Hybridisation between *Rumex rupestris* Le Gall (Polygonaceae) and other docks

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ABSTRACT

Hybrids of *Rumex rupestris* with *R. conglomeratus* are reported for the first time and named as ***R.*** × ***rosemurphyae*** D. T. Holyoak, **hybr. nov**. Other hybrids involving *R. rupestris* have been found at the same locality in West Cornwall (v.c. 1a), involving *R. pulcher* (= *R.* × *trimenii* Camus), probably *R. crispus*, and possibly *R. obtusifolius*. Evidence of introgressive hybridisation was found resulting from *R.* × *rosemurphyae* backcrossing with *R. conglomeratus*, but there was no evidence of introgression with other coexisting *Rumex* species.

KEYWORDS: conservation, Shore Dock, introgression, taxonomy.

INTRODUCTION

Shore Dock *Rumex rupestris* Le Gall is a rare European endemic species occurring on and near coasts from Wales southwards to north-western Spain (Jalas & Suominen 1979; Daniels *et al.* 1998). Many of its localities are on rocky sea cliffs where few other dock species grow, so that opportunities for it to be involved in interspecific hybridisation are less prevalent than with congeners that commonly grow together on disturbed ground inland. Indeed, the reviews by Lousley & Williams (1975) and Lousley & Kent (1981) reported few hybrids of *R. rupestris*, and those only with *R. pulcher* L. and *R. crispus* L. There do not appear to be any reports of hybrids involving *R. rupestris* from outside Britain.

R. rupestris was investigated from 1994–1998 in dune-slack like habitats at Penhale Camp, West Cornwall. During this period its population there increased from about 60 to 137 mature plants. At this site, four other dock species (*Rumex* subgenus *Rumex*) and several of their interspecific hybrids grow intermingled with, or close to, *R. rupestris*. It was expected that under these circumstances hybrids involving *R. rupestris* would occur, and, over the five years of study, a total of eight such hybrid plants was found, apparently representing four different hybrid combinations. This paper extends and partly revises the preliminary notes (Holyoak 1995, 1996) on the hybrids at Penhale Camp by giving descriptions of each of the hybrid taxa and naming the hybrid with *R. conglomeratus* Murray which has not been reported from elsewhere. In addition, previous records of hybrids involving *R. rupestris* are reviewed.

Results are also described of biometric investigation of apparent introgression of *R. rupestris* and *R. conglomeratus* at Penhale Camp. Potential threats to the survival of *R. rupestris* from introgressive hybridisation are discussed on the basis of these data.

METHODS

Penhale Camp (West Cornwall; c. SW/770.570) occupies an extensive area of coastal sand-dunes. In most winters water stands in several large and small pools and flows along an ephemeral stream, but all of these areas are usually dry in summer. These dune-slack like areas support vegetation characteristic of dune-slacks, fens and pool-margins, with locally dominant plants of different areas including *Eleocharis palustris* (L.) Roemer & Schultes, *Epilobium hirsutum* L., *Equisetum palustre* L., *Mentha aquatica* L., *Pulicaria dysenterica* (L.) Bernh. and *Rorippa nasturtium-aquaticum* (L.) Hayek. *Rumex rupestris* grows intermixed with these wetland plants in four separate small colonies.

TABLE 1. HYBRID FREQUENCY INDEX MEASUREMENTS OF *RUMEX RUPESTRIS*, *R. CONGLOMERATUS* AND INTERMEDIATE PLANTS FROM LOCALITIES IN WEST CORNWALL, AUGUST 1996

	Hybrid-index score															
Site	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Penhale Camp SW/769.569	22	7	4	2	-	-	-	1	-	-	2	4	7	16	22	28
Mount Field SW/781.571	-	-	-	-	-	-	-	-	-	-	-	-	1	2	14	20
near Ventongimps Moor SW/779.511	-	-	-	-	-	-	-	-	-	-	-	-	-	3	19	20
Bonython Estate SW/696.207	-	-	-	-	-	-	-	-	-	-	-	-	-	6	17	23

See Appendix 1 for details of the five characters used and the scoring system, with which a typical plant of *R. rupestris* scores 0 and a typical plant of *R. conglomeratus* scores 15. *R. conglomeratus* occurred at all four of these sites; *R. rupestris* was present with it only at Penhale Camp.

Other *Rumex* species present in the same wet areas are *R. conglomeratus* (hundreds of plants), *R. crispus* subsp. *littoreus* (J. Hardy) Akeroyd (many hundreds of plants, but most of them growing in drier edges of wetland vegetation) and *R. obtusifolius* L. var. *obtusifolius* (2 plants seen). In addition, *R. pulcher* occurs in very small quantity on dry slopes nearby. Other dock hybrids recorded in the same area were *R. conglomeratus* × *R. crispus* (5), *R. conglomeratus* × *R. pulcher* (1) and *R. crispus* × *R. obtusifolius* (c. 47) (Holyoak 1996 and subsequent pers. obs.).

The area was visited several times in August of each of the years 1994 to 1998, so that virtually all of the docks present could be identified and counted as their fruits ripened. Some plants were individually marked from 1995 onwards and by 1998 all plants of *R. rupestris* and its hybrids had been individually marked. In 1995, 1996 and 1998 specimens were collected from each of the marked hybrids involving *R. rupestris* at times when they had at least some mature fruits.

During August 1996 it was noticed that some fruiting plants of *R. conglomeratus* showed characters approaching those of the *R. rupestris* growing near them. Because these intermediate characters seemed likely to have resulted from hybridisation, their morphology and those of the closest plants of *R. conglomeratus* and *R. rupestris* were investigated using the "hybrid frequency index" technique of Anderson (1936). The scoring system used is explained in Appendix 1 and other details are given with the results in Table 1. Comparative data were obtained from three populations of *R. conglomeratus* growing at localities in West Cornwall that lacked *R. rupestris*.

Several counts of chromosomes at mitotic metaphase were obtained from root tips of seedlings germinated on moist filter paper in petri dishes. Excised root tips were fixed overnight in Farmer's fluid before squash preparations were prepared using acetic orcein stain.

RESULTS

Rumex* × *rosemurphyae D. T. Holyoak, **hybr. nov.**
(*Rumex conglomeratus* Murray × *R. rupestris* Le Gall) (Fig. 1)
Hybrida a *Rumice conglomerato* Murray et *R. rupestri* Le Gall genita et characteribus plerlsque intermedia; ab ambobus fructibus pro parte maxima abortivis et statura nonnunquam multo majore differt.

A hybrid between *Rumex conglomeratus* and *R. rupestris*, found within 2 m of plants of those two species. It is intermediate between them in most characters but differs from both in being mostly but not completely infertile and sometimes in its much greater size.

A robust perennial growing in a compact clump from a stout rootstock. The holotype was much larger than accompanying plants of *R. conglomeratus* and *R. rupestris*, on 8 August 1995 it had 35

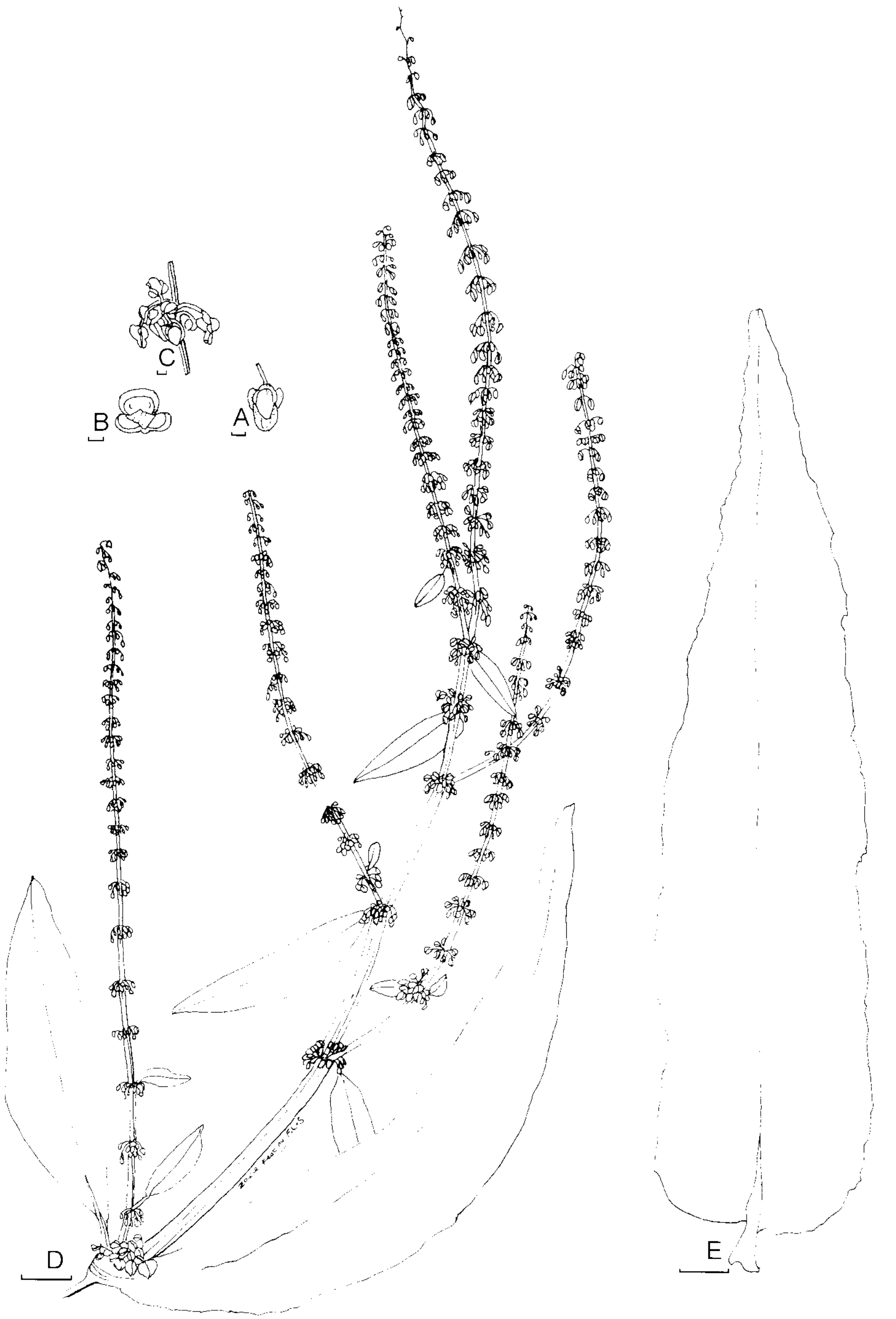

FIGURE 1. *Rumex* × *rosemurphyae*. A. Fruit (i.e. perianth enclosing nutlet) B. Diagrammatic section through fruit. C. Single whorl of inflorescence. D. Inflorescence. E. Leaf from lower part of stem. Scale bars represent 1 mm (A–C) or 10 mm (D, E).

stems up to 1·4 m long, the same plant on 18 July 1998 had 77 flowering stems up to 1·5 m long, in both years most stems had become decumbent before fruits ripened. Lower stem leaves with lamina at flowering up to 20 × 8 cm or more, but most lower leaves wither before fruits ripen. Upper stem leaves smaller, oblong-lanceolate to lanceolate. At least some leaves thicker than in accompanying plants of *R. conglomeratus*, but less thick than in some *R. rupestris*.

Panicles with many branches that mostly arise at about 45° from main stem, the branches more numerous than is usual in *R. rupestris*, but with branching at more acute angles than typical of *R. conglomeratus*. Each of the lower whorls of flowers on each branch subtended by an ovate-lanceolate to narrowly lanceolate leafy bract, the bracts becoming abruptly smaller towards the middle of each branch and absent near the branch apex, as in *R. conglomeratus*. On those parts of the inflorescence where fertile fruits occur, whorls of flowers appear less close and congested than in *R. rupestris*, more like those of *R. conglomeratus*. Where nutlets develop, inner perianth-segments oblong to oblong-lanceolate with bluntly rounded apex and sides subparallel in upper part, always entire. Where nutlets develop, inner perianth-segments very variable in size, some as small as in typical *R. conglomeratus* (length 1·7–2·5 mm) others as long as in typical *R. rupestris* (2·8–3·7 mm), but with many of intermediate lengths. Where nutlets develop, each of the inner perianth-segments has a swollen, rounded tubercle that varies from 70–120% of the maximum width of perianth segment and 40–65% of its length. The few well developed nutlets seen were trigonous, 1·4–1·6 mm long, brown, glossy, with acute angles.

Counts of mitotic chromosomes from three seedlings grown from seed collected from the Holotype were all n = 20. Identical counts were obtained from seedlings of *R. conglomeratus* (4) and *R. rupestris* (5) grown from seed collected from plants growing within 10 m of the holotype. Counts of n = 20 have been reported previously for both of these species (e.g. Degraeve 1975; Rechinger 1993; Kay 1996).

Named for Miss Rosaline J. Murphy in recognition of her work on the Cornish flora and as thanks for introducing the author to Penhale Camp.

HOLOTYPUS: W. Cornwall, v.c. 1a, Penhale Camp (SW/768.569), among *Epilobium hirsutum* in fen along course of ephemeral stream, 7–8 August 1995 and 18 July 1998, *D. T. Holyoak*, field labels C and 28 (**RNG**).

A smaller plant growing 6 m away from the holotype (field label D) was also identified as *R.* × *rosemurphyae*. On 8 August 1995 this plant had only two flowering stems, the longest 70 cm tall. It resembled the Holotype closely in other respects, including its low fertility.

In addition to the two plants described above as *R.* × *rosemurphyae* and interpreted as F_1 hybrids between *R. conglomeratus* and *R. rupestris*, at least six (and perhaps as many as 13) of the 40 plants of *R. conglomeratus* growing within 20 m of them in August 1996 showed characters that somewhat approached those of *R. rupestris* (Table 1, Appendix 1). As discussed below, these are believed to represent back-crosses between *R.* × *rosemurphyae* and *R. conglomeratus*.

On 13 September 1998 two more plants attributed to *R.* × *rosemurphyae* were seen in a dune-slack at Gear Sands (SW/7.5), about 700 m from the Penhale plants (marked by C. J. Neil as numbers 117 and 122; vouchers were given field labels DTH 4 and 6 respectively). They were again close to plants of both *R. conglomeratus* and *R. rupestris*. Both of these hybrids also had low fertility (<20% of nutlets developed) and both showed evidence of "hybrid vigour", one plant having about 20 flowering stems up to 1·3 m tall, the other 39 flowering stems up to 1·4 m tall. Details of the inflorescence and inner perianth-segments were similar to those described for the Holotype from Penhale Camp. Their (fertile) inner perianth-segments measured (2·0)3·0–3·3(3·7) mm on one plant and (2·2)3·0–3·2(4·0) mm on the other.

Probable *Rumex crispus* L. × *R. rupestris* Le Gall

A single plant tentatively attributed to this hybrid was found at Penhale Camp on 24 July 1996, close to both of the supposed parent species. It was about 60 cm tall with a single main stem. The lower stem leaves were lanceolate, up to 23 × 5 cm, rather thick and with somewhat crisped margins. The panicle had nine rather upright branches diverging at 10–20° from the main stem, several of the longer branches having several whorls in the lower half of the branch subtended by a narrowly lanceolate, petiolate bract. The whorls of the inflorescence appeared less crowded than in *R. crispus*, but this impression apparently resulted from low fertility, with many of the inner perianth-segments failing to enlarge after flowering. The minority of perianth segments that had enlarged were smaller and narrower than in *R. crispus*, but broader than in *R. rupestris* (reaching 3·7 mm long × 2·8 mm wide), with wider apices, three swollen tubercles and entire margins (occasionally with a few short or indistinct teeth).

While the balance of probabilities would suggest that this is a hybrid between *R. crispus* and *R. rupestris*, it may be impossible to discount other hybrid combinations using morphological characters. In particular, the parent with wide inner perianth segments might have been *R. crispus* × *R. obtusifolius* (= *R.* ×*pratensis* Mert. & Koch) rather than *R. crispus*, a possibility strengthened by the presence of short teeth on some inner perianth segments of the hybrid. Varied forms of *R.* × *pratensis* were growing nearby, some of them with up to 40% of nutlets well developed. It is even possible that this hybrid plant represents an extreme form of *R.* ×*pratensis* or a backcross between it and *R. crispus*, but some of its enlarged inner perianth segments appear too narrow for that to be likely. The second parent with narrow inner perianth segments might have been *R. conglomeratus* rather than *R. rupestris*, but that seems less likely in view of the upright branches of the panicle in the hybrid and the large size of some inner perianth segments and their tubercles. However, involvement of *R. conglomeratus* would explain the rather prominent bracts on some branches of the panicle. Because of these doubts about identification a new name for the hybrid combination of *R. crispus* × *R. rupestris* is not introduced here. The possible occurrence of "triple" hybrids involving *R.* ×*pratensis* is discussed further below.

Rumex crispus × *R. rupestris* has been reported from the Isles of Scilly (v.c. 1b) and Kenfig, Glamorgan (v.c. 41) (Lousley & Williams 1975; Lousley & Kent 1981; Stace 1991); there are specimens from both vice-counties at **RNG**. Dr J. R. Akeroyd (pers. comm.) has located an additional specimen collected above rocks just above HWM at Pendower Beach, E. Cornwall (v.c. 2) by Olga Stewart 277/82 on 13 September 1982 (**E**).

Kay (1996) mentions instances of *R. crispus* subsp. *littoreus* being mistaken for this hybrid. However, the Penhale plant and those discussed by Lousley & Williams (*loc. cit.*) differed from *R. crispus* subsp. *littoreus* not only in being largely infertile but also in having at least some inner perianth-segments narrower overall, or narrower apically, than in *R. crispus*.

Possible *Rumex obtusifolius* L. × *R. rupestris* Le Gall

Three dock plants growing close together in the edge of a fen area at Penhale Camp were studied on 8 August 1995 and on 24 July 1996. Two of them that survived were studied again on several visits during July–September 1998, allowing herbarium material to be collected at various stages of development. Their puzzling combination of morphological characters and consistently low fertility (with less than 20% of nutlets developing) implied they were hybrids, but although the three plants are rather similar to each other, they show an odd mixture of features that has prevented confident inference of the parent species.

All three plants grew as compact patches from stout rootstocks, with strong, erect flowering stems. In August 1995 one plant (field label E) had about 25 flowering stems up to 1·1 m tall, the other plant (G) had 11 stems up to 1·2 m tall. The basal and lower stem leaves were thick and fleshy, with strongly undulate margins; an immature basal leaf had petiole 7 cm, lamina 11 cm; the longest stem leaves were oblong-lanceolate and had petiole 6·5 cm, lamina 20·5 cm. The underside of the leaf midrib and some of its strongest veins had low conical papillae, recalling those in *R. obtusifolius*, but much smaller and less developed. The panicles were similar in habit to those of *R. rupestris*, with branches mainly rather erect (at 20–30° from main stem) and none widely divaricate. The inner perianth segments of the minority of fruits that ripen were wider than in *R. rupestris*, but narrower than in *R. crispus* (reaching 4·6 mm long and 3·0 mm wide), with a longer and more attenuate apex than in *R. crispus*, mostly with one or two short teeth on the basal margins. All three inner perianth segments on each well-developed fruit had a large swollen tubercle, that on one perianth segment being larger than those on the other two perianth segments.

Dock species growing within 20 m of these plants were *R. crispus*, *R. rupestris* and *R. conglomeratus*, along with numerous *R.* × *pratensis* and two *R.* × *rosemurphyae*; the only other dock species within many hundreds of metres being two plants of *R. obtusifolius* and a few of *R. pulcher*. Nevertheless, the distinct teeth on the inner perianth segments imply that among the dock species occurring nearby, either *R. obtusifolius* or *R. pulcher* was one of the likely parents of the hybrids. However, involvement of *R. pulcher* seems unlikely, as the hybrids gave no evidence of the divaricate branching, warty tubercles or other characters of that species. On the other hand, involvement of *R. obtusifolius* might be deduced from the presence of papillae on the back of the leaf midribs, albeit that these and other features of *R. obtusifolius* appear poorly developed.

Other features of these plants imply that *R. rupestris* was one parent, including the thick leaves, large to very large tubercles and rather narrow inner perianth segments with more or less attenuate apex. Nevertheless, a supposed parentage of *R. obtusifolius* × *R. rupestris* does not account for the strongly undulate leaf margins, for which it is tempting to infer some involvement of *R. crispus*. Since numerous plants of *R. crispus* × *R. obtusifolius* (*R.* × *pratensis*) were present nearby, whereas the only two plants of *R. obtusifolius* found were several hundreds of metres distant, the characters of the three hybrids might therefore be best explained by inferring their parentage as (*R. crispus* × *R. obtusifolius*) × *R. rupestris*.

Hybrids between *R. obtusifolius* or *R.* × *pratensis* and *R. rupestris* have not been reported before. Indeed, no "triple" hybrids have been reported for wild docks in Britain, although crosses involving three species have been produced experimentally and they are known in Europe (Lousley & Williams 1975). The absence of British reports of "triple" hybrids in *Rumex* might therefore result not from their absence but from the almost insuperable difficulties in identifying them from morphological characters.

Williams (1971) suspected from field observations that *R.* × *pratensis* back-crosses with both parental species and this suspicion was strengthened because *R. crispus* × *R.* × *pratensis* has been produced in cultivation. Holyoak (1996) noted that the numerous *R.* × *pratensis* at Penhale Camp vary widely in fertility and in characters of the inner perianth segments, concluding that it is uncertain to what extent their marked variability is due to back-crossing or merely the expression in F_1 hybrids of an independent assortment of varied characters from the parental genotypes.

Overall, it seems likely that the three puzzling plants described above originated either from *R. obtusifolius* or *R.* × *pratensis* hybridising with *R. rupestris*. Because analysis of their morphological characters alone may provide an insufficient basis to choose between these alternatives the hybrid combination is not named here.

Rumex* × *trimenii Camus
(*Rumex pulcher* L. × *R. rupestris* Le Gall)

A single plant of this hybrid grew close to numerous plants of *R. rupestris* at Penhale Camp from 1994–1996 (**RNG**); it was described and illustrated by Holyoak (1995). A similar, but smaller, plant was found in 1998 close to a different colony of *R. rupestris*. The nearest plants of *R. pulcher* to both of these hybrids were 200 m away and few in number.

Both of the Penhale hybrids had low fertility although at least some apparently fertile fruits were surrounded by perianth-segments that enlarged after flowering. Their widely divaricate branches resembled those of *R. pulcher* and the influence of that species was also apparent from the reticulate venation of the perianth segments, the presence on them of marginal teeth and the warty surface of their tubercles. Influence of *R. rupestris* was apparent in the hybrids from the strong stems, the rather thick leaves of broadly lanceolate shape and the narrowly lingulate inner perianth-segments. Lousley & Kent (1981) describe a similar combination of characters in *R.* × *trimenii*. There appear to be three previous records of this hybrid in the wild, each of single plants: in v.c. 1b from east coast of Samson, Isles of Scilly (**RNG**) and New Grimsby, Tresco, Isles of Scilly (**RNG**) , and in v.c. 2 at Whitesand Bay, E. Cornwall (**BM**); it also arose spontaneously in the garden of the South London Botanical Institute (Lousley 1971, 1983; Lousley & Williams 1975; Lousley & Kent 1981; Margetts & David 1981; Holyoak 1995, 1996).

DISCUSSION

Rumex rupestris at Penhale Camp has apparently produced hybrids involving all four of the other dock species that grow in the same area. The total population of *R. rupestris* there was about 60 mature (fruiting) plants in 1994, but it had increased to 132 by 1998. Although the number of hybrids involving this species at Penhale was small (eight plants), they apparently exceeded 10 % of the total *R. rupestris* population during 1994–1996. Moreover, six of the eight hybrids were found in one small fen area (SW/768.569) that supported a maximum of 18 plants of "pure" *R.*

rupestris. Two more hybrids were found at Gear Sands alongside a colony of about 27 plants of *R. rupestris*.

Most, if not all, of these hybrids produce at least some pollen and at least small amounts of viable seed. Hence, given the rather high frequencies of F_1 hybrids that have been found, there may be opportunities for introgression to occur between the dock species involved. The following discussion explores various possibilities of introgression between *Rumex* species at Penhale.

POSSIBLE INTROGRESSION OF *R. RUPESTRIS* GENES INTO *R. CRISPUS*

Lousley and Kent (1981) reported possible introgression of *R. rupestris* into *R. crispus* in the Isles of Scilly and at Kenfig, Glamorgan, noting that "in both these localities plants referred to *R. crispus* occur with exceptionally large, elongate tubercles recalling those of *R. rupestris* and indicating possible introgression". However, these may have been merely the coastal taxon now treated as *R. crispus* subsp. *littoreus* (e.g. in Stace 1991). Nevertheless, plants of *R. crispus* subsp. *littoreus* growing at Penhale Camp in the same areas as *R. rupestris* also include some with unusually elongate tubercles and it was tempting at first sight to suspect introgression had occurred between these species. However, the Penhale plants also grew alongside numerous *R.* × *pratensis* (26 were counted in 1995) and possible back-crosses of these to *R. crispus*, the plants showing considerable variability in morphology and in fertility (cf. Holyoak 1996). Hence there is no need to invoke introgression from *R. rupestris* to explain variability in the *R. crispus* growing close to it at Penhale Camp.

INTROGRESSION OF *R. RUPESTRIS* GENES INTO *R. CONGLOMERATUS*

In August 1996 the small fen area at Penhale Camp with the two plants of *R.* × *rosemurphyae* also had about 40 plants of *R. conglomeratus* and at least six and perhaps as many as 13 of these showed characters approaching those of *R. rupestris* (Table 1). Because no evidence of *R. conglomeratus* showing similar characters was found in 39 plants studied from other parts of Penhale Camp or in a total of 125 plants from three localities elsewhere in West Cornwall, the presence of *R. rupestris* seems to be associated with occurrence of some of its characters in the coexisting population of *R. conglomeratus* (Table 1). Since two F_1 hybrid plants (*R.* × *rosemurphyae*) were present at the site it seems likely that some of the plants of *R. conglomeratus* had acquired genes from *R. rupestris*, presumably as a result of back-crossing from F_1 hybrids.

Although fully adequate data on pollen fertility of *R.* × *rosemurphyae* are not available, freshly collected pollen from its Holotype mainly appeared well formed when examined microscopically in July 1998. The F_1 hybrid (*R.* × *rosemurphyae*) produces few fertile fruits so that few F_2 plants would be expected to occur, although some of its fruit has been successfully germinated in cultivation. In contrast, the plants of *R. conglomeratus* putatively introgressed with *R. rupestris* appear to produce mainly fertile fruits so these back-crosses would be expected to persist once established and this may explain the occurrence of at least six and perhaps as many as 13 such plants in one small fen area at Penhale Camp.

RISK OF INTROGRESSION OF *R. CONGLOMERATUS* GENES INTO *R. RUPESTRIS*

R. rupestris is regarded as a globally threatened species, which is included in the *British Red Data Book* (Wigginton 1999), placed on the "Biodiversity Short List" (B.S.G.R. 1995) and included in Schedule 8 of the Wildlife and Countryside Act, 1981. It is included in English Nature's "Species Recovery Programme" which is being undertaken collaboratively with Plantlife's "Back from the Brink" Project. Its population at Penhale Camp (137 fruiting plants in 1998) apparently includes at least 20 % of all *R. rupestris* plants currently known in the British Isles (cf. Daniels *et al.* 1998).

In these circumstances any "leakage" of genes from other docks into *R. rupestris* populations would complicate attempts to maintain a favourable conservation status for "genotypically pure" *R. rupestris*. The potential danger is evident from several well documented instances of the loss of flowering plant taxa through introgressive hybridisation, either locally (DePamphilis & Wyatt 1990; Klier *et al.* 1991), or over the whole range of geographically restricted taxa (Reiseberg *et al.* 1989). However, although the data presented in this paper appear to show "leakage" of genes out of *R. rupestris* into *R. conglomeratus* there is no direct evidence for genes of *R. conglomeratus* entering the *R. rupestris* genotype. This asymmetry might be genuine and have arisen because hybridisation was asymmetrical with respect to male and female parentage, or because of differential mortality in hybrid products.

However, this apparently fortunate result might be seriously misleading, both regarding the situation at Penhale Camp and elsewhere. Some doubts arise because few *R. rupestris* plants could be studied (although at least 130 have now been studied in detail, of which 35 were scored for hybrid index frequency in 1996), despite the Penhale Camp population being one of the largest known. Thus, relatively rare, introgressed, fruiting plants of *R. rupestris* might be absent merely as a result of stochastic processes operating during germination or causing mortality during growth, so that viable seed with an introgressed genotype might nonetheless be present at low frequency in the local seed-bank.

It is also possible that the mode of inheritance or mode of phenotypic expression of the characters used in deriving the hybrid frequency index means it is easier to recognise introgressed *R. conglomeratus* than introgressed *R. rupestris*. Although polygenic traits can be expected to show intermediate expression in hybrids, traits governed by one or two genes are more likely to show parental expression, which could include strong maternal effects. This may explain why, in a survey of morphological patterns in natural and experimental hybrids of flowering plants, Reiseberg & Ellstrand (1993) found that hybrids are no more likely to display intermediate morphological features than parental ones. The classic "hybrid frequency index" technique of Anderson (1936) can thus be viewed as applicable in only the minority of situations where hybrids are intermediate.

Considered against this background, the present lack of morphological evidence for introgression of *R. conglomeratus* genes into *R. rupestris* might well be misleading. It seems likely that if a theoretical introgressed *R. rupestris* was once established in a population, further back-crossing and introgression into that species could easily occur, much as appears to have happened with introgressed *R. conglomeratus*. In view of such dangers, further work on hybridisation of *R. rupestris* with other docks is desirable, for which morphological studies might usefully be supplemented by genetic studies that should provide additional characters.

Daniels *et al.* (1998) reported "preliminary" results of isozyme electrophoresis on samples of *R. rupestris* from south-western England, disclosing a high level of genetic diversity within some populations and significant differences between certain groups of populations. Nevertheless, it remains unclear how much of that genetic variation is intrinsic to *R. rupestris* and how much of it might be derived from introgressive hybridisation with congeners. This doubt becomes important if the species is to be introduced or reintroduced into the wild since it is then desirable to establish that genotypically "pure" *R. rupestris* plants are used. Otherwise, attempts to maximise genetic variation in the introduced populations might result in introgressed plants being chosen for introduction attempts.

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APPENDIX 1

Methods used for hybrid frequency index measurements of *Rumex rupestris*, *R. conglomeratus* and intermediate plants from localities in West Cornwall, August 1996.

The hybrid index was derived by scoring each of five characters on each plant. A score of 0 was assigned for character-states typical of *R. rupestris*, 3 for those typical of *R. conglomeratus* and 1–2 for intermediate states. Hence, summing data for five characters, a typical plant of *R. rupestris* would score 0, a typical plant of *R. conglomeratus* would score 15. Data were scored only from undamaged plants with mature (drying) perianths. The characters and scoring systems were as follows:

Length of longest inner-perianth segment: mean of 10 perianths examined from middle part of inflorescence; measurements made with eyepiece graticule to accuracy of ± 0·05 mm; 0 = > 3·0 mm, 1 = 2·5–3·0 mm, 2 = 2·0–2·5 mm, 3 = < 2·0 mm;

Length of tubercle as per cent of length of longest inner-perianth segment: mean of 10 perianths examined from middle part of inflorescence (same perianths as for preceding character); measurements made with eyepiece graticule to accuracy of ± 0·05 mm; 0 = > 60%, 1 = 55–60%, 2 = 50–55%, 3 = < 50%;

Angle of main branches of inflorescence: modal value; angle measured from main stem (not from vertical); measured only for branches > 5 cm long; 0 = < 50°, 1 = 50–60°, 2 = 60–70°, 3 = > 70°;

Number of bracts on longest three branches of inflorescence: using only branches > 10 cm long; 0 = 1–5 bracts, 1 = 6 or 7 bracts, 2 = 8 or 9 bracts, 3 = > 9 bracts;

Crowding of whorls on main branches of inflorescence: estimated as ratio of inflorescence whorl width (flowers + their pedicels)/ interwhorl width along the inflorescence axis (length of stem clear of all flowers + pedicels); modal value for all of main inflorescences; 0 = ratio <1·0/1, 1 = ratio 1·0–1·25/1, 2 = ratio 1·25–1·5/1, 3 = ratio > 1·5/1.