

CHROMOSOME NUMBERS OF *EPILOBIUM* IN BRITAIN

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ABSTRACT

The 14 species of *Epilobium* occurring in Britain are shown to have $2n = 36$. Chromosome numbers of *E. lanceolatum* and *E. tetragonum* subsp. *lamyi* are given for the first time and a further 11 species have not hitherto been counted from British material. The artificial F_1 hybrid *E. montanum* \times *adenocaulon* is of reduced fertility, but shows no meiotic irregularities. The rôle of self-pollination in reducing interspecific hybridization is stressed.

Chromosome numbers have been reported for the majority of European species of *Epilobium* and they were summarized by Löve & Löve (1961, p. 256–7), but there seems to have been only one published record dealing with British plants. Rutland (1941, p. 210) gave the somatic chromosome number of *Epilobium palustre* as $2n = 36$ without specifying the locality from which the material originated. A few of the counts reported in the present paper were mentioned by Clapham (1962).

All counts reported here were made during studies of meiosis in pollen mother cells, the anthers being fixed in 1:3 acetic alcohol and squashed in acetocarmine. With the exception of *E. alsinifolium*, all the chromosome numbers were determined by the senior author during the tenure of a United States National Science Foundation post-doctoral fellowship spent in London during 1960–61. The authors are grateful to Professor D. H. Valentine, Dr. C. R. Metcalfe and Dr. K. Jones for the facilities afforded Raven while he was making his cytological studies and to Mr. A. Eddy for collecting plants of *E. alsinifolium*. Vouchers for the chromosome counts are deposited in the herbarium, Department of Botany, British Museum (Natural History) and in the Dudley Herbarium, Stanford University. Details of the collections from which plants were counted are given in Table 1.

TABLE 1. Chromosome vouchers of British species of *Epilobium*.

<i>E. adenocaulon</i> Hausskn. MIDDLESEX, Chiswick, <i>Raven 18060</i> (garden progeny). SURREY, weed by the herbarium, Royal Botanic Gardens, Kew, <i>Raven 16086</i> .
<i>E. alsinifolium</i> Vill. WESTMORLAND, Moorhouse Nature Reserve, altitude <i>c.</i> 1,800 ft, <i>Moore 464</i> (garden progeny).
<i>E. anagallidifolium</i> Lam. WESTMORLAND, at head of Knock Ore Gill, by road to Radar Station, altitude <i>c.</i> 2,500 ft, <i>Raven 16277</i> (garden progeny).
<i>E. angustifolium</i> L. MIDDLESEX, Twickenham, <i>Raven 16490</i> .
<i>E. hirsutum</i> L. DERBYSHIRE, along hedgerow 2 miles north of Derby, <i>Raven 16194</i> .
<i>E. lanceolatum</i> Seb. & Mauri. SURREY, weed by the herbarium, Royal Botanic Gardens, Kew, <i>Raven 16087</i> .
<i>E. montanum</i> L. OXFORDSHIRE, Bagley Wood, <i>Raven, 15915</i> .
<i>E. nerterioides</i> A. Cunn. KENT, Bayham Abbey, <i>Raven 16168</i> (progeny grown at Chelsea Physic Garden).
<i>E. obscurum</i> Schreb. WESTMORLAND, Glencoyne Wood, Ullswater, <i>Raven 16226</i> .
<i>E. palustre</i> L. WESTMORLAND, Glencoyne Wood, Ullswater, <i>Raven 16225</i> .
<i>E. parviflorum</i> Schreb. SURREY, weed by the herbarium, Royal Botanic Gardens, Kew, <i>Raven 16488</i> .
<i>E. roseum</i> Schreb. SURREY, weed by the herbarium, Royal Botanic Gardens, Kew, <i>Raven 16193</i> .
<i>E. tetragonum</i> L. subsp. <i>lamyi</i> (F. W. Schultz) H. Lév. SURREY, Ewell, <i>Pennington in 1961</i> .
<i>E. tetragonum</i> subsp. <i>tetragonum</i> . KENT, sand pit behind Covers Farm, Westerham, <i>Raven 16485</i> .

All collections of *Epilobium* cited in Table 1, formed 18 bivalents at meiotic metaphase I; no meiotic irregularities were observed. All numbers except that for *E. palustre* are being reported from Britain for the first time; *E. lanceolatum* and *E. tetragonum* subsp. *lamyi* do not appear to have been counted before. The list includes all British species of *Epilobium*, including the two introduced ones, *E. adenocaulon* and *E. nerterioides*. The segregate genus *Chamaenerion* is not recognized here for reasons discussed in detail elsewhere (Raven 1962a, 1962b).



Fig. 1. Chromosome pairing at first meiotic metaphase in the artificial F_1 hybrid between *E. montanum* (Turkey) and *E. adenocaulon* (Middlesex) showing 18 bivalents.

DISCUSSION

These additional chromosome numbers re-emphasize that barriers to hybridization in *Epilobium* sect. *Epilobium* (*Lysimachion*) are not a result of aneuploid differences in chromosome number. Judging from reports in Britain and on the Continent, hybrids are probably possible between all combinations of species except those involving *E. angustifolium* and *E. nerterioides*. Many if not most of these hybrids are at least partly fertile.

Meiosis in interspecific hybrids in *Epilobium* has been studied by Hair (1942) and by Lewis & Moore (1962). These authors studied natural hybrids and in no case were meiotic irregularities observed. In an effort to extend their observations, we artificially duplicated one of the hybrids frequently encountered in Britain, that between *E. montanum* and the introduced North American *E. adenocaulon*. Our strain of *E. adenocaulon* was from Chiswick (see Table 1), whereas our seeds of *E. montanum* were from Turkey (Prov. Bolu, Ala Dağ, alt. 700 m, Khan, Prance & Ratcliffe 515). Both of the parents consistently formed 18 bivalents at meiotic metaphase I. The hybrid plants (Raven 18557) were more vigorous than the parents, with darker, larger flowers, irregularly lobed stigmas, and the short capsules caused by a low seed set (c. 10 per cent. and below). Judged by staining in acetocarmine, their pollen was approximately 15 per cent. fertile (based on 200 pollen grains from each of four F_1 plants). Just as in the cases of natural hybrids analyzed previously, meiosis in this hybrid was quite regular (Fig. 1).

The reduced fertility certainly may help to maintain species distinctions in such a case, but we are still in large measure faced with the problem, posed by Valentine (1951), as to how the species maintain themselves in the absence of strong genetical, geographical and ecological barriers to interbreeding. The relatively small percentage of hybrids found in mixed populations of two or more species of *Epilobium* in Britain suggests that a part of the answer may be in the high degree of self-pollination characteristic of most species of the genus. Of the 14 British species of *Epilobium*, only two are outcrossed to any appreciable degree—*E. hirsutum* and the very distinct *E. angustifolium*, which is presumably incapable of forming hybrids with the other species. In all other species found in Britain, the anthers surround the stigma and shed pollen directly on it, and the high degree of autogamy resulting from this doubtless tends to decrease sharply the proportion of hybrids that might otherwise be expected. This explanation was adduced by Lewis & Moore (1962) for the rarity of hybridization between the North American species *E. adenocaulon* and *E. brevistylum* Barbey in the Rocky Mountains. These authors also postulated that the hybrids they were studying were genotypically not so well adapted as the parental species to the communities in which the parents grew, and consequently they were less likely to become established

in the undisturbed habitats available. In Colorado, where Lewis & Moore studied hybridization in the genus, the summers are long and dry so that the habitats occupied by *Epilobium* are of rather limited extent, normally consisting of wet meadows and streamsides where the plants are members of relatively stable communities. In Britain, on the other hand, the climate is generally much moister throughout the year and many species of *Epilobium* are decidedly weedy, frequently growing in ecologically open communities in which there is a rapid turn-over of individuals. Even under these conditions the proportion of hybrids still remains extremely low. This tends to suggest that habitual autogamy and, possibly, lowered cross-compatibility (Valentine 1951, p. 86) may be far more important in maintaining the species as discrete units, at least for the 'weedy' species, although lowered hybrid fitness probably operates when interspecific crosses do occur.

The evidence presented here further emphasizes that the gross chromosomal rearrangements that have been so important in the evolution of the tribe Onagreae have apparently had no part in the differentiation of species in other tribes of the family (Lewis & Moore 1962, Raven 1963 and unpubl.).

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