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Palynology of a bumble-bee nest

By KNUT FAEGRI, Bergen

In the late summer of 1960, the curator of the entomological collection of the Bergen University Zoological museum, Miss ASTRID LØKEN, collected an exceptionally big nest of *Bombus lucorum* in Jæren, SW Norway (LØKEN 1961). She has given me the opportunity of taking a palynological survey of the nest, for which I am very grateful, as well as for our discussions and for references to relevant literature.

Pollen analyses were made on some different parts of the nest and its inhabitants, cf. tab. 1¹. The first column shows the composition of a lump of pollen taken directly from the leg of a worker. It is very uniform, and shows that this animal has been collecting almost, if not quite exclusively on *Erica tetralix*, which is a very common plant in that area, and which had then probably been flowering for some time. The small number of other pollen may even have been collected as impurities in the *Erica* flowers. The next pollen lump (column 2), taken from another worker, shows a much more varied picture, and there can hardly be any doubt that this animal has been visiting different plant species. In this case, however, the leg on which the pollen had been collected, broke loose and was prepared as a whole. There is thus a possibility that the *Campanula* etc. pollen grains did not belong to the pollen lump, but adhered as accidental admixtures to other parts of the body of the insect. The other pollen lump on the opposite leg had been lost, and only two small spots were left, at the upper and lower end of the corbicula. They were collected and prepared, and gave as result 100 % tetrad pollen with between 1 and 2 % *Calluna* (508 grain counted). On the other hand, pollen washed off the abdomen of the insect (cf. below) showed a more mixed composition (column 3). As the total number of pollen grains was in this case rather small, some 450 all told, it is difficult to see that an admixture of part of this pollen could change the figures as much as is the case in column 2. I therefore think that this worker must have collected pollen also in other flowers than those of *E. tetralix*. Probably the pollen from individual flowers may have been represented as discrete lumps within the pollen load, and the two remaining spots on the other leg both came from *Erica* visits. There is also the possibility that some of the "foreign" pollen may derive from regurgitated honey, used in the pollen packing process. As

¹ Samples were prepared by acetolysis-KOH treatment and Fuchsin b staining, or in some cases by 1 hr. boiling in 10 % KOH (cf. DEUSE and FAEGRI 1960), also followed by staining. It should be noted that some pollen species are destroyed by prolonged KOH treatment.

shown below, it is not probable that these pollen grains have been collected during nectar collecting. The great number of grains of anemogamous plants is noteworthy.

	1	2	3	4	5	6	7	8	9	10	11	12
	<i>Bombus lucorum</i>											
	Pollen load	do. with leg	Abdomen	Pollen cylinder	Honey pot	Feces	Feces	Cocoon, outside	Cocoon, in web	Cocoon, old	Pollen pocket	Feces
<i>Narthecium</i>	—	—	—	—	—	5.1	5.7	—	0.5	—	3.4	44.6
<i>Potentilla erecta</i> ..	—	—	—	0.8	—	0.6	0.6	0.3	0.5	3.7	5.6	3.7
<i>Filipendula</i>	—	1.1	5.4	2.4	0.4	28.2	18.6	13.5	11.4	21.0	—	7.1
<i>Trifolium</i>	—	2.9	0.8	1.8	84.1	5.1	8.6	10.6	4.3	17.4	—	—
<i>Lotus</i>	—	—	2.3	2.6	—	8.1	7.4	8.9	6.8	6.2	12.9	—
<i>Umbellifer</i>	—	0.4	0.8	0.5	0.2	3.1	4.3	2.6	1.1	0.7	—	—
<i>Erica</i>	97.6	89.3	81.3	81.3	12.7	42.4	42.9	49.6	60.9	32.6	76.0	44.4
<i>Calluna</i>	2.3	1.2	—	1.6	0.4	0.4	—	?	?	?	1.7	0.1
<i>Rhinanthoideae</i> ...	—	0.2	1.7	1.9	0.2	3.2	5.4	0.3	0.3	2.0	—	—
<i>Campanula</i>	—	4.8	2.3	5.7	1.7	3.7	6.3	13.8	14.1	11.4	—	—
<i>Composites</i>	—	—	0.3	—	—	0.1	0.3	0.3	—	—	0.3	—
<i>Anemogames</i>	—	0.2	4.9	0.2	0.2	—	—	—	0.3	0.2	0.1	—
<i>Others</i>	—	—	0.5	1.2	—	0.1	—	—	—	1.2	—	—
Total number counted	512	560	353	615	466	1403	350	349	368	596	1560	739

Within the nest, there were great quantities of pollen lying in storage (column 4). It will be seen that the composition of this stored pollen material is like that of the pollen collected on the second worker (col. 2).

In the lower layers of the nest, some cocoons were now utilized as honey pots, and an attempt was made to suck the honey out of some of them by means of an injection syringe. However, the honey was so viscid that it was a partial success only, and it is possible that some of the pollen observed may have been brought into the honey during the attempt at harvesting the pots. Apparently, small lumps of pollen were deposited along the edges of the pots, and may have been brought into them by the necessary manipulations. But certainly the honey—even if it was very clear—did also contain some pollen before I started working the pots. The composition of the pollen flora is radically different from that of the pollen storage (column 5): *Trifolium repens* pollen dominates in the honey as strongly as did *Erica* in the pollen store.

This may be due to two different causes which are not mutually exclusive. (1) We know nothing about the age of the honey. The cells used for the purpose belonged to an earlier generation, and may have been left by the larvae some time ago. The anthesis of *T. repens* and *E. tetralix*

are in western Norway in the main coincident, but *Trifolium* generally starts a little earlier. The dominance of that pollen may simply reflect the fact that *Erica* was not available when nectar was collected. However, one may also (2) presume that, for some reason or other, the workers do not care to collect *Trifolium* pollen grains when *Erica* tetrads are there. But as a nectar source, *Trifolium* is acceptable. The results of analysis of old cocoon material (column 10) indicates that the time factor cannot alone be responsible, but that there must be a certain factor of preference involved as well, cf. the great percentages of *Erica* and the relation between *Trifolium* and *Filipendula*. Similar discrepancies between pollen and honey brought home during the same period are known from literature, e. g. HASSELROT (1960 tab. 13-15). In some of these cases *T. repens* furnished the pollen, other plants the nectar.

Unfortunately, the animals had dried up, and their interior had therefore partly disintegrated. The worker represented by columns 2 and 3 was sacrificed, and its abdomen cut open after having been depilated and washed (column 3). From the plentiful occurrence of a clear, sticky fluid inside the abdomen, as well as from the odour, it was obvious that this worker had been collecting nectar as well as pollen. Ca. 20 *Erica* tetrads were found inside the abdomen. *B. lucorum* generally steals nectar from the flowers of *E. tetralix* (A. LØKEN comm.). In itself this is no obstacle against pollen collecting in the same species, contrary to what has been presumed by BRIAN (1951:193).

As is well known, the larvae do not defecate until the end of the larval period, when the rectum opens. The excreta were analysed in two larvae. In individual C, the larva was opened between the second and third abdominal segment—counted from the rear end—and a small sample of the contents of rectum taken out. Larva D had burst near the fifth segment and exposed the excreta, of which a sample was taken from the interior of the mass.

The palynological composition of the two masses of excreta is essentially similar (col. 6 and 7), and in the whole intermediate between that of the pollen and nectar collections, with a little more than 50%—by number—of small pollen grains. *B. lucorum* larvae are fed by injection into their cells of a mixture of pollen and nectar, which is beautifully reflected in the composition of the excreta, cf. the percentages in col. 4 and 5. If the *Erica* nectar is in all cases as free from pollen as in the one analysed worker, great quantities of that might have been involved without any palynological consequences.

To get an idea of the digestive activity of *B. lucorum* larvae I prepared out the digestive tract of two other workers, E and F, froze them and cut on the microtome. The sections show—especially distinctly in *Campanula*—that neither exine nor intine had been digested. Evidently there are

no cellulose-decomposing enzymes present in the intestines of the larvae. On the other hand, the onci (HYDE 1955) seem to have disappeared from the *Campanula* pollen grains, which would indicate that these plugs are of a different chemical composition from the intine s. s. (cf. BRIAN l. c.: 191, BAILEY 1960).

Pupating, the larva spins a cocoon round itself. Inside the cocoon, there are no pollen exines: in the excreta pollen exines adhere in great number to the outside of the lower part of the cocoon. In column 8 there is a sample from the outside of an upper-story cocoon, the pollen composition of which is very similar to that of the excreta of the larvae that had not yet pupated. Defecating and cocoon spinning evidently go hand in hand. Fig. 1 shows how the excreta (pollen masses) are interleaved by cocoon web. Col. 8 gives the composition of one of the inner pollen lumps, embedded in the cocoon. Its palynological composition is essentially similar to that of the outside—as could be expected. A third sample of the same kind was taken from the bottom of one of the oldest cocoons still available, a rather small one. Its palynological composition (col. 10) is very similar to that of the preceding columns, with the exception that *Erica* is less frequent and *Filipendula* more so—corresponding to the flowering periods of these plants.

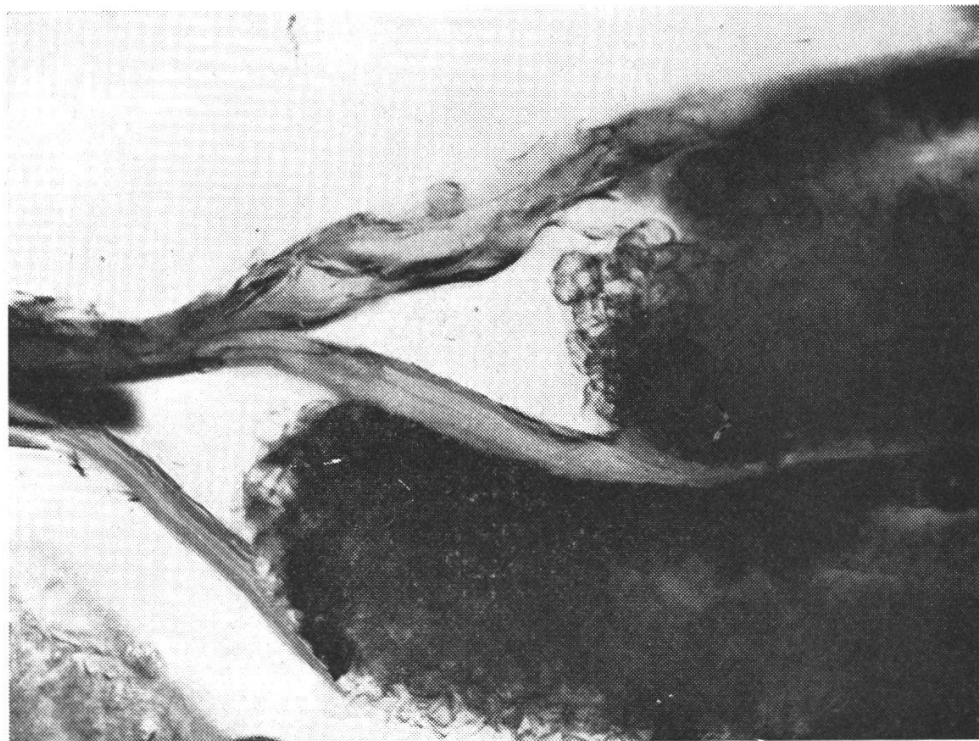


Fig. 1. Section through a cocoon wall,
showing the intercalation of meconia with cocoon web.
Inside of the cocoon up in the photograph.

A much smaller nest of *B. muscorum* was collected in the same summer, at some distance further south. Two analyses were made from that nest, one from a lump of pollen stored in the nest, and one from the excreta at one of the cocoons. The figures (col. 11-12) do not need much comment. They are more or less the same as those found in the other nest, with the interesting exception of the great number of *Narthecium* pollen grains met with in the excreta. I understand from Miss LØKEN that *Narthecium* is a plant that is generally not considered to be of great value for bumblebees. KNUTH's hand-book quotes some different insects: flies and hymenopters, as visitors of *Narthecium* flowers (1899 : 504), but as HAGERUP (1950 : 14) remarks: there is little to attract insects to the nectar-less flowers. HAGERUP (l. c.) has shown that pollination may take place by rain-induced autogamy, but evidently the observation from our *B. muscorum* nest shows that these flowers are actually visited by pollen collectors. There is not much pollen in the flowers, but it is interesting that it is highly conspicuous, due to its bright red colour, that contrasts vividly against the yellow filaments and perianth segments. The existence of a strong scent also indicates that *Narthecium* flowers are or have been adapted for insect pollination.

ON PALYNOLOGICAL IDENTIFICATION ²

Tetrad pollen. This was almost exclusively that of *Erica tetralix*, which is a very common plant within the area in question. There is not much callunoid pollen, but with the enormous number of *Erica* grains observed their variation was greater than indicated by OLDFIELD (1959, cf. OVERBECK 1934, BEUG 1961), and in some cases there was a certain overlap. In cases of doubt, the reinforced margins of the colpi were considered the decisive character. In the excreta, where state of preservation was less satisfactory, no attempt was made at a complete differentiation. Also in these cases, the *Calluna* percentage was very small.

Campanula. The only species occurring in any quantity near the sites is *C. rotundifolia*.

Leguminosae. Several types occurred. A small one could be identified as that of *Lotus corniculatus* (other *Lotus* species being absent). Of the other ones, the most frequent could be identified as *Trifolium repens* because of its weaker reticulation that did not reach the polar area (cf. FAEGRI 1956). Both *T. repens* and *T. pratense* are plentiful at Jæren, but in the sandy soil of the outer coast area, *T. repens* grows in many places

² My thanks are due to Mr. BENT FREDSKILD of the Copenhagen Nationalmuseum for identification of some pollen types, and for discussions.

where the other species has no chance. In columns 1-9 I believe that there are very few other leguminosae pollen grains except from the two species here indentified, also in the honey sample. The badly preserved pollen of col. 7-8 could not be quite properly indentified. In col. 10 the picture was more varied, and some few grains could easily be identified as derived from *T. hybridum* whereas no attempt was made to identify other, rarer types.

Umbelliferae. The pollen represented a certain difficulty, as the thorough work on the family by CERCEAU (1959) does not include some of the relevant species (*Ligusticum*, *Angelica littoralis*). The pollen belonged to a rather uncharacteristic type, the P/E ratio being a little more than 2, and the exine characteristics not too well developed. However, I think we may tentatively refer it to *Daucus carota*, and presume that the bumble-bees have been foraging in the extensive carrot fields near by. To what extent carrots were grown for seed, could not be ascertained.

Filipendula. *F. ulmaria* is the only species occurring in the region. By an oversight, some grains of *Sambucus nigra* were originally included in the *Filipendula* count. A later check proved them to constitute ca. 10% of the filipenduloid total. The provenance of the *Sambucus* grains is slightly enigmatic, but there may have been an elderberry bush in some near-by farmer garden.

Rhinanthoideae. The majority of the grains had burst, and presented themselves as small, rolled-in, boat-shaped fragments. A generic identification is hardly feasible. Some of the better preserved ones were by Mr. FREDSKILD referred to *Euphrasia*. I am inclined to think that many of the fragments came from *Pedicularis*, of which both *P. palustris* and *P. silvatica* are frequent in the area, and which are also bumble-bee pollinated (cf. NORDHAGEN in LAGERBERG et al. 1957 : 141 seq.).

The occurrence of pollen of anemogamous species is interesting. In most samples, one or two grains were counted, but in col. 3 there was a considerable number, viz. 7 grass, 3 *Corylus*, 2 each of *Alnus* and *Plantago*, one each of *Pinus* and *Betula* plus a *Polypodium* spore. Cf. the great number of pollen of anemogamous plants found adhering to bees by FREDSKILD (1955 : 79).

ON FLOWER CONSTANCY

The flower "constancy" of bees and bumble-bees has been under discussion since the concept was formulated, and I refer to a forthcoming discussion (FAEGRI and v. d. PIJL).

There is no doubt that *Bombus lucorum* and *B. muscorum* in our two nests have exhibited strong preference for *Erica tetralix*, but it is also obvious that they are not absolutely constant. A great number of pollen

types occur in so great quantities that they cannot be considered accidental. The question arises how these secondary (pollen) sources are utilized. Are there some individuals that show a different preference from that of the majority of individuals, do all or some of the ordinary workers at some foraging flights visit other plants than at the usual flights, or do they visit these accidental plants during ordinary flights? Since we do not usually know how much and what kind of pollen a worker may have taken out of the nest when starting on a pollen collecting flight, the interpretation of a mixed load will always be open to doubt. When, as in the case of col. 1 a whole pollen load consists almost exclusively of one pollen type, we have a positive proof for a very high degree of preference on this particular flight, but the opposite case: a mixed load, is open to different interpretations. It is noteworthy that the composition of the presumably latest pollen collections (col. 1-4) show a very high degree of preference of *Erica tetralix*. Evidently, this plant exercises such a great attraction on *B. lucorum*, that it is less interested in other species after *Erica* has come properly into bloom, i. e. a marked preference for *E. tetralix*, but no monotropic constancy. It is interesting to note that according to Miss LØKEN the *B. lucorum* nest was found under a vigorous plant of *Anchusa officinalis*, which was visited by other bumble-bees. *Anchusa* pollen was met with only in the oldest sample (col. 10), and then in 0.7 %. Obviously, there is a strong negative preference against *A. officinalis*.

Flower preferences are of great interest both from the point of view of pollinator psychology and of pollination ecology. "Constancy" has been considered a prerequisite for successful pollination. That this is not so, is obvious: whether the composition of the pollen present on the surface of a bumble-bee includes 100 or 80 or even 60 % *Erica tetralix* pollen, is not very important from the point of view of pollination effectivity. A certain degree of preference is undoubtedly necessary for the pollination effect, but a mixed preference is just as advantageous as the absolute constancy. The pollen composition quoted in the table suggests that *B. lucorum* may be an effective pollinator of both *Erica tetralix*, *Narthecium*, and *Trifolium repens*. A mixed load will make the insect a more effective pollinator as such, even if an absolute preference would give a higher number of visits to the one species in question.

In the case of our two nests, the positive preference for *Erica* is obvious. Without a close study of the vegetation it is difficult to state anything about negative preferences (except for *Anchusa*), but the almost complete absence of pollen of composites is noteworthy. A couple of species from that family were certainly flowering then and there. *Calluna* is another species of which one should have expected more pollen.

BRIAN (1951 tab. 2) has analysed meconia adhering to discarded cocoons, and in her material *Ericaceae* also dominate for *B. lucorum* together

with *Trifolium repens* and *Lotus corniculatus*, with *Filipendula* and *Potentilla erecta* as secondary constituents.

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