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DIFFERENT BUMBLE BEES VISITING *DIGITALIS PURPUREA* AND ITS FORMA *HEPTANDRA*

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1. INTRODUCTION

Some years ago observations on the morphology and the width of variation of *Digitalis purpurea* L., f. *heptandra* DE CHAMISSO have been presented (1). The plants concerned were all derived from a single specimen of a typical *heptandra* which appeared spontaneously in the laboratory garden in 1964. Descendants were propagated in free mutual pollination, and during the last 6 to 8 years we had some rather large fields in which a fair percentage of the plants consisted of *heptandra*'s in various stages of deviation from the typical *purpurea*. Notwithstanding the fact that good evidence has been presented in early literature (2) that *heptandra* differs in a single, recessive factor from *purpurea*, the expression of this factor underlies a wide variation so that flowers are present without nearly any corollar development and 9 stamens onto fairly tubular flowers differing from *purpurea* only by the fact that they have 3 additional pairs of anthers on the rim of the flower tube (in the positions 5, 6 and 9, see ref. (1)).

Variation of corollar development is not only present between plants, but also between flowers of the same spike. We have detailed observations on this subject which are being prepared for publication (3).

2. RELATION TO INSECTS

Altogether, *heptandra* presents a flower type, very different from the well-known 'fox-glove' type shown by *purpurea*. The lack of the long, tubular corolla

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implies that the stamina are no longer pressed together against the inner dorsal surface of the corolla but emerge freely to all sides. Since they are (mostly) seven, they constitute the most impressive part of the flower, yielding a picture which, in total, is very different from that of *purpurea*.

It seems of interest that this also affects the insects visiting the flower stalks. *Digitalis purpurea* is, like many Scrophulariaceae with large flowers (*Scrophularia*, *Antirrhinum* and others) a typical bumble bee flower. This has been observed already by H. MÜLLER (4) and even by SPRENGEL (5).

MÜLLER (l.c., p. 285) mentions three species of bumble bees which are preferent visitors of *Digitalis purpurea*, viz. *Bombus terrestris*, *hortorum* and *agrorum*, cf. fig. 1, B, C, D. The first two are large, black bumble bees with white and yellow bands, the last one is a smaller species with a rust coloured

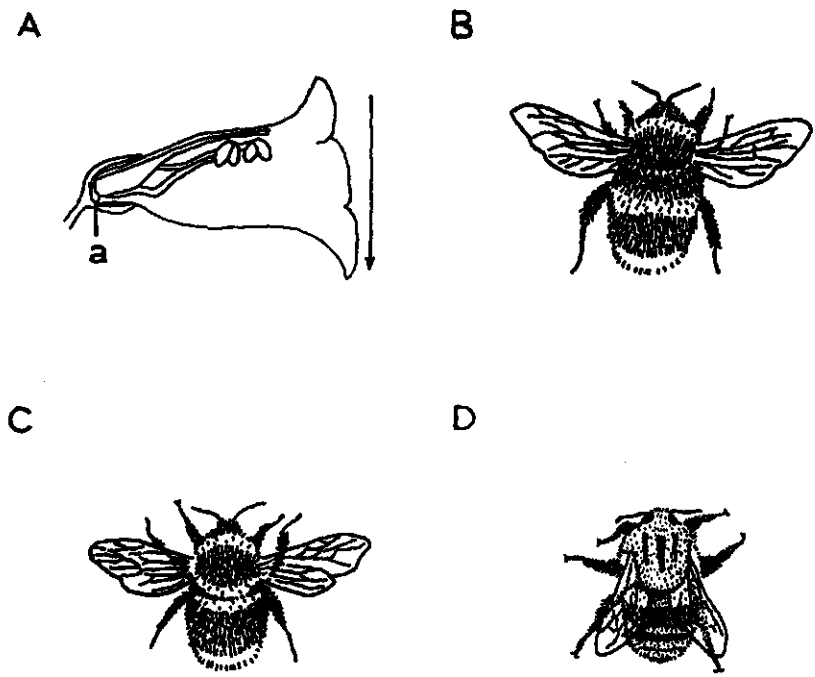

FIG. 1 A. Flower of *Digitalis purpurea* L., median section to show the place of nectar secretion (a). Note the position of stamens and pistil rather pressed against the upper wall of the corolla.
B. *Bombus terrestris*
C. *B. hortorum*
D. *B. agrorum*
Natural size. Drawn by Miss M. E. VAN DEN NOORT, A after H. MÜLLER, ref. (4); B, C, and D after various sources.

thorax and no very definite bands. I do not pretend any detailed knowledge about bumble bees, but specimens which correspond to the first two species, can be seen climbing into the tubular flowers, the dimensions of which very well agree with those of their own bodies. Notwithstanding the fact that MÜLLER also mentions *B. agrorum* as a regular visitor of *D. purpurea*, in the mixed fields in our experimental garden the specimens of this species showed a distinct preference for the flowers of the *heptandra* plants.

One is inclined to think that perhaps the length of the 'tongue' of the various species might be responsible for this behaviour. This, however, can hardly be true, since (according to KNOLL, 6) the only species with a rather long tongue is *hortorum* (ca. 21 mm), i.e. about twice that of *terrestris* (8–11 mm). We have no data on the tongue length of *agrorum*, it probably is in the range of *terrestris* or smaller. The tongue length does not seem to play a differentiating rôle in the visiting of the *Digitalis* flowers.

According to more recent observations (e.g. BRIAN, cf. ref. 7, p. 180), the behaviour of *B. agrorum* with respect to tongue length seems to be much like that of *B. hortorum*. This confirms the impression that with respect to *Digitalis purpurea* and *heptandra* tongue length is not a differentiating factor.

It was already mentioned that the *heptandra* form is held to differ from the normal *purpurea* in one recessive (Mendelian) factor. This would lead to the supposition that in sufficiently large fields (about 10×20 m) in free pollination about $\frac{1}{4}$ of all plants would show the *heptandra* features which, within the large width of variation in degree of expression of these features may be about true.

I have repeatedly observed during the last few years that small bumble bees which show the *agrorum* type very definitely move from one *heptandra* plant to another, and so on, neglecting the visually move obvious typical *purpurea* plants which, moreover, are present in higher numbers.

To this behaviour we observed one fascinating 'exception'. The *agrorum* type of bumble bees may visit *purpurea* stalks but they restrict themselves to the flowers from which the corolla (with the stamens) has just dropped, leaving the still fresh white pistil protruding very obviously from the green calyx (cf., e.g., ref. 1, plate I, fig. 2, plate II, fig. 3, plate III, fig. 6). Probably, the bees obtain from a number of flowers near together at this stage an impression similar to that of *heptandra* flowers with their protruding stamens.

It is difficult to say whether the pistils of the *purpurea* flowers still have a chance to be fertilized by pollen from *heptandra*'s, supplied by the *agrorum* type of bumble bees. It seems likely that their chance to have been fertilized with *purpurea* pollen by the larger bumble bees in an earlier stage is far greater.

Visiting these late stage *purpurea* flowers, the *agrorum* type of bumble bees search for nectar at the bottom of the calyx, which probably still is there or even may still be excreted, *D. purpurea* being rather strongly protandrous.

MÜLLER has explained that nectar is being excreted in a rim at the foot of the gynoeceum (l.c., fig. 100, see also this paper, fig. 1A).

3. Discussion

The visits to just post-floral *purpurea's* by the small bumble bees may be considered as an indication that the overall near-by picture of *heptandra* is the image that leads the short distance search for *heptandra* by *agrorum* bumble bees that are already flying in a large mixed field. Direct experiments to prove this have not yet been tried. It also seems of interest to investigate in how far the attraction depends on the visibility of the remainder of corolla-development in the various *heptandra* variations. Like Plates XIII–XIV in (1) show, there is a fairly continuous range of corollar depression between *purpurea's* and extreme *heptandra's*. We do not know yet at what stage visits by *agrorum* shift to those of *hortorum/terrestris*. This is rather difficult to explore since not all stages are always present, or only present in small numbers. One is inclined to believe that flowers which require entry by the insect of a clearly tubular flower will be avoided by *agrorum*. This would agree with their tendency to avoid the typical *purpurea* and moreover with the supposition that they are trained on the total image of a flower with protruding filaments (stamens or pistils, see above).

It is well-known that in *D. purpurea* specimens with white flowers exist aside of the (more frequent) red ones. The *heptandra* forms exist also in the white flowering types, as well as in the intermediate pink ones. We do not know in how far the colour affects the visiting by insects, it does not seem to have a definite effect.

Systematic observations concerning the bumble bees visiting the different forms, and countings of their number, have not yet been made, but qualitatively, the preference of the *heptandra's* for the *agrorum* type seems beyond doubt. A few times the larger types of bumble bees visit the *heptandra*-type flowers; the *agrorum* type very rarely visits the *purpurea* flowers. Theft of nectar by piercing the bottom part of the corolla was not observed, by far the majority of the insects seem to go the legal way!

Certainly, from a distance, the impression of a mixed *purpurea/heptandra* field, resulted from spontaneous pollination, as exists in our garden, is that of a *purpurea* field. One may ask what leads the *agrorum* type bumble bees to such a field, since, once there, they appear to neglect the true *purpurea*'s. Two types of explanation would appear possible, viz., 1°-They may be lead by their experience that these fields, looking like *purpurea*, contain the *heptandra's* which they want to visit. This type of explanation has a certain probability, since in our garden there are a few fields of more or less this same composition, whereas there are, in the neighbourhood, no pure *purpurea*-fields of similar size. 2°-Another type of explanation might be that the *agrorum* bees indeed are attracted by the general image of *purpurea*, which they may really intend to visit. (It may be recalled in mind that Müller (4) mentions *agrorum* under the regular visitors of *D. purpurea*). If so, once there, the *agrorum* bees may find the *heptandra's* the 'easier preys' which they then furtheron give preference. This type of explanation, however, might be somewhat less probable, since the binding to *heptandra*

appears well developed, and, along this line, one would expect rather more intermediate visits to *purpurea*.

4. Additional comments

Heptandra's appear to be less abundant seed producers than the normal *purpurea*'s. This goes along with a production of more vegetative buds in the axils of the lower leaves, so that the plants tend to become perennials. We have specimens of several years old with some 10–12 flower stalks. The phenomenon may be used for vegetative propagation for physiological and experimental-morphological studies. Inverse relationships between seed production and vegetative propagation have also been reported by other plants, e.g. potatoes with respect to seed production and tuber formation.

We have observed that not many botanists appear ever to have seen *D. purpurea* f. *heptandra*. A much more common deviation is the formation of *peloria* at the end of the flower stalks, i.e. the formation of a terminal more or less radial-symmetric flower which mostly contains a large number of staminae and appears to be composed of several flower initials. We once (1974) have observed *peloria* formation in a *heptandra* plant. Unfortunately, any sort of propagation material from this plant was lost, e.g. also because the possibility of propagation by low axillary buds had not yet sufficiently been realized.

5. Summary

In a mixed field containing *Digitalis purpurea* L. f. *heptandra* De Chamisso among a majority of the typical *D. purpurea*, the *purpurea* flowers are regularly visited by large bumble bees of the types *Bombus hortorum* and *B. terrestris* whereas the smaller *B. agrorum* shows a strong binding to the *heptandra* plants in their flying from one *heptandra* plant to another, disregarding the *purpurea*'s.

Features of this binding are discussed and some additional observations regarding the relation between seed formation and vegetative propagation are mentioned.

Notwithstanding the fact that a number of reports on *heptandra* exist in earlier and more recent literature, not many botanists appear to have ever seen this deviation.

6. Acknowledgement

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