

STUDIES ON BRITISH POPPIES

II. SOME OBSERVATIONS ON HYBRIDS BETWEEN *PAPAVER RHOEAS* L. AND *P. DUBIUM* L.

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ABSTRACT

The observations reported here on interspecific hybrids between *Papaver rhoeas* and *P. dubium* are in general agreement with those given by McNaughton & Harper (1960b). Irregular germination of the hybrid seed is thought to be due to poor embryo development. The total failure of the F₁ hybrids to produce viable gametes would seem to preclude the possibility of any gene-flow between the two species. Observations of meiotic behaviour in the hybrids, however, suggests that the two species may have a genome in common, though its members appear to have undergone structural changes in the two species. No evidence has been obtained regarding the identity of the other *P. dubium* genomes, but the species seems likely to be of hybrid origin.

INTRODUCTION

In spite of the fact that *P. rhoeas* and *P. dubium* frequently occur together in the same habitat, gene interchange between them seems unlikely on account of their differing levels of polyploidy and an effective discrimination shown by the principal pollinating insect, *Apis mellifera* (McNaughton & Harper 1960a).

Presumed hybrids are however reported from time to time and artificial hybrids have been raised both by McNaughton & Harper (1960b) and by the present writer in an attempt to ascertain whether gene flow between the two species is possible.

METHODS

Parent plants were raised in an unheated greenhouse using seed collected from wild populations. Emasculations and pollinations were carried out in a similar manner to that described by McNaughton & Harper (1960b).

<i>Pollinations</i>	<i>Attempted</i>	<i>Successful</i>
<i>P. rhoeas</i> × <i>dubium</i>	41	10
<i>P. dubium</i> × <i>rhoeas</i>	14	3

For cytological observations, the Feulgen technique (Darlington & LaCour 1950) was used, following 1:3 acetic alcohol fixation. Hydrolysis times were 9 minutes in the case of root tips and a maximum of 6 minutes for pollen mother cells.

SEED GERMINATION AND EMBRYO DEVELOPMENT

Contrary to the result reported by McNaughton & Harper (1960b), germination of the hybrid seed was poor and the subsequent seedling mortality rate high, only 16 out of 48 seedlings ultimately developing to maturity.

Embryos were examined from some of the hybrid seed to ascertain whether their development might account for its poor germination. Fifty embryos were dissected out from the seeds resulting from three separate crosses, all having *P. rhoeas* as the seed parent. Twenty-six of these had very small or rudimentary embryos with the cotyledons not or barely differentiated. Eleven had small but fully differentiated embryos, and in the remaining thirteen the embryos were well developed though smaller than those of *P. rhoeas*. Some typical examples are illustrated in Figure 1a. There was insufficient seed to examine

embryos resulting from the reciprocal cross. Variation in the size of hybrid embryos has been reported by Valentine (1953) in *Primula* where it is also associated with poor seed germination.

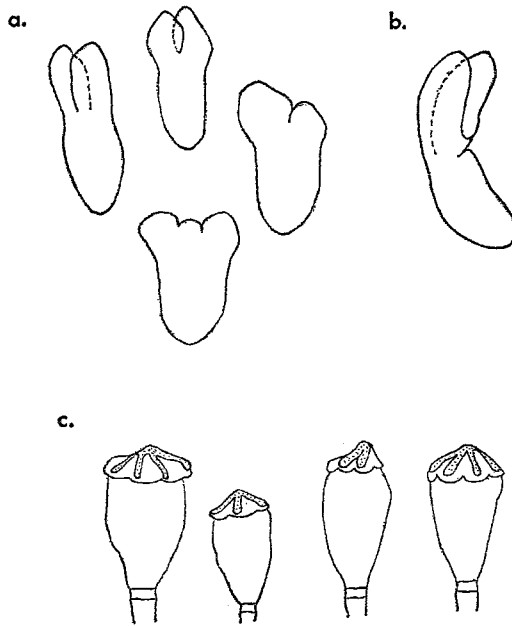


Fig. 1.

- A. Embryos from ripe seed of *Papaver rhoeas* × *dubium*.
 B. *P. rhoeas* embryo for comparison.
 C. Capsules *P. rhoeas* × *dubium*. (a) and (b) × 50, (c) × 2.

GROWTH OF THE HYBRID PLANTS

Similar abnormalities to those reported by McNaughton & Harper (1960b) were observed in the growth of the young hybrid plants. The foliar distortion and chlorosis became less marked with age and the plants ultimately flowered. All were male sterile, though in some the anthers were well developed and contained recognizable but shrivelled pollen grains. The ovary was intermediate in form between those of the parents having a length/breadth ratio between 1.7 and 2.2 (Fig. 1c).

CYTOLOGICAL OBSERVATIONS

Root tip squashes from both *P. rhoeas* × *dubium* seedlings and the reciprocal cross gave chromosome counts of $2n = 28$, thus confirming the hybrid nature of the seedlings (Fig. 2a).

Examination of the pollen mother cells showed that both the first and second divisions of meiosis are negotiated. The onset of meiosis is simultaneous in all the pollen mother cells in an anther, but proceeds at different rates so that both 1st division metaphases and tetrads may be found within the same anther, a condition frequently encountered in interspecific hybrids.

Observations of diakinesis and metaphase I indicate that between three and seven bivalents are formed, the residual chromosomes remaining unpaired (Fig. 2b, 2c). There is also evidence from the configurations at diakinesis that chiasmata are established between the pairing chromosomes, indicating a certain degree of homology. The unpaired chromosomes at anaphase I fail to get on to the spindle and form two groups of irregular numbers near the poles of the spindle. There is no evidence of a precocious division of the unpaired chromosomes at this stage and they all appear to become incorporated in the interphase

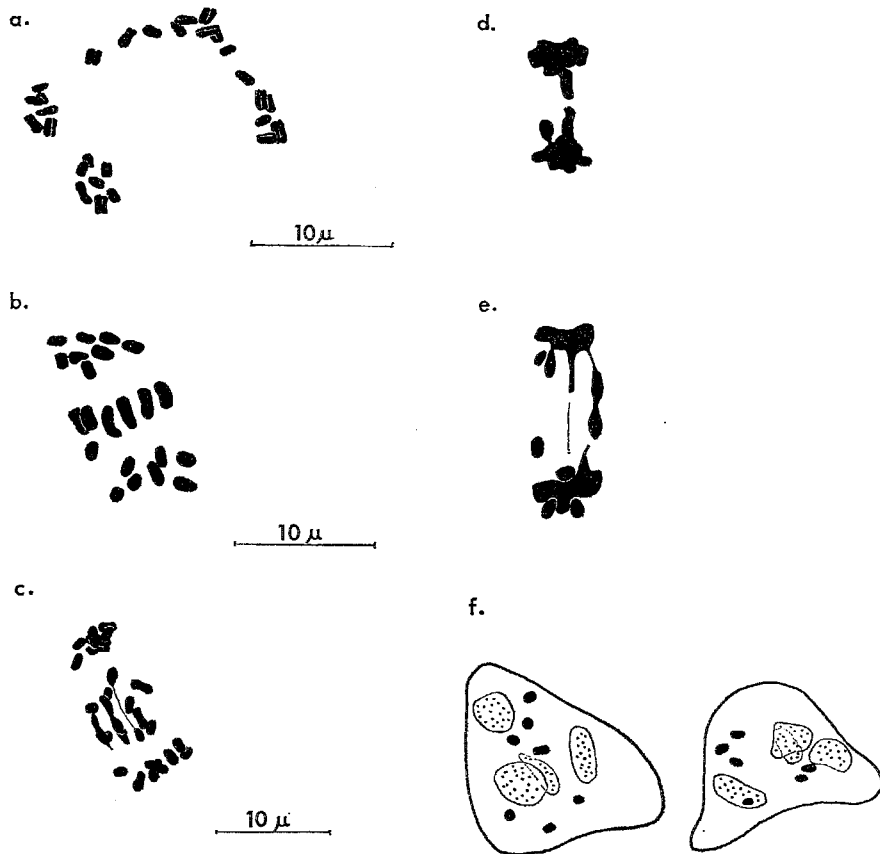


Fig. 2. *Papaver rhoeas* × *dubium*

(a) Root tip squash $2n = 28$.

(b) Meiosis in pollen mother cells: 6 bivalents and 16 univalents.

(c) 7 bivalents separating and 13 univalents.

(d) and (e) Anaphase bridges.

(f) Uneven nuclei and excluded chromosomes at the end of the second division.

nuclei and thus enter the second division. Anaphase bridges occur in many nuclei when the bivalents separate (Fig. 2d, e) and this not only provides further evidence of the establishment of chiasmata but also indicates that the pairing chromosomes differ structurally. In the majority of the pollen mother cells the second division is completed and tetrads are produced. The nuclei of these are of very uneven size (Fig. 2f) and invariably some chromosomes are excluded from them. The 'tetrad stage' frequently contains only two or three nuclei and in these cases there are many excluded chromosomes.

The meiotic behaviour here described indicates strongly that there is homology between the chromosomes of *P. rhoeas* and one of the genomes constituting the hexaploid *P. dubium*. The formation of a maximum of seven bivalents could only be explained otherwise as being the result of pairing between members of two of the *P. dubium* genomes. In this case the formation of tri- and quadrivalents and the consequent irregularities in meiosis and reduction of fertility would be expected in populations of *P. dubium*. Observations of meiosis and pollen development in *P. dubium* provide no evidence of this. The formation of anaphase bridges indicates that the common genome has undergone structural modification within the two species which result in its constituent chromosomes not being homologous along their entire length.

While no evidence has been obtained regarding the identity of the other *P. dubium* genomes, a hybrid origin for this hexaploid does not seem unlikely and might provide an alternative explanation to the possession of weak incompatibility alleles, for the partial self-compatibility in this species.

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