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

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ABSTRACT

A morphological comparison has been made between British plants of *O. rapum-genistae* and plants referable to subsp. *rigens* from Corsica, which is endemic to that part of the Mediterranean. Characters which best separate the two taxa are indicated and it is concluded that the latter is more appropriately placed at species level as *O. rigens* Loisel.

KEYWORDS: Orobanche rapum-genistae subsp. rigens, Corsica, taxonomy.

INTRODUCTION

BACKGROUND

Orobanche rapum-genistae sensu lato comprises a small but widespread group of western European taxa thought to be distributed eastwards as far as Germany and Italy (limit at Val Vestino, south Tirol (Gilli 1965)) and southwards to Spain and Portugal (Beck 1926–28); it is also recorded for Algeria (Battandier 1890) and other north African countries, although its presence in some may be doubtful. The current northern limit is in Scotland.

Fournier (1937) recognised three taxa at subspecific level. These were the type (subsp. *rapum-genistae*), subsp. *benthamii* (Timb.-Lagr.) P. Fourn., differing from the former by its extremely long bracts and a distinctly bilobed upper lip to the corolla, which had been recorded from Spain, Portugal and northern Italy, and subsp. *rigens* (Loisel.) P. Fourn., apparently similar to the type but almost glabrous, from Corsica and Sardinia and the associated small off-shore islands. It is not definitely known whether the distributional ranges of the latter two taxa overlap with subsp. *rapum-genistae*. More recent treatments (Chater & Webb 1972; Pignatti 1982) have supported Fournier's approach.

The host plants are usually leguminous shrubs (Fabaceae), especially the genera *Cytisus, Ulex* and *Genista*, but with subsp. *rigens* apparently restricted to species of *Genista* (Chater & Webb 1972; Camarda 1981; Pignatti 1982).

Throughout most of its European range *O. rapum-genistae* is represented by subsp. *rapum-genistae*. In the British Isles this occurs southwards from southern Scotland and is widespread but local, having substantially declined during the past century (Foley 1994) and receded into a predominantly south-westerly distribution pattern, but with substantial populations remaining in Wales; it also occurs in south-east Ireland. In the British Isles the host is invariably either *Cytisus scoparius* (L.) Link or *Ulex europaeus* L., although there is an old record from Kent on *Genista tinctoria* L. The procumbent, maritime subspecies of *C. scoparius* (subsp. *maritimus*) is parasitised on sea cliffs in the Channel Islands (Rumsey & Jury 1991).

In France, from where the type (*O. rapum-genistae* Thuill.) was originally described, it is widely distributed up to subalpine levels (Rouy & Foucaud 1909) and records for Switzerland are also mainly from montane and (rarely) subalpine localities (Hess *et al.* 1972). In Germany it is restricted to the west, known from the Rheinland and Schwarzwald eastwards to Westphalia (Gilli 1965); it is also present (as subsp. *rapum-genistae*) in Belgium and Holland (Chater & Webb

1972). In Italy, Pignatti (1982) gave all three subspecies: the type, widespread throughout; subsp. *benthamii* from the alpine foothills of Piedmont and Lombardy; and subsp. *rigens* from Corsica, Sardinia and Sicily. Also for Corsica, Gamisans & Jeanmonod (1993) recorded all three taxa but the presence of two of them (the type and subsp. *benthamii*) is doubtful, whilst Camarda (1981) also gave localities for subsp. *rigens* (as *O. rigens*) in Sardinia. Both the type and subsp. *benthamii* are known from the Iberian peninsula (Willkomm 1893; Merino 1906; Coutinho 1913; Cadevall 1932; de Lima 1947; Franco 1984). For Algeria only the type was recorded by Battandier (1890) and Quezel & Santa (1963) although there is a record for subsp. *benthamii* by Beck (1930). *O. rapum-genistae s. l.* is apparently present in Morocco (Greuter *et al.* 1989) but doubtful in Tunisia (Bonnet & Barratte 1896).

BASIC TAXA RELATED TO O. RAPUM-GENISTAE AND SUBSEQUENT TREATMENTS

O. rapum-genistae was described from near Paris, France (Thuillier 1799) where it parasitised *Cytisus scoparius* and flowered in June: "*caule crasso, conspicue pubente et angulato: spica longissima: confertiflora, bracteis calycibusque villosissimis: corollis rufescentibus, brevi-tubulatis*". The description is barely adequate, although the reddish (but shortly tubular) corollas give some indication of its appearance. The type specimen is possibly in LE.

O. rigens was first described from Corsica (Loiseleur 1807) from specimens seen in Richard's herbarium "caule simplicissimo glabro, squamis lanceolatis rigentibus imbricatis, corollis quadrifis, staminibus inferne nudis, stigmate 2-lobo, lobis distantibus, stylo glaberrimo, simillima praedenti [O. major L.], sed discrepare videtur squamis rigentibus subpungentibus, et glabritie omnium parte, exceptis bractaeis quae leviter pubescunt. Flores rubiginosi ut planta ipsa". According to this description, one of the main characters relates to the more or less glabrous nature of the stem, style and lower part of the filaments - and indeed of most parts other than the lightly pubescent bracts. The imbricate, lanceolate scale-leaves are rigid, the stigma lobes apparently well separated and the flowers and the whole plant are of a reddish coloration. No specimen was mentioned by Loiseleur but his description indicates that it was based on Corsican material collected by Richard and retained in the latter's herbarium; however such potential type material appears now to be lost or destroyed. Loiseleur's herbarium at Avignon (AV) also contains no relevant material collected by Richard (Camarda 1981) but the Paris herbarium (P) has a Corsican specimen gathered by Soleirol in 1826 and presumably studied by Loiseleur "au mont d'Oro près des neiges eternelles". This has been proposed as the neotype for *O. rigens* (Camarda 1981).

O. benthamii Timb.-Lagr. was based upon the earlier *O. rapum* var. *bracteosa* which was described by Reuter (1847) as "*spicâ valde elongatâ, bracteis flores superantibus apice comosâ*". Reuter's diagnosis referred to plants collected by Bentham at Collioure in southern France and by Moris in the subalpine region of Piedmont, Italy. There is a fuller description of the same plant collected at les Basses Corbières hills, near Durban, southern France as *O. benthamii* (Timbal-Lagrave 1874). Again the bract character is referred to: "bractées.....dépassant de beaucoup les fleurs, ce qui rend l'inflorescence chevelue" - i.e. making the inflorescence "hairy". The corolla is stated to be very large, bright red - is the stem - and with lobes with fimbriate teeth. The filaments are glabrous and inserted at the base of the corolla and the stigma is white or yellow.

Beck (1930) placed all these taxa in his Grex Arcuatae, members of which were characterised as follows. The corollas were broad and more or less ventricose above the point of filament attachment and of similar internal and external colour, their dorsal line was strongly curved over the whole length, the margins of the corolla lobes were glandular-ciliate, the filaments inserted very low near the corolla base and the stigma lobes yellow. Within the Arcuatae he recognised three species: *O. rapum-genistae, O. rigens* and *O. anatolica* Reuter (1847) - the last is non-European, being from the Caucasus and Iran.

As regards *O. rapum-genistae* itself, Beck (1930) recognised two varieties in addition to the type. One of these was var. *bracteosa* (= *O. benthamii* Timb.-Lagr.) described above, the other, var. *insolita*, was based upon Guimarães' description of *O. insolita* from Bussaco, Portugal (Guimarães 1904) where it apparently parasitised *Eryngium campestre*. This is the usual host for *O. amethystea* and it is possible that *O. insolita* may be a variant of this, although filament, bract and inflorescence characters and the presence of abundant white, glandular hairs (Guimarães 1904) are consistent with *O. rapum-genistae s. l.* Unfortunately, no material of *O. insolita* that is known to have been seen by Guimarães has been located.

		CORSICA	CORSICA	BRITAIN	BRITAIN	BRITAIN	
Locality		Tassenita valley Asco	Haut Asco Asco	Haydon Bridge Northumberland	Cyttir Mawr Anglesey	Amisfield Dumfries	
Number		10	7	10	10	10	
Date		10.6.1997	10.6.1997	12.6.1993	5.6.1993	12 & 19.6.1993	
Species		rigens	rigens	rapum-genistae	rapum-genistae	rapum-genistae	
Grid Ref./Coordinates		42 26'N; 8 58'E	42 26'N; 8 58'E	NY8565	SH5774	NY0083	
Plant	height	213.5 ± 16.7	165 ± 13.9	415.5 ± 18.7	360 ± 14.9	379.9 ± 20.5	
Stem	width pubescence	10.1 ± 1.0 0.8 ± 0	8.9 ± 0.5 0.9 ± 0	10.8 ± 0.3 1.5 ± 0	11.6 ± 0.3 1.7 ± 0.1	13.1 ± 0.8 1.8 ± 0.1	
	colour	pink-mauve - yellow	pink. pink-yellow, yellow	pink-yellow	pink-pale brown	pale brown-pink	
Inflorescence length density		133.0 ± 9.8 1.7 ± 0.1	105.7 ± 10.1 1.8 ± 0.1	224.8 ± 18.0 1.3 ± 0.1	195.7 ± 15.8 1.9 ± 0.1	175.0 ± 14.8 1.6 ± 0.1	
Leaf	width	6.9 ± 0.4	6.8 ± 0.4	6.7 ± 0.2	6.7 ± 0.2	8.0 ± 0.4	
	shape	0.8 ± 0 ovate-tapering	0.9 ± 0 ovate-lanceolate	0.9 ± 0.1 linear-lanceolate	1.0 ± 0 triangular- lanceolate	1.2 ± 0.1 tapering	
	colour	pink-slt. mauve	pink-yellow	brown	medium brown	fawn-dark brown	
Bract	length shape	16.7 ± 0.7 ovate-lanceolate	18.4 ± 0.8 ovate-lanceolate	27.6 ± 0.5 lanceolate	21.9 ± 1.1 lanceolate	$25 \cdot 1 \pm 1 \cdot 0$ lanceolate	
	colour	1.5 ± 0.1 darkish mauye	1.4 ± 0.1	2.0 ± 0	1.0 ± 0.1	dark brown	
Corolla	length	23.2 ± 0.6	21.6 ± 0.6	24.4 ± 0.3	22.2 ± 0.5	25.6 ± 0.6	
Corona	height	9.1 ± 0.3	7.7 ± 0.5	10.0 ± 0.3	10.4 ± 0.4	10.3 ± 0.2	
approximate sha		subcampanulate	subcampanulate	\pm infundibuliform	buliform \pm infundibuliform \pm infundibuliform		
	attitude	$1 \cdot 1 \pm 0 \cdot 1$	1.0 ± 0	1.3 ± 0.1	1.6 ± 0.1	1.4 ± 0.1	
	dorsal line	2.5 ± 0.1	2.4 ± 0.1	$2 \cdot 2 \pm 0 \cdot 1$	2.9 ± 0.1	2.6 ± 0.1	
	colour	1.0 ± 0	0.8 ± 0.1	1.5 ± 0.1	1.2 ± 0.1	1.4 ± 0.1	
	colour	pink-mauve	pink-yellow	pink-rawn	pink-paie rawn	pink-rawn	
Upper lip	divided	0.5 ± 0.2	0	0	0.1 ± 0.1	0	
Lower lip	ciliate	0.2 ± 0	0.1 ± 0.1	1.0 ± 0	0.3 ± 0.1	0.7 ± 0.1	
sł	ape of lobes	0	0	0.8 ± 0.1	0.8 ± 0.1	0.8 ± 0.1	
relative size		1.0 ± 0	1.0 ± 0	1.4 ± 0.1	1.3 ± 0.1	1.3 ± 0.1	
(cer	tral to lateral)						
Bracteole		0	0	0	0	0	
Calyx	length	13.6 ± 0.3	13.0 ± 0.9	15.0 ± 0.5	13.0 ± 0.4	15.8 ± 0.6	
segn	nent division	1.8 ± 0.4	1.0 ± 0	1.0 ± 0	1.4 ± 0.2	1.2 ± 0.1	
shap	pubescence be of teeth	1.4 ± 0.1 elongated	1.2 ± 0.1 triangular-	2.0 ± 0 tapering	1.2 ± 0.1 ± acuminate	1.7 ± 0.1 tapering	
	colour	mauve	lanceolate mauve-pink	pale fawn	pale pink-fawn	pale fawn	
Filaments	insertion	2.9 ± 0.1	2.6 ± 0.1	3.4 ± 0.2	2.0 + 0.1	3.8 ± 0.2	
	height	27201	20201	51202	20101	50101	
pilosity above		0	0	1.0 ± 0	0.9 ± 0.1	1.0 ± 0	
phosity below		0	0	0	0	0	
Anthers pilose		0	0	0	0	0.1 ± 0	
Stigma lobes separation colour		$2 \cdot 1 \pm 0$ pale yellow	2.0 ± 0 pale yellow	3.0 ± 0 bright yellow	2.9 ± 0.1 bright yellow	2.9 ± 0.1 bright yellow	
Apparent host		Genista salzmannii var. lobelioides	Genista salzmannii var. lobelioides	Cytisus scoparius	Ulex europaeus	Cytisus scoparius	

TABLE 1. COMPARISON OF MORPHOLOGICAL CHARACTERS OF POPULATIONS OF OROBANCHE RIGENS AND O. RAPUM-GENISTAE

Mean values and standard errors (in mm)

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Beck (1930) maintained *O. rigens* as a separate species from *O. rapum-genistae* on the basis of the former's more or less glabrous corolla, filaments and style. In contrast, Fournier (1937) in his French Flora placed all the principal European Arcuatae taxa at subspecific level under *O. rapum-genistae*. Such a treatment has been maintained by several later workers (Chater & Webb 1972; Pignatti 1982) but modified by others. For example *O. rigens* was ranked at species level by both Camarda (1981) and Uhlich *et al.* (1995) despite having much earlier been considered a variety by Fiori (1926). In other instances some of the taxa have been simply omitted or ignored completely.

METHODS

Three British populations of subsp. *rapum-genistae* (two parasitic upon *Cytisus scoparius* and one upon *Ulex europaeus*) were morphometrically compared with two Corsican populations of subsp. *rigens* parasitic upon *Genista salzmannii* var. *lobelioides* (see Table 1 for locality details). Characters measured or assessed and the methods used were as described in a prior paper (Foley 2000). Mean values and standard errors of the relevant characters are summarised in Table 1 and the quantifiable numerical elements of these data have been subjected to PCA (Figure 1) in a similar manner to that previously decribed (Foley *op. cit.*). 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.

RESULTS AND DISCUSSUION

In Figure 1 it can be seen that the Corsican plants are clearly separated from the British on the PC1 axis. Within the British plants there is only slight overlap between plants at Cyttir Mawr, Anglesey (on *Ulex europaeus*) and those of the other two populations on *Cytisus scoparius* (at Amisfield and Haydon Bridge). Whether this difference is significant, possibly due to the influence of the different hosts on the plant's morphology, is open to question but this could additionally be investigated by cultivation experiments.

When the characters of the two taxa (subsp. *rapum-genistae* and subsp. *rigens*) are compared (Table 1), it can be seen where the principal differences lie. It is true that there is quite a close similarity in many of them but relatively intangible morphological differences, readily apparent in living plants in the field, are reflected in at least some of these.

Plants of subsp. *rigens* appear to be less robust than those of subsp. *rapum-genistae* (overall height, inflorescence length, stem width etc.) - but this may in part be due to their occurrence at a higher average altitude. In many plants the inflorescence occupies a higher proportion of the overall height of the plant and often reaches close to ground level. Leaf and bract shape is distinctly ovate (rather than lanceolate) and the corolla is subcampanulate rather than ventricose-infundibuliform as in subsp. *rapum-genistae* (the latter is also somewhat carinate dorsally), with the lobes of the lower lip much more rounded and of equal size. Corolla colour (and general plant coloration - stem, leaves, calyces) differs, being markedly mauve-pink in subsp. *rigens* rather than pink-fawn. Perhaps the clearest character difference lies in filament pubescence. Whilst the filaments are inserted at similar heights, they are glabrous throughout their entire length in subsp. *rigens* whereas those of subsp. *rapum-genistae* are very distinctly glandular-pilose in their upper portion. The style and ovary are also distinctly pilose, being provided with colourless, few-celled, glandular hairs; in contrast subsp. *rigens* is glabrous in this respect. Stigma lobe colour is also much paler in this taxon and the stigma lobes are noticeably less separated.

Another character difference which is very apparent is the overall level of pubescence, this being very much reduced in subsp. *rigens* compared to *O. rapum-genistae*. Since subsp. *rigens* appears to be a much more montane-subalpine plant than subsp. *rapum-genistae*, it might be expected that if the former were merely a close variant of the latter then the pubescence, as in other montane plants, would be much greater (not less) in the higher altitude taxon.



FIGURE 1. First two axes of Principal Components Analysis for individual plants of *Orobanche rigens* and *O. rapum-genistae.* PC1 & PC2 jointly account for 43.6% of the total variance.

CONCLUSIONS

It is clear that whilst both subsp. *rapum-genistae* and subsp. *rigens* are quite similar, they also possess several distinctive characters. In contrast to subsp. *rapum-genistae*, the following characters are diagnostic for subsp. *rigens*: the very low level of overall pubescence, the differering corolla shape and coloration, the more ovate leaf and bract shape, the glabrous filaments and the differing stigma lobe characters. In the absence of evidence of intermediates between the two, it is concluded that these differences are sufficient for subsp. *rigens* to be separated at species level as *Orobanche rigens* Loisel. Other work, based mainly upon herbarium specimens of Sardinian *O. rigens* (Camarda 1981), reached a similar conclusion; both those findings and the present ones contrast with the approach taken by most other workers subsequent to Fournier (1937), who have maintained *O. rigens* at subspecific level.

The situation regarding subsp. *benthamii* is less easy to resolve as it is a little-known taxon of limited and relatively unknown distribution; it is not recorded for Britain. During this work no living plants and only three herbarium specimens (out of many hundreds of this group examined) could reasonably be referred to this taxon and even those differed from subsp. *rapum-genistae* only in their significantly longer bracts. Other differences indicated in Chater & Webb (1972), e.g. an erect, distinctly bilobed upper corolla lip in subsp. *benthamii*, were not evident in these specimens. It is concluded that the latter should be considered to be merely a form of *O. rapum-genistae*.

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TAXONOMIC DESCRIPTION

OROBANCHE RAPUM-GENISTAE THUILL.

(syn.: O. major L. pro parte; O. palatina Schultz; O. rapum var. bracteosa Reuter; O. bracteosa (Reuter) Nyman; O. elatior Horn; O. foetida Duby, O. sarothamnophyta St Lager, O. benthamii Timb.-Lagr., O. rapum-genistae subsp. benthamii (Timb.-Lagr.) P. Fourn.)

Described from near Paris, France. Type possibly in LE.

Typically 250–450 mm tall, with a quite dense, long, many-flowered inflorescence. *Stem*: 8–15 mm wide immediately below the inflorescence, distinctly glandular-pubescent, pink-yellow to pink-brown. *Leaves*: maximum width 6–8 mm, \pm lanceolate, fawn-brown. *Bracts*: 20–28 mm long, linear-lanceolate, light brown, distinctly glandular-pubescent. *Calyx*: 13–16 mm long, segments fairly equally divided, tapering, pale pink-fawn, glandular-pubescent. *Corolla*: 22–26 mm long, sub-erect, \pm infundibuliform, ventricose, somewhat carinate dorsally, pink-fawn, glandular-pubescent, dorsal line distinctly curved; upper lip \pm entire, margins of lower lip somewhat ciliate, not denticulate, rather acute, the central lobe often larger than the laterals. *Filaments*: inserted 2–4 mm above the corolla base, glabrous below, distinctly glandular-hairy above. *Stigma lobes*: deep yellow, well separated. Parasitic mainly upon species of *Ulex* and *Cytisus*.

This is a plant of scrub-invaded areas such as rocky hillocks, field margins and headlands, roadside verges and other habitats typical of its hosts. Within Britain, observations have suggested a possible west-east cline in host preference with *Ulex europeaus* apparently being preferred in the west (especially Wales) and *Cytisus scoparius* the preferred host further east. Flowers April–July. The species is apparently widespread but often very local in western Europe extending north to southern Scotland and east to the Italian south Tirol.

The long-bracted form (syn.: *O. rapum-genistae* var. *bracteosa* Reuter; *O. benthamii* Timb.-Lagr.) appears to differ from the above only in its exceptionally long bracts. Suggested differences in corolla lip characters have not been confirmed. It is apparently of very limited occurrence and recorded only very locally in southern France, Italy, parts of the western Mediterranean and the Iberian peninsula.

OROBANCHE RIGENS LOISEL.

(syn.: O. condensata Moris pro parte; O. thyrsoidea Moris; O. rapum var. glabrescens Gren. & Godr., O. rapum-genistae subsp. rigens (Loisel.) P. Fourn.)

Described from Corsica. Type thought to be lost (Richard herb.), neotype: "au mont d'Oro [Corsica] près des neiges eternelles, 1826, leg. Soleirol" (**P**!).

Typically 150–230 mm tall, with a fairly dense, many-flowered inflorescence which sometimes extends to most of the length of the spike. *Stem:* 8–10 mm wide immediately below the inflorescence, slightly glandular-pubescent to nearly glabrous, pink-yellow to somewhat mauve. *Leaves:* maximum width 6–7 mm, usually \pm ovate, pink-yellow to pink-mauve. *Bracts:* 16–20 mm long, \pm ovate, pink-mauve, somewhat pubescent. *Calyx:* 13–14 mm long, segments fairly equally divided, teeth elongated, triangular-lanceolate, mauve-pink, somewhat glandular-pubescent. *Corolla:* 21–24 mm long, erect to suberect, \pm subcampanulate, not noticeably carinate dorsally, pink-mauve sometimes tinged yellowish, only slightly glandular-pubescent, dorsal line distinctly curved. Upper lip sometimes noticeably divided, margins of lower lip sometimes slightly ciliate, not denticulate, rounded, lobes of \pm equal size. *Filaments:* inserted 2–3 mm above the corolla base, glabrous throughout their length. *Stigma lobes:* pale yellow, only moderately separated. Parasitic upon species of *Genista*, in Corsica usually only on *Genista corsica*. There is a suspicion that *Anthyllis hermanniae* may also be parasitised (D. Jeanmonod, pers. comm. 1996).

In Corsica, this is a plant of montane-subalpine habitats mainly found in the *Thymus-Genistetum* association of dwarf spiny shrubs at an altitudinal range of (600–) 900–c.2000 m, but in Sardinia it occurs down to sea-level (Camarda 1981). Flowers (March–) May–June (–July at high altitudes). It is endemic to Corsica and Sardinia and the associated off-shore islands. It is widespread but local in suitable habitats but may be under-recorded. Records for Sicily are probably errors for other taxa.

Although both *O. rapum-genistae* and its long-bracted form (var. *bractosa*) have been recorded for Corsica, it is possible that these are errors and that *O. rigens* is the only member of the group present.

ACKNOWLEDGMENTS

I am most grateful to the trustees of the Welch Bequest Fund of the Botanical Society of the British Isles and to the Botanical Research Fund (Kew) for financial assistance during this project.

I am also grateful to D. Jeanmonod (Geneva) and I. Guyot (Bastia) for providing me with information regarding Corsican localities for *O. rigens*, and to all those vice-county recorders who have similarly helped with information on *O. rapum-genistae* in Britain. I also wish to thank the curators of the following herbaria for their loan of specimens: **B**, **BM**, **E**, **LIV**, **MA**, **P**, **SEV**.

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(Accepted July 1999)