Reassessing the *Odontites purpureus* group (Orobanchaceae) from south-east Spain and north-west Africa

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We describe a species of *Odontites*, *O. bolligeri* E.Rico, L.Delgado & Herrero, endemic to the south-eastern Iberian Peninsula and north Africa, from Morocco to Tunisia. This species belongs to the *O. purpureus* group and corresponds to the taxon that the monographer Markus Bolliger called *O. squarrosus* subsp. *squarrosus*. However, according to the International Code of Botanical Nomenclature (ICBN), this is an invalid name, and hence we propose a new name for these plants here. Drawings of the new species are also supplied. In addition, we compare and discuss the other species of the *O. purpureus* group, propose a key for them and include a karyological study of the two Iberian species of the group. © 2008 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2008, 158, 701–708.


INTRODUCTION

The genus *Odontites* Ludw. comprises, in a restricted sense, 26 species (Bolliger, 1996), as Rothmaler (1943), based on characters of the corolla, excluded some species that were separated and included in smaller genera. This splitting of the genus was later taken up by Bolliger & Wick (1990), who considered exine ornamentation to be of great importance in this context. *Odontites* species have a wide distribution, ranging from Madeira and the north of Africa to northern Europe and eastern Asia. However, most species are endemic to the Mediterranean region and, in addition, the genus shows the greatest diversity in the western part of this region (Bolliger, 1993: 354).

The western Mediterranean, particularly northern Morocco and Algeria, Tunisia and the south-eastern Iberian Peninsula, harbours the taxa that Bolliger (1996), mainly based on morphological data, included in the *O. purpureus* group. According to this author, there are two species of this group in south-eastern Spain: *O. squarrosus* (Salzm. ex Rchb.) Bolliger subsp. *squarrosus* and *O. squarrosus* subsp. *foliosus* (Pérez Lara) Bolliger.

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check the variation of several morphological (e.g. colour of corolla and habit) and ecological characters.

Chromosome counts were mostly made using young floral buds, from which immature gynoecia were selected, although sometimes meiosis was observed in anther cells. The material was fixed in 3 : 1 absolute ethanol–glacial acetic acid. The fixed material was stored at 4 °C until required. It was then stained with 2% acetic orcein and squashed in 45% acetic acid (La Cour, 1945). From each population, at least two counts were made, from which chromosomes were drawn and photographs were taken with a Nikon Optiphot microscope. Drawings and negatives are deposited at the Department of Botany of the University of Salamanca.

The classification of Stebbins (1938) was followed to assign chromosome size. The interchromosomal asymmetry index (A_A) was calculated according to the formula proposed by Romero Zarco (1986).

RESULTS

**Odontites bolligeri** E.Rico, L.Delgado & Herrero, sp. nov.

*Odontites squarrosus* (Salzm. ex Rchb.) Bolliger in Willdenowia 26: 148 (1996), nom. inval., subsp. *squarrosus* [description (in German), excl. type].


**Type:** Almegjar (Espagne, prov. Granada), Las Alpujarras, aux abords du fleuve Guadalfeo, UTM 30S VF 7284, alt. 900 m, maquis thermophile sur des sols calcaires, Saturejo-Coriodythymion Rivas Goday & Rivas-Martínez 1964, 4.x.1979, M. Ladero, J. Molero & F. Pérez Raya [sub *O. purpureus* (Desf.) G.Don]. Holotype G 278400; isotypes B 10 0264914, MAF 123093, JACA 447384, RNG, SALA 68772, SEV 112540.

**Diagnosis:** Suffrutex non longaevus, plerumque e basi in caules aliquot divisus, puberulus, non viscosus vel ad apicem tantum leniter viscosus. Caules ad 60 cm alti, pilis brevibus unicellularibus eglandulosis abundantibus, retrorsis, rectis vel parum recurvatis, ad basin haud vel parce dilatatis, adpressis vel fere adpressis vestiti, sine glandulis vel paucis glandulis minutis sessilibus vel subsessilibus instructi. Bracteae minus quam 5(–6.5) mm longae, ovale–lanceolatae (longitudine 2.1–2.8plo majore quam latitudine), calycem plerumque non superantes. Calycis dentes breviros quam tubus, pilis antrorse eglandulosis paucis et saepe pluricellularibus glanduliferis numerosis instructi. Corolla (5)–6–7.5 mm, labis ambobibus purpureis vel interdum roseis, extus glabra. Capsula 3–4.8 × 1.8–2.2(–2.5) mm, intus pilis rigidis juxta septum praedita. Semina 1.1–1.7 × 0.5–0.7 mm, in capsula unaquaque plura quam quattuor.

**Description:** Short-lived suffruticose plant, generally each individual plant with several main stems, puberulent, non-viscid or only weakly viscid on the apical part. Stem up to 60 cm, with abundant unicellular hairs, up to 0.5 mm, eglandular, retrors, straight or slightly curved, not or sparingly widened at base, adpressed or almost adpressed, without minute glands or with very few of them at the base at the start of ramifications or in inflorescence. Leaves (5)10–30 × 1–4 mm, linear, linear-lanceolate or triangular-lanceolate, entire, generally with eglandular hairs, antrorse, with or without a few minute glands. Inflorescence 1–1.5(2) cm (during flowering), basipetal; bracts of less than 5(6.5) mm, 2.1–2.8 times longer than wide, in general not exceeding the calyx, oval-lanceolate, hairiness similar to that of the leaves, usually less hairy. Calyx (2.5)3–4(4.5) mm in flowering, up to 4.8 mm during fruiting, lobes shorter than tube, with few antrorse eglandular hairs, often with numerous pluricellular glandular hairs, with two to three cells and a thick pluricellular gland, at least on lobes, and rarely without them. Corolla (5)6–7.5 mm, with both lips purple or sometimes pink, occasionally with a whitish band, glabrous on the external face; tube 2.5–3.5(4) mm, shorter than lips, shorter or slightly exceeding the calyx. Staminodes with smooth or finely papillose filaments, twisted 90° under anther, so that the latter is arranged almost perpendicularly to the filament; anthers 1.1–1.5(1.7) mm, hidden or slightly protruding from corolla, dehiscent along almost the whole length, with an apical tuft of hairs ± twisted and glabrous on rest, exceptionally with some isolated hairs. Style 4.5–6 mm during fruiting, glabrous or with only a few hairs on basal half. Capsule 3–4.8 × 1.8–2.2(2.5) mm, with rigid hairs inside, near to septum. Seeds 1.1–1.7 × 0.5–0.7 mm, several (more than four well developed or aborted) per capsule.

**Etymology:** Dedicated to Markus Bolliger, the Swiss botanist who recognized this taxon for the first time, and author of the most exhaustive revision available of *Odontites*.

**Iconography:** Figure 1A–K. Bolliger in Willdenowia 26: 149 (1996) [sub *O. squarrosus* subsp. *squarrosus*].

**Chromosome number:** The chromosome numbers 2n = 22, 24, 26 and n = 11 were found in four populations investigated (Figs 2–6).

**Ecology and phenology:** Thermophile shrubland belonging to the phytosociological class *Rosmarinetea officinalis* Rivas Mart., Fern. Gonz., Loidi, Lousa & Penas. Usually grows together with *Rosmarinus*.
officinalis L. and Thymbra capitata (L.) Cav., on basic substrates at elevations of 130–1350 m a.s.l. Flowering usually between September and November (exceptionally from July to January). Fruiting generally from September to December.

Distribution: Northern Africa (from central-northern Morocco to Tunisia) and south-eastern Iberian Peninsula (parts of western Andalusia, provinces of Málaga and Granada). The plant is found at locations not far from the Mediterranean coast: in Africa, north of the

Rif and north of the Atlas mountain ranges, and on the Iberian Peninsula on the southern slopes of the Sierra Nevada and Sierra Almijara.

Conservation status: In the fairly small area of Spain where the species is represented, it is a relatively common plant, although not frequent, and there are some populations with many individuals. Accordingly, for the time being, it is not endangered, although there are no detailed studies on possible threats. In the Red List of Endangered Plants of Andalusia (Cabezudo et al., 2005: 103), it is included in section DD (Deficient data) under the name *O. squarrosus* subsp. *squarrosus*. With regard to the northern African populations, the data are insufficient for conclusions to be drawn.

**TAXONOMIC DISCUSSION**

The taxa included in the *O. purpureus* group (Bolliger, 1996: 144) are perfectly recognizable by a set of morphological characteristics, such as a stem without long pluricellular hairs, a basipetal inflorescence, a calyx with hairs ending in a thick pluricellular gland, a wholly or partially purple and glabrous or subglabrous corolla and the presence of more than four seeds per capsule. Several of these characters are shared with *O. viscosus* (L.) Clairv., one of the most polymorphic species of the genus that is distributed from north-western Africa to western Switzerland and Italy, and that is frequent on the Iberian Peninsula. However, the presence of long pluricellular hairs, at least at the base of the stems, and of only four seeds per capsule, clearly separates this species from all those of the *O. purpureus* group. Moreover, an additional character, the existence of a line of hairs inside the capsule next to the septum, also seems to be of general occurrence in the group, although this could not be confirmed in *O. ciliatus* Pomel.

This character is also shared by *O. viscosus* and is almost completely lacking in the remaining species of the genus. Rothmaler (1943: 229) placed *O. purpureus* G.Don together with *O. viscosus* in section *Dispermotheca* (Beauv.) Rothm.

Several species in the group have been described, especially from northern Africa. However, the authors, prior to the revision made by Bolliger, had grouped all the European material of this group in a single species: *O. purpureus*. Thus, for example, *O. purpureus* is cited in Lange (1870: 616) and Webb & Camarasa (1972: 267). Bolliger (1996) reported the intraspecific morphological diversity of these plants and, on the basis of morphological characters, such as habit, the size of the corolla, calyx and bracts, type of hairiness and corolla colour, recognized the following taxa as a reflection of the described diversity: *O. purpureus*, *O. discolor* Pomel subsp. *discolor*, *O. discolor* subsp. *ciliatus* (Pomel) Bolliger, *O. squarrosus* subsp. *squarrosus* and *O. squarrosus* subsp. *foliosus*.

**Figures 2-7. Odontites bolligeri.** Fig. 2. Mitotic metaphase, 2n = 22 (SALA 103768)*. Fig. 3. Mitotic metaphase, 2n = 24 (SALA 103764)*. Fig. 4. Mitotic metaphase, 2n = 24 (SALA 103767)*. Fig. 5. Mitotic metaphase, 2n = 26 (SALA 103767)*. Fig. 6. Meiotic anaphase I, n = 11 (SALA 103770)*. **Odontites foliosus.** Fig. 7. Mitotic metaphase, 2n = 26 (SALA 103775)*. Scale bar, 10 μm.
After our revision of abundant material from the Iberian Peninsula and part of northern Africa, including types, we agree with most of the nomenclatural and taxonomic proposals made by Bolliger (1996), with the exception of one nomenclatural aspect and the ranking of two clearly distinguishable taxonomic entities within this group.

With regard exclusively to the nomenclatural problem, although the plants that Bolliger included under the name *O. squarrosus* subsp. *squarrosus* can be differentiated from the remaining taxa in this group, above all because they are the only suffruticose plants within it, and hence merit independent taxonomic recognition, it is not possible to name them *O. squarrosus* (Salzm. ex Rchb.) Bolliger. The latter is a nomen nudum, as neither the basionym *Euphrasia squarrosa* Salzm. ex Rchb., which has never been described (ICBN Art. 32.1 d; McNeill et al., 2006), nor the combination under *Odontites* (Bolliger, 1996: 148), which is not accompanied by a description or diagnosis in Latin or with a reference to a previous description (ICBN Art. 36.1; McNeill et al., 2006), has ever been published validly. After a careful revision of all the names that have been used for the plants of this group, we have not found any validly published available as a substitute the invalid *O. squarrosus*, and it is therefore necessary to propose a new name. We could have attempted to maintain the name ‘*O. squarrosus*’ associated with the Latin description given here, but, on studying the original material of Saltmann deposited in G and P, correspondingly selected as neotype and isoneotype by Bolliger (1996: 148), we have seen that these materials correspond to the closely related taxon *O. foliosus* Pérez Lara (‘*O. squarrosus* subsp. *foliosus*’) and not to ‘*O. squarrosus* s.s.’ (‘*O. squarrosus* subsp. *squarrosus*’). Although it is not possible to appreciate the colour of the corolla in these herbarium specimens, in our opinion, the unmistakable hairiness of the stem leaves us in no doubt. Owing to this problem, we have preferred not to preserve this name.

There is a further name related to this case, *Euphrasia recurvata*, proposed by Schousboe directly and only on a herbarium label for plants collected in the surroundings of Tangier. However, owing to the hairiness, this original material of Schousboe (deposited in P) would again correspond to *O. foliosus* and not to *O. squarrosus* s.s., such that it does not seem advisable to maintain the epithet *recurvata* to refer to the plants that Bolliger includes under ‘*O. squarrosus* subsp. *squarrosus*’.

With regard to taxonomic issues, in our opinion *O. bolligeri* (‘*O. squarrosus* subsp. *squarrosus*’) and *O. foliosus* (‘*O. squarrosus* subsp. *foliosus*’) should be considered as independent species, as the latter is clearly differentiated from the former in that the stem has hairs that are strongly recurved and broadened at the base and there are abundant minute sessile glands (Fig. 1L). In addition, the corolla is bicoloured, with a purple or pink upper lip and a whitish or yellow lower lip, and it is an annual plant. The colour of the corolla and the hairiness of the stem are characters exclusive to *O. foliosus* within the group of *O. purpureus*. Also Valdés (1987: 547) considered *O. foliosus* to be a separate taxonomic unit at the species rank. It is a taxon endemic to the southern extreme of the Iberian Peninsula (province of Cádiz and west of the province of Málaga) and north-west of Morocco (around Tangier); that is, it is found at the westernmost edge of the area of distribution of the whole group.

Accordingly, in our opinion, the group should comprise four species, one with two subspecies. Below, we offer a dichotomous key for the five taxa and a summary of the nomenclature and chorology of the taxa most closely related to *O. bolligeri*. These results are the combined product of the revision of material and taxonomic studies performed by us and the data provided by Bolliger (1996).

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**KEY TO THE *ODONTITES PURPUREUS* GROUP**

<table>
<thead>
<tr>
<th>Key</th>
<th>Description</th>
</tr>
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<tbody>
<tr>
<td>1.</td>
<td>Flowers 7.5–11 mm; calyx 4–7 mm; corolla concolorous, purple; annual</td>
</tr>
<tr>
<td>1b.</td>
<td>Flowers 5–7.5(8.5) mm; calyx 2.5–4(4.8) mm; corolla concolorous or bicoloured; annual or suffruticose plant</td>
</tr>
<tr>
<td>2.</td>
<td>Leaves with dense hairs beneath; corolla 8–11 mm</td>
</tr>
<tr>
<td>2b.</td>
<td>Leaves glabrous beneath, with hairs restricted to the margins; corolla 7.5–8.2 mm</td>
</tr>
<tr>
<td>3.</td>
<td>Bracts lanceolate, 5–11 mm in length, 3.5–5.6 times longer than wide, clearly longer than calyx; corolla concolorous, purple; annual</td>
</tr>
<tr>
<td>3b.</td>
<td>Bracts oval-lanceolate, less than 5 mm in length, 2.2–2.9 times longer than wide, nearly always equal to or shorter than calyx; corolla concolorous or bicoloured; annual or suffruticose plant</td>
</tr>
<tr>
<td>4.</td>
<td>Stem with straight or slightly recurved hairs, without or with few minute sessile or subsessile glands; corolla purple or pink; suffruticose plant</td>
</tr>
<tr>
<td>4b.</td>
<td>Stem with strongly recurved hairs and with abundant minute sessile or subsessile glands; corolla bicoloured, with upper lip purple or pink and lower one whitish or yellow; annual</td>
</tr>
</tbody>
</table>

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**Illustration:** Bolliger in Willdenowia 26: 146 (1996).

**Distribution:** Endemic to north-eastern Algeria.


**Illustration:** Bolliger in Willdenowia 26: 146 (1996).

**Distribution:** Endemic to north-eastern Algeria.


**Illustration:** Valdés, Talavera & Galiano (eds.), Fl. Andalucía Occid. 2: 547 (1987).

**Distribution:** Endemic to southern Spain and north-western Morocco.

**Karyology**

The number of chromosomes for the taxa within this group of *Odentites* remained unknown until Bolliger (1996: 55) first published $2n = 24$ for *O. squarrosus*. No voucher was indicated by this author, and so we cannot check to which species the studied material belongs. Moreover, no locality of provenance of the material was indicated.

We counted the number of chromosomes in plants from four populations belonging to *O. bolligeri* and two to *O. foliosus*; in the case of the latter species, these are the only two populations currently known on the Iberian Peninsula.

For *O. bolligeri*, the chromosome numbers obtained are $2n = 22$ (Fig. 2), $2n = 24$ (Figs 3, 4), $2n = 26$ (Fig. 5) and $n = 11$ (Fig. 6). The diploid counts were carried out on mitotic prometaphases and metaphases of cells of the gynoecium, and the haploid count in microsporocytes. The diploid numbers $2n = 22, 24$ were each found in two populations, and the number $2n = 26$ in one population. The most frequent number was $2n = 22$ (three counts), followed by $2n = 24, 26$ (two counts). No anomaly was observed in the different stages of meiosis studied.

In *O. foliosus*, we observed the same diploid numbers as in the previous species, that is $2n = 22, 24, 26$ (Fig. 7), although no haploid count was obtained. The diploid numbers $2n = 24, 26$ were found in a population from Barbate, whereas, in the population from Manilva, a single chromosome number was found: $2n = 22$.

The karyotypes of *O. bolligeri* and *O. foliosus* are similar with regard to several characters: both show a predominance of small, metacentric chromosomes, a varying number of telocentric chromosomes (2–6) and a similar length range of the chromosomes. There are no significant differences with regard to overall size of the chromosomes; in *O. bolligeri* they range from 0.7 to 2 μm and in *O. foliosus*, from 0.4 to 1 μm (measurements carried out in cells with $2n = 26$). However, they differ in that the number of chromosomes smaller than 1 μm in *O. foliosus* (20 chromosomes) is much larger than that in *O. bolligeri* (eight chromosomes), such that the karyotype of *O. bolligeri* ($A_2 = 2.5$) is more asymmetric than that of *O. foliosus* ($A_2 = 0.4$).

**SELECTED MATERIAL**

(Asterisks indicate populations used for karyological studies.)

**Odontites bolligeri**

**ALGERIA.** Oran, Vallon de Noiseux, broussailles, 16.x.1910, A. Faure (G 86547); ibid., 24.xi.1912, A. Faure (G 86548, MA 114034). Oran, à Santa-Cruz, broussailles, 13.xi.1939, A. Faure (BCF 30845, G 86549, MA 114035). Oran, Djebel Santo, ix.1848, Munby (C). Oran, iv.1849, Reuter (G 86551). Oran, Sidi-bel-Abbès, 21.ix.1874, A. Warion (G 86546). Oran, montagne des Lions, 10.xii.1852, Balansa (G 86543). **MOROCCO.** Ker-Ker, 600–1000 m, 14.vi.1933, Sennen et Mauricio (MA 114033). Tafersit, ad pedem
Odontites discolor subsp. discolor
ALGERIA. Souk-Ahras, xi.1873, Reboud (MPU 5743, lectotype, Photo!).

Odontites discolor subsp. ciliatus
ALGERIA. Bône, Fradin (MPU 5742, lectotype, Photo!).

the project Flora iberica VII (CGL2005-05471-C04-03/BOS and CGL2005-05471-C04-01).

REFERENCES


