Taxonomic separation of *Ulex minor* Roth. and *U. gallii* Planch.: morphometrics and chromosome counts

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ABSTRACT

Morphological separation of species in the genus *Ulex* (Fabaceae) is difficult because they and their hybrids seem to show overlaps in the ranges of all characters. Chromosome counts offer a method of accurately assigning plants to species, which can then be used to obtain definitive measures of character ranges. This study was carried out in order to address the issue of the identification of the two closely related species *Ulex gallii* Planch. and *Ulex minor* Roth., and to investigate hybridisation between the two species. Chromosome counts from 135 individuals growing at a site in Dorset gave results of n = 16 for 53 plants and n = 32 for 82 plants. These counts are those usually reported for *U. minor* and *U. gallii* respectively. There was no chromosomal evidence for any *U. gallii* × *U. minor* hybrids.

Using chromosomal identification of species, measures of one vegetative and five floral characters were compared. All characters showed species differences, but all overlapped to a greater or lesser degree and could not be used individually to separate the species consistently. Use of a suite of characters gave more reliable separation of the species, but a small proportion of plants (1·5–2·5%) were misclassified. Use of the character ranges reported by Proctor (1965) gave less reliable identification, with 7% of plants misclassified.

Two possible barriers to hybridisation between the two species were investigated. The species show slightly asynchronous flowering, but this is probably insufficient to prevent cross-fertilisation. Both species had very similar insect pollinator assemblages, and it is concluded that interspecific pollen transfers between *U. gallii* and *U. minor* can and do occur.

KEYWORDS: *Ulex gallii* × *U. minor*, discriminant analysis, gorse, phenology, pollinators.

INTRODUCTION

Ulex minor Roth. and *U. gallii* Planch. (Fabaceae) are very similar morphologically and difficult to separate (Gloaguen 1986; Proctor 1965). Following a study by Proctor (1965) they are usually distinguished by measures of particular characters such as lengths of standard, calyx or primary spine, or bush size. Studies which have measured large numbers of plants sampled over southern Britain (Proctor 1965), Brittany, France (Gloaguen 1986) and Dorset, England (Bullock *et al.* 1998) have demonstrated that the two species can be largely separated by morphometrics, but a substantial minority of plants of both species have character values which overlap with those of the other species. Therefore, the problem arises of whether it is possible to assign plants with intermediate characters to one or the other *Ulex* species with confidence.

Cytological methods provide an unambiguous way of separating the two species. *U. minor* is diploid (2n = 32) (Alvarez Martinez *et al.* 1988; Bullock *et al.* 1998; Castroviejo & Valdes-Bermejo 1990; Fernandez Prieto *et al.* 1993; Misset 1990; Misset & Gourret 1996) and *U. gallii* has been shown to be either tetraploid (2n = 64) (Bullock *et al.* 1998; Fernandez Prieto *et al.* 1993) or hexaploid (2n = 96) (Misset 1990; Misset & Gourret 1996). Although several studies have reported both tetraploid and hexaploid *U. gallii* (Alvarez Martinez *et al.* 1988; Castroviejo & Valdes-Bermejo 1983; Fernandez Prieto *et al.* 1993), it is sufficient for taxonomic separation that the two species have consistently different ploidy levels.

However, the link between chromosome number and morphology in these two *Ulex* species has never been made explicitly. The consistent ploidy differences between the species in the studies reported above would suggest that the authors have had few problems in distinguishing the species

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when sampling in the field. However, it is not clear whether difficult or intermediate specimens have been avoided in these studies. Bullock *et al.* (1998) went one stage further and carried out chromosome counts on specimens identified in the field using Proctor's characters. This paper takes the final step and provides numerical data on the correlation between chromosome number and the values of a range of morphological characters. The strategy is to use chromosome counts to assign plants definitively to one ploidy level and thus (by extension) to one species, and then to investigate whether one or (more probably) a combination of morphological characters serve to separate the species accurately and completely. This approach was used recently by Cubas & Pardo (1997) to investigate differences between *U. europaeus* subsp. *europaeus* and *U. europaeus* subsp. *lactobractaeus* in the Iberian peninsula. We also used this methodology to determine to what extent the widely-used character values reported by Proctor (1965) gave accurate identification of plants when tested against chromosome counts.

Taxonomic problems are complicated further by the possibility of hybridisation between the two *Ulex* species. Such hybrids were suggested by Corillion (1950) and Lambinon (1962), but these observations are not convincing as they are based on morphological observations. A survey carried out by Bullock *et al.* (1998) in a mixed population in Dorset found 84 plants with $2n = 32$ or $2n = 64$, but one plant had $2n = 48$ chromosomes. If this count, which had never been reported before, does indicate the existence of hybrids between *U. minor* and *U. gallii*, then such hybrids appear to be extremely uncommon. A secondary aim of the study reported here was to search for plants with this intermediate chromosome number and to characterize them morphologically.

U. gallii and *U. minor* are strictly insect-pollinated, allogamous plants. Little work has been carried out on the ecology of these species, so we used this opportunity to obtain information on their flowering phenology and insect pollinators. These data were used to carry out a preliminary investigation into the reasons behind the very low proportions of hybrids even in mixed populations (Bullock *et al.* 1998). Barriers to the hybridisation of two species can be due to geographical, ecological or phenological factors (Leebens-Mack 1998; Weiblen & Brehm 1996). There are many factors controlling the production of hybrid plants, such as pollen-stigma interactions, ovule abortion, viability of seed, or fitness of the hybrid offspring (Carney *et al.* 1996; Weiblen & Brehm 1996). However, here we look at just two: the identity of pollinators and the degree of synchrony in flower production.

To summarize, the following questions were addressed in this study:

1. Can *U. minor* and *U. gallii* always be distinguished accurately using morphometrics, when checked against chromosome counts?
2. Are there *U. gallii* × *U. minor* hybrids, as detected using chromosome counts?
3. Are there any differences between *U. gallii* and *U. minor* in flowering phenology?
4. Are there differences in pollinator assemblages and/or pollinator behaviour which could act as a reproductive barrier between *U. gallii* and *U. minor*?

METHODS

The distributions of *U. gallii* and *U. minor* overlap in Dorset, England, but most heaths only contain one of these species of *Ulex* (J. M. Bullock unpublished data). The study site was Gore Heath (SY/924.900), where the two species are intermingled and grow in close proximity. This was ideal as it provided a situation where separation of the species was most difficult, where hybrids were most likely to occur, and where pollinator behaviour on both species could be observed. This is an area of mixed dry and humid heath, dominated by the two *Ulex* species, *Calluna vulgaris*, *Erica cinerea*, *Erica tetralix*, *Ulex europaeus*, *Molinia caerulea*, *Agrostis curtisii* and *Agrostis capillaris*, with scattered *Pinus sylvestris* and *Betula pendula*.

In early July 1998, four 50 m transects were laid out in Gore Heath: two in areas where *U. minor* was more abundant than *U. gallii*, and the other two in areas where *U. gallii* was the predominant species. Along the transects, each bush of either *Ulex* species touching the transect line was marked – 135 plants in all. These plants were then sampled in different ways.

CHROMOSOME COUNTS

Chromosome counts were made using the same methods as Bullock *et al.* (1998). During mid- to late July flower buds of c. 2 mm length were collected from each plant and fixed in the field in Carnoy's fixative (3:1 glacial acetic acid:ethanol). The buds were refrigerated for at least 48 hours. The anthers were then dissected out on a microscope slide in a drop of aceto-carmine, and squashed under a coverslip. Gametophytic counts of stained chromosomes were made from pollen cells at metaphase 1 for at least two buds from each plant.

MORPHOMETRICS

One vegetative character and four floral characters were measured on each of the marked plants during mid-August 1998, but measures of the flower parts were not taken for seven individuals which were not in flower by that time. Measurements of the length of the longest primary spine on the flowering shoot were taken in the field: five measures were taken on different branches for each bush.

For the floral characters, five fully opened flowers were picked from each bush and kept chilled. Within 24 hours of collection each flower was measured for the length of the calyx, standard, keel and wings to the nearest 0·5 mm. The five measures taken for the five characters were used to calculate the mean of each character for each bush.

PHENOLOGY

Gloaguen (1986) described three phenological stages for *U. gallii* and *U. minor*. Stage 1, the closed flower bud. The size of the bud can be variable but only the sepals are visible. Stage 2, the more-or-less opened flower before fertilization. This is from the stage the flower begins to open showing the tip of the standard, to the fully opened flower. Stage 3, the flower after fertilisation. The flower withers and the petals burnish and fade. Once they have dropped, the pod becomes visible.

We monitored all three stages, but only stage 2, the receptive flower, is considered as this is the stage of relevance to hybridisation. Between 13 July and 10 November 1998, at intervals of an average of 11 days, the stage 2 flowers were counted on two branches for each of the 135 bushes. The amount of each branch sampled was restricted to the last 12 cm of the main branch and side branches within a 12 cm spread from the main branch. This was to keep the length of branch sampled roughly equivalent between bushes. The same branches were sampled at each census. As far as possible, the branches sampled were chosen in two different parts of each bush – for example one on the top and one on the lower part of the plant – in order to take into account the flowering heterogeneity within each individual.

POLLINATOR OBSERVATIONS

The pollination of *Ulex* spp. is described by Proctor *et al.* (1996). The flowers lack nectar, but are freely visited by bees. When a bee forces entry into a fresh flower, this causes the keel petals, which are held straight by the stamen tube and the style, to break apart. The uncovered stamens and style are brought sharply into contact with the underside of the insect, so dusting it with pollen. This is an explosive pollen-presentation mechanism. Once "exploded", the spent flower hangs limply open and is seldom visited again by insects.

Monitoring of flower visitations was carried out over eight 30 minute periods for both species of *Ulex*. During these periods, the number of individuals of each pollinator species visiting bushes of a single species (identified by chromosome counts) growing within a 2×2 m area was counted. Individuals were only counted if they showed pollination behaviour. All observations were made between 12 and 14 August and during the peak of insect activity between 11 a.m. and 5 p.m. The same number of observation periods for each of the two gorse species was carried out each day, so variation in weather conditions would not bias the comparison of the insect visitation rates between the *Ulex* species. A reference collection of insect visitors to the *Ulex* flowers was made and used to identify individuals in the field.

QUANTIFICATION OF OVERLAP

The overlap between *U. gallii* and *U. minor* in both flowering phenology and pollinator assemblage was calculated using the Proportional Similarity Index (Colwell & Futuyma 1971; Rozzi *et al.* 1997):

$$Ps = 1 - 0{\cdot}5\Sigma \mid P_{ij} - P_{ik} \mid \quad (1$$

$P_{ij} = N_{ij} / Y_j$ and j and k represent the two species. For flowering periods, N_{ij} is the number of flowers for the species j on date i, and Y_j is the total number of flowers counted over all census dates for species j. For pollinator assemblages, N_{ij} is the number of flower visits made by insect species i on *Ulex* species j, and Y_j is the total number of flower visits by all pollinator species recorded on species j. The index Ps takes its maximum value of 1 when the proportional distributions of species j and species k among the categories (flowers among dates, or pollinators among insect species) are the same, and its minimum value of 0 when the two species share none of the categories.

RESULTS

CHROMOSOME COUNTS

Of the 135 plants sampled, 53 individuals had gametophytic counts of n = 16 and 82 individuals had counts of n = 32. No cytotypes with an intermediate number of chromosomes were observed. In the subsequent analyses of morphology, flowering phenology and pollinator assemblages, plants were classified according to their chromosome counts: plants with n = 16 chromosomes were assumed to be *U. minor*, and those with n = 32 chromosomes were assumed to be *U. gallii*.

MORPHOMETRICS

Four floral characters and one vegetative character were compared between the two (cytologically-identified) species, with the mean character value for each plant being taken as a sample. Proctor

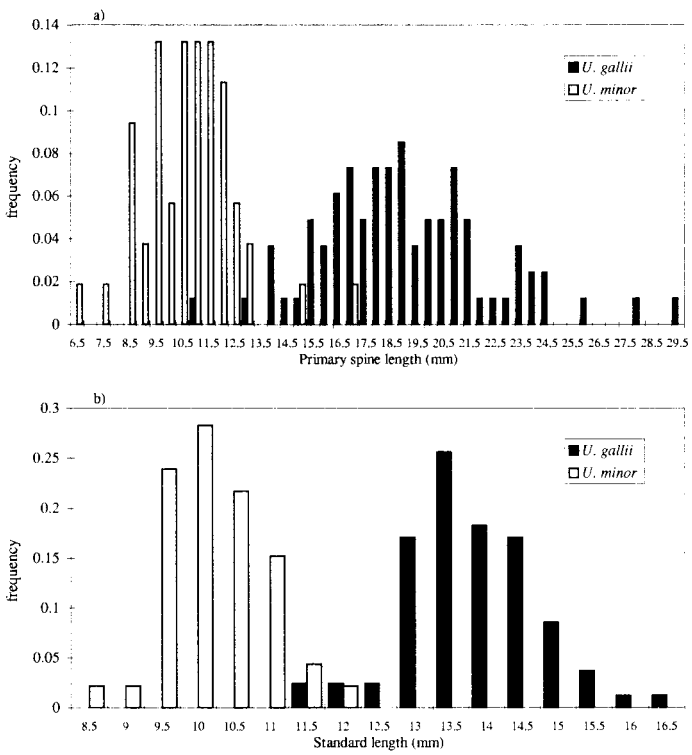
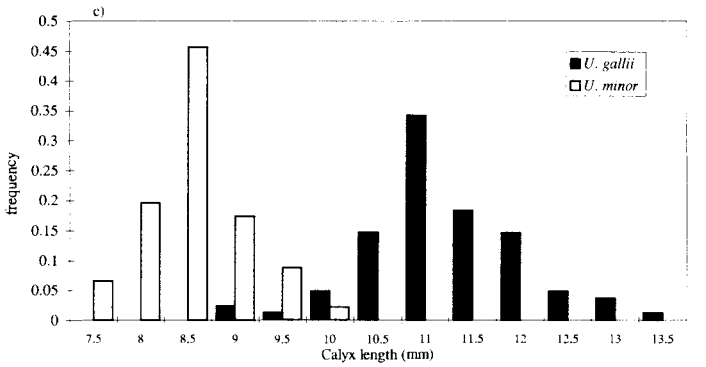


FIGURE 1. The frequency distributions of the floral and vegetative characters of the plants identified as *Ulex gallii* and *U. minor*.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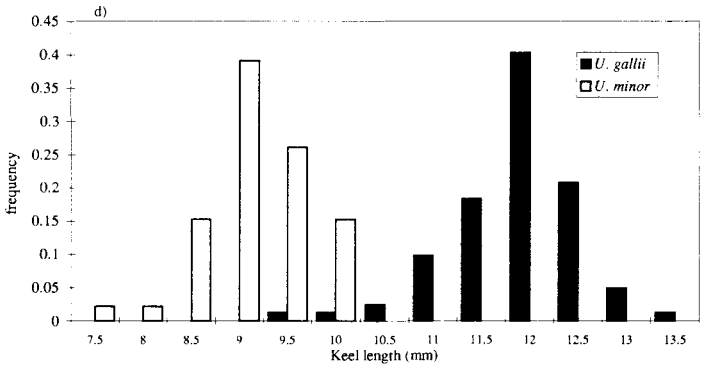
Calyx length (mm)
U. gallii
U. minor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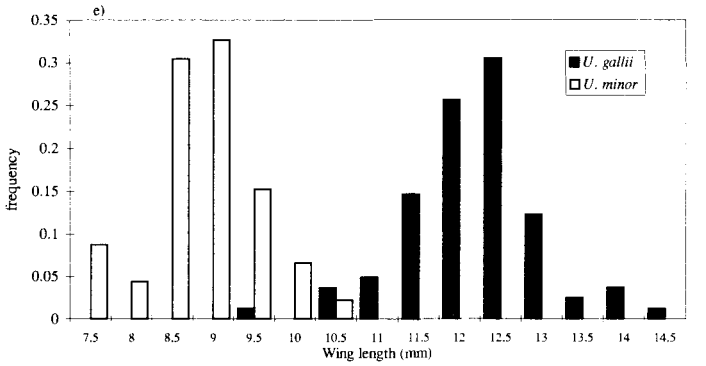
Keel length (mm)
U. gallii
U. minor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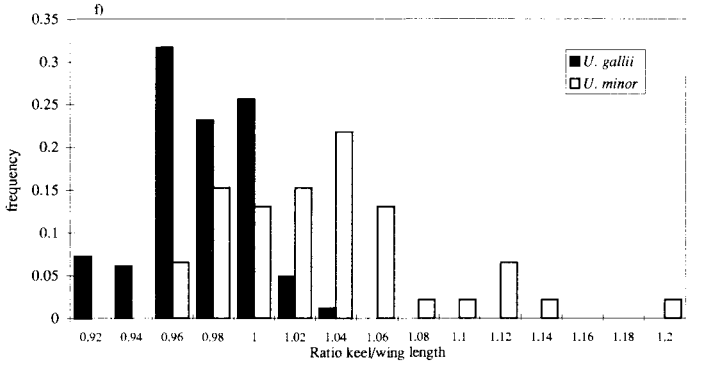
Wing length (mm)
U. gallii
U. minor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Ratio keel/wing length
U. gallii
U. minor

TABLE 1. THE DIFFERENCES BETWEEN *ULEX GALLII* AND *U. MINOR* (AS IDENTIFIED BY CHROMOSOME COUNTS) IN EACH CHARACTER WITH THE RESULTS OF T-TESTS.

	Ulex gallii	*Ulex minor*	
	Mean ± se	Mean ± se	*t*
Primary spine length (mm)	19·0 ± 0·36	10·7 ± 0·25	19·04
Standard length (mm)	13·8 ± 0·10	10·2 ± 0·10	24·49
Calyx length (mm)	11·2 ± 0·09	8·6 ± 0·07	22·23
Keel length (mm)	11·9 ± 0·08	9·1 ± 0·07	26·35
Wings length (mm)	12·2 ± 0·09	8·9 ± 0·08	25·09
Keel/wing ratio	0·98 ± 0·003	1·03 ± 0·007	7·48

Means are calculated using the *per* bush means as samples. The variances of the two species differed in each comparison, so t-tests were carried out using separate variance estimates. In this method, the degrees of freedom are modified using the sample standard deviations of the two species. All tests were significant at $P<0.0001$

(1965) and Gloaguen (1986) reported that relative lengths of the wings and the keel can show some difference between *U. gallii* and *U. minor*. The ratio keel/wing length was included in the analyses, by calculating the ratio for each flower on a bush and taking the mean value per bush. Frequency histograms for primary spine, standard, calyx, keel and wing lengths of all plants sampled showed bimodal distributions (Fig. 1). These were formed by unimodal distributions of character values for each species (Fig. 1) and the peaks of each distribution appeared well separated between the species for each character. However, all distributions overlapped to a greater or lesser extent: 0·5 mm of overlap for standard and keel lengths, 1 mm of overlap for calyx and wing lengths, and 6·5 mm of overlap for primary spine lengths. The keel/wing ratio showed less of a species difference. Although the means were <1 for *U. gallii* and >1 for *U. minor*, as reported by Proctor (1965) and Gloaguen (1986), this character showed no clear bimodal distribution and substantial overlap (Fig. 1f). Despite these overlaps, t-tests showed significant differences between the two species in all six characters (Table 1).

The overlaps in individual character values between the species means that identification based on single characters will always have some degree of error. The question is therefore, can a suite of characters be used to separate the two species completely and consistently? Discriminant analysis (Seber 1984) on all six characters was carried out using PROC DISCRIM in SAS (1990). This gave a good, but not perfect, discriminant function: all *U. minor* plants were classified correctly, but three *U. gallii* plants were misclassified (a success rate of 96·3%). This is illustrated in Fig. 2, which gives the graphic representation of the separation of the species based on the canonical discriminant functions. Most *U. gallii* plants have a score <0, but three have a score characteristic of *U. minor* plants, >0.

Another way to address this question is to determine to what extent the measured ranges of each character can be used individually or in combination with other characters to separate the species. To do this we calculated which *U. minor* (or *U. gallii*) individuals had character values which fell within the ranges shown by the *U. gallii* (or *U. minor*) samples, for certain combinations of characters. The total of those individuals which would be classified as the wrong species using this method was used as a measure of the discriminating power of that character or group of characters. When carried out using the ranges measured by us at Gore Heath, no single character gave good discrimination between the species, but use of all characters together or all characters without spine length or keel/wing ratio accurately identified all but one of each species (Table 2). Proctor (1965) sampled plants from a large geographical spread of sites in Britain and his character values should be more representative of variation over Britain, so we repeated the analyses using Proctor's (1965) character ranges. This gave worse results. Individual characters, especially spine and standard lengths, gave high proportions of misclassification, and combined characters still misclassified 15% of *U. minor* plants and 2% of *U. gallii* plants (Table 2).

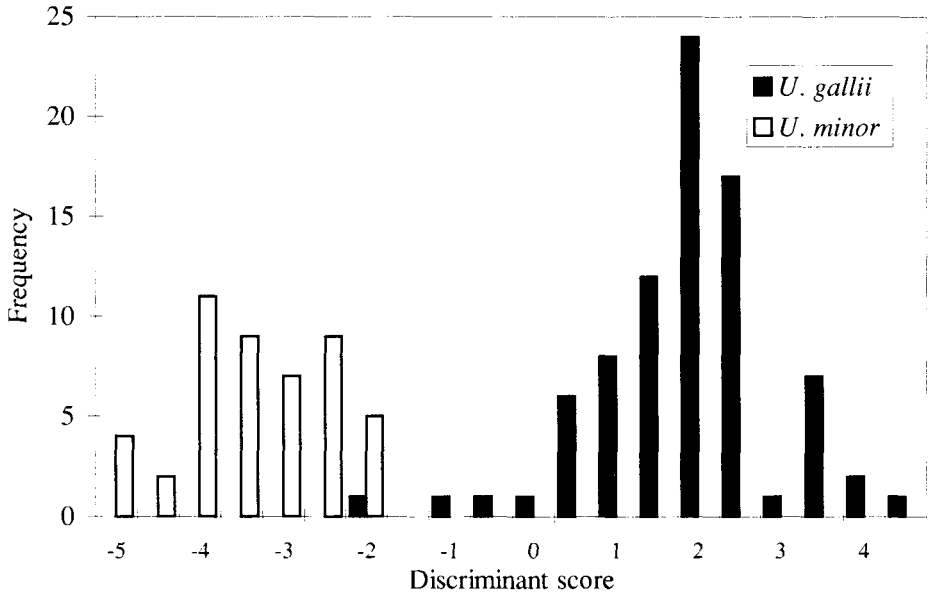

FIGURE 2. The distributions of the canonical discriminant scores for the 82 *U. gallii* plants and 46 *U. minor* plants, derived from the six measured characters. All *U. minor* scores are <0, and all *U. gallii* scores are >0 apart from three misclassified plants.

TABLE 2. THE RANGES OF CHARACTER VALUES FOR *ULEX MINOR* AND *U. GALLII* FROM THIS STUDY AND AS REPORTED BY PROCTOR (1965).

Characters used	*Ulex gallii*		*Ulex minor*	
Measures from this study	Range	Misclassified (%)	Range	Misclassified (%)
Primary spine length (mm)	11·1–29·5	24 (29)	6·5–17·1	22 (48)
Standard length (mm)	11·5–16·4	4 (5)	8·7–12·13	2 (4)
Calyx length (mm)	9·1–13·5	4 (5)	7·5–9·8	5 (11)
Keel length (mm)	9·25–13·3	1 (1)	7·7–10·0	19 (41)
Wing length (mm)	9·25–14·3	1 (1)	7·5–10·3	11 (24)
Keel/wing ratio	0·91–1·05	63 (77)	0·96–1·20	33 (72)
All		1 (1)		1 (2)
All except spine and ratio		1 (1)		1 (2)
Measures from Proctor (1965)				
Primary spine length (mm)	8–34	79 (96)	6–25	45 (98)
Standard length (mm)	10·5–18	5 (6)	6–12·5	16 (35)
Calyx length (mm)	8·5–14·5	15 (18)	5·5–10·5	30 (65)
Keel length (mm)	9–15·5	3 (4)	5·5–10·5	13 (28)
Wing length (mm)	9·5–15·5	5 (6)	5–11	9 (20)
All		2 (2)		7 (15)
All except spine		2 (2)		7 (15)

The ranges of one or more characters for a species were used to classify plants of the second species as overlapping with the first species (i.e. misclassified), or not overlapping. The numbers of misclassified plants in each species are given.

TABLE 3. INSECT SPECIES OBSERVED VISITING, AND PROBABLY POLLINATING, *ULEX MINOR* AND *U. GALLII* FLOWERS. TOTAL NUMBERS OF OBSERVATIONS ALONG WITH THEIR RELATIVE FREQUENCIES ARE LISTED FOR EACH SPECIES.

		Ulex gallii		*Ulex minor*	
	Insect species	number	frequency	number	frequency
Bumblebees	*Bombus terrestris/lucorum*	28	0·364	16	0·356
	Bombus humilis	5	0·065	4	0·089
Bees	*Andrena ovatula*	5	0·065	2	0·044
	Apis mellifera	2	0·026	0	0
Hover-flies	*Sphaerophoria scripta*	9	0·117	3	0·067
	Syritta pipiens	21	0·273	19	0·422
	Eristalis sp.	3	0·039	1	0·022
	Episyrphus sp.	4	0·052	0	0

PHENOLOGY

The two species showed some differences in flowering phenology (Fig. 3). Phenology was examined in terms of the changes in mean number of flowers per plant (i.e. on the branches sampled) (Fig. 3a) and the proportion of plants in each census which reached their peak flower number at that census (Fig. 3b). The first *U. gallii* flowers were seen on 13 July, but *U. minor* started flowering later on 23 July. While the *U. gallii* population reached maxima in both the mean flower number and the proportion of plants at peak flower production on 18 August, these maxima were attained by the *U. minor* population on 9 September. Chi-square tests showed that the relative distribution of flower numbers between the censuses differed significantly between the species ($\chi^2 = 557$, $df = 10$, $P<0·001$), and the average date of the peak in flower number per bush was later for *U. minor* (median = 28 August) than *U. gallii* (median = 18 August) (Mann Whitney $W = 4676$, $P<0·001$). However, the species showed a large overlap in phenology as measured by the Proportional Similarity Index, Ps = 0·78.

POLLINATOR OBSERVATIONS

Five bee species were recorded visiting flowers (Table 3). Workers of the Buff-tailed and White-tailed Bumblebees *Bombus terrestris* and *B. lucorum* are difficult to separate with confidence, so we did not distinguish them in the field. Five hoverfly (Syrphidae, Diptera) species visited flowers (Table 2), but one, *Paragus* sp., was observed only once. Over the eight hours of observation, 77 insect visits were recorded for *U. gallii*, and 45 for *U. minor* (Table 3). *Bombus terrestris/lucorum* and *Syritta pipiens* were by far the most frequent insects seen visiting *Ulex* flowers, with *Bombus humilis*, *Andrena ovatula* and *Sphaerophoria scripta* also frequent. Fisher's Exact Test (used rather than a Chi-square test because of the small numbers of observations for several species) showed the pollinator communities of *U. gallii* and *U. minor* did not differ significantly ($P = 0·546$). This was illustrated by the high degree of overlap in the assemblages, as quantified by the Proportional Similarity Index, Ps = 0·83.

DISCUSSION

IDENTIFICATION OF *ULEX* SPECIES

In accordance with other workers in Europe, we have assumed plants with chromosome counts of n = 32 to be *U. gallii* and with n = 16 to be *U. minor* (Alvarez Martinez *et al.* 1988; Bullock *et al.* 1998; Castroviejo & Valdes-Bermejo 1983; Fernandez Prieto *et al.* 1993). Using chromosome counts as an absolute method for distinguishing the two species, we were able to assess accurately the degree to which the species show overlaps in morphology and other traits. Other studies have been hampered by the circularity which results from assessing morphological overlaps using plants which have been identified to species using morphology. We found that the species showed clear differences in the average values of all the measured characters, with all apart from the keel/wing

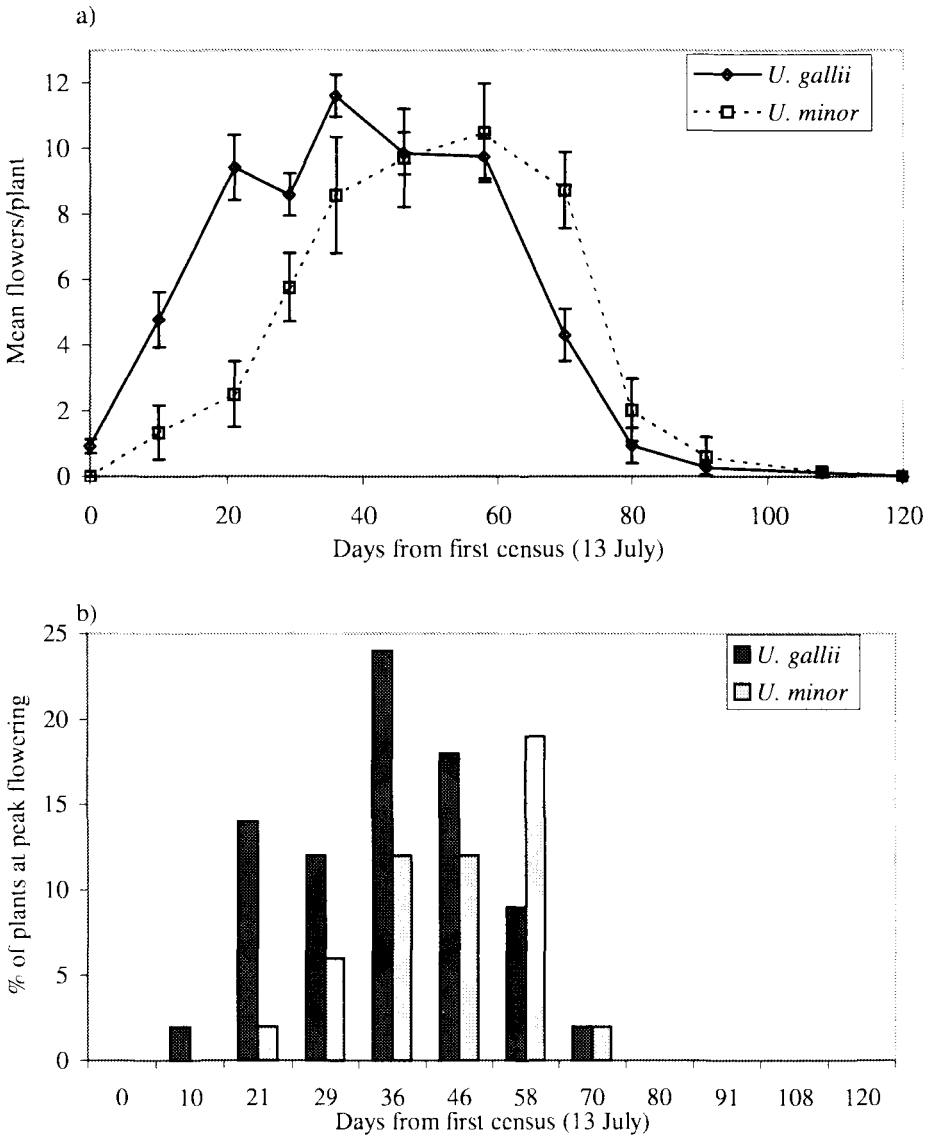

FIGURE 3. The flowering phenology of *Ulex minor* and *U. gallii*. a) Changes in the mean number of flowers per bush, with one standard error. b) The proportion of plants in the populations showing peaks in flower number at each census date.

ratio showing bimodal distributions (Note: Proctor 1965 did not find a bimodal distribution for spine length). However, all characters showed some degree of overlap, and use of one character alone would give a minimum of 5% (using standard length) and a maximum of 77% (using keel/wing ratio) of plants being misidentified. Using a suite of characters was more successful: discriminant analysis using all six characters gave only 2·3% misclassification. More useful to field botanists is defining what suite of characters should be measured to best identify species accurately. Using the ranges in character values measured in this study, we found that the use of standard, calyx, keel and wing lengths resulted in misidentification of only two of the 128 plants, 1·6%. The

keel/wing ratio is less useful for separating the two species. Proctor (1965) cast doubt on the idea that this ratio is always >1 for *U. minor* and <1 for *U. gallii*, although Gloaguen (1986) reiterated that this is a distinguishing feature. If this criterion is applied to the 128 plants sampled, 14 *U. minor* and 20 *U. gallii* plants are misclassified. Similarly, due to high plasticity, the length of the primary spine cannot be considered as a useful distinguishing character.

We achieved 98·4% accuracy in identification using the character ranges of the plants measured on Gore Heath in Dorset. The ranges given by Proctor (1965) were from plants sampled from Plymouth in the west to Woking in east-central England, and so these better represent the variation in characters in England (although identification was not supported by chromosome counts). These gave a much worse result: when all four floral characters were used 7% of plants were misclassified. It is clear, therefore, that morphological characters cannot be relied upon to give a completely accurate separation of *U. minor* and *U. gallii*. Although we had a very high success rate using the character ranges measured at our study site, it is more relevant to use Proctor's (1965) ranges when considering identification in Britain and Europe. Here, the 7% failure rate may sound small, but it translates to a large number of misidentifications if these character values are used extensively.

Our plants were sampled from a mixed heath in an area of range overlap. The ranges of these species are largely disjunct (Bullock *et al.* 1998; Gloaguen 1986; Proctor 1965). In Britain *U. minor* is virtually confined to the south-east of England, whereas *U. gallii* occurs mostly in the west and north-west of England, Wales and the extreme south-west of Scotland. The distributions can be divided coarsely by a line running from Dorset to the Humber estuary, roughly halfway up the east coast. Therefore, it might be tempting to use geographical location as a distinguishing character (e.g. Cuba & Pardo 1997). However, this is a dangerous strategy and may lead to misidentification of plants occurring outside their recognised range limits. In this way responses to climate change, or other factors which may change plant distributions, may go undetected. There are several cases where the *Ulex* species are found well outside any simply-described range limits. *U. gallii* is found in a few locations in south-eastern England, most notably in Kent in the extreme south-east and, in large numbers, on the East Anglian coast. *U. minor* has some records in north Wales and on the south-western Scottish border (current distribution maps are held by the Natural Environment Research Council Biological Records Centre). It would be useful to check these records with chromosome counts from these disjunct populations.

U. GALLII × *U. MINOR* HYBRIDS

The chromosome counts performed on the 135 plants did not provide any evidence for the occurrence of *U. gallii* × *U. minor* hybrids. These results – together with those of Bullock *et al.* (1998) who found a single putative hybrid (n = 24) out of 85 bushes sampled at Gore Heath – suggest that hybrids between *U. gallii* and *U. minor* are extremely uncommon. Therefore, the occurrence of hybridsation must be constrained in some way.

INTERSPECIFIC POLLEN TRANSFERS.

This study shows that the constraints on hybridisation are not flowering phenology or pollinator behaviour. It is an interesting and unexpected finding that *U. minor* had a significantly later start and peak in flower production than *U. gallii* (Fig. 3). Gloaguen (1986), working in Brittany, found that for *U. minor* flowering began in August, peaked in October (in terms of flower numbers) and finished in November. Flowering phenology differed between two *U. gallii* populations: flowering began in both during August, but one population peaked at the end of September and finished at the end of November, while the second peaked at the end of October and finished at the end of December. Therefore the species' differences we found may not be repeated in other sites. Despite differences in start dates and peaks, the flowering periods of the two species overlapped to a large degree (Ps = 0·78) and there was high intraspecific variation in the flowering period for both species (Fig. 3). Individuals of the two species bearing fully opened flowers simultaneously could be seen at any time during the flowering season.

The insect species seen visiting the flowers of the two species of *Ulex* were the same, and the relative abundance of the insect species showed no significant difference between *U. gallii* and *U. minor*. It seems that exactly the same pollinator assemblage was visiting both *Ulex* species and that the insects were not distinguishing between the species. Given their overlapping phenologies and pollinator assemblages and the large degree of physical intermingling between plants, pollen

transfer between *U. gallii* and *U. minor* probably occurs frequently. Indeed, over the eight hours of observation, there was one definite sighting of a *Bombus terrestris/lucorum* worker moving from *U. gallii* to *U. minor*. Therefore, other factors may act as barriers to hybridisation between the two species. Alternatively, if hybrid seed is formed, the lack of hybrid plants may be caused by very poor germination or establishment of hybrids. Neither hypothesis has been explored fully.

CONCLUSIONS

Given the taxonomic difficulties within the section *Neowilkommia* of the genus *Ulex*, there is a need to use chromosome counts to investigate further the morphological and ecological correlates of groupings such as *U. gallii, U. minor, U. europaeus*, and *U. europaeus* × *U. gallii*. It is insufficient to rely on morphology alone to distinguish species or hybrids definitively. Other authors have reported the use of traits other than the gross morphological characters used in this paper, such as pollen grain size (Misset *et al.* 1982), epidermal structure (Godeau 1977), stoma size (Cuba & Pardo 1997) or isoenzymes (Misset & Fontenelle 1992). However, chromosome counts provide a discontinuous measure allowing definitive separation of species and hybrids. Problems may arise in cases where *U. gallii* plants appear to show 2n = 96 (e.g. Misset 1990; Misset & Gourret 1996), the same number as shown by *U. europaeus*. However, there is continuing controversy about such counts and there is a need to investigate ploidy levels in these species further.

This study was carried out on one heath in Dorset. To expand this work and test the conclusions over the full geographic distribution of both species, the next stage should be to repeat the study at a range of sites over Britain, France and the Iberian peninsula.

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REFERENCES

ALVAREZ MARTINEZ, M. J., *et al.* (1988). El genero *Ulex* en la Cornisa Cantabrica. I. *Ulex* gr. *gallii-minor*. *Candollea* **43**: 483–497.

BULLOCK, J. M., CONNOR, J., CARRINGTON, S. & EDWARDS, R. J. (1998). Chromosome numbers and flower sizes of *Ulex minor* Roth. and *Ulex gallii* Planch. in Dorset. *Watsonia* **22**: 143–152.

CARNEY, S. E., HODGES, S. A. & ARNOLD, M. L. (1996). Effects of differential pollen-tube growth on hybridisation in the Louisiana irises. *Evolution* **50**: 1871–1878.

CASTROVIEJO, S. F. L. S. & VALDES-BERMEJO, E. (1990). On the identity of *Ulex gallii* Planchon (Leguminosae). *Botanical journal of the Linnean Society* **104**: 303–308.

COLWELL, R. K. & FUTUYMA, D. J. (1971). On the measurement of niche breadth and overlap. *Ecology* **52**: 567–576.

CORILLION, R. (1950). Phanérogames intéressantes pour la Bretagne. *Bulletin de la Société scientifique de Bretagne* **25**: 131–140.

CUBAS, P. & PARDO, C. (1997). Correlations between chromosomal and morphological characters in subspecies of *Ulex europaeus* L. (Genisteae, Leguminosae) from the north-west of the Iberian Peninsula. *Botanical journal of the Linnean Society* **125**: 229–243.

FERNANDEZ PRIETO, J. A., *et al.* (1993). Chromosome numbers and geographic distribution of *Ulex gallii* and *U. minor* (Leguminosae). *Botanical journal of the Linnean Society* **112**: 43–49.

GLOAGUEN, J. C. (1986). Les ajoncs de Bretagne. *Bulletin de la Société botanique de France – Lettres botanique* **133**: 363–385.

GODEAU, M. (1977). Observation au microscope électronique à balayage de l'épiderme séminal d'*Ulex europeaus* L., *U. minor* Roth, *U. gallii* Planchon. *Bulletin Société science naturelle Ouest de la France* **75**: 83–89.

LAMBINON, J. (1962). Note sur les *Ulex* du Massif Armoricain. *Lejeunia* **9**: 64–66.

LEEBENS-MACK, J. & MILLIGAN, B. G. (1998). Pollination biology in hybridising *Baptista* (Fabaceae) populations. *American journal of botany* **85**: 500–507.

MISSET, M. T. (1990). Données caryologiques chez le genre *Ulex* L. (Papilionidae) dans le Massif Armoricain. *Taxon* **39**: 630–635.

MISSET, M. T. & FONTENELLE, C. (1992). Protein relationships between natural populations of *Ulex europaeus* and *U. gallii* (Faboideae, Genisteae) and their hybrids. *Plant systematics and evolution* **179**: 19–25.

MISSET, M. T. & GOURRET, J.-P. (1996). Flow cytometric analysis of the different ploidy levels observed in the genus *Ulex* L. Faboideae-Genisteae in Brittany (France). *Acta Botanica* **109**: 72–79.

MISSET, M. T., GOURRET, J.-P. & HUON, A. (1982). Le pollen d'*Ulex* L. (Papilionoideae): morphologie des grains et structure de l'exine. *Pollen et spores* **24**: 369–395.

PROCTOR, M. C. F. (1965). The distinguishing characteristics and geographical distributions of *Ulex minor* and *Ulex gallii*. *Watsonia* **6:** 177–187.

PROCTOR, M., YEO, P. & LACK, A. (1996). *The natural history of pollination*. Bath Press, Bath.

ROZZI, R., ARROYO, M. K. & ARMESTO, J. J. (1997). Ecological factors affecting gene flow between populations of *Anarthrophyllum cumingii* (Papilionaceae) growing on equatorial- and polar-facing slopes in the Andes of Central Chile. *Plant ecology* **132**: 171–179.

SAS (1990). *SAS/STAT users guide*. SAS Institute, Carey, North Carolina.

SEBER, G. A. F. (1984). *Multivariate observations*. John Wiley & Sons, New York.

WEIBLEN, G. D. & BREHM, B. G. (1996). Reproductive strategies and barriers to hybridisation between *Tellima grandiflora* and *Tolmeia menziesii* (Saxifragaceae). *American journal of botany* **83**: 910–918.

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