A morphological comparison between some British Orobanche species (Orobanchaceae) and their closely-related non-British counterparts from continental Europe: Orobanche reticulata Wallr. s. l.

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ABSTRACT

A morphological comparison has been made between lowland British plants and those of the European mountains, both referable to *O. reticulata s.l.* A brief summary is given of the previous taxonomic treatments which have been applied to this group. It is concluded that two separate but closely-related taxa exist, and that these are best treated at subspecific level, the British plant being referred to subsp. *procera* (Koch) Dostál. A possible third taxon, perhaps no more than a pale colour form of one or both of the above, has been described at various ranks under the epithet '*pallidiflora*'. No direct support for its continued recognition has been established.

KEYWORDS: Taxonomy, root parasites, broomrape.

INTRODUCTION

BACKGROUND

Orobanche is a genus of obligate root parasites, which completely lack chlorophyll and are therefore unable to photosynthesise and so independently sustain themselves. To do so they parasitise a wide range of (usually) dicotyledonous, and very often herbaceous, hosts. The genus is distributed throughout much of the world's northern temperate latitudes and has a northern limit in southern Scandinavia. Only relatively few species occur in the southern hemisphere and some of these are probably introductions.

In comparison to continental Europe, the British Isles have a very limited *Orobanche* flora, only ten species being recognised by Stace (1991). This is in contrast to mainland Europe where even the conservative treatment in *Flora Europaea* (Chater & Webb 1972) describes 45 at species level. Apart from the relatively widespread *O. minor* Sm., which in fact may have been largely introduced into this country, all the other British species are apparently native and several are very rare. Four of the latter have been accorded *British Red Data Book* status (Wigginton 1999): *O. artemisiae-campestris* Gaudin (= *O. loricata* Rchb.), *O. caryophyllacea* Sm., *O. purpurea* Jacq., and *O. reticulata* Wallr. In Europe, however, these and many others are much more frequent, and the abundance and species diversity increases appreciably as one moves south, with the Mediterranean area having an especially rich *Orobanche* flora. Many species show close morphological similarities one to another and can therefore be difficult to separate taxonomically.

In this paper, the relationship is examined between British plants referable to *O. reticulata* Wallr. and those from continental Europe. In doing so, much reliance has been placed on the morphometric assessment of living populations of plants, with additional information obtained from the study of preserved herbarium material.

PROBLEMS ENCOUNTERED IN THE STUDY OF THE GENUS

This is acknowledged to be a taxonomically difficult genus (*e.g.* Chater & Webb 1972, Pignatti 1982, Rumsey & Jury 1991) and meaningful work, whether in the field or in the herbarium, is difficult to achieve. For instance, these morphologically very similar taxa possess few readily

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quantifiable characters. The above-ground plant comprises little more than an inflorescence, the stem of which bears simple, sessile, scale-like leaves which rapidly become brittle soon after emergence. This lack of normal leaves is therefore a major loss of potential taxonomic information and the inflorescence is the only part of the living plant which it is feasible to study.

Being fleshy and lacking chlorophyll, *Orobanche* plants make poor herbarium specimens, sometimes forming a rather amorphous mass so that important characters are lost. This is especially true of corolla and stigma colours and subtleties of corolla shape. However, from well-pressed specimens with accompanying field colour notes, useful information can be gained. Unfortunately, a large proportion of specimens are not preserved to such a high standard, and so it is better to study the genus as living plants.

There are also other difficulties. Many of the original authors' descriptions are very brief and inadequate or even ambiguous. In such cases, recognition of the taxon to which the description is applied may be almost impossible to achieve. Very often descriptions refer to non-diagnostic characters, such as leaf and stem, whilst information on much more important characters is generalised or even omitted. Type specimens are rarely indicated by these authors and when they are known, they may be very old and by now seriously fragmented, and so taxonomically almost worthless.

OROBANCHE RETICULATA s. l.

O. reticulata s. l. is widespread but local throughout much of the montane/subalpine region of Europe and is also recorded from lowland habitats elsewhere on the continent. However, it was not until shortly after the start of the twentieth century that plants apparently corresponding with the description of continental *O. reticulata* were recognised in Britain. These occurred (and still do so) in a very limited area of Yorkshire, as lowland plants, usually on the magnesian limestone where they mainly parasitise *Cirsium arvense*, growing on rough calcareous grassland and scrub, and especially on river margins and flood plains. Since there must be many similarly suitable habitats throughout the rest of the country, this very restricted British range is difficult to explain. The discovery in Britain in 1907 is of some interest and has been summarised elsewhere (Foley, 1993). I have examined both the British plant and those of the European mountains on several occasions in the field and certain morphological differences between the two are apparent which suggest the existence of separate taxa.

BASIC TAXA RELATED TO O. RETICULATA AND SUBSEQUENT TREATMENTS

O. reticulata was first described by Wallroth (1825) from plants collected near Toulouse, France. His description is quite vague and does not especially differentiate it from other similar taxa. He described the calyx as divided into simple, linear-lanceolate teeth, shorter than the tubular, inflated, 20 mm long corolla. The lobes of the lower lip were rounded and equal in size and the filaments and style were more or less glabrous. His most significant statement referred to the purple coloration of the corolla caused by the reticulate veining of the upper lip, and this appears to be a consistent character of *O. reticulata s. l.* as seen in the field. The type specimen (Toulouse, 1807, *Flügge*) is held in **LE**(!) and, although comprising only the upper part of the inflorescence, equates satisfactorily with living plants seen in mountain areas of southern France, but much less so with those from Britain.

Shortly after Wallroth's description of *O. reticulata*, Wimmer & Grabowski (1829) described *O. pallidiflora* from a specimen collected in Poland. This plant was pubescent with flowers in a lax spike. The calyx segments were described as ovate-acuminate and the corolla as curved, tubular-ventricose, with glands and purple veins distally. The corolla lobes were crenulate margined and the filaments pilose at the base and \pm glabrous above. There is very little information here to separate it from Wallroth's *O. reticulata*. Type material of *O. pallidiflora* has not been located but specimens in several herbaria are referred to this species.

Another worker who described similar plants from Germany was Koch. His description of *O. procera* (Koch 1833) stated that the calyx segments were uniformly divided or entire, the corolla yellow-brown, campanulate, inflated towards the base and curved, and the lobes of the lips denticulate and ciliate. The filaments, inserted at the base of the corolla, were sparsely hairy below with a few glandular hairs above. In Koch's opinion the plant lay taxonomically close to

O. rapum-genistae but the corolla and filament characters given clearly differentiate the two. The plants upon which he provided his description apparently grew close to the Rhine and, from his comments, it is clear that Koch knew the living plant from this same area.

At the same time as he published this description, he also described *O. scabiosae* (Koch 1833) based on plants from a mountain area near Berchtesgaden, Germany, growing at an altitude of 5500 feet and apparently parasitising *Scabiosa columbaria*. His diagnosis described the calyx segments as entire or divided into teeth of equal length; the corolla campanulate, slightly curved, glandular-hairy with the margins of the lobes wrinkled, the filaments inserted low in the corolla with scattered hairs in their lower part but almost glabrous above. He made interesting comments on the corollas being basically bright ochre-yellow but tinged reddish-orange on the lip margins, violet in the dorsal area and also violet-veined on the lips.

Most subsequent workers have treated *O. scabiosae* as a synonym of *O. reticulata* Wallr.. This seems justified in view of Koch's description, especially of the corolla colour and its montane habitat. It is clear, however, that Koch considered it to be quite separate from his *O. procera* which is described almost immediately before it in the same paper (Koch 1833). From this it might be assumed that *O. reticulata* and *O. procera* are themselves morphologically quite separate. No type specimens of either of the two species described by Koch have been located and none of either is indicated as having been seen by Beck (1930).

Beck (1890) recognised three varieties within *O. reticulata*: the type (var. *typica*), and vars. *pallidiflora* and *procera*. Later, he largely adhered to this treatment (Beck 1930), retaining the three taxa at varietal level and providing a key to their identification where var. *procera* was separated from the others chiefly by the shape of its broad, tubular-campanulate, completely curved corollas, 15–18 mm in length. In the other varieties he considered the corollas to be tubular or campanulate, longer than wide, with the dorsal line straight or only slightly curved, 20–23 mm long or occasionally shorter. He separated var. *pallidiflora* from the type mainly by its paler corolla, especially the degree of venation and presence of violet glandular hairs, and also in its slightly more hairy filaments and choice of host (*Cirsium* and *Carduus* spp., rather than members of the Dipsacaceae or other members of the Asteraceae).

In their French Flora, Rouy & Foucaud (1909) placed these taxa under *O. platystigma* Rchb. based on a specimen of Reichenbach *f*. The first, var. *scabiosae* (based on Koch's *O. scabiosae*) had a tubular corolla 20–22 mm long, yellow at the base, then amethyst or purple distally and covered with coloured glandular hairs. Another variety, var. *procera*, had a much broader, subcampanulate, shorter corolla (16–18 mm long), weakly veined violet or purple but only on the upper lip and generally with fewer, less strongly coloured glandular hairs.

Gilli (1965), working on central European taxa, recognised two subspecies of *O. reticulata*: the type and subsp. *pallidiflora*. He described subsp. *pallidiflora* as having corollas which were whitish or yellowish but pale lilac distally with few dark-coloured glandular hairs. In their upper part, the filaments were sparsely glandular hairy to glabrous. He considered this taxon to occur only in low-lying areas in Germany and Austria north of the Alps, where it parasitised species of *Cirsium* and *Carduus*. Under subsp. *reticulata* he described the corolla as usually longer than broad (20–23 mm long) and the dorsal line straight or only slightly curved. Within this he included var. *procera* (Koch) Beck, characterised by a quite different corolla shape: broader, tubular-campanulate and 15–18 mm long with the dorsal line completely curved. Gilli described the type (subsp. *reticulata*) as differing from subsp. *pallidiflora* mainly in corolla colour, which was yellow only at the base and otherwise intensely coloured violet to purple with dark veins and glandular hairs.

In *Flora Europaea*, Chater & Webb (1972) described only one species, *O. reticulata* Wall., placing *O. pallidiflora* under synonymy; there was no mention of *O. procera*. However Pignatti (1982) recognised two taxa in Italy: subsp. *reticulata* from the alpine area and subsp. *pallidiflora* from lower altitudes. He separated the latter from the typical form by its paler corolla colour and less glandular-pilose filaments. This was largely supported by Uhlich *et al.* (1995) when considering European taxa as a whole but Hartvig (1991), who distinguished the two taxa in a somewhat similar way, considered that for the montane areas of Greece most plants belong to var. *pallidiflora* rather than var. *reticulata*. More recently, Kreutz (1995) recognised two taxa at species level in Europe: *O. reticulata* from the alpine areas and *O. pallidiflora* from lower altitudes. He placed the British plant under the latter whilst including var. *procera* within *O. reticulata*.

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From the varied treatments outlined above it is apparent that much confusion exists regarding the taxonomy of *O. reticulata s.l.*, but that it includes at least two taxa which differ mainly in their corolla shapes. These are the montane/subalpine *O. reticulata* and the lower-altitude *O. procera*. Plants with a paler corolla often appear to be referred to *O. pallidiflora*.

METHODS

A fundamental approach in this work has been to carry out detailed field examinations of the morphology of living plants in their natural habitats. From personal field experience on the genus and also from that of other workers (e.g. Beck 1890, 1930; Guimarães 1904; Wilkomm & Lange 1870; Wilkomm 1893; Coutinho 1913; Schiman-Czeika 1964; Gilli 1965, 1982; Chater & Webb 1972; Feinbrun-Dothan 1978; Pignatti 1982; Meikle 1985; Valdés *et al.* 1987; Jones 1989; Rumsey & Jury 1991), the characters described below and listed in Table 1 appear to be the most useful in circumscribing closely related *Orobanche* taxa. Many taxa are best described by using several characters in combination.

The methods used were as follows. A random selection was made of ten plants within a population, all of which were in full flower. By "full flower" was meant plants in which the lowest third of the inflorescence had fully open corollas, one of which was utilised for the morphological evaluation of floral characters. For this purpose, only freshly-opened corollas were used. This approach is similar to that previously employed for the assessment of taxa within other genera (e.g. Roberts & Gilbert 1963; Roberts 1966, 1988; Bateman & Denholm 1983; Foley 1990) and has also been recently applied to populations of British *Orobanche* taxa by Jones (1989). With practice, selection bias can be avoided and a representative sample of plants assessed. The raw data obtained from each of the populations studied are given in Foley (1998).

Measurements were achieved in two ways. Dividers used in conjunction with a ruler calibrated to 0.5 mm were found convenient and very satisfactory for dimensions upwards of 20 mm. For smaller values, a Leitz Wetzlar measuring lens possessing a built-in scale calibrated to 0.1 mm was used. For the very largest dimensions such as plant height and inflorescence length it was often not possible to measure reliably to less than 5 mm due to slight vagaries in stem contortions etc.. All values were taken in a direct line and therefore lengths of curvature (for instance of corollas) were ignored in such measurements.

Quantifiable numerical data obtained from the morphometric measurements of many of the characters shown in Table 1 were also subjected to Principal Components Analysis (PCA) using the Clustan 4 computer programme (Wishart 1987). By this technique, each specimen measured is located in a multidimensional array, in which the number of dimensions is equal to the number of characters measured, and where the most similar specimens are placed closest together. This technique extracts the axes of greatest variation from the multidimensional space, thereby simplifying the space to a few (usually 2 or 3) dimensions, so allowing the location of each specimen to be visualised. Qualitative characters (34-45) and those of a binary nature could not be used in PCA. Several of these are known to be important diagnostic characters for Orobanche taxa and, of course, were fully considered alongside the PCA data and in the subsequent description and delimitation of the individual taxa. Of especial significance are corolla colour and shape, calyx shape and stigma lobe colour. Binary characters which clearly separate sections or groups within the genus (e.g. presence or absence of stem branching (character 7) or presence or absence of bracteoles (character 22), were not analysed further. The following characters (enumerated in Table 1) were employed in the PCA: 1-6, 8-15, 18-20, 23-29b, 33. In the diagrams, the component accounting for the greatest variance (PC1) is represented by the x-axis, that of next significance (PC2) by the y-axis.

Photographic records were also made of plants within each population studied; many of these are illustrated in Foley (1998). Whenever conservation considerations allowed, a typical specimen was pressed for the herbarium (E, LANC) and inflorescences preserved in 70% alcohol (now in LANC).

Most major British herbaria likely to contain material of the genus were visited during this work; and a great number of loans were also obtained from European institutions. The internal flower structures of preserved specimens were examined by detaching individual corollas and gently boiling them for c. 10 minutes in water to which a small amount (<0.01%) of surfactant had been

TABLE 1. CHARACTERS AND SCORING SYSTEM UTILISED IN THE MORPHOMETRIC ANALYSIS (ALL MEASUREMENTS IN MM)

- 1 PLANT HEIGHT: measured from ground level to the uppermost tip of the inflorescence.
- 2 STEM WIDTH: measured immediately below the lowest corolla in the inflorescence.
- 3 STEM PUBESCENCE: estimated on the scale shown below *.
- 4 INFLORESCENCE LENGTH: measured from the point of attachment of the lowest corolla to the uppermost tip of the inflorescence.
- 5 INFLORESCENCE DENSITY: estimated on the scale:- 0 = lax; 1 = fairly lax; 2 = fairly dense;
 3 = very dense.
- 6 COROLLA ATTITUDE: estimated on the scale:- 0 = almost erect to 3 = almost level, patent.
- 7 STEM HABIT: 0 = simple, unbranched; 1 = pedicellate at least below; 2 = branched.
- 8 MAXIMUM LEAF WIDTH: as measured.
- 9 LEAF PUBESCENCE: estimated on the scale shown below *.
- 10 COROLLA LENGTH: measured in a direct line from base of the corolla to the extremity of the upper lip.
- 11 COROLLA VERTICAL HEIGHT: measured distally at a point just prior to reflexing of the lips.
- 12 DORSAL LINE CURVATURE: estimated on the scale:- 1 = almost straight; 2 = slightly curved; 3 = strongly curved; 4 = genuflexed.
- 13 DIVISION OF UPPER LIP: estimated on the scale:- 0 = entire; 1 = notched; 2 = slightly bilobed; 3 = strongly bilobed.
- 14 LOWER LIP CILIATE OR OTHERWISE: 0 = not; 1 = yes.
- 15 LOWER LIP DENTICULATE OR OTHERWISE: 0 = not; 1 = yes.
- 16 & ATTITUDE OF UPPER AND LOWER LIPS OF COROLLA: estimated on the scale:- 1 = reflexed;
- 17 0 = upright; 1 = intermediately forwards; 2 = forward.
- 18 RELATIVE SIZE OF THE CENTRAL LOBE OF THE LOWER LIP OF COROLLA IN RELATION TO THE LATERAL LOBES: ratio estimated.
- 19 SHAPE OF THE LOBES OF THE LOWER LIP OF COROLLA: estimated on the scale:- 0 = rounded, distinctly obtuse; 1 = more or less acute.
- 20 COROLLA PUBESCENCE: estimated on the scale shown below *.
- 21 COROLLA CONSTRICTED DISTALLY: estimated as:- 0 = not; 1 = yes.
- 22 BRACTEOLE: 0 = absent; 1 = present.
- 23 BRACT LENGTH: measured from the point of attachment to the tip.
- 24 BRACT PUBESCENCE: estimated on the scale shown below *.
- 25 CALYX LENGTH OF SEGMENTS; if divided, includes the longest tooth.
- 26 CALYX SEGMENTS DIVIDED INTO SEPARATE TEETH OR OTHERWISE: Degree of division estimated on the scale:- 1 = equally divided; 2 = unequally divided; 3 = very unequally divided; 4 = entire.
- 27 CALYX PUBESCENCE: estimated on the scale shown below *.
- 28 TYPICAL HEIGHT OF INSERTION OF THE FILAMENTS ABOVE THE COROLLA BASE: measured from the point of attachment of the lowest
- 29a FILAMENT PILOSITY (UPPER PORTION): estimated on the scale shown below *.
- 29b FILAMENT PILOSITY (LOWER PORTION): estimated on the scale shown below *.
- 30 ANTHERS OR STYLES EXSERTED: estimated on the scale shown below *.
- 31 ANTHERS PILOSE: estimated on the scale shown below *.
- 32 STYLE PILOSITY: estimated on the scale shown below. *
- 33 STIGMA LOBE SEPARATION: estimated on the scale:- 0 = fused to 3 = well separated.

GENERAL SCALE: 0 = not, absent; 1 = slightly; 2 = appreciably; 3 = very, densely, excessively. (Values intermediate between those given above may, in some cases, be arrived at).

NOTE: Additional characters (e.g. leaf length, bract width, maximum width of corolla tube, maximum distance between the extremities of the lateral lobes of the lower lip of the corolla) were also measured during the early stages of this work. However, some of these were later abandoned when the character states were found to yield information of little value.

The following additional characters were recorded descriptively or photographically since they are not readily quantifiable. They were recorded from fresh material in full flower.

34. STYLE COLOUR, 35. STIGMA LOBE COLOUR, 36. COROLLA SHAPE, 37. COROLLA COLOUR, 38. LEAF SHAPE, 39. LEAF COLOUR 40. BRACT SHAPE, 41. BRACT COLOUR, 42. CALYX SHAPE, 43. CALYX COLOUR, 44. FILAMENT BASE SHAPE, 45. STEM COLOUR.

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added. Formerly dry, brittle material could then be softened and more easily handled and dissected. It was therefore possible to measure the height of filament insertion and the degree, type, and distribution of pilosity along their length. Also, if the stigma and style were first softened by a similar process and carefully pressed with clean filter paper, an indication of stigma lobe colour could sometimes be obtained.

RESULTS AND DISCUSSION

A COMPARISON BETWEEN BRITISH POPULATIONS AND PLANTS FROM MONTANE/SUBALPINE HABITATS IN EUROPE

A morphological evaluation was carried out on plants referred to *O. reticulata* from three British populations within the plant's very restricted British range in Yorkshire (see Table 2 for locality details). These populations were compared one to another as well as to plants from montane localities in eastern France. In the latter area, however, although several populations were located and examined, only one population was found (Petit Mont Rond, Jura) which had plants in sufficiently large numbers and in a suitable condition for a morphological evaluation to be made. This was despite searches on several field visits over three seasons (1995–1997) and was mainly due to their unpredictable flowering behaviour at higher altitudes.

Mean values and standard errors of the relevant characters are summarised in Table 2 and the quantifiable numerical elements of these data have been subjected to Principal Components Analysis (PCA). Examination of PCA data (Figure 1) for the three British populations shows good overlap on the PC1 axis but with some separation for the Aberford population on the PC2. This appears to be mainly due to their less robust habit (reflected in reduced height, inflorescence length, stem width, and leaf, bract and calyx dimensions (Table 2)). On the other hand there is very clear separation on the PC1 axis between the British and the French plants and an examination of



FIGURE 1. First two axes of Principal Components Analysis for individual plants from populations referred to *Orobanche reticulata* from Yorkshire, England and France. PC1 & PC2 jointly account for 43.6% of the total variance.

TABLE 2. COMPARISON OF MORPHOLOGICAL CHARACTERS OF POPULATIONS OF BRITISH AND ALPINE O. RETICULATA S.L.

		BRITAIN	BRITAIN	BRITAIN	FRANCE
Locality		Aberford Yorkshire	Oxclose Yorkshire	Ripon Yorkshire	Petit Mont Rond Jura
Number		10	10	5	10
Date		2 vii 1994	9 vii 1994	13 vii 1994	6 viii 1995
Grid Referenc	e/Coordinates	SE/43 35	SE/36.46	SE/31 73	46 20'N: 6 02'E
Plant height		327+3.55	520 + 22.2	481 + 51.0	40.20 10, 0.02 L 324 ± 10.7
Flaint height		407 ± 10.5	529 ± 55.2	401 ± 31.0	524 ± 19.7
Stem	pubescence colour	3.0 ± 0.4 2.5 ± 0 fawn-violet	9.2 ± 0.5 2.0 ± 0 cream-mauve	10.4 ± 0.7 2.0 ± 0 deep violet	2.0 ± 0 cream-mauve
Inflorescence	length density	130.3 ± 10.1 2.1 ± 0.1	181 ± 17.7 1.9 ± 0.1	156 ± 19.6 2.0 ± 0.1	155 ± 14.5 2.5 ± 0
Leaf	width pubescence shape colour	4.5 ± 0.1 1.5 \pm 0 linear-lanceolate cream	$5 \cdot 2 \pm 0 \cdot 3$ $1 \cdot 6 \pm 0$ linear-lanceolate mauve-cream	4.7 ± 0.2 1.5 ± 0 linear-lanceolate violet-fawn	4.0 ± 0.1 1.5 ± 0 linear-lanceolate yellow-cream
Bract	length shape pubescence	17.9 ± 0.8 linear-lanceolate 2.1 ± 0.1	19.6 ± 0.8 linear-lanceolate 2.0 ± 0	21.9 ± 0.8 linear-lanceolate 2.0 ± 0.1	16.6 ± 0.9 linear-lanceolate 2.0 ± 0
Carralla	loweth	cream-purple		mauve-violet	
Corona	height approximate shape	20.4 ± 0.4 6.8 ± 0.3 ± campanulate	21.7 ± 0.3 8.1 ± 0.3 ± campanulate	21.1 ± 0.4 6.9 ± 0.2 ± campanulate	18.5 ± 0.4 6.7 ± 0.3 tubular-tubular- campanulate
	attitude dorsal line pubescence colour	1.5 ± 0 3.0 ± 0 1.6 ± 0.1 cream-purple	1.5 ± 0 2.3 \pm 0.1 1.5 \pm 0 cream-purple	1.5 ± 0 2.6 ± 0.1 1.5 ± 0 cream-purple	1.0 ± 0 2.2 ± 0.4 1.7 ± 0.1 cream-vellow-purple
Upper lip	divided	1.7 ± 0.1	1.8 ± 0.1	1.6 ± 0.2	1.3 ± 0.1
Lower lip	ciliate denticulate shape of lobes relative size entral to lateral)	$0 \\ 0 \\ 0 \\ 1 \cdot 1 \pm 0$	$ \begin{array}{c} 0 \\ 0 \\ 0 \\ 1 \cdot 0 \pm 0 \end{array} $	$0 \\ 0 \\ 0 \\ 1 \cdot 0 \pm 0$	$ \begin{array}{c} 0.8 \pm 0.1 \\ 1.0 \pm 0 \\ 0 \\ 1.1 \pm 0 \end{array} $
Bracteole	entrui to futorui)	0	0	0	0
Calyx	length segment division	11.4 ± 0.4 2.5 ± 0.3	12.6 ± 0.5 2.9 ± 0.3	15.1 ± 0.6 3.3 ± 0.3	11.4 ± 0.4 3.1 ± 0.3
	pubescence shape of teeth colour	2.0 ±0 tapering mauve-purple	1.6 ± 0.1 narrow acuminate cream-violet	1.8 ± 0.1 broadly tapering mauve-violet	2.0 ± 0 narrow, tapering cream-yellow
Filaments	insertion height pilosity above	$3 \cdot 2 \pm 0 \cdot 1$ $0 \cdot 1 \pm 0$	$3 \cdot 2 \pm 0 \cdot 1$	3.4 ± 0.2	2.4 ± 0.1 0.2 ± 0.1
	pilosity below	0.2 ± 0.1	0.4 ± 0.1	0	0.3 ± 0.1
Anthers	pilose	0	0	0	0
Stigma lobes	separation colour	1.7 ± 0.1 mauve-purple	1.7 ± 0.1 brown-purple	1.9 ± 0 brown-purple	2.4 ± 0.1 brown-purple
Apparent host		Cirsium arvense	Cirsium arvense	Cirsium arvense	Carduus defloratus

Mean values and standard errors (in mm)

Table 2 shows where the main differences lie. Other than in the different degree of robustness mentioned above, the three British populations show close agreement in almost all important characters (Table 2 and Figure 1). This is especially notable for those related to the corolla (shape, size, height of filament insertion, filament pilosity and stigma lobe separation). Corolla shape, being relatively broad in relation to length and strongly curved, is especially characteristic and constant for the British plants and differs appreciably from the more tubular, much less curved corollas of those from mountain areas of France. Being qualitative, however, this character is not included in the PCA. The French plants also differ from the British in their lower level of filament insertion, their wider stigma lobe separation and in the presence of ciliate, denticulate lobes to the lower lip of the corolla. Corolla length in this population is also less than for British plants, but this may not be significant as it was found to be somewhat longer in other French populations seen but which were not morphologically assessed in detail. Broad similarities in corolla height of all four populations did not reflect the characteristic corolla shape apparent in the British plants, i.e. relatively broad in relation to length.

During the course of this work and earlier, 44 populations of the British plant have been examined (Foley 1992a). All appeared to be morphologically similar but showed appreciable variation in colour, especially that of the stem, calyx and corolla. A few populations had individuals with very atypical coloration (Foley 1992b), some being uniformly rich yellow or occasionally pure white. Apart from these exceptional plants, corolla colour differences were usually due to the varying presence of mauve-purple glandular hairs and purple corolla venation. This could vary widely and sometimes partially obscured the basic cream to greyish base colour of the corollas. Plants seen in French montane/subalpine populations were similarly, but less variably, veined and embellished with mauve-purple glandular hairs, usually over a deeper, almost yellow, background.

The above observations suggest that the French montane/subalpine and British plants belong to *O. reticulata s. s.* and *O. procera* respectively. Whether *O. reticulata s. s.* is a plant wholly restricted to higher altitudes may be open to question since Wallroth's type specimen was collected from near Toulouse (France), some distance north of the Pyrenees, but no locality details are indicated. Although not in an ideal condition, the specimen conforms satisfactorily to plants seen by myself in the French mountains and, in corolla shape especially, it differs from the British plant in ways similar to those mentioned above.

The British plants on the other hand largely agree with the description given by Koch (1833) for *O. procera*, which occurs in lowland habitats in Germany and elsewhere. This applies especially to corolla shape which is campanulate distally, inflated towards the base and curved; his description is much closer to the British plant than to that from the Jura. A similar comment regarding the distinctive corolla shape of *O. procera* is given by Rouy & Foucaud (1909) under *O. platystigma* var. *procera*: "corolle plus large, subcampanulée, et plus petite", i.e. broader and shorter; this in comparison to other similar taxa within the group. Koch's *O. procera* grew in fields close to the River Rhine; the British plant is also most frequently found near river margins and flood plains (Foley 1993) where it usually parasitises *Cirsium arvense*.

Despite similarities existing between the lowland British and the European montane/subalpine plant, they can be readily distinguished by several clear-cut character differences. Due to this and the fact that they appear to occupy quite distinct habitats, often parasitise a different host genus and have a somewhat different geographical range, their appropriate taxonomic rank appears to be at the subspecific level. The lowland plant of Britain and Europe therefore becomes *O. reticulata* subsp. *procera* (Koch) Dostál and the montane/subalpine plant subsp. *reticulata*.

The status of *O. pallidiflora* Wimmer & Grabowski, however, remains uncertain. From its original description it is unclear whether its affinities lie closer to subsp. *reticulata* or to subsp. *procera*. By its specific epithet (= pale-coloured flowers) and the authors' brief reference to corolla colour, it would appear that this is its most distinctive character. If so, it may well be that light-coloured variants of subsp. *reticulata* (and even subsp. *procera*) are routinely referred to it. Although I have seen an appreciable number of herbarium specimens referred to *O. pallidiflora* (placed at that or lower ranks), most of these are closer to subsp. *reticulata* than to subsp. *procera*. In this genus, however, subtlety of colour is one of the first characters lost on preservation and it is one reason why investigations into this taxon have not been pursued here. It is possible that taxa referred to *O. pallidiflora* are mere colour forms of one or both subspecies of *O. reticulata*. No living populations were discovered during this work which could be reliably referred to this plant.

CONCLUSIONS

There are two distinctive, yet closely allied taxa: (a) *O. reticulata* subsp. *reticulata*, a plant of montane-subalpine occurrence, usually found at altitudes between 1000 and 2500 metres and apparently widespread but local in suitable areas of continental Europe, where its main host is *Carduus defloratus*, and (b) *O. reticulata* subsp. *procera*, a plant of lowland Europe (including Britain), often found in agricultural areas and in the vicinity of major rivers or flood plains where seed may dispersed by water-borne means. There are also other superficially similar lowland European plants which have been referred to *O. pallidiflora* but which are somewhat problematic. It is possible that these are simply colour variants and that such morphological differences as exist are at least partly determined by the different hosts parasitised. J. Zázvorka (litt. comm.), based on his experience in (the then) Czechoslovakia, goes even further and considers that all taxa embraced by *O. reticulata s. l.* are really a single taxon whose differing morphology is host-determined. There is no clear evidence for this, but the varying degree of robustness is one character which may well be host-determined.

TAXONOMIC DESCRIPTION

OROBANCHE RETICULATA WALL. SUBSP. RETICULATA

(syn.: O. scabiosae Koch; O. pallidiflora auct., O. platystigma Rchb.; O. carlinoides Miégeville; O. cardui Sauter; O. scabiosifixa St Lager).

Described from southern France "In agro Tolotono". Type collected at Toulouse in 1807 by D. Flügge (LE!).

Typically 300–350 mm tall, with a fairly dense, many-flowered inflorescence. *Stem*: 6–8 mm wide immediately below the inflorescence, distinctly glandular-pubescent, cream-mauve. *Leaves*: maximum width c. 4 mm, linear-lanceolate, yellow-cream, glandular-pubescent. *Bracts*: 12–18 mm long, linear-lanceolate, cream, rapidly darkening with age. *Calyx*: c. 10–12 mm long, segments usually unequally divided, sometimes entire, teeth narrow, tapering, cream-yellow, glandular-pubescent. *Corolla*: 18–22 mm long, suberect, tubular to tubular-campanulate, yellow-deep cream with mauve-purple veins and varying amounts of purple glandular hairs mainly distally on upper lip, dorsal line not strongly curved. Upper lip slightly bilobed; lobes of lower lip somewhat ciliate and denticulate, rounded, \pm similar in size. *Filaments*: inserted at 2·0–2·5 mm above the corolla base, very slightly glandular-pilose to glabrous above, \pm glabrous below but sometimes with a few hairs at the actual base. *Stigma lobes*: dark purple-brown with yellow undertones, distinctly separated. Parasitic mainly upon *Carduus defloratus*, but probably also on other taxa including *Knautia* spp.

A plant mainly of montane to subalpine habitats over a range of substrates, perhaps descending to lower altitudes close to its main area of distribution. Flowers June–August (–September). Widespread but local in suitable mountain habitats of mainland Europe including the Alps, the Pyrenees and the Balkans. Its distribution outside this area is unclear at present.

OROBANCHE RETICULATA SUBSP. PROCERA (KOCH) DOSTÁL

(syn.: O. pallidiflora auct.; O. cirsii Fries; O. mathesii Schultz: O. serotina Kirschleger).

Described from Germany "auf lehmigen Aeckern in Gegend von Mannheim in der Rheinpfalz... [etc.]". Specimens collected by Schimper but type not located.

Similar to subsp. *reticulata* but more robust and taller (400–550 mm); *corolla*: broader and almost campanulate, quite strongly curved, lobes of lower lip not noticeably ciliate or denticulate; *filaments*: inserted higher (3.0–3.5 mm) above the corolla base; *stigma lobes*: less widely separated. Parasitic on *Cirsium* spp., especially *Cirsium arvense* and related genera.

A plant mainly of lowland habitats, river banks and flood plains, field borders, ruderal habitats, roadsides, unimproved pastures, scrub, woodland clearings and perhaps occasionally reaching submontane grasslands. Flowers June–August. Widespread throughout much of central Europe north of the Alps, including Germany and Poland and with disjunct occurrences in eastern England (Yorkshire).

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