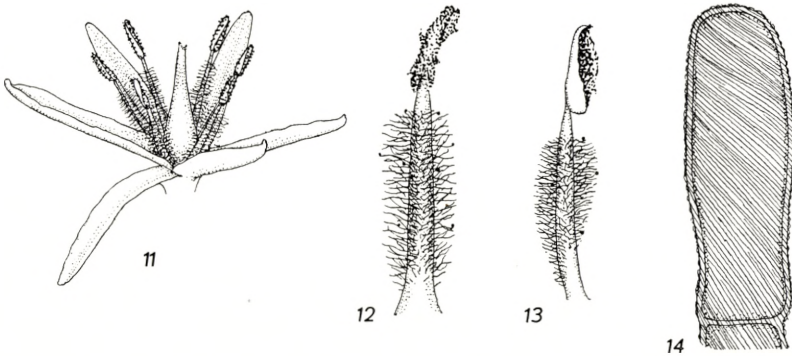
The method of pollination is mysterious. Knuth has observed the flowers being visited by bees and other insects as well and gives a list of these; but the flowers have no honey, so the insects may have been attracted by the scent or the conspicuous colour.

But insect pollination at any rate is not necessary, for the plant fructifies abundantly in the Faroes, where there are no bees. Only once I have seen a fly on the flowers there, and such a sparing visit by insects cannot play any role worth mentioning to the multitude of flowers found everywhere in Faroes, where I have examined a large material.



Only a few times I have observed spontaneous self-pollination in flowers in which a few anthers had opened in the bud and given off pollen direct on to the stigma. Wind pollination as well is extremely rare. Both this and insect pollination are made difficult by rain, and further the plant fructifies excellently in such localities where there are no pollinating insects.

In the Faroes I witnessed the rare phenomenon that there was no rain for about a fortnight. I then sought out a fairly large population of *Narthecium* with flowers newly out. Half of



Figs. 11—14. *Narthecium ossifragum*. Fig. 11: flower seen obliquely from above.  $\times 4$ . Figs. 12—13: stamens with nonabsorbent hairs seen from behind (fig. 12) and from the side (fig. 13). After rain pollen may be found everywhere in the interior of the flower.  $\times 7$ . Fig. 14. Tip of hair on stamen with nonabsorbent spiral ledges.  $\times 800$ . The Faroes.

the area was now sprinkled with water several times during a few days. After about ten days the flowers that had received the artificial rain had withered because they had been pollinated and the ovaries had begun growing; but the flowers which had not been sprinkled with water were still fresh because they had not been pollinated. Thus there is a probability that *Narthecium* can be pollinated by rain even though artificial sprinkling with water has not quite the same effect as natural rain.

If a whole, young flower is dipped into water it proves to be nonabsorbent in most places, only that it gets moist at the bottom of the flower and on anthers and stigmas. This faculty, however,—as in *Ranunculus*—is lost with age or when the flower has been exposed to plenty of rain. The possibilities of pollination therefore must be investigated in newly opened flowers.

Of particular interest to the pollination are the curious stamens (figs. 12—13), which in nearly the whole of their length are covered by long coloured hairs, which are nonabsorbent. This faculty perhaps (?) is connected with the fact that the surface of the hairs is provided with very fine spiral lines (fig. 14), which make the hairs scabrous, the physical significance of which I have not investigated.

The pollen hangs together in clots, but if it is put into a drop of water, the various grains separate and float on the surface.

If a single drop of water is dripped into the flower, it will mostly come to rest as shown in fig. 15, the stamens forming a partly water-stopping cup of a similar function as the corolla in *Ranunculus*. If more water enters the flower, it collects as a connected ring round the style, which rises above the surface as a skerry (fig. 16).

In natural rain some of the obliquely placed anthers are hit by the drops at an angle of about  $45^{\circ}$ . By the force of the drops pollen is now flung to the sides, but—because of the oblique position of the anthers—particularly towards the style and on the surface of the water.

The deep red grains of pollen are easy to see in a magnifying glass. They are moving remarkably rapidly, whirling round on the surface of the water, some of them, however, easily getting stranded on the nearest fixed points, viz. anthers and stigma, which thus may be pollinated.

If the rain-water could flow out of the flower at the top, much pollen would be washed away; but this catastrophe is avoided by the flower having a similar outlet at the bottom as *Ranunculus*.

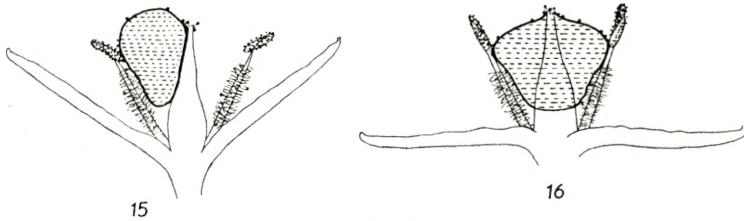
If there is plenty of water in the flower, the blows from falling drops and the water's own weight will force the water down to the bottom of the flower, which is nonabsorbent, among other things because the lower parts of the filaments are without the above-mentioned water-stopping hairs.

When the water has passed the bases of the stamens, the stream is again delayed by the petals found immediately outside, which are also nonabsorbent both inside and outside. However, these are always—even in rainy weather—separated from each other so that all the surplus water can finally leave the flower through the spaces between the petals.

The flowers are always stiffly upright and wide open, so that they receive as much water as possible. After a heavy rain the flower is wet inside. Even the hairs on the stamens have become moist, and if, further, water is dripped into such a moist flower, it runs right through.

After rainy weather pollen may be found everywhere in the interior of the flower, but also on the stigma. The pollination takes place at the beginning of the rain.

From a genetic point of view rain-pollination must be considered autogamy.



Figs. 15—16. *Narthecium ossifragum*. Longitudinal section of flowers with water (dotted), on the surface of which pollen floats from anther to stigma.  $\times 4$ .  
The Faroes.

In *Menyanthes* the inside of the corolla is set with similar hairs as are found on the stamens of *Narthecium*. The behaviour of the flower of *Menyanthes* during rain should be explained in detail.

In general it should be investigated what influence is exerted by precipitation on all our flowers, many of which are wide open in rainy weather. Such observations must be considered necessary links in future investigations within floral biology.

## 5. Summary.

(1) It has been investigated how the flowers of the following species behave during the rain: *Ranunculus* species (figs. 1—10), *Calltha palustris* (fig. 5), and *Narthecium ossifragum* (figs. 11—16).

(2) In *Ranunculus* the flowers of the commonest species may be pollinated in three different ways:

(3) First (entomophily), the just opened flower may be pollinated by insects (particularly flies). The inmost anthers then are unopened



and prevent the outermost open anthers from transferring their pollen directly to the stigmas. Conditions in the Faroes show that several species can completely do without visits by insects, as the flowers can be pollinated by rain.

(4) During heavy rain the flower is not filled with water, which would wash the pollen away.

(5) Only the bottom of the flower is covered with water, on the surface of which pollen is floating (fig. 2). The pollen-bearing water is by capillary action sucked up between the stamens and carpels which are placed close together, and thus pollen gets stranded on the stigmas (figs. 3, 5, 8).

(6) The surplus water is slowly drained off through narrow and sinuous outlets in the bottom of the flower, from where it slowly runs down the stalk.

(7) Insect pollination is most pronounced in *R. acer* (the flower of which bends in the rain). The outlet is most highly developed in species with grooved stalks (figs. 6, 7).

(8) The third method of pollination (autogamy) is used at the very last, if both insects- and rain-pollination have failed, pollen then from the inmost stamens falling direct on to the stigmas.

(9) In *Narthecium* (figs. 11—16) the very hirsute stamens form a water-stopping cup round the style. The flower has a similar outlet at the bottom as that of *Ranunculus*.

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