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POLLINATION IN  
THE FAROES - IN SPITE OF RAIN  
AND POVERTY IN INSECTS

BY

O. HAGERUP



København

i kommission hos Ejnar Munksgaard

1951

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## 1. The Problems.

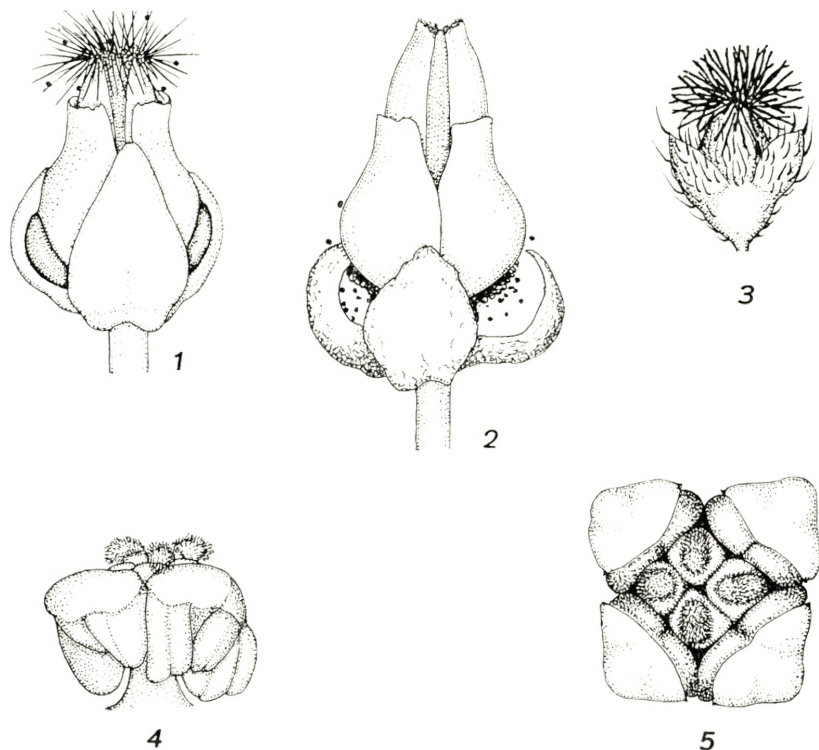
During a stay in the Faroes in 1922—23 it struck me that a number of plants were found there which in Denmark were considered typical entomophiles, such as *Calluna*, *Lychnis flos cuculi*, *Ranunculus* species, *Hypericum pulchrum*, *Armeria*, and others. But in the Faroes bees and butterflies are nearly completely absent, or they are present in so small numbers that they practically do not play any part in the pollination. In nature in the Faroes there are therefore particularly good opportunities to investigate the importance of insects for pollination.

From observations in nature in Denmark one is easily tempted to form a high estimate of the importance or even the absolute necessity of insect pollination; but conditions in the Faroes, Greenland, and other regions in the north poor in insects made me doubt the universal validity of the views mentioned above. During a stay in the Faroes in 1947 it proved that some plants can be pollinated in several different ways, which are realized in accordance with conditions in the various habitats. Thus *Calluna* in Denmark is mostly pollinated by bees and butterflies, but this does not take place in the Faroes. Other species are self-pollinating if cross-pollination fails.

In what follows instances will be adduced of conditions of pollination in a typical Faroese locality, viz. the neighbourhood of Thorshavn, where I have examined practically all the species growing in the environs of the town within a radius of up to one mile.

The world of insects is remarkably poorly represented in the Faroes, as appears from the list of names in NIELSEN (1908). Very few species are present in so great numbers of individuals that they can be of any importance to the pollination worth mentioning. During a month's stay in the Faroes in the middle of

the flowering season (July 1947) I observed neither humble-bees (*Bombus*) nor honey-bees (*Apis*). In the same period only one butterfly was present in rather a large number, viz. the little grey *Cidaria albulata* SCHFF. (*Geometridae*), but this rarely sucks



Figs. 1—5. Anemophilous flowers. Figs. 1—2, *Triglochin palustre* at a female (fig. 1) and a male stage (fig. 2).  $\times 12$ . Fig. 3, *Urtica dioica*.  $\times 40$ . Figs. 4—5, *Potamogeton polygonifolius*, side view (fig. 4) and seen from above (fig. 5).  $\times 12$ .

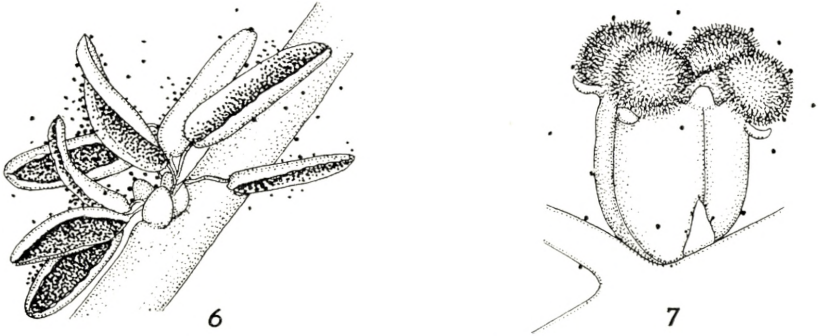
honey from the flowers. Because of the small numbers in which they occur neither bees nor butterflies nor most of the other large insects usually occurring in the Faroes are of any appreciable importance for the pollination.

The flies are an exception. Travelling in the Faroes one arrives at the result that the only insects present in so great amounts that they can really play any part in the pollination, are certain rather big flies (*Diptera*).

The importance of the flies, however, is remarkably restricted by the fact that generally they are abundant only in rather sharply

defined localities, which again is due to the conditions of breeding of the flies.

Certain significant rather large species are particularly found near the dwellings of man, where dung and refuse from animals and man are present. (The dunghills are not covered.) On the bird-cliffs, too, the insects are attracted by the dung; finally in places where seaweeds are rotting, e. g. on low beaches and on cultivated fields.



Figs. 6—7. Anemophily in *Myriophyllum alterniflorum*. Male (fig. 6) and female (fig. 7) flower.  $\times 20$ .

The dung of the sheep is so widely spread on the mountains that there is almost no pollinating insects (only a few flies) or—in certain places—no pollinating insects at all.

There is, therefore, a remarkably great difference between the vegetation on isolated, uncultivated mountains and the flora growing near the villages (the home-field), on the bird-cliffs, and on low beaches. These differences are of course chiefly conditioned by the supplies of dung, but also by the flies, as certain plants the fructification of which succeeds only after pollination by flies, are particularly found in the three localities mentioned, but are rarer or completely absent in the hill pastures.

Pollination by flies is, however, greatly influenced by rain and gales, which for a long time can prevent the activities of the insects. During storms the animals sit still and hide e. g. in the nodding flowers of *Ranunculus acer*, or they allow the rain to pour down upon them in the open flowers of *Archangelica*.

The rain may last for days. In such cases the plants must be capable of self-pollination without the assistance of insects.

We shall therefore examine the individual species and shall see that most Faroese species can really have autogamy, as already suggested by WARMING (1908).

## 2. Wind Pollination.

Numerically the Faroese vegetation is dominated by *Gramineae*, *Cyperaceae*, and *Juncaceae*. Some of these may be autogamous, but most of them are anemophilous. There is always plenty of wind in the Faroes. The value of this way of pollination is, however, greatly reduced during the constant and prolonged heavy showers of rain, which beat the suspended pollen to the ground.

The defects of wind pollination are illustrated in an interesting manner by conditions within the genus *Empetrum*, represented in the Faroes by two species, which often grow promiscuously. They are closely related, but *E. nigrum* has unisexual flowers, while *E. hermaphroditum* is bisexual. The latter fructifies abundantly, because its flowers either pollinate themselves or receive pollen from neighbouring flowers on the same shoot.

The pollen of the dioecious species must be transported a relatively long distance through the air, and the defects of this method of pollination manifest themselves in the fact that the species fructifies poorly in the Faroes. In Denmark, where conditions of the weather are much more favourable to wind pollination the same species mostly fructifies abundantly.

In spite of the difficulties of wind pollination, many Faroese species are exclusively anemophilous. This is unmistakable e. g. in the protogynous flowers (or inflorescences) of *Potamogeton polygonifolius* (figs. 4—5), *Triglochin palustre* (figs. 1—2), *Myriophyllum alterniflorum* (figs. 6—7) and *Plantago major*, the methods of pollination of which, for that matter, are well-known.

*Potamogeton polygonifolius* POURR. figs. 4—5.

Such amounts of pollen are transferred that the whole inflorescence is powdered over. Furthermore there is a great waste of pollen, which floats on the surface of the water. In this way there will hardly be any pollination as the spikes are raised out of the water during the flowering. Mostly few of the carpels are pollinated. This may be due to the fact that the flowers producing



pollen are situated below the flowers which are in a female stage.

*Juncus squarrosus* L.

The large protogynous flowers are wide open and during rain are filled with water. Great quantities of pollen may be found everywhere in the interior of the flower after a shower. In not a few cases, however, the flowers were visited by flies. Still, wind pollination is no doubt the commonest method of pollination,



Figs. 8—9. Anemophilous flowers. Fig. 8, *Agrostis canina*,  $\times 18$ . Fig. 9, *Rumex domesticus*,  $\times 13$ .

even though the other methods may now and then be used. In many flowers the ovary withers without developing seeds.

Many species of *Glumiflorae* have not only a chance of wind pollination when the flower opens in favourable weather; but if they are homogamous there is also a valuable possibility of autogamy (see fig. 8). As most of the species have dense inflorescences, they may also have geitonogamy. The fact that there are so many different possibilities must involve increased certainty of obtaining a favourable pollination in spite of the fact that conditions are both variable and often direct unfavourable.

The possibility of wind pollination even at comparatively long distances is seen in *Rumex* (fig. 9), among the species of which (*R. domesticus*, *crispus*, *obtusifolius*, *acetosa*, *acetosella*) there are frequently hybrids.

Plants with unisexual flowers also show the value of wind pollination, e. g. *Callitriche*, *Atriplex glabriusculum*, *Litorella*, and *Urtica dioica* (fig. 3).

Furthermore wind pollination is found in *Oxyria digyna*, *Thalictrum alpinum*, and occasionally in *Calluna*.

Within the family of grasses autogamy is found e. g. in *Poa annua*, the flowers of which are nearly always closed. Cross-pollination is typical of protogynous species, e. g. *Alopecurus pratensis*.

In *Festuca rubra* the spikes are non-absorbent because they are covered both with hairs and a thin layer of wax. Therefore open flowers are not spoilt by rain. The relation to rain of the other common grasses requires further investigation.

### 3. Insect Pollination.

In accordance with the statements above as to the areas of distribution of pollinating insects, entomophilous plants are found remarkably locally, and furthermore are few in number.

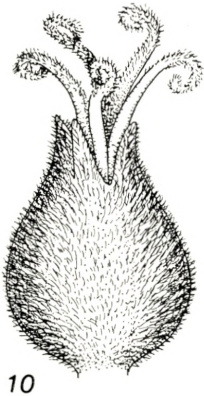
As mentioned above, most of these flowers are particularly found near (1) inhabited places, (2) bird-cliffs, and (3) low beaches with rotting seaweed and animals.

Such plants as can only be pollinated by bees, butterflies, and wasps are not found in the Faroes. The possibility of other forms of insect pollination in this climate, which is so difficult to insects, is clearly illustrated by the fact that some of the entomophilous plants are dioecious (e. g. *Melandrium dioicum*, *Sedum roseum*) and by the fact there is a hybrid, *Orchis maculatus* × *O. purpurella*. The pollinators in this case are flies.

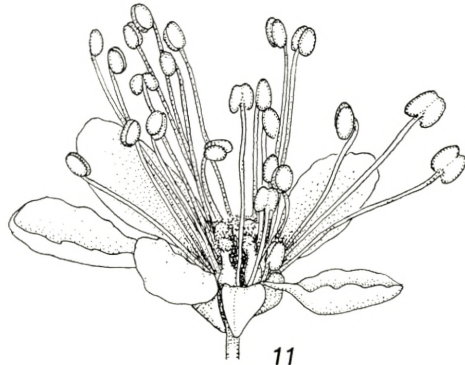
The only insects playing any quantitative role as pollinators worth mentioning are a few big flies. A list of the names of these is found in I. C. NIELSEN (1908). There are also many small *Diptera* occurring abundantly in damp places and e. g. seen continually on the leaves of *Pinguicula*. It is particularly a question of various *Chironomidae*, which are also often found sticking to the stigmata of *Orchis*, the honey of which they have tried to get at in the spur. The wings of the insects then have touched the stigmata, but the animals cannot pollinate the flower as they are too small to remove and transport the pollinia.

*Archangelica officinalis* HOFFM.

This is the Faroese species whose fly pollination is most easily observed. Even at a distance one may often observe a dark layer of insects covering the inflorescences. It is found either near inhabited places or on bird-cliffs, where also *Angelica silvestris* and *Haloscias scoticum* can be found. All these three *Umbelliferae* are pollinated by flies (WARMING 1908, p. 1060).



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11

Fig. 10. *Melandrium dioecum*. Female flower (corolla removed),  $\times 3$ .

Fig. 11. *Filipendula ulmaria*, anemophilous flower,  $\times 5$ .

*Geranium silvaticum* L.

This is also found both on bird-cliffs and near inhabited places where numerous flies swarm about it. Only on one single occasion I have seen a flower pollinate itself by direct contact between anther and stigma. Flowers which are isolated in a room do not fructify. Often some of the flowers are unisexual, and in the bisexual flowers the anthers are turned away from the stigmata so that visits by insects must normally be considered necessary for pollination.

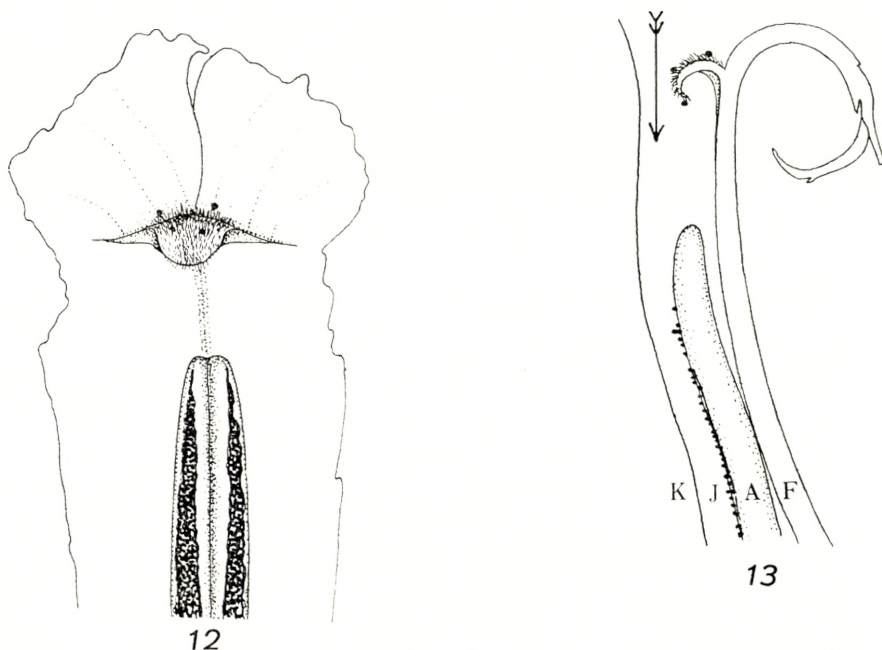
*Melandrium dioecum* L. (fig. 10).

This also grows in the fly areas on bird-cliffs and near inhabited places. The corollas are conspicuous and spread out flat so as to form a convenient landing-place for the flies, which easily strike against the projecting anthers or stigmata. The stigmata are twisted and long so that the flies can hardly avoid touching them when landing on the flower. During pairing flight the flies

roam about fast between the male and female flowers as very effective pollinators.

*Filipendula ulmaria* L. (fig. 11).

In accordance with the pollination by flies the plant is particularly found near inhabited places. The fragrant and conspicuous flowers are frequently visited by flies which with vigorous



Figs. 12—13. *Iris pseudacorus*. Fig. 12, style seen from below. Fig. 13, longitudinal section of style (F) and anther (A). The arrow indicates the route of the insect (J); K, corolla.  $\times 3$ .

movements work about the inflorescences touching the anthers, the light pollen thus being shaken out in all directions so that it can both hit the flower itself (autogamy), the neighbouring flowers (geitonogamy), or the flowers below. Furthermore the insects are powdered over and may perform normal entomogamy.

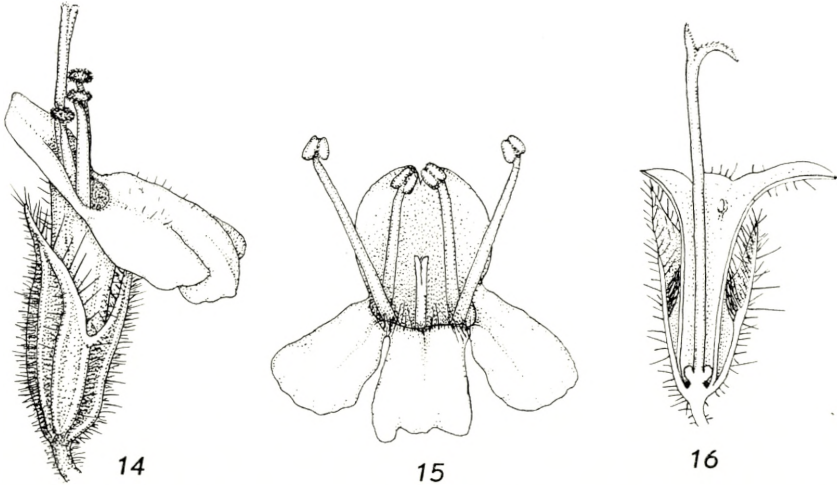
In Denmark the plant is pollinated as in the Faroes.

No doubt wind pollination is of the greatest importance for the flowers. If these are shaken, clouds of pollen are thrown into the air from the long and mobile stamens. In the damp Faroese climate this method of pollination is hardly so secure as in Denmark.

*Iris pseudacorus* L. (figs. 12—13).

The pollination takes place in the well-known way that flies crawl down into the cleft between style (F) and perianth (K). The route of the insect is in fig. 13 indicated by an arrow. There the animals have a good hiding-place during any kind of storm. Homogamy.

*Thymus serpyllum* L. var. *prostrata* HORNEM. (figs. 14—16).  
Even in purely female flowers (fig. 16) there is often pollen



Figs. 14—16. *Thymus serpyllum*. Fig. 14, bisexual flower at the female stage. Fig. 15, bisexual flower at the male stage. Fig. 16, female flower.  $\times 6$ .

on the stigma. Visits by insects have been observed by both WARMING and me. The plant has plenty of nectar and the big *Eristalis intricarius* may be seen crawling over the dense inflorescences.

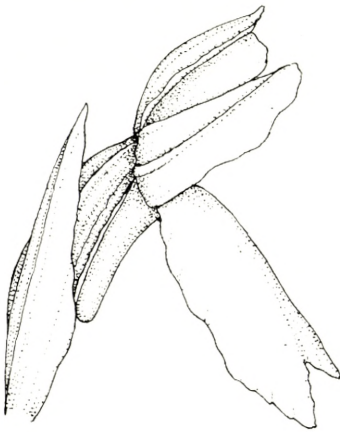
In the bisexual flowers the anthers dehisce first,—already while the style is still quite short (fig. 15). Later the style grows up among the anthers and the stigmas spread out so that auto-gamy may be obtained if insect pollination should fail.

*Orchis maculatus* L. (figs. 17, 19, 57).

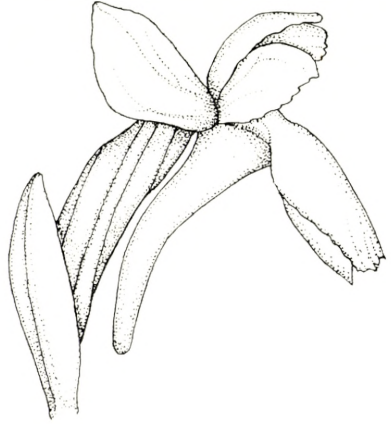
The very complicated structure and function of the flower has rightly made it an object-lesson of insect pollination; but MARTENS (1926) has shown that even this ingenious flower may have autogamy like a number of other orchids. In the Faroes, where

*O. maculatus* is very abundant, I have been unable to find any form of self-pollination in this species; but still numerous fruits develop without any visits by bees and butterflies.

Observations in nature by R. RASMUSSEN and me have shown that *Orchis* is visited and pollinated by a big and long-haired fly, *Eristalis intricarius* L. (fig. 57), which strangely resembles a small dark humble-bee, a resemblance expressed in the synonym *Eristalis bombyliiformis* FABR. This big beautiful fly can easily pull out pollinia and carry them to the stigmata of other flowers.



17



18

Fig. 17. *Orchis maculatus*; exterior perianth leaves directed forward. Fig. 18. *Orchis purpurella*; exterior perianth leaves directed backward.  $\times 3$ .

On a single occasion I have also seen the minor species, *Eristalis lucorum* MEDG. on the flowers.

*Eristalis intricarius* is nearly  $1\frac{1}{2}$  cm long and just under 1 cm broad. The body is densely set with long stiff hairs, which make it non-absorbent; but the insect prefers flying in dry weather and then sweeps fast through the air in wide turns. It breeds in damp places, preferably near human dwellings. During the pairing flight it generally lands on the large leaves of *Calltha*; but when the insect wants to eat it roams about and searches many different flowers, e. g. *Ranunculus*, *Thymus*, *Orchis*. This fly is perhaps the most important of all the pollinating insects in the Faroes. It also occurs in Denmark and is distributed from Northern Scandinavia to Italy. Without it the magnificent abundance of *Orchis* flowers was hardly found in the Faroes.

The Faroese form of *O. maculatus* has so short a spur that its bottom can be reached by the proboscis of the fly. This can be stretched out remarkably far (3—5 mm), so that the fly can easily reach the bottom of the spur when squeezing its head into the flower, which is thus pollinated in the usual way. On the very hairy head of the fly there is a hairless spot at the very place where the adhesive disk of the pollinia is touched and sticks fast (fig. 57).

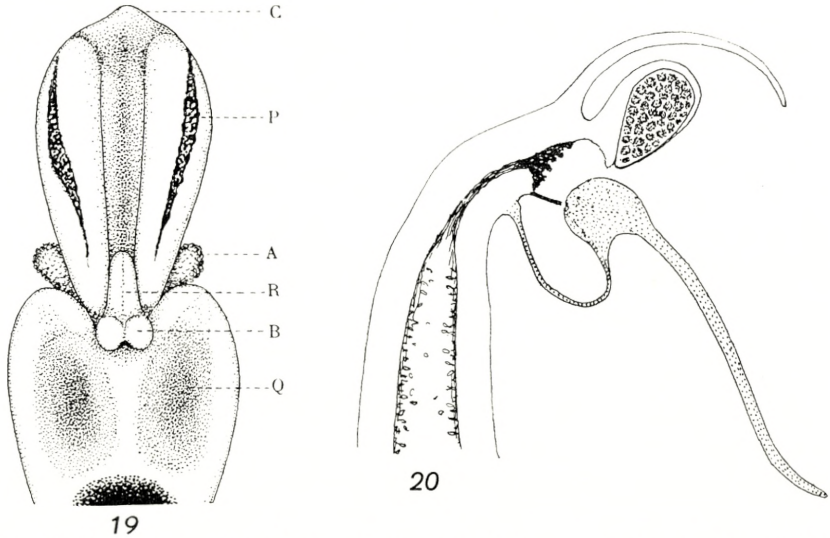


Fig. 19. *Orchis maculatus*. Flower with perianth leaves removed. A, auricula; B, bursicula; C, anther; P, pollinium; Q, stigma; R, rostellum.  $\times 20$ .  
 Fig. 20. *Habenaria viridis*. Median longitudinal section through flower. Entrance to spur closed with membrane (black).  $\times 16$ .

The Faroese *Orchis maculatus* flowers further seem to be especially adapted to hold their own in rainy weather; for they are assembled much more densely than on the Danish plant. Therefore the lip of one flower hangs as a protecting roof over the flower below, and drops of rain trickle from one lip to the next without penetrating into the interior of the flowers. Not rarely it happens that some of the flowers in the short dense spikes cannot get room enough to unfold themselves completely. The outer leaves of the flower then cannot bend back as is normally the case, but are directed forward so that they, too, can protect the interior of the flower from drops of rain coming from the side. This forward-directed position is also particularly con-

spicuous in *Coeloglossum (Habenaria) viride*, which looks as if the flower is always in bud.

*Coeloglossum (Habenaria) viride* L. (figs. 20—24).

The entrance to the flower is extremely narrow so that only the heads of small insects can be introduced into it. That the flower has come out at all only appears from the fact that the long narrow lip hangs obliquely downwards when the flower can be pollinated. The narrow aperture of the flower somewhat reminds of the entrance to a mouse-trap and it may be surmised that a visiting insect must struggle to get out of the flower, there being thus a greater chance of having some pollinium removed.

The flower being nearly completely closed does not mean that it is autogamous, at any rate not always. I have found a few pollinated flowers which had all of their own pollen situated in its original place, for which reason the pollen found on the stigma must have been transferred from another flower by an insect. I have not, however, seen any insect visit the flowers. There are still some traits missing in our knowledge of the biology of this strange species. An account of these will be published later.

In order to examine the peculiar short spur from which the plant has got its name, I cut some series of sections medianly through the flower. It then appeared that the broad entrance to the saccate spur is closed with a thin membrane, a fact which has never been recorded from any other orchid.

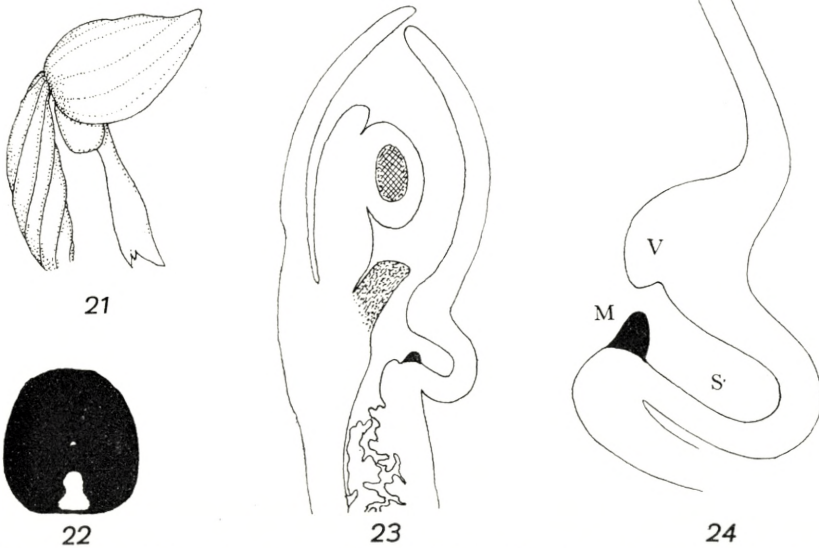
In order to get hold of the nectar in the spur, the visiting insect must first squeeze its proboscis through the membrane, which effort increases the chance that the insect both receives and gives off pollen. It is not necessary, however, that it should be insects with pricking mouth-parts which perforate the membrane, for such insects do not occur in the Faroes, where all the pollinated flowers examined had a burst membrane. Direct observation in nature has provided interesting information of the process of the visit by the insect (SILÉN, 1906). Only when a non-pollinated flower begins withering (with age) the membrane bursts without the action of insects.

The morphology of this peculiar spur was examined in series of young stages of development. The membrane is started very early as a nearly crescent-shaped circular pad round the entrance



to the spur so that the membrane is broadest at the back and has a narrow aperture in front. In the full-blown flower the membrane covering the entrance to the spur looks as shown in fig. 22, where the perforation is white. It is somewhat triangular in shape and is situated in front.

The lip is peculiar by having a median vertical pad at the base of the upper side. This pad swells greatly during the flowering



Figs. 21—24. *Habenaria viridis*. Fig. 21, flower. Fig. 22, the membrane (black) over the entrance to the spur is perforated in front.  $\times 12$ . Fig. 23, median longitudinal section of young flower with initial development of the membrane (black).  $\times 28$ . Fig. 24, median longitudinal section through spur (S) with initial development of membrane (M); V, circular pad.  $\times 50$ .

season, thus forcing the lip down vertically when the flower comes out. It projects over the hole in the membrane, which thus becomes more difficult to find by a visiting insect.

The inconspicuous flower of *Coeloglossum* thus makes a fresh contribution to the curious pollination biology of the orchids.

#### *Habenaria albida* L.

For comparison it may be mentioned that *Habenaria albida* (L.) has a short saccate spur similar to that of *Coeloglossum*, but it is not closed with a membrane. Preliminary investigations of *H. albida* made in Denmark show that the flowers are autogamous and accordingly have a rich fructification. Conditions of pollina-

tion need further investigations and therefore will be discussed in a paper to be published in the future.

*Caltha*, *Ranunculus*, and *Calluna*, which have previously been described (HAGERUP 1950) should be mentioned among the entomophilous plants. Particular attention should be given to the pollination by means of *Thrips*, which was previously nearly unknown, but which is probably rather widely distributed and valuable, e. g. in *Compositae*. In the Faroes *Thrips* thus was found in a number of flowers the pollination of which seems somewhat puzzling, e. g. *Silene acaulis*, *Armeria*, *Leontodon*, and others which need further investigations.

#### 4. Geitonogamy.

In most plants with fairly large, dense inflorescences it cannot be avoided that neighbouring flowers should pollinate each other. This applies to *Glumiflorae*, *Rumex*, *Filipendula*, and others, thus both anemophilous and entomophilous plants. Geitonogamy is particularly conspicuous in *Umbelliferae*, where flies crawl from flower to flower all over the umbel.

*Cornus suecica* L. (fig. 26).

The stamens are directed obliquely outward and half way over the adjoining flowers so that the heavy pollen will drop direct on to the stigmata when the flowers are shaken by wind, insects, or rain. The fructification is abundant in the centre of the inflorescence, where most of the anthers are assembled. The marginal flowers are often sterile.

The flowers are non-absorbent, surplus rain water being drained off along the stalk of the inflorescence, which is remarkably stiff, grooved, and hairy, a fact which reminds of the rain pollination in certain *Ranunculaceae* (HAGERUP, 1950).

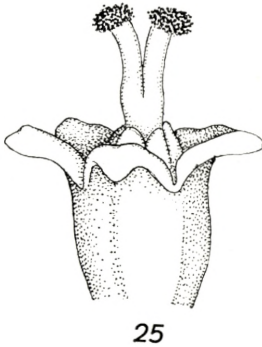
*Leontodon autumnalis* L.f. *nigro-lanata* Fr. (fig. 27).

The pollination takes place already when the first corollas open; for when the flower head takes up its right position it closes and then all the long projecting styles, which have pollen on the outside, are squeezed among each other in a dense con-

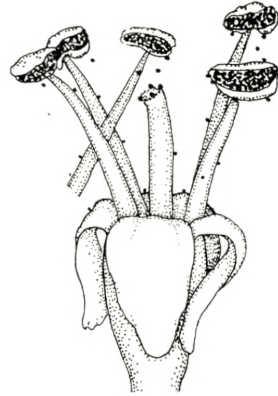
fusion so that they cannot avoid having the pollen of the neighbouring flowers left on their stigmata.

Furthermore autogamy will easily take place, because the two long stigma lobes have papillae right out to their margins, where pollen has often stuck fast when the styles grew out among the anthers.

Particularly in the centre of the flower head there are often exclusively female flowers and the fructification is poor.



25



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Fig. 25. *Matricaria ambigua*. The flower's own pollen is seen on the apical stigma.  $\times 20$ .

Fig. 26. *Cornus suecica*. Geitonogamy.  $\times 12$ .

In Denmark the pollination takes place in a way similar to that in the Faroes. Here, too, visits by big insects are comparatively rare; but *Thrips* individuals are often found in the flowers.

### 5. Autogamy.

In the Faroes there is a good number of flowers characterized both by fragrance, colour, and size; but in spite of this the insects present are not attracted. Many of the most beautiful flowers of the Faroes call in vain and are not visited by insects. In many conspicuous flowers a visit by insects would, indeed, be in vain because the flower pollinates itself either (1) before, (2) during, or (3) after flowering, when the corolla has withered and the beauty is gone. Such futile visits by insects are, however, of frequent occurrence. Thus a fly may settle almost anywhere on

a plant or other objects without this visit necessarily having anything to do with pollination. Therefore visits by insects and pollination should not be identified as a matter of course.

Still, one of the rare and accidental visits by insects may, to a normal autogamous flower, mean a chance of cross-pollination, which perhaps is not always without importance.

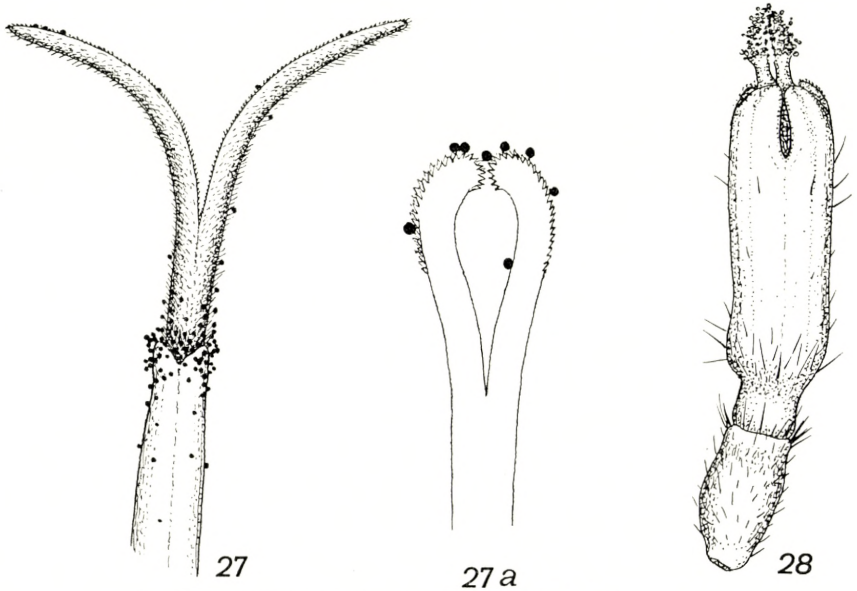


Fig. 27. *Leontodon autumnalis*. Stigma and anthers.  $\times 25$ .

Fig. 27 a. *Bellis perennis*. Longitudinal section of stigma.

Fig. 28. *Bellis perennis*. Projecting stigma covered by the flower's own pollen.  $\times 25$ .

### A. Pollination after Flowering.

*Hypericum pulchrum* L. (figs. 29—30).

At a first view of this large, pretty flower it is tempting to assume insect pollination. Indeed, I have on rare occasions seen a fly moving about the long erect stamens in search of nectar. But it soon disappeared, and visits by insects are of no value for the pollination as the anthers are closed and the stigmata unable to receive pollen as long as the flower is open. In spite of assiduous search the pollination of this flower long continued being a puzzle to me.

The fructification is perfect. Every flower develops a large capsule which remains on the plant during the winter until the next flowering season or sometimes still longer (two years). Strangely enough the withered corolla (as on *Calluna* and *Erica*) remains round the wintering capsule.

During the flowering both the corolla and the outer stamens are spread out horizontally; but when the flower for a few days has in vain displayed its tempting beauty, the corolla rather

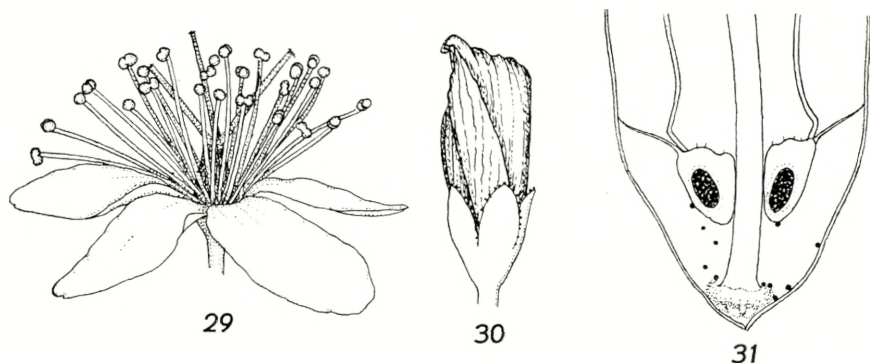


Fig. 29—30. *Hypericum pulchrum*. Fig. 29. Before pollination the flower is open, but the anthers are closed.  $\times 3$ . Fig. 30. At the stage of pollination the corolla is closed, but the anthers have dehisced.  $\times 3$ .

Fig. 31. *Erica cineria*. Longitudinal section of bud in autogamy immediately before it comes out.  $\times 12$ .

suddenly closes tightly by the perianth leaves standing up vertically, and by the withering movements the tips of the corollas twist themselves round each other so as to form a remarkably firm knot, which is not opened later. The bases of the corollas do not work loose, and the stamens remain in their original places. By the vigorous movements of the withering corolla all the stamens are squeezed densely together into a bunch in the centre of the flower, where the three styles are also imprisoned and are squeezed in among the stamens, whose anthers do not dehisce until then. The interior of the withered flower thus is filled with pollen and at the same time the stigma becomes susceptible to pollination, which is performed with automatic certainty. Without any inconvenience caused by bad weather the stigmata are covered with pollen and the fructification is secured.

The Faroese plant is a special variety. It should be investigated how the species is pollinated in other countries, in particular whether it may also have a chance of cross-pollination.

Some individuals were planted in the Botanical Garden of Copenhagen. The plants thrived and in the flowering season (in 1949) the weather was both dry and warm with plenty of sunshine. Under these conditions unusual to a Faroese plant, the flowers opened much more than in their native country so that the petals even were somewhat retrorse. It is, however, of special interest that the anthers were open already during the flowering (thus not only when the flower had faded, as in its native country), i.e. that the pollen on possible visits by insects had a chance of being transferred to other flowers and pollinating these. There is no chance like this in the comparatively damp and cold Faroese climate poor in insects and sunshine, in which the flower is autogamous.

*Lychnis flos cuculi* L. (figs. 33, 34).

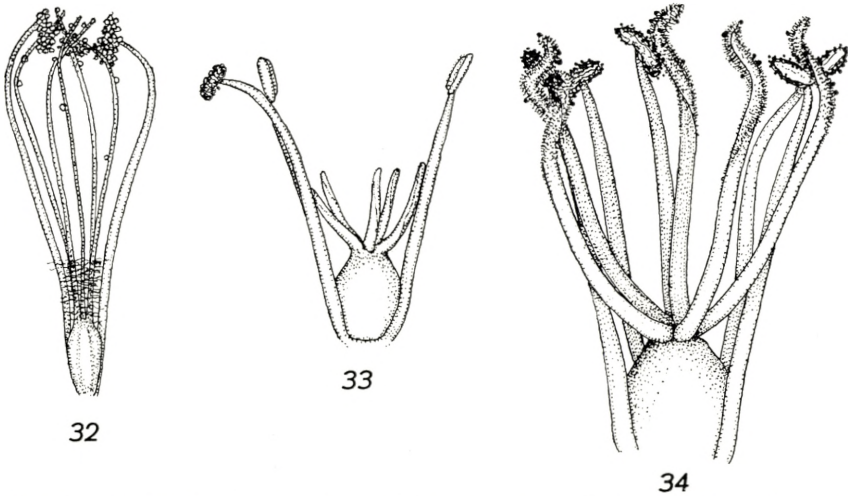
This well-known large, beautiful flower embellishes the Faroese meadows and fields in such a way as to suggest entomogamy. It was, however, impossible, in spite of intense search, to ascertain the occurrence of visits by insects. Furthermore, the flower is so deep that none of the insects present have proboscises long enough to reach the bottom of the calyx. Consequently the flower must somehow be autogamous.

KNUTH has a long list of insects which in countries farther south visit the flower, but it should be verified whether these insects are of any importance for the pollination. In the Faroes, at any rate, such visits would be of no value as the stigma is not at all mature for receiving pollen during the flowering (fig. 33). The styles then are quite short and without any developed papillae. The plant, however, fructifies abundantly and at a ripe stage bears numerous large capsules tense with seeds and suggesting that there is an absolutely effective pollination.

During the flowering season the anthers are open and project high above the short styles, which are hidden in the flower.

If rainy weather sets in (as very often happens), some of the pollen is washed down into the flower, where it gets stranded on the inside of the corolla, the lower parts of the stamens, etc. Still, the greater part of the pollen remains in the anthers.

When the flower begins withering, the styles start growing vigorously in length. During this growth, however, they wind several times round their own axis, and furthermore the stigma bends aside. During these characteristic growing movements the papillae develop on the stigma, which is then receptive to pollination. When the stigma moves up through the narrow tube of the corolla, it will touch the organs placed there, which are mostly set with pollen that has dropped down or been washed down.



Figs. 32—34. Pollination in withered flowers, the corolla having been removed. Fig. 32. *Armeria vulgaris*.  $\times 8$ . Fig. 33. *Lychnis flos cuculi*. Flowering stage with undeveloped stigma, but some dehiscent anthers.  $\times 4$ . Fig. 34. *Lychnis flos cuculi*. Pollination in withered flower.  $\times 6$ .

The growth of the stigmata stops when they have got on a level with the anthers. Then stamens and styles are twisted round each other and this bunch is squeezed into a dense lump by the withering petals bending towards the centre of the flower. Finally the stigmata have clasped the stamens as with the arms of an octopus so that autogamy is performed with perfect certainty.

Danish individuals are pollinated quite like the Faroese ones.

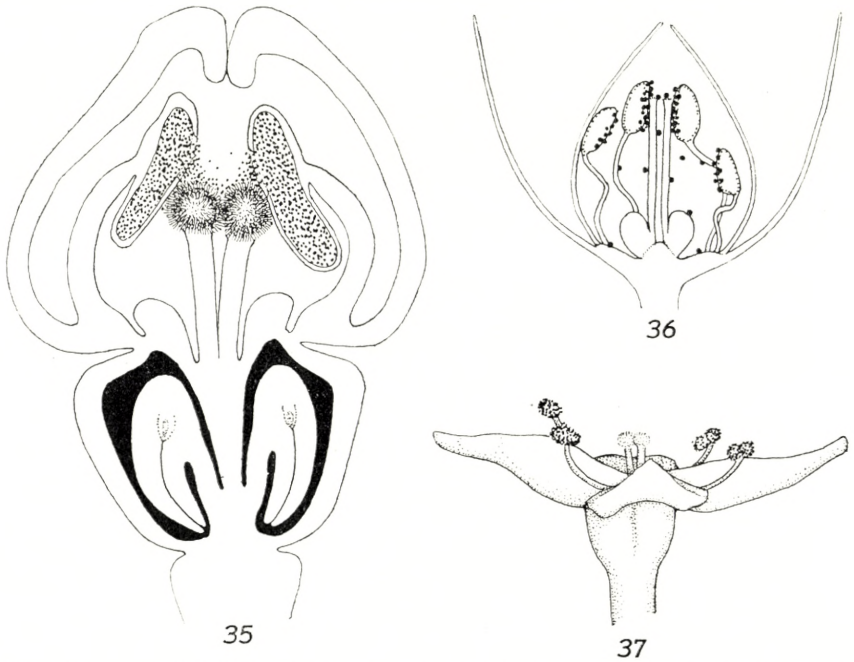
*Armeria vulgaris* WILLD. (fig. 32).

As this flower has already been described by WARMING (p. 1056), I shall confine myself to the following additions:

In the full-blown flower there is a chance of avoiding auto-

gamy as the styles are bent aside and can only with difficulty touch the anthers. But I have never been able to observe any visit by insects.

When the flower withers the styles and stamens bend closely together in the centre of the flower and are further squeezed together by the petals which surround this "bud" as a tight



Figs. 35—36. Pollination before the flower comes out. Longitudinal section of buds of *Galium saxatile* (fig. 35,  $\times 40$ ) and *Potentilla erecta* (fig. 36,  $\times 12$ ).  
Fig. 37. *Galium saxatile*. The flower has already been pollinated when it opens.  $\times 12$ .

protecting cover inside which autogamy is inevitable as the stigmata have fresh papillae and the anthers still contain pollen. According to IVERSEN the flower's own pollen yet does not germinate upon its own stigmata. It is markedly self-sterile. I do not know how the transport of foreign pollen takes place. It may be the flies of the coastal area which perform the pollination. This needs further investigation. The plant propagates exclusively by seeds, which are present in abundance.

Danish individuals showed the same conditions of pollination as the Faroese ones.



There are probably more flowers than the three mentioned here which have "withering pollination" at last if the other methods of pollination should fail.

### B. Pollination before Flowering (Bud-Autogamy).

There was a number of other Faroese flowers whose conditions of pollination to begin with seemed unintelligible, e. g.

*Galium saxatile* L. (figs. 35 and 37).

Already WARMING (1908, p. 1059) investigated this species, but he did not find out the method of pollination, because the stamens in the open flower are bent outward and away from the styles. Still, such a multitude of fruits is produced that all flowers would seem to have been pollinated.

The numerous flowers are gathered in dense growths, which make the plant conspicuous, and it belongs to the commonest species. In the flowering season, however, the anthers are nearly emptied of pollen and it is extremely rare that a casual insect should be allured by the flowers. Visits by insects are of no value at all for the flowers, which for that matter not only are conspicuous, but also have a large circular nectary which is quite open and easily accessible even to insects with short proboscises (flies).

In order to discover the method of pollination the flower must be examined while it is still in bud shortly before it comes out. Fig. 35 shows a longitudinal section of such a bud. It is seen that the anthers are pressed tightly against the stigmata, which have long papillae. The anthers have dehisced and large quantities of pollen pour out on to the stigmata. This is a very secure form of autogamy. The stamens cannot at that stage be damaged by rain.

During rain the flowers are wide open and the last pollen is washed away, but as the flower has already been pollinated before it opens, its possibilities of fertilization are not reduced by storms.

KNUTH (1898, p. 548) supposes that the plant reproduces by geitonogamy and gives a list of visiting insects; but at any rate in the Faroes visits by insects are of no value whatever.

*Potentilla erecta* L. (fig. 36).

This is one of the commonest species in the Faroes, which embellishes the vegetation with its numerous yellow flowers. These are wide open and apparently ready to receive visits by insects. But insects are seen so rarely on the flower that they cannot be of any importance worth mentioning for the pollination. In the full-blown flower the stamens, in addition, are turned away from the styles so that they cannot leave pollen direct on the stigmata. Still, all flowers are fertilized and seedlings are common.

WARMING tried in vain to discover the method of pollination, which also at first seemed puzzling to me until the buds were examined immediately before they opened. It then appeared that the innermost anthers were already open and bent towards the stigma where they leave pollen. This mechanism functions very securely and all carpels are fertilized.

Danish individuals have bud-pollination in the same way as the Faroese ones.

*Erica cinerea* L. (fig. 31).

This is one of the most beautiful species of the Faroese flora. It has not only colour and beauty of form, but it also has a pleasant fragrance and a well developed nectary. Besides, the anthers are provided with the horns so characteristic of most *Bicornes*, which—in other species perhaps rightly—are considered an adaptation to entomophily.

One would therefore beforehand be inclined to consider it a matter of course that the flower should be entomophilous, and indeed KNUTH gives a long list of visiting insects.

In spite of this no insects are seen on the flowers. Even though there may be flies in the neighbourhood these will not be allured by *Erica cinerea*, but seek out certain other species (e. g. *Umbelliferae*).

There does not seem to be any pollen on the sticky stigma of the full-blown flower either. Furthermore the anthers have long been open and have already given off most of their content.

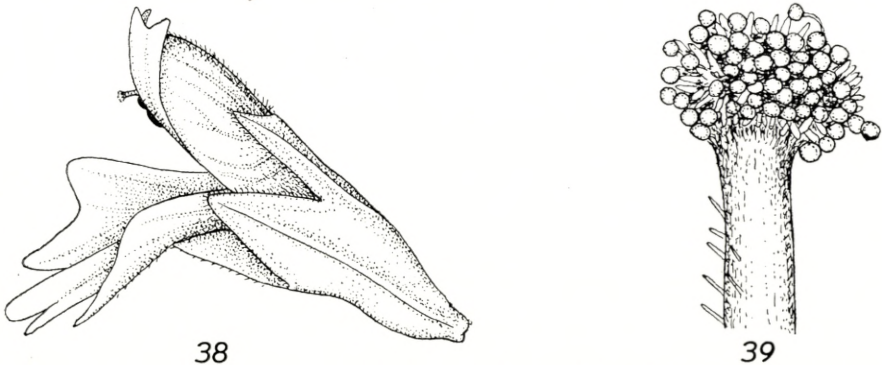
The flower hangs obliquely downwards already while in bud. The stigma is placed in its very lowest tip. The anthers dehisce before the corolla and pollen at once falls into the funnel-

shaped cavity between the tips of the petals, where the sticky stigma cannot avoid being filled with pollen, which is absorbed so quickly in the mucilage that it cannot immediately be seen in the full-blown flower.

This bud-autogamy functions so securely that all possible later visits by insects seem of no use for the pollination. It would be interesting to investigate whether the species is pollinated by insects in other countries.

*Euphrasia borealis* (TOWNS.) WETTST. (figs. 38, 39).

This flower has already been described by WARMING (1908, p. 1059), who found that the stigma at the flowering stage projects



38

39

Figs. 38—39. Autogamy. *Euphrasia borealis*.

Fig. 38. Full-blown flower after pollination.  $\times 5$ .

Fig. 39. Stigma with the flower's own pollen prepared from bud.  $\times 50$ .

in front of the anthers so that no self-pollination can take place.

However, if the bud is examined immediately before it opens it appears (fig. 39) that the stigma is already full of pollen from the flower's own anthers. This pollen has already germinated.

The corolla always keeps dry because it is covered by non-absorbent hairs. The upper lip is spatulate and envelops the anthers, which in the bud are pressed close together round the stigma.

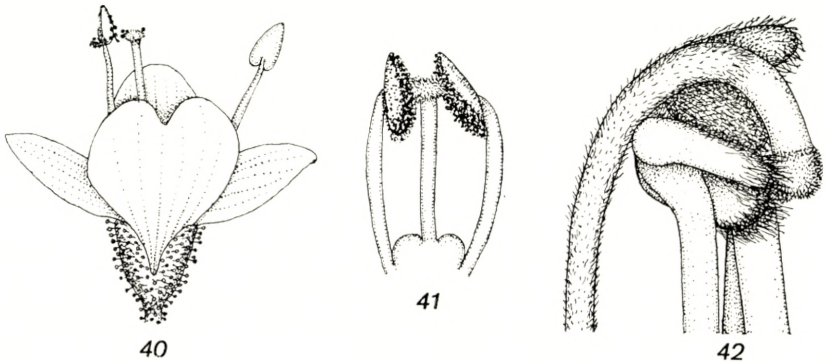
The pollen is dry and in the bud is found everywhere between anthers and stigma. The anthers are densely hairy so that pollen does not spread too much in the anterior of the bud, but is kept together near the stigma. Abundant fructification.

*Alectorolophus (Rhinanthus) minor* EHRH. (fig. 42).

This flower has a bud-autogamy reminding very much of conditions in *Euphrasia*. See further WARMING 1908, p. 1055.

*Veronica beccabunga* L. (fig. 41).

In the bud the anthers are pressed tightly against the stigma. They open inward immediately before the flower comes out and then pollen is with great certainty left on the stigma.



Figs. 40—42. Autogamy. Fig. 40. *Veronica officinalis*.  $\times 7$ . Fig. 41. *Veronica beccabunga*.  $\times 18$ . Fig. 42. *Alectorolophus minor*. Stigma bending in among the anthers.  $\times 12$ .

In the open flower the stamens are moved somewhat outward and inward.

Once I have seen a small moth, *Cidaria albulata* SCHIFF., flying from flower to flower and sticking its proboscis into the corollas; but such visits are of no importance to the plant as the flowers have already been pollinated.

The Danish plants are different from the Faroese ones both in appearance and biologically. The flowers are smaller and not so purely blue as in the Faroes. In Denmark the anthers do not dehisce in the bud, but only when the flower has come out. In the young flower there is a chance of insect pollination because the anthers are turned outward and away from the style. As a last chance of pollination, however, the stamens in the older flower bend inward and leave pollen on the stigma.

*Cerastium caespitosum* GILIB. var. *fontanum* BAUMG. (fig. 43).

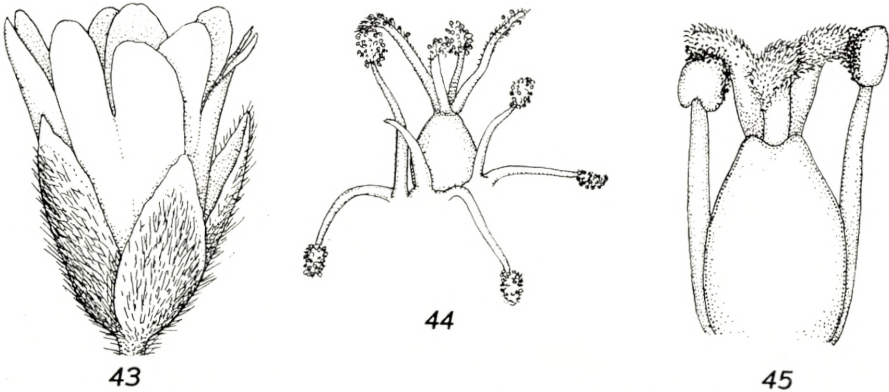
The Faroese form has relatively large corollas, which often open more than in Denmark. I have not, however, seen any

insects on the flower. Still, there may be a chance of cross-pollination in other countries richer in insects (Norway) where var. *fontanum* also occurs.

In the Faroes the anthers dehisce immediately before the flower comes out and pollen is then left direct on the stigma because the anthers are still pressed tightly together round the stigmata. Fructification is abundant.

*Stellaria media* (L.) VILL.

It has bud-autogamy like *Cerastium*, and all flowers fructify.



Figs. 43—45. Autogamy. Fig. 43. *Cerastium caespitosum*.  $\times 5$ . Fig. 44. *Stellaria uliginosa*. An anther pollinating a stigma.  $\times 12$ . Fig. 45. *Sagina procumbens*.  $\times 18$ .

*Lotus corniculatus* L. f. *carnosa* PERS. (figs. 50—52).

Pollination has been studied thoroughly in Central European localities. As to the main species e. g. KNUTH (1898, p. 303) has arrived at the result that it can only be pollinated by insects. This is not correct at any rate as regards the Faroese form, for this form does not receive visits by insects and besides none of the insects occurring there are heavy and vigorous enough to start the well-known mechanism of pollination. And even if they would have been able to do so it would be too late; for already before the flower opens, the stigma is completely surrounded by large amounts of pollen, which is ready to germinate on the stigma as soon as it becomes susceptible.

It should be investigated whether this form of autogamy is something special to the Faroese variety. KNUTH's long list of visiting insects need not mean that these are necessary for pollination.

A. PEDERSEN (1949, II, p. 311) writes about the form cultivated in Denmark that it is "pronouncedly self-sterile". Pollination in the different forms of this greatly polymorphous species should obviously be studied in more detail. It fruits sparingly.

### C. Autogamy during Flowering.

Most of the species belonging here are homogamous and the pollination takes place during the flowering itself. If the flower opens, there is a possibility of insect pollination in such coun-

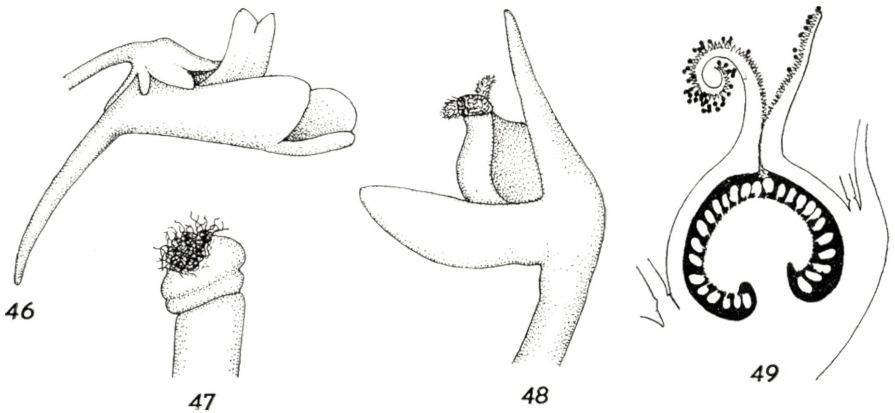


Fig. 46—49. Autogamy. *Pinguicula vulgaris*. Fig. 46, flower in stage of fertilization.  $\times 3$ . Pollen germinates in the anther (fig. 47,  $\times 16$ ), which is pressed tightly against the stigma (fig. 48,  $\times 6$ ). Fig. 49, longitudinal section of gynaecium.  $\times 14$ .

tries in which there are many insects; but as this is not the case in the Faroes, cross-pollination is without practical importance there.

In a number of species the flower is open in rainy weather and a filling with water will then often cause pollen to be transported to the stigmata. Autogamy functions with great precision and fructification is abundant. Most of the Faroese species which are not anemophilous belong here.

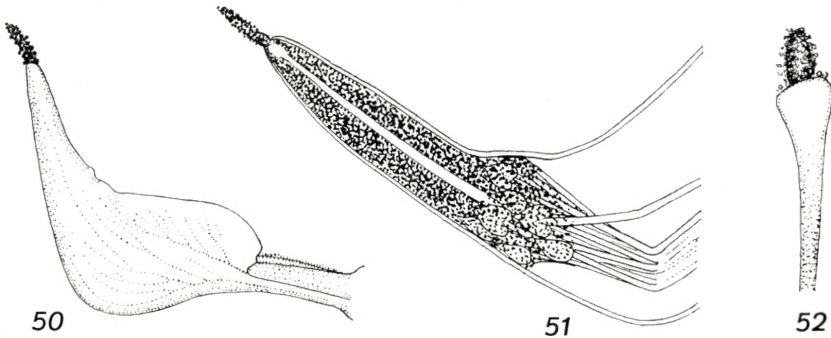
(a) *The flower is open during pollination and has a slight chance of cross-pollination.*

*Pinguicula vulgaris* L. (figs. 46—49).

There is some uncertainty as to the pollination, as KNUTH is of opinion that autogamy is excluded. WARMING (1912, p. 389), on the other hand, assumes that both insect- and self-pollination can be practised.

In the Faroes I examined a large material in nature without observing conditions which might in any way support KNUTH'S views. Still, it should be investigated how pollination takes place in localities farther south, where KNUTH made his studies.

The anthers of the Faroese plant press tightly against the stigma, which is soon covered with pollen. If one pulls at a stamen it appears that it clings to the stigma and this adhesion is due to the fact that all pollen grains have germinated even though they remain in the anther. Pollen tubes form a dense cotton-like mass of fine interwoven filaments most of which have



Figs. 50—52. Autogamy. *Lotus corniculatus* var. *carnosa*. Fig. 50, carina,  $\times 3$ . Fig. 51. Longitudinal section of apex of carina showing stigma surrounded by masses of pollen.  $\times 6$ . Fig. 52. Filament with tumid apex.  $\times 17$ .

penetrated into the stigma. At high magnification it is easy to follow the tracks of the pollen tubes among the long papillae of the stigmata and farther down to the ovules. The autogamy of the Faroese plant functions very precisely and seedlings are abundant. Once I even found a capsule the seeds of which had not even been dispersed but which had germinated inside the fruit.

Danish individuals showed quite the same conditions of pollination as the Faroese ones.

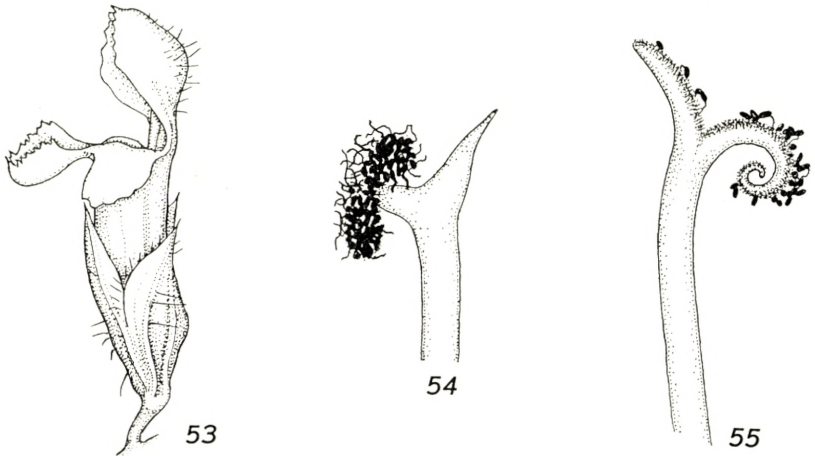
#### *Vicia sepium* L.

This species is also generally considered exclusively entomophilous in Central Europe. Not so in the Faroes, where pollen is left direct on the stigma in the homogamous flowers. Fructification is abundant although I have not seen insects on the flowers. The current view of the pollination may also in the case of this species be based on the tempting confusion of visits

by insects with pollination. Flowers from Denmark behave almost in the same way as the Faroese ones. The anthers are open and the stigma is pollinated before the flower opens. The chance of cross-pollination is very poor.

*Trifolium repens* L.

This species, which is dominant on the low-lying Faroese pastures, is autogamous in a similar way to the two preceding



Figs. 53—55. Autogamy. *Prunella vulgaris*. At the flowering stage (fig. 53,  $\times 5$ ) the pollen tubes have already grown out of the anthers (fig. 54,  $\times 20$ ) and have penetrated into the stigma (fig. 55,  $\times 20$ ).

*Papilionaceae*, as the ripe stigma is jammed in between the open anthers. The strong fragrance and conspicuous colour of the flower do not attract the few insects. Rain does not penetrate into the flower in *Papilionaceae* because of the form of the petals and their mutual position.

A. PEDERSEN (1949, II, p. 298) states about the forms cultivated in Denmark that they are "pronouncedly self-sterile". The various forms of the species thus ought to be investigated thoroughly and apart as they may show different conditions of pollination. It fruits sparingly.

*Prunella vulgaris* L. (figs. 53—55).

The large coloured inflorescences everywhere embellish the Faroese pastures, thus in advance suggesting insect pollination, a view which is indeed shared by the early floral biologists (KNUTH, 1898—99, p. 283). WARMING (1908, p. 1057), on the



other hand, states the occurrence of autogamy. As a matter of fact the Faroese flies are not attracted by the flowers.

The position of the flower is nearly horizontal, and the stamens are protected from rain by the vaulted upper lip, which on top is set with non-absorbent hairs.

The anthers are pressed firmly against the stigma, which is mature simultaneously with the release of pollen. The pollen germinates quickly. Even if it remains in the anther, pollen tubes grow to the stigma. As in *Pinguicula* the lowest branch of the stigma rolls back spirally, thus obtaining an extra chance of being powdered with the pollen. The mechanism of autogamy functions perfectly, and seedlings are common.

Still, it is possible that some of the southern forms of this polymorphous species can be pollinated by some of the numerous insects included in KNUTH'S lists. The Danish flowers, however, behave like the Faroese ones. If an anther is taken out with a pair of tweezers, pollen tubes may already be seen in a magnifying glass. Furthermore, the Danish flowers are much smaller than the Faroese ones and have hardly any chance of cross-pollination worth mentioning.

*Galeopsis tetrahit* L. (fig. 56).

Autogamy mainly takes place as in *Prunella*. Two of the anthers press tightly against the stigmata and pollen is left upon these. I have not observed any visits by insects in the Faroes, but in Central Europe the flowers are visited by humble-bees (KNUTH, p. 264).

Fructification is plentiful.

In the Danish flowers the anthers are far from being so tightly pressed against the stigma. Hence there is presumably a much greater chance of cross-pollination than in the Faroes.

*Polygala serpyllacea* WEIHE. (figs. 58—60).

Although the flower both in form and colour seems to have been made for insect pollination it is an inveterate self-pollinator. Visits by humble-bees have been observed in localities farther south (KNUTH, p. 153), but in the Faroes I have never seen any insect on the flower and still fruit is developed by nearly all flowers. (Furthermore, the seeds are remarkable by having elaiosome, although there are no ants.)

Already WARMING (1908, p. 1062) found autogamy in *Polygala*. I shall therefore only refer to the figures below. The thick layer of pollen on the stigma exclusively derives from the flower's own anthers.

*Veronica officinalis* L. (fig. 40).

The corolla is funnel-shaped and directed obliquely upwards. Inside it is non-absorbent like the anthers, but outside it gets wet in the rain. The two anthers, which do not open at the same

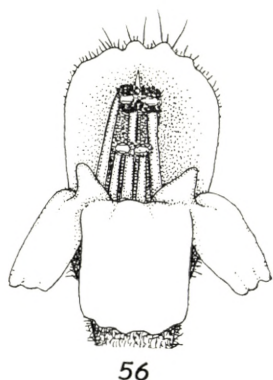


Fig. 56. Autogamy. *Galeopsis tetrahit*. The anthers pressed against the stigma.  $\times 4$ .  
Fig. 57. Pollinia of *Orchis purpurella* on head of *Eristalis intricarius*.  $\times 6$ .

time, are both of the same length as the style; but at the beginning of the flowering they are bent outwards and away from the stigma. So at this stage the flower has a chance of insect pollination. In the Faroes, however, I have never seen any insect on the flowers.

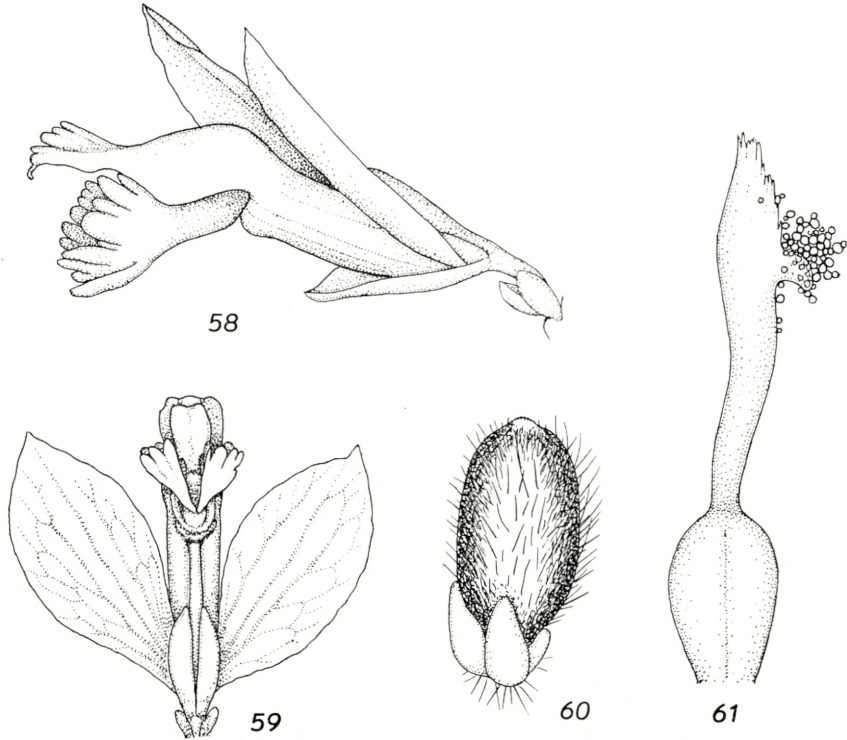
When the flowering is being finished the anthers move towards the centre of the flower and the anther is pressed against the stigma, which in this way receives pollen. This form of autogamy thus is the last chance of the flower, and it is probably nearly always efficient.

The style, too, may move a little aside and towards the anthers.

The Danish plants behave nearly as the Faroese ones, but are more open and have a greater chance of insect pollination in the beginning of the flowering.

*Veronica serpyllifolia* L.

The corolla is wide open, but the stamens are mostly upright, with the anthers being placed very close to the stigma, autogamy thus being secured.



Figs. 58—61. Autogamy. *Polygala serpyllacea*. Fig. 58. Side view of flower.  $\times 12$ . Fig. 59. Flower seen from below.  $\times 6$ . Fig. 60. Seed. Fig. 61. Stigma with the flower's own pollen prepared from bud.  $\times 16$ .

The flower is self-pollinating in Denmark as well, often before the corolla is quite open. The stamens make spontaneous movements. The anthers dehisce simultaneously with the corolla or shortly before.

*Viola Riviniana* RCHB. (figs. 62—64).

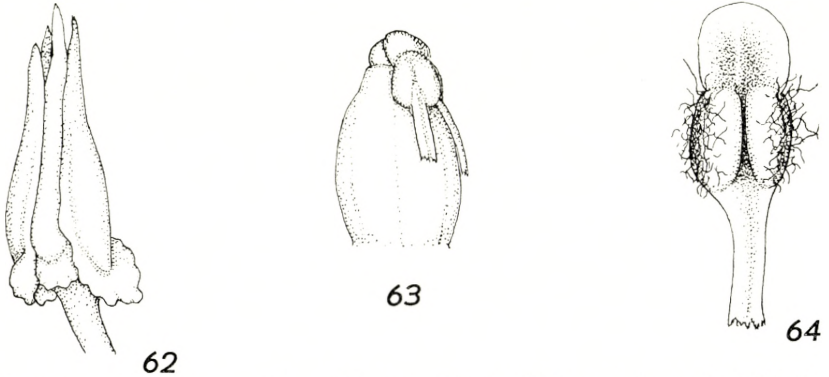
The Faroese plants have closed flowers similar to e. g. the Danish ones. Pollen germinates in the anthers and pollen tubes grow direct down into the stigma.

See further KNUTH's account (1898, pp. 138—140).

*Bellis perennis* L. (fig. 27 a).

This species is abundant in the meadows and its fructification is plentiful; but only rarely a stray fly is seen on the flowers, and if so, it does not pollinate them. During rain or in the dark the inflorescences close nearly completely.

The stigma is strange because it is not, as in other *Compositae*, situated on the inside of the apex of the style. But the sticky papillae are placed both on the apex and on the outside of the



Figs. 62—64. Autogamy. *Viola Riviniana*. Fig. 62. Flower at stage of fertilization.  $\times 7$ . Fig. 63. Anthers sticking to stigma.  $\times 13$ . Fig. 64. Pollen tubes growing out of anthers.  $\times 20$ .

style. When the latter grows up through the tube formed by the stamens, the anthers have already dehisced on the inside, and great quantities of pollen are transferred to the stigma.

From localities farther south KNUTH reports plenty of visits by insects. He does not count on a possibility of autogamy. Danish individuals behave like the Faroese ones.

*Senecio vulgaris* L.

This species has autogamy similar to *Bellis*. KNUTH counts on autogamy, but also reports scarce visits by insects.

In Denmark, too, the species is autogamous.

*Matricaria ambigua* (LEDEB.) (fig. 25).

This species is pollinated in a way similar to *Bellis*. The stigma, however, is placed only on the extreme apex of the style, which is pushed like a piston through the anther tube, where it receives plenty of pollen. In Denmark the same method is found in the case of the inner flowers of the main species. The marginal

flowers have spread-out styles, which have a great chance of being insect-pollinated, e. g. by *Thrips*, which often—in great amounts and powdered over by pollen—crawl about the flowers.

*Cirsium palustre* L. (Scop.) (figs. 65—66).

In structure the style reminds of the ordinary style of *Compositae*, as on the outside it is set with stiff hairs which sweep the pollen out of the anther tube, while the stigmatic papillae are found to be covered on the inside of the style, autogamy thus generally being avoided.

In the present species, however, there are stigmatic papillae not only on the inner surface, but right out to the margin of it and even some short distance down the outside surface. Indeed, it is just along the margins that the germinating pollen grains are found and perform this special form of autogamy.

The flowers have both fragrance and nectar, and KNUTH gives long lists of visiting insects from southern localities, assuming that the flower is entomophilous. This needs critical investigation.

In Denmark numerous *Thrips* powdered over with pollen move about the flowers. Visits by larger insects are often seen, too.

Flowers from all localities were peculiar by the two stigma branches (facing each other) during the greater part of the flowering season being pressed tightly together. Only during the last stage of the flowering the two branches bend a little apart, but then only at their extreme tips. So at this late stage there is a chance for the flower to receive pollen from other flowers; but as a rule there is still some of the flower's own pollen on the back of the stigma. This is easily transferred to the margin of the stigma, which may thus be pollinated, e. g. when the long stalks are shaken by the wind. Conditions in the Faroes at any rate show that visits by insects are not necessary for the pollination.

One of the two stigmata is nearly always longer and broader than the other (fig. 66). Consequently both apex and margins are exposed during the whole flowering season. The flower's own pollen is often found in the places mentioned, having been left there at an early stage when the flower was coming out, for which reason possible later visits by insects are hardly of

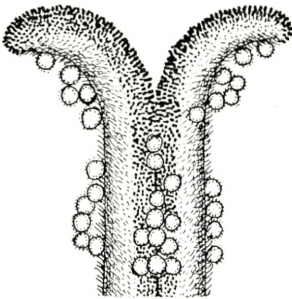
any appreciable importance for the pollination. Autogamy is probably the normal.

*Sedum villosum* L.

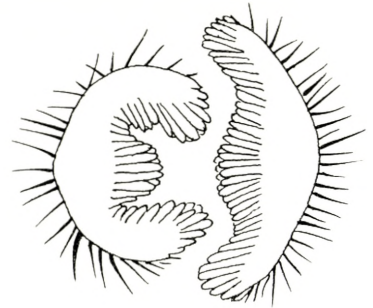
The flower has been described by WARMING (1908, p. 1064). In the stellate flower the stamens are moved inward towards the centre, where they cannot avoid touching the stigma. Autogamy thus is normal.

*Saxifraga stellaris* L.

As in *Sedum villosum* the stamens make great movements,



65



66

Figs. 65—66. *Cirsium palustre*. Fig. 65. Apex of stigma with pollen.  $\times 90$ .  
Fig. 66. Cross-section of stigma.  $\times 200$ .

ending in the anthers touching the stigma, where they leave pollen. Abundant fructification.

KNUTH reports visits by insects and states that as a rule the species is not autogamous.

*Stellaria uliginosa* MURR. (fig. 44).

Pollination in this species reminds remarkably of pollination in *Sedum* and *Saxifraga*. The flower is wide open and the stamens make great movements to and fro so that some of them may be bent right back, while at the same time others are nearly upright in the middle of the flower; but just there the stigma is found and is inevitably pollinated. All flowers set fruit.

Autogamy in this species was described by KNUTH, who also, however, observed visits by insects.

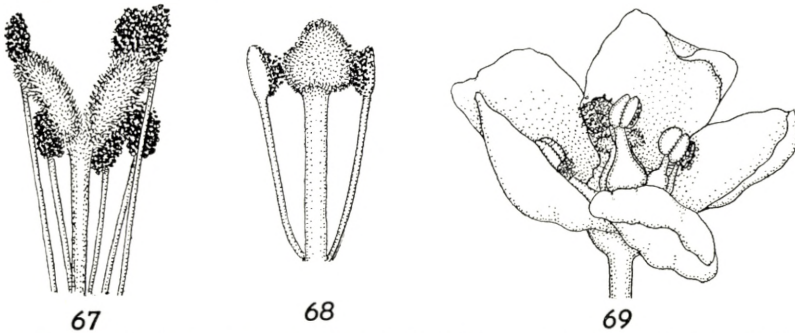
*Polygonum aviculare* L. (fig. 69).

In fine weather the flower is wide open and the stamens are

first bent outwards; but when the anthers dehisce, they bend one by one towards the middle of the flower and leave pollen on the stigma. Finally the whole flower closes, all the stamens are pressed tightly together, and autogamy is secured.

*Epilobium montanum* L. (fig. 67).

The flower has already been examined by KNUTH and WARMING, who found that the anthers even adhere to the stigma. The Danish flower has a considerably greater chance of cross-pollination as both stigma and anthers are spread out much more widely than in the Faroes.



Figs. 67—69. Contact-autogamy. Fig. 67. *Epilobium montanum*.  $\times 5$ . Fig. 68. *Epilobium palustre*. Fig. 69. *Polygonum aviculare*.  $\times 16$ .

*Epilobium palustre* L. (fig. 68).

This species shows a form of autogamy similar to *E. montanum*. The anthers are open already in the bud and pressed tightly against the stigma. On Danish material the style is somewhat longer than on the Faroese material. Thus at any rate the apex of the style can be receptive to cross-pollination. The flowers are rarely visited by insects; but in Denmark they are more open than in the Faroes and the stamens are also spread out more.

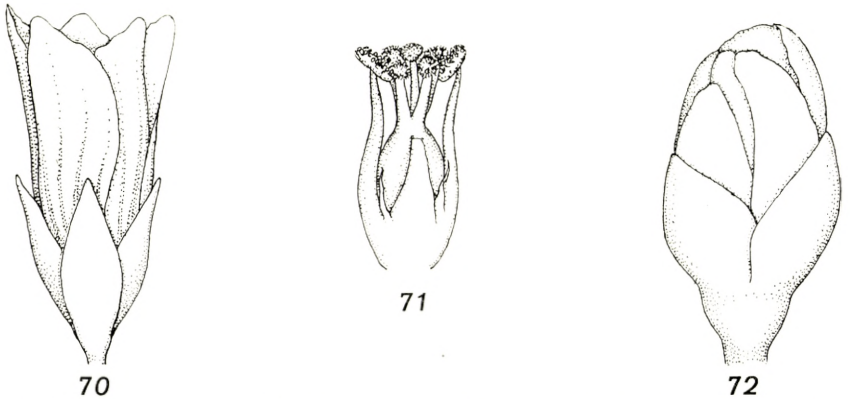
*Myosotis palustris* (L.) var. *strigulosa* (RCHB.).

When the sun shines on the dense carpets of the conspicuous, beautiful flowers, big flies roam about in the air. They often with predilection settle on *Myosotis* and place their proboscises in the entrance to the narrow corolla tube. In a *Myosotis* locality it is thus possible to observe the humble-bee-like *Eristalis intricarius*, which is of so great importance for the pollination of *Orchis*.

The flower is wide open, the large corollas thus offering good landing-stages for insects; but the insects cannot reach the bottom of the corolla tube with their proboscises because the entrance is completely barred by the stigma and anthers.

The stamens together form a narrow tube similar to that of the *Compositae* and the stigma grows up through this like a piston. During its growth the anthers are open and inevitably leave pollen on the stigma.

The visits by insects, however, offer a chance of cross-pollina-



Figs. 70—72. Autogamy. Fig. 70. *Linum catharticum*.  $\times 8$ . Fig. 71. *Linum catharticum*. The anthers place pollen on the stigma.  $\times 16$ . Fig. 72. *Montia lamprosperma*.  $\times 20$ .

tion which perhaps is not quite without importance even though autogamy is the normal, particularly in bad weather. Rain water cannot penetrate into the narrow aperture of the corolla tube. Therefore the well-protected anthers are always dry, even if the exposed parts of the petals get wet.

The Danish flowers behave like the Faroese ones.

*Myosotis arvensis* (L.).

This smaller species has a spontaneous autogamy similar to that of *M. palustris*. I have never seen insects on the small flowers.

*Linum catharticum* L. (figs. 70—71).

The flowers do not open so wide as in Denmark and have hardly any chance of cross-pollination.



The dehisced anthers are tightly pressed against the stigmata, which are pollinated with great certainty.

*Cochlearia officinalis* L. (figs. 73—74).

At the stage when the flower is opening, there is, in the Faroes, a direct contact between the mostly just dehisced anthers and the stigma, autogamy thus being inevitable in bad weather.

If the air is dry, the flower comes out earlier and the stamens are not pressed so tightly against the stigma. The petals spread out horizontally and the anthers get more space. Autogamy then can easily be avoided. On a dry sunny day in the Faroes the conspicuous flowers are not rarely visited by flies, thus getting a chance of cross-pollination. This possibility is still more pronounced in Denmark.

The species often grows in the coastal fly areas.

*Cardamine hirsuta* L.

In the Faroes neither calyx nor corolla open, but they are pressed together to form a tube. By this means the anthers of the four long stamens (the anthers dehisce inward) are pressed tightly together in the middle of the flower, but exactly there the stigma is found both before and during the flowering. Autogamy thus is inevitable, and all flowers set fruit.

In Denmark the flowering is somewhat different, the flowers here opening completely as shown in figs. 75—76. This may possibly mean a chance of cross-pollination, which is not possible in the Faroes. Furthermore, the stigma on the Danish plants is found a little higher than the anthers so that as a rule these cannot reach high enough to leave pollen direct on the stigma.

*Cardamine silvatica* LINK.

The flower is a little more open than that of *C. hirsuta*, but still autogamy is practised in the same way in Denmark and in the Faroes.

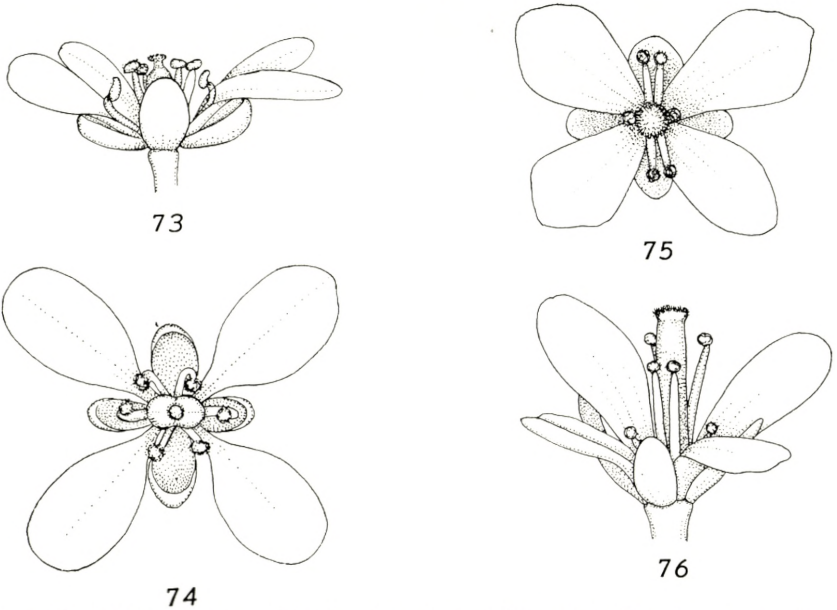
*Cardamine pratensis* L.

The large beautiful flowers also in the Faroes are wide open, but still they pollinate themselves in the same way as the two preceding species.

In southern localities insect pollination according to KNUTH is the commonest method, and he mentions visits by many different insects.

*Capsella bursa pastoris* (L.) MOENCH.

In the Faroes mostly in part closed and autogamous. In Denmark visits by insects to the open flowers are not rare, but also there the flowers nearly always pollinate themselves.



Figs. 73—74. *Cochlearia officinalis*, side view of flower (fig. 73), flower seen from above (fig. 74). Figs. 75—76. *Cardamine hirsuta*.  $\times 10$ .

(b) The flower is closed during pollination so that no cross-pollination can take place.

*Koenigia islandica* L.

In Greenland the flower is completely open in fine weather so that the three yellow nectaries can be seen; but still the anthers touch the stigma and places pollen direct upon it.

In the Faroes the flower is nearly always closed and the mechanism of autogamy functions with great certainty.

*Sagina procumbens* L. (fig. 45).

In Denmark it sometimes happens that the flower of this species is slightly open; but in the Faroes it is always closed firmly.

By this means the anthers are pressed against the stigma and places pollen direct upon it. The flower always sets fruit. When this is mature, the valves spread like a star. In other countries visits have been observed by flies and bees, and even ants have been seen in the flowers, which have nectaries.

*Montia lamprosperma* (CHAM.) (fig. 72).

The small white flowers are always closed and the anthers cannot avoid touching the stigma. In Denmark the flowers open somewhat in dry weather and in Scotland visits by flies have even been observed (KNUTH, II, 1, p. 424).

## 6. General Remarks.

A study of conditions of pollination in the individual species in a Faroese local flora thus has shown that many of the species are not pollinated in the same way as in southern localities.

The present investigations were made in a locality where a number of apparently entomophilous species fructify excellently without visits by insects, the purpose being to find out of how great or small importance visits by insects may be. Some flowers (e. g. those of *Erica*) have both fragrance, nectar, and colour, but they tempt insects in vain. Detailed morphological investigations of such structural features as invite interpretation as adaptations to entomophily (WARMING) thus may actually lead the student astray. This applies e. g. to the horns on the stamens in *Erica cinerea*, the flowers of which are pollinated before the horns can be touched by any insect. The horns in *Calluna* and many other "adaptations" in other flowers are just as superfluous in the Faroes.

Morphological investigations indoors thus are not sufficient. The decisive observations must be made in nature, where the student should not least be attentive to the question whether species considered autogamous really produce seed capable of germinating after self-pollination.

The methods of pollination may be very different in different localities within the total area of distribution of the species. This is most clearly illustrated by *Calluna* (HAGERUP, 1950), the flowers of which may be pollinated by e. g. bees, butterflies, *Thrips*, wind, and autogamy. The method to be realized depends

on ecological conditions in the various stations, e. g. by wind and weather and the species of insects found in the place. These circumstances may again vary from year to year. Consequently the flower need not be pollinated in the same way every year. Thus, if continuous rain sets in, the insects are prevented from flying about and no air transport of pollen can take place. The flower then must fall back on one of the other methods of pollination, e. g. by means of *Thrips* or autogamy. But then, if the weather is dry next year during the flowering, the same individuals perhaps are pollinated in quite different ways, e. g. by bees or the wind.

In the damp climate of the Faroes *Calluna* thus is pollinated by *Thrips* or the wind, while in Denmark the species is often pollinated by bigger insects. In some localities the morphological adaptations then may be of importance while elsewhere they seem of no value. There is thus a certain plasticity in the conditions of pollination of certain flowers, a fact of which already WARMING was aware. The somewhat schematic and stiff descriptions of conditions of pollination in certain textbooks should sometimes be taken with a grain of salt, and many of the classic observations of floral biology should be taken up for renewed investigations. The necessity of this is illustrated e. g. by conditions in *Orchis*, which, indeed, is a classic example of one of the most ingenious forms of entomophily; but here MARTENS has found occasional autogamy, as is also found normally in a number of other orchids (*Epipactis*, *Liparis*, etc.), which indeed have just as ingenious morphological "adaptations" as *Orchis*. All the usual strange forms of pollination in orchids are superfluous in the case of this species. Still, the flower receives visits by insects (just as *Taraxacum* does).

The discrepancies between the observations of pollination in the various species in the Faroes and in southern localities need not be due to erroneous observations, but may simply be due to the fact that various species (e. g. *Prunella*) have developed particular autogamous races in the Faroes, whereas e. g. in Germany they are visited more or less frequently and perhaps also may be pollinated by insects.

The fact that flowering and pollination can be influenced direct by the climate (and thus need not be exclusively genetic-

ally conditioned) is beautifully illustrated by conditions in the Faroese form of *Hypericum pulchrum* (see above, pp. 18-20).

Self-sterility is a possibility which should be considered in the case of the relatively small number of entomophilous species. Thus it is stated that *Ranunculus acer* is sometimes self-sterile; but the great number of autogamous species which are not visited by insects cannot be self-sterile, as it is always easy to find the flower's own pollen germinating on the stigma. Such autogamous species have a remarkably rich fructification.

The flora of the Faroes in respect of nutrition offer conditions of a much richer fauna of insects than is actually found there. In the great number of fragrant, coloured, and attractive flowers there are quantities of pollen and nectar which are not used as food, but simply are wasted (e. g. in *Erica*). For comparison it may be mentioned that in Greenland, in latitudes much farther north, there is a relatively much greater number of pollinating insects (e. g. humble-bees and butterflies) than in the Faroes. This poverty in insects in the Faroes should be investigated by zoologists. The causes may be either the present climatic conditions or conditions of immigration.

In corresponding latitudes on e. g. the west coast of Norway there is also a much richer fauna of insects than in the Faroes.

Similar problems crop up concerning the fly areas which—as mentioned above—are so characteristic of the closest surroundings of (1) inhabited places, (2) beaches with rotting plants and animals, and (3) bird-cliffs and the flora conditioned by these.

Have the inhabitants of the fly areas been imported by man or do these insects belong to the original fauna of the islands as it existed already before man immigrated? Both possibilities seem to have been realized. The house-fly (*Musca domestica*) has obviously immigrated in the company of man. The same perhaps also holds good of other flies whose larvae live in the dung of human beings or domestic animals (sheep). When the domestic animals were imported it was necessary to import fodder for them, too, and this may have contained both the brood of flies and seeds of the plants of the fly areas.

HØEG writes the following passage about the corresponding conditions in Spitsbergen, which in a remarkable degree remind of the above-mentioned conditions in the Faroes:

“This abundance of flowers may indeed arouse feelings of summer; but still it is as if something is missing: all the pullulating life of insects which belongs to our picture of a summer’s day and which is part of its atmosphere. Not one honey-bee, not one humble-bee or a butterfly. The flowers come out in vain. They smarten themselves up, tempt and pose,—and then there is nobody for which to pose. Only some disgusting big, fat flies fly about. They are said to have come to Spitsbergen in recent years and now the mining towns teem with them, at any rate Longyear City, so that they sweep them up with vacuum cleaners.—Looking more closely, one finds some small flies and some other still smaller vermin. That is all—indeed nothing to pose for! The poverty in the insect world is very remarkable in the pronounced arctic regions.”

But besides all the species imported in the company of man, there are also such carnivorous and coprophagous flies as may very well have been established inhabitants of the bird-cliffs before man immigrated.

I am therefore of opinion that the fly areas house both imported and spontaneous species of pollinating insects as well as plants.

The question whether a given imported species can continue existing in the Faroes thus is conditioned by the possibility of its managing the problems of pollination in spite of the poverty in insects and the bad weather.

## 7. Summary.

1. The present work is a study on the pollination of the species in a local flora (around Thorshavn) in the Faroes where poverty in insects and violent and prolonged rains and gales put obstacles in the way of cross-pollination.

2. Therefore most plants must either be able to pollinate themselves or utilize the wind.

3. Anemogamy: Some of the flowers pollinated by means of the wind are protogynous, e. g. *Myriophyllum*, *Triglochin*, *Plantago*, *Potamogeton*. Others are homogamous and then mostly autogamous, e. g. *Rumex* and many *Glumiflorae*.

4. Entomogamy: The only insects playing any significant

part in the pollination are some species of flies. These *Diptera*, however, are very local in distribution because their larvae subsist on putrefying animal substances. Therefore there are entomophilous flowers particularly near (1) human dwellings, (2) on bird-cliffs, and (3) on beaches with putrefying algae and animals.

5. No plants collect so many flies as *Archangelica* and other *Umbelliferae*. *Orchis* is pollinated by *Eristalis intricarius*. Fly-pollination is furthermore found in *Geranium*, *Sedum*, *Ranunculus acer*, *Caltha*, *Thymus*, *Melandrium*, *Filipendula*, and *Iris*. *Calluna* is pollinated by *Thrips* and the wind (Hagerup, 1950).

6. A particularly strange species is *Coeloglossum* (*Habenaria*) *viride*, in which the entrance to the spur is closed by a membrane which the insect must penetrate before it can reach the nectar.

7. Rain can pollinate certain flowers: *Ranunculus* sp., *Narthecium*, and *Caltha* (HAGERUP, 1950).

8. Autogamy: Most flowers can occasionally or always pollinate themselves. This mostly takes place by the anthers placing pollen direct on the stigmata of homogamous flowers: *Prunella*, *Montia*, *Caryophyllaceae*, *Polygala*, *Cardamine*, *Epilobium*, *Euphrasia*, *Galeopsis*, *Koenigia*, *Linum*, *Lotus*, *Matricaria*, *Myosotis*, *Pinguicula*, *Rhinanthus*, *Trifolium*, *Veronica*, *Vicia*, and *Viola*. In these species pollination takes place during the flowering.

9. Bud-Pollination: In some species the flower is pollinated already while it is in bud (thus before flowering): *Erica*, *Galium*, *Potentilla*.

10. "Withering-Pollination." In some species the flower is not pollinated until the perianth is withering (thus after flowering): *Lychnis*, *Hypericum*.

11. Geitonogamy. The dense inflorescences are closed in the dark, the styles and stamens thus touching and effecting pollination (*Leontodon*): night-pollination. Neighbouring flowers also pollinate each other in a number of other species with dense inflorescences: *Cornus* and many *Glumiflorae*.

12. The faculty of managing by means of autogamy and anemogamy is characteristic of the original species of the Faroes, whereas some entomophilous species presumably have been imported by man.

13. In many cases the Faroese plants are systematically different from the corresponding southern species and should

be subjected to detailed taxonomic and cytological investigations.

14. The characteristic conditions of pollination in many species are genetically conditioned, whereas e. g. autogamy may be due to the direct influence of ecological factors (p. 18-20).

15. The main rule thus is that entomogamy is remarkably rare. The greatest part by far of the area of the Faroes is covered by autogamous and anemophilous plants.

To judge from WARMING's investigations in Greenland autogamy (and anemophily) is to a remarkable degree predominant in other arctic regions poor in insects—even in *Bicornes*.

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### 8. Literature.

- GODFERY, M. (1931): The Pollination of *Coeloglossum*, *Nigritella*, *Serapias*, etc. Journ. of Bot. vol. 69, p. 129.
- HØEG, O. A. (1925): Blomsterbestøvningen paa Spitsbergen. Naturen pp. 202—220.
- (1932): Blütenbiologische Beobachtungen aus Spitzbergen. Norges Svalbard- og Ishavs-Undersøgelser. No. 16.
- HAGERUP, O. (1950): *Thrips* Pollination in *Calluna*. Dan. Biol. Medd. **18**, no. 4.
- (1950): Rain-Pollination. Ibidem **18**, no. 5.
- IVERSEN, J. (1940): Blütenbiologische Studien. I. Dimorphie und Monomorphie bei *Armeria*. Dan. Biol. Medd. **15**, no. 8.
- JAMES, W. O., and CLAPHAM, A. R. (1935): The Biology of Flowers. Oxford.
- KNUTH, P. (1898—99): Handbuch der Blütenbiologie. I—II.
- MARTENS, P. (1926): L'autogamie chez l'*Orchis* et chez quelques autres Orchidées. Bull. Soc. Roy. Bot. Belgique. Tom. LIX, Fasc. I, p. 69.
- NIELSEN, I. C. (1908): The Insect-Fauna of the Færøes. Bot. of the Færøes. III, p. 1066.
- OSTENFELD, C. H., and GRØNTVED, JOHS. (1934): The Flora of Iceland and the Færøes. Copenhagen.
- PEDERSEN, A. (1948—50): Landbrugets Plantekultur. I—II.
- SILÉN, F. (1906): Blombiologiska iakttagelser i Kittilä Lappmark. Medd. Soc. Fauna et Flora Fennica. XXXI, S. 98.
- WARMING, E. (1908): Field-Notes on the Biology of Some of the Flowers of the Faeroes. Botany of the Faeroes. III, p. 1053.
- (1912): Froplanterne. København.

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