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Micromorphological Studies on Seeds of *Orobanche* Species from the Iberian Peninsula and the Balearic Islands, and Their Systematic Significance

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• *Background and Aims* Previous research has made clear the intrinsic taxonomic difficulties in identifying species in the genus *Orobanche*. The aim of this study, therefore, was to investigate the systematic utility of seed characteristics.
• *Methods* Light and scanning electron microscopy was used to examine the seeds of 33 taxa of *Orobanche* from the Iberian Peninsula and the Balearic Islands.
• *Key Results* Characters such as size, shape and ornamentation of the seeds were not found to be very useful in differentiation of taxa; however, other characters of the epidermal seed coat cells proved to be very helpful in this respect. Ornamentation of the periclinal walls could be used to discriminate four morphological types. Other features related to the anticlinal walls of the cells, such as thickness, presence/absence of a narrow trough, or relative depth, all contributed to the characterization of a large number of species.
• *Conclusions* The usefulness of micromorphological studies on seeds of *Orobanche* in relation to differentiating taxa is demonstrated, and a key is provided to distinguish species or groups of species.

Key words: *Orobanche*, seed, seed-coat, morphology, systematic significance, SEM.

INTRODUCTION

Orobanche is a large genus mainly distributed throughout subtropical and temperate regions of the northern hemisphere, with the Mediterranean region one of the most important centres of diversity. *Orobanche* is a genus with approx. 100 species, 30–35 % of which are present in the Iberian Peninsula and the Balearic Islands. Thirty-two taxa were recognized by Foley (2001), although the floristic contributions of Pujadas and Lora González (1995, 1996, 1997), Pujadas *et al*. (1997), Pujadas (1997, 2000), Pujadas and Gómez (2000) have indicated that there are 34 taxa (Pujadas, 2002).

The genus *Orobanche* is divided into two well-delimited sections, *Trionychon* Wallr. and *Orobanche* L., traditionally recognized by authors such as Beck von Mannagetta (1930) and Chater and Webb (1972), and more recently by Foley (2001) and Pujadas (2002). The most important differential characteristics of the section *Trionychon* are branched stems, bracteolate flowers, an entire and campanulated calyx, a blue or purple corolla, white anthers, and the stigma usually white. This contrasts with the single stems, non-bracteolate flowers, calyx divided into two lateral segments, corolla white, yellow, brown, amethyst or red, anthers yellow, brown-grey or greyish, and stigma yellow, orange, red or purple of the section *Orobanche* (Pujadas, 2002). From a molecular point of view, according to Schneeweiss (2001), the separation of both sections is pronounced, and supports the treatment of the section *Trionychon* as a separate genus *Phelipanche*, as previously stated by Teryokhin (1991, 1997).

The Orobanchaceae is a family of holoparasitic plants, which has been traditionally considered to be closely related to the Scrophulariaceae. Some authors, like Stace (1985), have pointed out the absence of a clear separation between the families, and have highlighted the relationship between hemiparasitic and holoparasitic taxa of both families due to the continuity of their morphological features (Kuijt, 1969; Weber, 1980). Previously, Boeshore (1920) had carried out a study concerning morphological continuity between the Scrophulariaceae and Orobanchaceae based on different characters such as roots, leaves or inflorescences in order to delimit these families. Other authors such as Hutchinson (1969), Takhtajan (1980) and Cronquist (1981) consider Orobanchaceae as a different and more advanced family, probably originating from the subfamily Rhinantoideae of the Scrophulariaceae. Later work by Teryokhin (1997) considered it as a subfamily Orobanchoideae within the Scrophulariaceae. Recent molecular phylogenetic research on the Scrophulariaceae and Orobanchaceae has provided new data about their delimitation. Young *et al*. (1999) suggest that the traditional Orobanchaceae, the hemiparasitic Scrophulariaceae, and the *Lindenbergia* genus should make up the family Orobanchaceae. Finally, Olmstead *et al*. (2001) suggest that this complex should be subdivided into at least five different families and that the Scrophulariaceae parasites should be included within the Orobanchaceae.

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The difficulty in identifying species in the genus *Orobanche* has been shown by the research of various authors. Among these, we can highlight the palinology carried out by Minkin (1987), Minkin and Eshbaugh (1989) and Abu Sbaih *et al*. (1994), and the biomolecular studies by Schneeweiss (2001), Benharrat *et al*. (2001), Román *et al*. (2003). The intrinsic taxonomic difficulties of the genus *Orobanche* are further increased by the fact that important differential characters are observed only with difficulty, or not at all, on dried specimens. With regard to seeds, there are several studies that analyse different aspects such as their chemical composition (Velasco *et al*., 2000), observations through fluorescence microscopy techniques (Joel, 1987*a*), or research with scanning electron microscopy (SEM; Abu Sbaih and Jury, 1994*a*, *b*; Musselman and Mann, 1976; Joel, 1987*b*, 1988*a*, *b*; Deif *et al*., 2000).

The use of SEM allows for the observation of structures which would be difficult by other means, and some authors have highlighted the importance of this technique for the study of seed-coats, especially for those families in which identification is complicated, such as the Portulacaceae (Danin *et al*., 1979) and, particularly, the Scrophulariaceae (Canne, 1979; Sutton, 1988; Juan *et al*., 1994, 1997, 1999, 2000), where features of seed morphology have been widely used to distinguish the different taxa or to find affinities between them.

The aim of the present study was to illustrate the role of seed features in the identification of species of *Orobanche* in the Iberian Peninsula and the Balearic Islands as an aid to agriculture by identifying soil-born pathogens, and to relate such characters to the systematics of the group.

MATERIALS AND METHODS

Seed morphology was studied in 33 taxa of the *Orobanche* L. genus from the Iberian Peninsula and the Balearic Islands. For every taxon, specimens from the populations within the study area were sampled, except for *O. teucrii* and *O. reticulata*. In these cases, it being impossible to obtain samples from Iberian populations, specimens from France (courtesy of the Herbarium at the Pirenaic Institute of Ecology, CSIC, Jaca) and from Germany, respectively, were used. For *O. artemisiae-campestris*, which is present in the Iberian Peninsula, it proved impossible to find seeds for analysis.

The study was based on dry herbarium specimens from the Department of Sciences and Agronomy and Forestry Resources of the University of Córdoba (COA), although some of the samples used came from specimens provided by the herbaria of the Aranzadi Science Society in San Sebastián (ARAN) (*O. caryophyllaceae*), by the Department of Science and Natural Resources at the University of Alicante (ABH) (*O. olbiensis*) and by the Pirenaic Institute of Ecology (JACA) (*O. teucrii*). Collectors and localities are shown in the Appendix.

Data on the width and length of seeds is based on the measurement of 30–150 seeds per taxon, by means of direct observation under optical microscopy.

For scanning electron microscopy, dry seeds were mounted directly on stubs using double-sided adhesive tape and coated with gold/palladium in a sputter coater. Morphological observations were made using a Philips XL-30 microscope of the Electronic Microscopy Service of the University of Seville.

The terminology of seed-coat surface sculpturing basically follows Stearn (1992) and Font Quer (1993). The abbreviations of the authorities of plant names follow the standard of Brummit and Powell (1992), and acronyms of the herbariums follow Holmgren *et al*. (1990).

RESULTS

Seeds of *Orobanche* are extremely small, being less than 1 mm in size, with a wide variety of shapes (ellipsoid, oblongoid, ovoid, globose, trigonous or tetragonous) and a terminal funicular attachment. The seed coat is reticulated with polygonal cells, which range from more or less isodiametric to tangentially elongated, being sometimes irregular. *Orobanche* seeds usually have a smooth membranous outer periclinal wall, although they can sometimes have a fibrillar aspect due to epicuticular waxes. Both kinds collapse on the inner periclinal wall, thus showing the structure of the latter, which is of very changeable aspect (perforate, granulate, rugulose, etc.).

Observations made using scanning electron microscopy indicated that there are four morphological seed types, recognizable as listed in Table 1.

Type I

Seeds 0·28–0·47 × 0·17–0·30 mm, ellipsoid to ovoid shape; very dark brown. Seed-coat surface of isodiametric cells, 0·06–0·11 × 0·04–0·06 mm; anticlinal walls with remarkably deep thickening at the vertex, and with a narrow trough marking the wall junctures between cells; outer periclinal walls smooth, impeding vision of the inner one (Fig. 1A–C).

Among the taxa examined, only seeds of *O. rapum-genistae* have this seed type.

Type II

Seeds 0·27–0·57 × 0·14–0·41 mm, ovoid, oblongoid, ellipsoid, trigonous, tetragonous or subglobose; dark brown to greyish. Epidermal seed-coat of polygonal ± isodiametric cells or tangentially elongated 0·06–0·2 × 0·04–0·10 mm, with anticlinal walls from slightly to remarkably deep, evenly or unevenly thickened, and with a narrow trough

TABLE 1. *Four morphological seed types of* Orobanche *as indicated by observations made using scanning electron microscopy*

1.	Epidermal cells with fibrillar outer periclinal wall	Type IV
1′.	Epidermal cells with smooth outer periclinal wall	2
2.	Outer periclinal walls impede vision of the inner one	Type I
2′.	Outer periclinal walls allow vision of the inner one	3
3.	Inner periclinal wall perforate	Type II
3′.	Inner periclinal wall granulate or rugulose	Type III

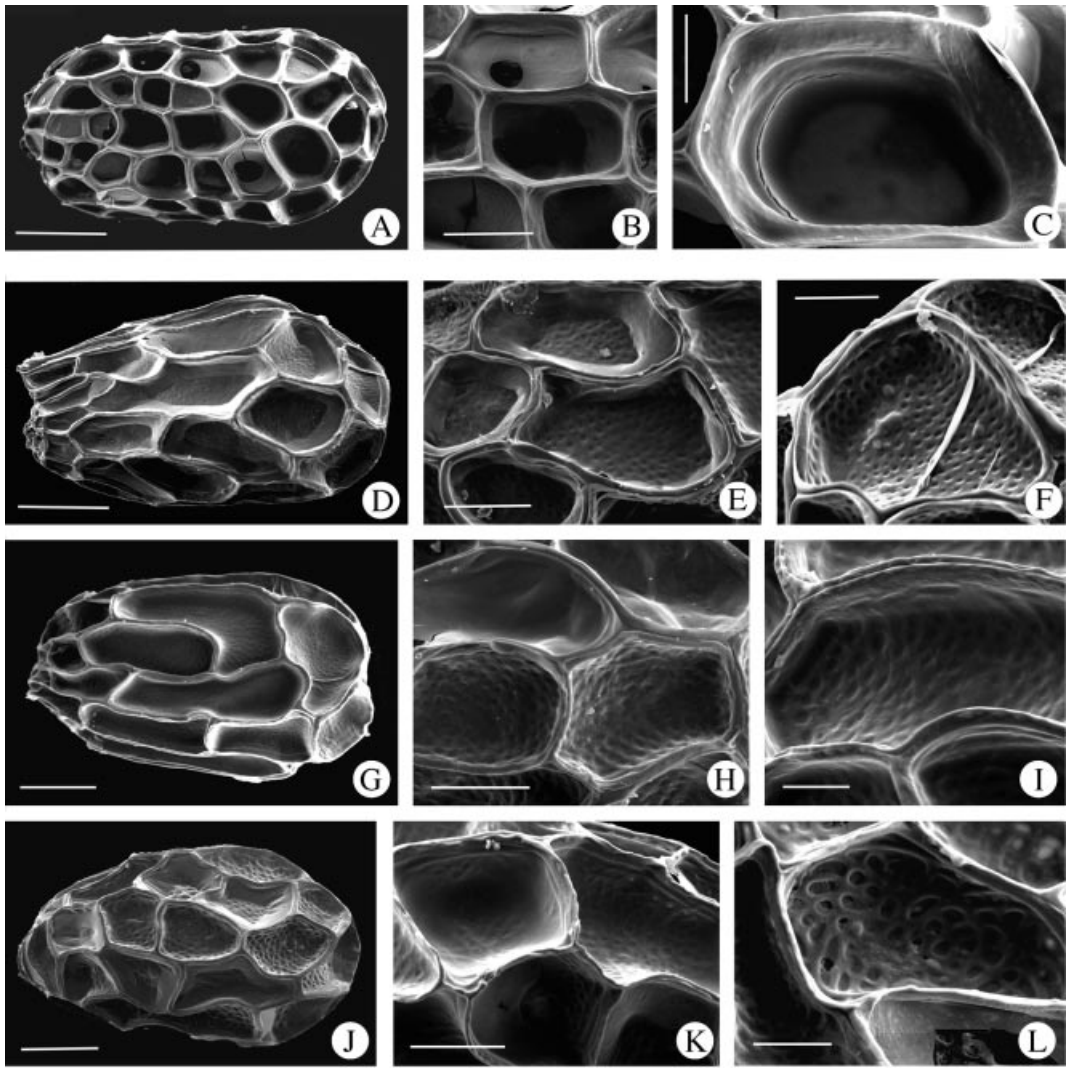

FIG. 1. Scanning electron micrographs of *Orobanche* seeds. (A–C) Type I, *O. rapum genistea*. (D–L) Type II. (D–G) Subtype II_A: (D) *O. alba*, (E) *O. reticulata* subsp. *reticulata*, (F) *O. minor*, (G) *O. calendulae*. (H, I) Subtype II_B: (H) *O. elatior* subsp. *icterica*, (I) *O. amethystea*. (J–L) Subtype II_C: (J) *O. laserpitii-sileris*, (K, L) *O. clausonis*. Scale bars = 100 μm (A, D, G, J); 50 μm (B, E, H, K); 20 μm (C, F, I, L).

marking the wall junctures between cells, sometimes just evident at the vertex; inner periclinal wall perforate (Fig. 1D–L; Table 2).

The differences observed in the diameter of the perforations of the inner periclinal wall suggest separation into three subtypes, as shown in Table 3.

Subtype II_A. Epidermal seed coat cells more or less isodiametric to tangentially elongated, anticlinal walls of medium depth and evenly thickened, with a narrow trough that is noticeable all around the edge of the cells or just at the vertices. Inner periclinal wall of epidermal seed coat cells with perforations of smaller diameter than the thickness of the walls that separate them, sometimes with a small central mammilla. This subtype includes *O. alba*, *O. ballotae*, *O. calendulae*, *O. crenata*, *O. minor* and *O. reticulata* subsp. *reticulata.*

Subtype II_B. Epidermal seed coat cells more or less isodiametric to tangentially elongated, anticlinal walls very deep or of medium depth and evenly thickened with a narrow trough that is evident all around the edge of the cells or just at the vertices. Inner periclinal wall of epidermal seed coat cells with perforations of similar diameter to the thickness of the walls that separate them. This subtype includes *O. amethystea*, *O. caryohyllaceae*, *O. cernua*, *O. crinita*, *O. elatior* subsp. *icterica*, *O. foetida*, *O. gracilis*, *O. hederae*, *O. montserratii* and *O. teucrii*.

Subtype II_C. Epidermal seed coat cells more or less isodiametric, slightly to very deep and anticlinal walls evenly or unevenly thickened, with a narrow trough that is noticeable just at the vertices of the cells. Inner periclinal wall of seed coat cells with perforations of larger diameter than the thickness of the walls that separate them. This

TABLE 2. *Relation of characters studied for species included in Type II (II_A, II_B, II_C)*

Seed subtype	Taxon	Seed shape	Seed size (mm)	Cell shape	Depth of anticlinal walls	Thickness of anticlinal walls	Narrow trough
II_A	*O. alba*	Oblongoid to ellipsoid	0.29–0.46 × 0.17–0.28	Isodiametric to tangentially elongated	Medium (Fig. 1D)	Even	Evident all around the edge
	O. ballotae	Ovoid	0.29–0.43 × 0.19–0.29	Isodiametric	Medium	Even	More evident at the vertices
	O. calendulae	Ovoid	0.30–0.41 × 0.18–0.27	Isodiametric	Medium (Fig. 1G)	Even	More evident at the vertices
	O. crenata	Ellipsoid	0.28–0.48 × 0.19–0.30	Isodiametric	Medium	Even	Evident all around the edge
	O. minor	Oblongoid to ellipsoid	0.27–0.36 × 0.15–0.24	Isodiametric to tangentially elongated	Medium (Fig. 1F)	Even	Evident all around the edge
	O. reticulata subsp. *reticulata*	Ellipsoid to ovoid	0.32–0.48 × 0.18–0.31	Isodiametric	Medium (Fig. 1E)	Even	More evident at the vertices
II_B	*O. amethystea*	Ovoid to ellipsoid	0.27–0.43 × 0.17–0.28	Isodiametric	Medium (Fig. 1I)	Even	More evident at the vertices
	O. caryophyllaceae	Ovoid to ellipsoid	0.25–0.47 × 0.16–0.30	Isodiametric	Medium	Even	More evident at the vertices
	O. cernua	Oblongoid to ovoid	0.30–0.50 × 0.17–0.24	Isodiametric to irregular	Medium	Even	Evident all around the edge
	O. crinita	Ovoid	0.24–0.40 × 0.14–0.23	Tangentially elongated	Medium	Even	More evident at the vertices
	O. elatior subsp. *icterica*	Ellipsoid to ovoid	0.30–0.45 × 0.20–0.27	Isodiametric	Medium (Fig. 1H)	Even	More evident at the vertices
	O. foetida	Ellipsoid to ovoid	0.27–0.39 × 0.14–0.23	Isodiametric to tangentially elongated, irregular	Medium	Even	Evident all around the edge
	O. gracilis	Subglobose to ovoid	0.31–0.49 × 0.17–0.31	Isodiametric	Remarkable	Even	More evident at the vertices
	O. hederae	Ovoid – oblongoid to ellipsoid	0.33–0.48 × 0.20–0.31	Isodiametric to tangentially elongated	Medium to remarkable	Even	Evident all around the edge
	O. montserratii	Ovoid to subglobose	0.31–0.52 × 0.20–0.40	Isodiametric	Remarkable	Even	Evident all around the edge
	O. teucrii	Ellipsoid to subglobose	0.33–0.47 × 0.22–0.30	Isodiametric	Medium	Even	Evident all around the edge
II_C	*O. clausonis*	Ellipsoid to ovoid	0.30–0.50 × 0.16–0.28	Isodiametric	Remarkable (Figs. 1K, L)	Uneven	More evident at the vertices
	O. haenseleri	Trigonous or tetragonous	0.29–0.57 × 0.18–0.41	Isodiametric	Medium to slight	Even	More evident at the vertices
	O. laserpitii-sileris	Ovoid to oblongoid	0.25–0.46 × 0.16–0.29	Isodiametric	Medium (Fig 1J)	Even	More evident at the vertices

subtype includes *O. clausonis*, *O. haenseleri* and *O. laserpitii-sileris*.

Type III

Seeds 0·25–0·50 × 0·16–0·30 mm, ovoid, oblongoid or ellipsoid, dark brown. Epidermal seed coat made up of polygonal, more or less isodiametric, tangentially elongated, or irregular cells 0·07–0·20 × 0·03–0·07 mm; anticlinal walls medium to very deep and evenly thickened, with a narrow trough marking the wall junctures between cells, noticeable all around the edge of the cells, inner periclinal walls granulate or rugulose (Fig. 2A–C, Table 4). This type includes *O. cumana*, *O. densiflora* and *O. santolinae*.

Type IV

Seeds 0·28–0·61 × 0·17–0·41 mm, ovoid, oblongoid, globose to ellipsoid, light or dark grey-brown. Epidermal seed coat made up of cells that are polygonal, more or less isodiametric to tangentially elongated, or irregular cells 0·07–0·15 × 0·03–0·08 mm; anticlinal walls slightly to very deep, evenly or unevenly thickened, with a narrow trough marking the wall junctures between cells more evident at the vertices; outer periclinal walls fibrillar, through which the

TABLE 3. *Three subtypes of Type II seeds as indicated by differences observed in the diameter of the perforations of the inner periclinal wall*

1.	Inner periclinal walls of epidermal seed coat cells with perforations smaller in diameter than the thickness of the walls that separate them; a small central mammilla sometimes present on cells	Subtype II_A
1′.	Inner periclinal walls of epidermal seed coat cells with perforations similar in diameter or superior to the thickness of the walls that separate them; small central mammilla absent on cells	2
2.	Inner periclinal walls of epidermal seed coat cells with perforations similar in diameter to the thickness of the walls that separate them	Subtype II_B
2′.	Inner periclinal walls of epidermal seed coat cells with perforations larger in diameter than the thickness of the walls that separate them	Subtype II_C

reticulate inner ones can sometimes be seen (Fig. 2D–I, Table 4).

The appearance of periclinal walls suggests separation into two subtypes:

Subtype IV_A: inner periclinal walls hidden by the outer.

Subtype IV_B: reticulate inner periclinal wall visible through the outer.

Subtype IV_A. Seed shape from ellipsoid to ovoid. Epidermal seed coat cells with inner periclinal wall hidden by fibrillar outer periclinal wall; anticlinal walls of slight or medium depth. This subtype includes *O. arenaria*, *O. latisquama*, *O. nana* and *O. ramosa*.

Subtype IV_B. Seeds oblongoid, ellipsoid, ovoid to globose. Epidermal seed coat with reticulate inner periclinal wall visible through the fibrillar outer periclinal wall; anticlinal walls slightly to very deep. This subtype includes *O. lavandulaceae*, *O. mutelii*, *O. olbiensis*, *O. purpurea*, *O. schultzii* and *O. tunetana*.

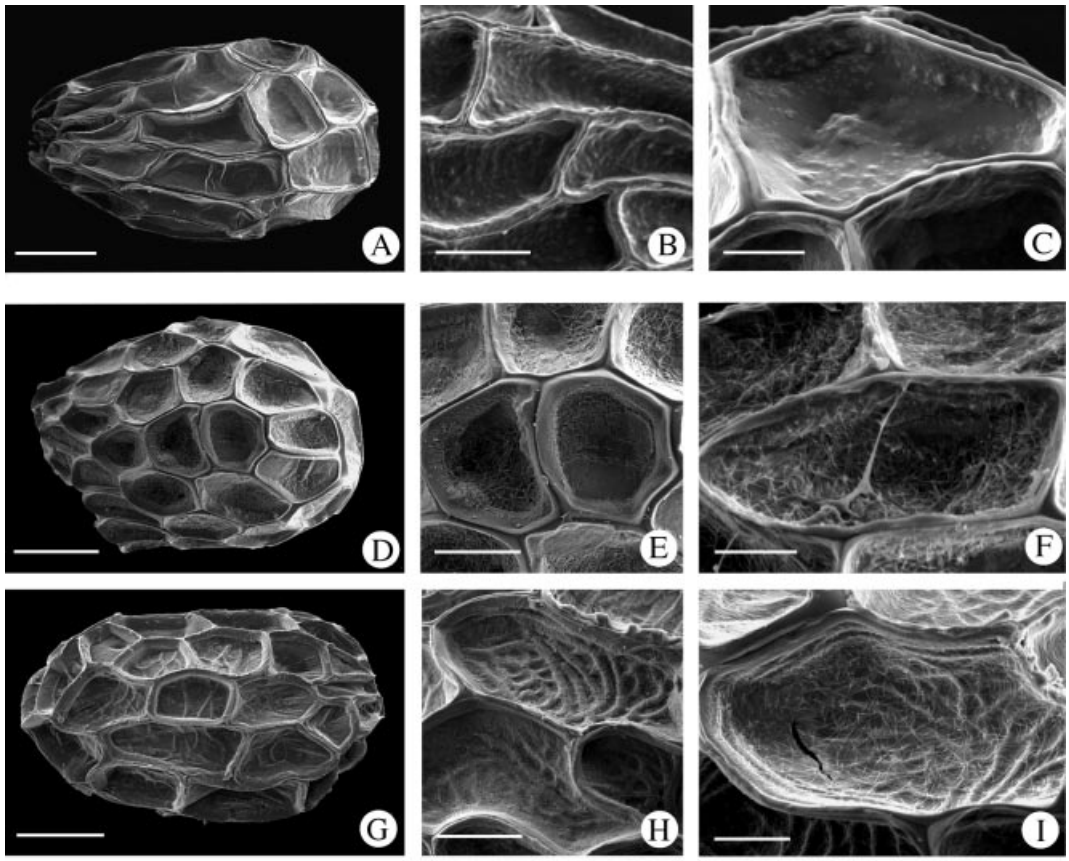

FIG. 2. Scanning electron micrographs of *Orobanche* seeds. (A–C) Type III: (A) *O. densiflora*, (B) *O. cumana*, (C) *O. santolinae*. (D–I) Type IV. (D–F) Subtype IV_A: (D, E) *O. latisquama*, (F) *O. ramosa*. (G–I) Subtype IV_B: (G) *O. purpurea*, (H) *O. schultzii*, (I) *O. lavandulacea*. Scale bars = 100 μm (A, D, G); 50 μm (B, E, H); 20 μm (C, F, I).

TABLE 4. *Relation of characters studied for species included in Types III and IV (IV_A, IV_B)*

Seed type or subtype	Taxon	Seed shape	Seed size (mm)	Cell shape	Depth of anticlinal walls	Thickness of anticlinal walls	Narrow trough
III	*O. cumana*	Oblongoid	0·36–0·50 × 0·16–0·25	Tangentially elongated or irregular	Medium (Fig. 2B)	Even	Evident all around the edge
	O. densiflora	Ovoid to ellipsoid	0·27–0·43 × 0·17–0·27	Isodiametric to tangentially elongated	Medium (Fig. 2A)	Even	Evident all around the edge
	O. santolinae	Ellipsoid to ovoid	0·26–0·48 × 0·16–0·29	Isodiametric to irregular	Remarkable (Fig. 2C)	Even	Evident all around the edge
IV_A	*O. arenaria*	Ovoid to ellipsoid	0·35–0·58 × 0·23–0·38	Isodiametric	Medium	Even	More evident at the vertices
	O. latisquama	Ellipsoid to ovoid	0·30–0·45 × 0·18–0·28	Isodiametric	Slight (Figs. 2D, E)	Even	Evident all around the edge
	O. nana	Ovoid to ellipsoid	0·29–0·51 × 0·17–0·30	Isodiametric to irregular	Medium	Even	More evident at the vertices
	O. ramosa	Ellipsoid to ovoid	0·33–0·52 × 0·19–0·33	Isodiametric	Medium (Fig. 2F)	Uneven	More evident at the vertices
IV_B	*O. lavandulacea*	Ovoid to oblongoid	0·32–0·52 × 0·18–0·38	Isodiametric	Remarkable (Fig. 2I)	Uneven	More evident at the vertices
	O. mutelii	Ovoid	0·35–0·53 × 0·21–0·35	Isodiametric to irregular	Remarkable	Even	More evident at the vertices
	O. olbiensis	Ellipsoid to ovoid	0·28–0·61 × 0·17–0·41	Isodiametric	Slight	Uneven	More evident at the vertices
	O. purpurea	Ellipsoid to ovoid	0·36–0·48 × 0·19–0·31	Isodiametric	Medium (Fig. 2G)	Even	More evident at the vertices
	O. schultzii	Ellipsoid to ovoid	0·39–0·57 × 0·26–0·38	Isodiametric to tangentially elongated	Remarkable (Fig. 2H)	Uneven	More evident at the vertices
	O. tunetana	Ellipsoid to globose	0·28–0·37 × 0·22–0·30	Isodiametric	Medium	Even	More evident at the vertices

DISCUSSION

The results obtained confirm the usefulness of seed characters for the identification of most of the species studied, and highlight the division of the genus into two sections (*Trionychon* and *Orobanche*), as has been traditionally recognized (Beck von Mannagetta, 1930; Chater and Webb, 1972; Foley, 2001; Pujadas, 2002).

Within each taxon, the size of the seeds is very variable. This is the reason why this character is not very useful for distinguishing groups of species below the category section, such as the 'grex' established by Beck von Mannagetta (1930). However, at species level, seed size helps to identify some taxa such as *O. reticulata*, *O minor*, *O. nana* and *O. arenaria*. Seed shape is also a variable character, ranging from oblongoid, ellipsoid to ovoid, although they are sometimes globose or subglobose. This character is related to its relative position in the capsule, as in the case of the Scrophulariaceae (Juan *et al*., 2000). The most extreme case is *O. haenseleri*, whose seeds allow the separation of this species from the rest of the taxa under study.

As far as ornamentation is concerned, our results agree with other authors (Ungurean, 1986; Joel, 1987*a*, *b*; Abu Sbaih and Jury, 1994*a*, *b*), showing that the genus *Orobanche* has reticulate seeds, although Teryokhin (1997) described them as alveolate due to invagination of the thin outer wall of the epidermal seed coat cells. The periclinal walls of the epidermal seed coat cells are of particular taxonomic interest, especially the inner wall, which remains intact since it is lignified. However, Abu Sbaih and Jury (1994*a*) pointed out that this wall is perforate-reticulate in all the species that they studied. Therefore, they considered the outer wall to be of greater interest as it allowed them to distinguish four groups of species.

In the present study, the epidermal seed coat cells permitted the discrimination of four morphological types, based on observations of both inner and outer periclinal walls. Among the four established types, Type IV corresponds to the section *Trionychon*, except for *O. latisquama*, whereas Types I, II and III are included in section *Orobanche*. The differences found in the periclinal walls of the epidermal cells support the morphological differentiation of the taxa of both sections, thus corroborating the taxonomic separation that Beck von Mannagetta (1890, 1930) established and which has been noted by other authors, including Polo (1988), Valdés and Díez (1990), and Abu Sbaih *et al*. (1994) based on pollen data; Andary (1994) in a chemotaxonomical study; and Velasco *et al*. (2000) in their study concerning fatty acid and tocochromanol compositions of seeds. However, it has not been possible to find any correlation between the types or subtypes established in the present study and the sections or groups (grex) based on the vegetative characters of the different taxa established by

TABLE 5. *Key to Iberian Peninsula and the Balearic Islands species of* Orobanche *based on seed features*

1.	Epidermal seed coat cells with smooth outer periclinal walls	2
1′.	Epidermal seed coat cells with fibrillar outer periclinal walls	20
2.	Outer periclinal walls impede vision of inner ones; anticlinal walls thickening at the vertices	*O. rapum-genisteae*
2′.	Outer periclinal walls allow vision of inner ones; anticlinal walls of even or uneven thickness	3
3.	Epidermal seed coat cells with perforate inner periclinal wall	4
3′.	Epidermal seed coat cells with rugulose or granulate inner periclinal wall	18
4.	Cells of inner periclinal wall with a small central mammilla	5
4′.	Cells of inner periclinal wall without a central mammilla	6
5.	Anticlinal walls with a narrow trough that is more evident at the vertices; seeds 0·32–0·48 mm	*O. reticulata* subsp. *reticulata*
5′.	Anticlinal walls with a narrow trough that is visible all around the edge; seeds 0·27–0·36 mm	*O. minor*
6.	Inner periclinal wall of epidermal seed coat cells with perforations of smaller diameter than the thickness of the walls that separate them	7
6′.	Inner periclinal wall of epidermal seed coat cells with perforations of diameter similar to or greater than the thickness of the walls that separate them	9
7.	Epidermal seed coat cells in the mid and insertion areas tangentially elongated and isodiametric at the opposite end	*O. alba*
7′.	Epidermal seed coat cells isodiametric on the entire surface	8
8.	Anticlinal wall junctures with a narrow trough that is visible all around the edge of the cells	*O. crenata*
8′.	Anticlinal wall junctures with a narrow trough that is evident at the vertices of the cells	*O. ballotae*, *O. calendulae*, *O. reticulata* subsp. *reticulata*
9.	Perforations with a similar diameter to the thickness of the wall that separates them	10
9′.	Perforations with a diameter which is larger than the thickness of the separating wall	16
10.	Epidermal seed coat cells with anticlinal walls of remarkable depth	11
10′.	Epidermal seed coat cells with anticlinal walls of medium depth	13
11.	Anticlinal wall junctures with a narrow trough that is evident at the vertices of the cells	*O. gracilis*
11′.	Anticlinal wall junctures with a narrow trough that is visible all around the edge of the cells	12
12.	Tangentially elongated epidermal seed coat cells, whose size decreases at the area of insertion; seeds ovoid to oblong	*O. hederae*
12′.	Isodiametric epidermal seed coat cells on the entire surface; seeds ovoid to subglobose	*O. montserratii*
13.	Anticlinal wall junctures with a narrow trough that is visible all around the edge of the cells	14
13′.	Anticlinal wall junctures with a narrow trough that is evident at the vertices of the cells	15
14.	Epidermal seed coat cells tangentially elongated which and narrow and decrease at the area of insertion	*O. foetida*, *O. hederae*
14′.	Epidermal seed coat cells more or less isodiametric or irregular	*O. cernua*, *O. elatior* subsp. *icterica*, *O. teucrii*
15.	Epidermal seed coat cells tangentially elongated	*O. crinita*
15′.	Epidermal seed coat cells more or less isodiametric	*O. amethystea*, *O. caryophyllaceae*
16.	Epidermal seed coat cells with anticlinal walls of remarkable depth and unevenly thickened	*O. clausonis*
16′.	Epidermal seed coat cells with anticlinal walls of slight or medium depth and evenly thickened	17
17.	Seeds trigonous to tetragonal	*O. haenseleris*
17′.	Seeds ovoid to oblongoid	*O. laserpitii-sileris*
18.	Epidermal seed coat cells with anticlinal walls of remarkable depth	*O. santolinae*
18′.	Epidermal seed coat cells with anticlinal walls of medium depth	19
19.	Epidermal seed coat cells tangentially elongated or irregular; seeds oblongoid	*O. cumana*
19′.	Epidermal seed coat cells more or less isodiametric at the vertices, tangentially elongated over the rest of the surface; seeds ovoid to ellipsoid	*O. densiflora*
20.	Inner periclinal wall hidden by the outer one	21
20′.	Reticulate inner periclinal wall visible through the outer one	24
21.	Epidermal seed coat cells with anticlinal walls of slight depth, and a narrow trough that is visible all around the edge of the cells	*O. latisquama*
21′.	Epidermal seed coat cells with anticlinal walls of medium depth and a narrow trough that is evident just at the vertices	22
22.	Epidermal seed coat cells with anticlinal walls unevenly thickened	*O. ramosa*
22′.	Epidermal seed coat cells with anticlinal walls evenly thickened	23
23.	Seeds <0·40 mm; epidermal seed coat cells isodiametric to irregular	*O. nana*
23′.	Seeds ⩾0·40 mm; epidermal seed coat cells isodiametric	*O. arenaria*
24.	Epidermal seed coat cells with anticlinal walls of slight depth; seeds light grey-brown	*O. olbiensis*
24′.	Epidermal seed coat cells with anticlinal walls of medium or remarkable depth; seeds dark grey-brown	25
25.	Epidermal seed coat cells with anticlinal walls of medium depth	*O. tunetana*, *O. purpurea*
25′.	Epidermal seed coat cells with anticlinal walls of remarkable depth	26
26.	Anticlinal walls evenly thickened	*O. mutelii*
26′.	Anticlinal walls unevenly thickened	*O. lavandulaceae*, *O. schultzii*

Beck von Mannagetta (1930), or on the results of the recent molecular analyses by Schneeweiss (2001), Benharrat *et al*. (2001) and Román *et al*. (2001, 2003).

Type I, which includes *O. rapum-genistae* (section *Orobanche*), is clearly separate from the other three established types because the epidermal cells present a smooth outer periclinal wall, which impedes vision of its inner one. Previously, Andary (1994) had already found morphological differences in the seeds of this taxon when comparing them with those of other species in the section *Orobanche*. In a phylogenetic study carried out on 20 Andalusian *Orobanche* taxa belonging to both sections, Román *et al*. (2003) showed this species (*O. rapum-genistae*) as the most different (with a distance of 0·864). Its genetic and morphological separation in relation to the rest of the species of the section *Orobanche* is therefore obvious.

Type II (section *Orobanche*), which shows the epidermal seed coat cells with perforate inner periclinal wall that are visible through the smooth outer periclinal wall, includes a greater number of species. Abu Sbaih and Jury (1994*a*) observed that in four species of the section *Orobanche* (*O. al*ba, *O. cernua*, *O. crenata* and *O. minor*), which were also analysed in our study, the outer wall is perforate. Moreover, it has been observed that within this group the diameter of such perforations on the inner wall vary amongst species, thus allowing for the distinction of three separate subgroups. This character has previously been used in species of the section *Trionychon* by Ungurean (1986), who distinguished two groups: one with numerous and small perforations, and the other with scarce, large ones. We agree with this author that the thickening of the inner wall gives seeds their reticulate aspect.

In Type III only three species of the section *Orobanche* are included, in which the outer periclinal wall shows a granulated-rugulose inner wall. This pattern has not previously been observed by other authors (Ungurean, 1986; Joel, 1987*a*, *b*; Abu Sbaih and Jury, 1994*a*, *b*). Even through they show the same seed type, these species (*O. cumana*, *O. densiflora* and *O. santolinae*) are different from a genetic point of view, as shown in the dendrogram reported by Román *et al*. (2003) in which these species are not clustered together, despite two of them belonging to same grex (grex *Minores* Beck).

Type IV, as has been pointed out above, includes all species belonging to the section *Trionychon* except for *O. latisquama*, which is found in the section *Orobanche* grex *Galeatae* Beck. The separation of *O. latisquama* from the section *Orobanche* has been supported by several authors, some of whom have even placed it under a different genus. Thus, Schultz (1848) includes it in *Boulardia* under the name of *B. latisquama*, whereas others such as Cosson (1848) and Lange (1864) consider it to be within the genus *Ceratocalyx* as *C. macrolepis* and *C. fibriata*, respectively. More recently, Schneeweiss (2001), despite the fact that he includes it once again within the genus *Orobanche* as *O. macrolepis*, regards it as a complex taxon that remains in a middle position between the rest of the taxa in the genus *Orobanche* (section *Trionychon*) and the genus *Cistanche*, thus constituting a separate clade.

This type shows a fibrillar periclinal outer wall, as 'group A' recognized by Abu Sbaih and Jury (1994*a*), who also include within it species of the section *Trionychon*. Previously, some authors such as Teryokhin (1991) have included certain species of the *Orobanche* genus (section *Trionychon*) in the genus *Phelipanche*, the presence of fibrillar outer periclinal walls of epidermal seed coat cells being one of distinctive characters. Results subsequently obtained in the molecular study carried out by Schneeweiss (2001) support this separation. However, in the present work it has been shown that *O. latisquama* (section *Orobanche*) features a fibrillar outer periclinal wall, a character more compatible with the section *Trionychon* or genus *Phelipanches*. Besides, a recent phylogenetic study points out that *O. clausonis*, another species of the section *Orobanche*, is closer to the taxa of the section *Trionychon* than to those of the section *Orobanche* (Román *et al*., 2003). In conclusion, it is clear that there are still several issues to solve.

Regarding the two subgroups, IV_A and IV_B, established on the basis of the visibility of the inner wall of the epidermal cells, these differ from subgroups obtained by other means of analysis (Velasco *et al*., 2000; Schneeweiss, 2001; Román *et al*., 2003) and from the groups proposed by Novopokrovsky and Tzvelev (2000): *Holocladas* Novopokr. and *Pleioclada* Novopokr. (depending on whether they present a simple or a ramificated stem, respectively).

In spite of the homogeneity of the seeds in this genus, pointed out by Abu Sbaih and Jury (1994*a*, *b*), our results have enabled us to produced a key (Table 5) in a similar manner to the one designed by Joel (1988*a*) for six species from Israel. In our key, most taxa have been separated except for six cases where two or three species have been grouped together (*O. foetida* and *O. hederae*; *O. amethystea* and *O. caryophyllaceae*; *O. tunetana* and *O. purpurea*; *O. lavandulaceae* and *O. schultzii*; *O. ballotae*, *O. calendulae* and *O. reticulata*; *O. cernua*, *O. elatior* and *O. teucrii*), even though they are taxa that are not close phylogenetically.

Some of the features of the *Orobanche* seeds, such as the terminal insertion and the reticulate ornamentation, show the similarity that exists between this genus and the hemiparasite species of Scrophulariaceae (Chuang and Heckard, 1972; Musselman and Mann, 1976; Canne, 1980; Juan *et al*., 1998), with which the Orobanchaceae family has some morphological characters in common (see above).

In addition, the results of the present study highlight, to some extent, the importance of the morphology of seeds in relation to dispersal or to the establishment of new plants. Thus, due to their small size, *Orobanche* seeds can be regarded as 'dust-seeds' that are mainly dispersed by wind, and which are frequent in other families with parasitic or hemiparasitic representatives, such as Orchidaceae (van der Pijl, 1982). According to Musselman and Mann (1976), the size of the seeds could be the result of an adaptation of these plants in an attempt to be dispersed through vegetation so as to be as close as possible to the host plant. Similarly, according to Stace (1985), the high production of seeds per

capsule is an adaptation of this type of plant aimed at increasing the probability of finding an appropriate host. The membranous outer periclinal wall of the epidermic cells would favour water absorption, thus enhancing the adherence and germination capacity, as in some examples of the family Lamiaceae (Ryding, 1992).

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LITERATURE CITED

Abu Sbaih HA, Jury SL. 1994*a*. Seed micromorphology and taxonomy in *Orobanche* (Orobanchaceae). *Flora Mediterranea* **4**: 41–48.

Abu Sbaih HA, Jury SL. 1994*b*. The seed micromorphology of the genus *Orobanche* (Orobanchaceae). In: Pieterse AH, Verkleij JAC, ter Borg SJ, eds. *Proceedings of the 3rd International Workshop on Orobanche and related Striga research.* Amsterdam, The Netherlands: Royal Tropical Institute, 112–120.

Abu Sbaih HA, Keith-Lucas DM, Jury SL, Harborne JB, Tubaileh AS. 1994. Pollen morphology of the genus *Orobanche* (Orobanchaceae). In: Pieterse AH, Verkleij JAC, ter Borg SJ, eds. *Proceedings of the 3rd International Workshop on Orobanche and related Striga research.* Amsterdam, The Netherlands: Royal Tropical Institute, 99–111.

Andary C. 1994. Chemotaxonomical study of the genus *Orobanche*. In: Pieterse AH, Verkleij JAC, ter Borg SJ, eds. *Proceedings of the 3rd International Workshop on Orobanche and related Striga research*. Amsterdam, The Netherlands: Royal Tropical Institute, 121–126.

Beck von Mannagetta G. 1890. Monographie der Gattung *Orobanche*. *Bibliotheca Botanica* **19**: 1–275.

Beck von Mannagetta G. 1930. Orobanchaceae. In: Engler A, ed. *Das Pflanzenreich,* vol IV. Leipzig: Verlag von Wilhelm Engelmann, 1–348.

Benharrat H, Théodet C, Veronesi V, Thalouarn P. 2001. Broomrape identification using inter simple sequence repeat (ISSR). Application to *Tryonychon* Wallr and *Osproleon* section species. In: Fer A, Thalouarn P, Joel DM, Musselman LJ, Parker C, Verkleij JAC, eds. *Proceeding of the 7th International Parasitic Weed Symposium.* Nantes, France, 79.

Boeshore I. 1920. The morphological continuity of Scrophulariaceae and Orobanchaceae. *Contributions from the Botanical Laboratory of the Morris Arboretum of the University of Pennsylvania* **5**: 139–177.

Burmmit RK, Powell CE. 1992. *Authors of plant names*. Richmond: Royal Botanic Gardens, Kew.

Canne JM. 1979. A light and scanning electron microscope study of seed morphology in *Agalinis* (Scrophulariaceae) and its taxonomic significance. *Systematic Botany* **4**: 281–296.

Canne JM. 1980. Seed surface features in *Aureolaria*, Brachystima, *Tomanthera*, and certain South American *Agalinis* (Scrophulariaceae). *Systematic Botany* **5**: 241–252.

Chater AO, Webb DA. 1972. Orobanchaceae. In: Tutin TG, Heywood VH, Burges NA, Moore DM, Valentine DH, Walters SM, Webb DA, eds. *Flora Europaea, 3*. Cambridge: Cambridge University Press, 285–294.

Chuang TI, Heckard LR. 1972. Seed coat morphology in *Cordylanthus* (Scrophulariaceae) and its taxonomic significance. *American Journal of Botany* **59**: 258–265.

Cosson ESC. 1848. Sur un genre nouveau de la famille des Orobanchées. *Annales des Sciences Naturelles Botanique Paris, series 3* **9**: 145–147.

Cronquist A. 1981. *An integrated system of classification of flowering plants*. New York: Columbia University Press.

Danin A, Baker HG, Baker I. 1979. Cytogeography and taxonomy of the *Portulaca oleracea* L. polyploid complex. *Israel Journal of Botany* **27**: 177–211.

Deif HAR, Al-Menoufi OA, Ahmed MF. 2000. A taxonomic study on the populations of three common species of the genus *Orobanche* L. (Orobanchaceae) in Egypt. 2. Macro- and micromorphology of the seeds and their taxonomic implications. In: Nordernstam B, El Ghazaly G, Kassas M, eds. *Plant systematics for the 21st Century*. London: Portland Press, 251–266.

Foley MJY. 2001. *Orobanche*. In: Paiva J, Sales F, Hedge IC, Aedo C, Aldasoro JJ, Castroviejo S, Herrero A, Velayos M, eds. *Flora Iberica,* 14. Madrid: CSIC, 32–72.

Font Quer P. 1993. *Diccionario de Botánica*. Barcelona: Labor.

Holmgren PK, Holmgren NH, Barnett LC. 1990. *Index Herbariorum. Part 1. The herbaria of the world*, ed. 8. Regnum Vegetabile 120. New York: New York Botanical Garden.

Hutchinson J. 1969. *Evolution and phylogeny of flowering plants*. New York: Academic Press.

Joel DM. 1987*a*. Detection and identification of *Orobanche* seeds using fluorescence microscopy. *Seed Science and Technology* **15**: 119–124.

Joel DM. 1987*b*. Identification of *Orobanche* seeds. In: Weber HC, Forstreuter W, eds. *Parasitic flowering plants. (Proceedings of the 4th ISPFP)*. Marburg: Philipps-Universität, 437–444.

Joel DM. 1988*a*. A key for the identification or *Orobanche* seeds. *Phytoparasitica* **16**: 376–377.

Joel DM. 1988*b*. *Orobanche cumana*, a new adventive weed in Israel. *Phytoparasitica* **16**: 375.

Juan R, Fernández I, Pastor J. 1997. Systematic consideration of microcharacters of fruits and seeds in the genus *Verbascum* (Scrophulariaceae). *Annals of Botany* **80**: 591–598.

Juan R, Pastor J, Fernández I. 1994. Seed morphology in *Veronica* L. (Scrophulariaceae) from south-west Spain. *Botanical Journal of the Linnean Society* **115**: 133–143.

Juan R, Pastor J, Fernández I. 1998. Estudio de frutos y semillas en *Parentucellia* Viv. (Scrophulariaceae) y sus implicaciones taxonómicas. *Acta Botánica Malacitana* **23**: 51–57.

Juan R, Pastor J, Fernández I. 1999. Morphological and anatomical studies of *Linaria* species from south-west Spain: seeds. *Annals of Botany* **84**: 11–19.

Juan R, Pastor J, Fernández I. 2000. SEM and light microscope observations on fruit and seeds in Scrophulariaceae from southwest Spain and their systematics significance. *Annals of Botany* **86**: 323–338.

Kuijt J. 1969. *The biology of parasitic flowering plant*. Berkeley and Los Angeles, California: University of California Press.

Lange JMCh. 1864. *Pugillus plantarum imprimis hispanicarum, quas in itinere 1851–52 legit Jon. Lange. III*. Videnskabelige Meddelelser Dansk Naturhistorisk Forening Kjøbenhavn 1861.

Minkin PJ. 1987. Pollen morphology of the Orobanchaceae and rhinanthoid Scrophulariaceae with reference to their taxonomy. In: Weber HC, Forstreuter W, eds. *Parasitic flowering plants (Proceedings of the 4th ISPFP)*. Marburg: Philipps-Universität, 575–589.

Minkin PJ, Eshbaugh WH. 1989. Pollen morphology of the Orobanchaceae and rhinanthoid Scrophulariaceae. *Grana* **28**: 1–18.

Musselman LJ, Mann WF. 1976. A survey of surface characteristics of seeds of Scrophulariaceae and Orobanchaceae using scanning electron microscopy. *Phytomorphology* **26**: 370–378.

Novopokrovsky NN, Tzelev P. 2000. Orobanchaceae. In: Schischkin BK, ed. *Flora of the U.S.S.R. Vol. XXIII* (English edition). Enfield, NH: Science Publishers, 21–145.

Olmstead RG, de Pamphilis CW, Wolfe AD, Young ND, Elisens WJ, Reeves PJ. 2001. Disintegration of Scrophulariaceae. *American Journal of Botany* **88**: 348–361.

van der Pijl L. 1982. *Principles of dispersal in higher plants*. Berlin: Springer-Verlag.

Polo JM. 1988. Aportación a la morfología polínica del género *Orobanche*

L. Significados taxonómicos. In: Civit J, Valle MF, eds. *Actas VI Simposio de Palinologia APLE*. Salamanca: 137–140.

Pujadas A. 1997. *Orobanche ballotae* A. Pujadas (Orobanchaceae), especie nueva. *Acta Botánica Malacitana* **22**: 29–34.

Pujadas A. 2000. *Orobanche* L. (Orobanchaceae), Sect. Trionychon Wallr. en Andalucía. *Acta Botánica Malacitana* **25**: 93–106.

Pujadas A. 2002. *Orobanche* L. In: López JA, Catalán P, Sáez LI, eds. *Plantas parásitas de la Península Ibérica y Baleares*. Madrid: Mundi-Prensa.

Pujadas A, Gómez D. 2000. *Orobanche montserratii* A. Pujadas & D. Gómez (Orobanchaceae), especie nueva del pirineo oscense. *Anales del Jardín Botánico de Madrid* **57**: 267–275.

Pujadas A, Lora González A. 1995. *Orobanche almeriensis* A. Pujadas (Orobanchaceae), nueva especie del sureste de la Península Ibérica. *Anales del Jardín Botánico de Madrid* **53**: 47–53.

Pujadas A, Lora González A. 1996. El género *Orobanche* L. (Orobancheceae) en la provincia de Almería SE de España. *Acta Botánica Malacitana* **21**: 199–220.

Pujadas A, Lora González A. 1997. Distribución de *Orobanche clausonis* Pomel (Orobanchaceae) en la Península Ibérica y Baleares. *Anales del Jardín Botánico de Madrid* **55**: 477–479.

Pujadas A, Lora González A, Crespo MB. 1997. *Orobanche tunetana* G. Beck (Orobanchaceae), especie nueva para el continente europeo. *Anales del Jardín Botánico de Madrid* **55**: 277–283.

Román B, Alfaro C, Torres A, Satovic Z, Pujadas A, Rubiales D. 2003. Genetic relationship among *Orobanche* species as revealed by RAPD analysis. *Annals of Botany* **91**: 637–642.

Román B, Alfaro C, Torres A, Satovic Z, Kharrat M, Pujadas A, Rubiales D. 2001. An analysis of genetic variation in natural populations of *Orobanche foetida* from Spain and Tunisia. In: Fer A, Thalouarn P, Joel DM, Musselman LJ, Parker C, Verkleij JAC, eds. *Proceeding of the 7th International Parasitic Weed Symposium.* Nantes, France, 57–60.

Ryding O. 1992. Pericarp structure and phylogeny within Lamiaceae subfamily Nepetoideae tribe Ocimeae. *Nordic Journal of Botany* **12**: 273–298.

Schneeweiss GM. 2001. Relationships within *Orobanche* sect. Tryonychon: insights from its sequences markers. In: Fer A, Thalouarn P, Joel DM, Musselman LJ, Parker C, Verkleij JAC, eds. *Proceeding of the 7th International Parasitic Weed Symposium.* Nantes, France, 49–52.

Schultz FW. 1848. *Archives de la flore de France et d'Allemagne*. Bitche: Haguenau & Deux-Ponts, 99–154.

Stace CA. 1985. Orobanchaceae. In: Heywood VH, ed. *Las plantas con flores*. Barcelona: Reverté, 244–245.

Stearn WT. 1992. *Botanical Latin*. London: David & Charles.

Sutton DA. 1988. *A revision of the tribe Antirrhineae*. London: British Museum (Natural History)/Oxford: Oxford University Press.

Takhtajan A. 1980. Outline of the classification of flowering plants (Magnoliophyta). *Botanical Review* **46**: 225–339.

Teryokhin ES. 1991. Orobanche research in the USSR. In: Wegman K, Musselman LJ, eds. *Progress in Orobanche research. Proceedings of the International Workshop on Orobanche Research*. Tübingen, Germany: Eberhard-Karls University, 30–34.

Teryokhin ES. 1997. *Weed broomrapes, systematics, ontogenesis, biology, evolution*. Landshut: Aufstieg-Verlag.

Ungurean L. 1986. Recherches sur le tegument seminal dans le cadre des espèces de la section Trionychon Wallr. du genre *Orobanche* L. *Revue Roumaine de Biologie, Série de Biologie Végétale* **31**: 121–125.

Valdés B, Díez M J. 1990. Aportación de los datos polínicos en taxonomía vegetal. In: Blanca G, Díaz de la Guardia C, Fernández MC, Garrido M, Rodríguez-García MI, Romero AT, eds. *Polen, esporas y sus aplicaciones.* Granada: Facultad de Ciencias, 153–165.

Velasco L, Goffman FG, Pujadas A. 2000. Fatty acids and tocochromanols in seeds of *Orobanche*. *Phytochemistry* **54**: 295–300.

Weber HC. 1980. Zur Evolution des parasitismus bei den Scrophulariaceae und Orobanchaceae. *Plant Systematics and Evolution* **136**: 217–232.

Young ND, Steiner KE, de Pamphilis CW. 1999. The evolution of parasitism in Scrophulariaceae/Orobanchaceae: plastid Gene sequences refute an evolutionary transition series. *Annals of the Missouri Botanical Garden* **86**: 876–893.

APPENDIX

Localities and dates of collections studied.

Orobanche alba Stephan ex Willd. SPAIN. Almería, Peña Lobera, Sierra Lúcar, 15 Jun. 1994, *Pujadas* and *Pallarés* (COA 17323). Granada, Sierra Nevada, Nigüelas, Pista barranco de los Alisos, 22 Jul.1997, *Prados*, *Parra* and *Jiménez* (COA 17635). Jaén, Sierra Mágina, El Almadén, 13 Jun. 1997, Pujadas (COA 23546). Jaén, Sierra Mágina, Torres, base de Monteagudo, 4 Jul. 1998, *Pujadas* and *Plaza* (COA 29897).

Orobanche amethystea Thuill. SPAIN. Alicante, Cap de les Hortes, 17 Apr.1997, *Pujadas* and *Aguilella* (COA 23735). Almería, Cóbdar, Cerro Pinar, 25 May 1994, *Pujadas* (COA 16475). Burgos, Villabáscones, 26 Jul.1991, *Pujadas* and *García Salmones* (COA 17608). Cádiz, Jerez de la Frontera, 11 May 1988, *Pujadas* and *Oliveira* (COA 13539). Girona, El Port de la Selva, naer Tamariua beach, 15 May 1998, *Pujadas* (COA 30473).

Orobanche arenaria Borkh. SPAIN. Almería, Sierra de las Estancias, Puerto Santa María de Nieva, 17 Jun. 2000, *Pujadas* (COA 29507). Granada, Puebla from Don Fadrique to Santiago de la Espada, Km 6, 19 Jul. 1999, *Pujadas* (COA 28906). Granada, Km 4 N from Trevélez, near Río Trevélez, 19 Jul. 2000, *Pujadas* and *López* (COA 30477). Murcia, Sierra Espuña, Pico Espuña, 17 Jun. 2000, *Pujadas* (COA 29508).

Orobanche ballotae A. Pujadas SPAIN. Almería, Agua Amarga, 6 May 1994, *Pujadas* (COA 17427). Almería, Níjar, N del Barranco Sabinar, 19 Apr. 1994, *Pujadas* and *Jiménez* (COA 17447). Almería, Níjar, Cerro de Los Frailes, 2 May 1994, *Pujadas* (COA 17446). Jaén, Los Villares, Los Cañones, 12 Jun. 1991, *Pujadas* and *Lora* (COA 17618).

Orobanche calendulae Pomel SPAIN. Ciudad Real, Piedrabuena, 10 May 1992, *Carrasco*, *Garrido* and *Blanco* (COA 22062). Toledo, Borrox, 24 May 1995, *Pujadas* (COA 30527).

Orobanche caryophyllaceae Sm. SPAIN. Álava, Peñalta, Arán, 10 Jun. 1983. Huesca, La Muria, Bisaurri, Ribagorza, 1 Jul. 2001, *Pujadas* (COA 31075).

Orobanche cernua L. SPAIN. Almería, Cerro Santa Fe, near Cerro Los Carneros, SE de la Mina Santa Bárbara, 23 Mar. 1994, *Pujadas* (COA 17355). Jaén, Bélmez de la Moraleda, Sierra de la Cruz, 3 May 1998, *Pujadas* (COA 25297). Granada, Cullar-Baza, El Margen, Arroyo El Margen, 08 Jun. 2000, *Pujadas* (COA 29902).

Orobanche clausonis Pomel SPAIN. Córdoba, Km 5 from Rute to Carcabuey, 15 Jun. 1995, *Pérez* (COA 17591). Granada, Sierra Parapanda, 28 Jun. 2000, *Pujadas*, *Plaza*

and *Román* (COA 29903). Murcia, Sierra Espuña, Río Espuña, 15 Apr. 1997, *Peláez* (COA 23732).

Orobanche crenata Forssk. SPAIN. Cádiz, near Grazalema, 20 Apr. 1995, *Pujadas* (COA 17507). Córdoba, Km 24 Puente Genil – Écija, 17 Jun.1987, *Hernández et al.* (COA 13682). Granada, Trevélez, near Río Trevélez, 30 Jun. 1990, *Pujadas* and *Poyato* (COA 13583). Málaga, near Guaro, 24 Jun.1992, *Lora*, *Prados* and *Pujadas* (COA 17519).

Orobanche crinita Viv. SPAIN. Baleares, Menorca, Sant Lluis, Biniancolla, 13 Agu. 2000, *Fraga*, *Poyato* and *Pujadas* (COA 29572). Menorca, ES Castell, 13 Apr. 2001, *Fraga* and *Pujadas* (COA 31046).

Orobanche cumana Wallr. SPAIN. Córdoba, Huerta San Luis, 2 Jul. 1996, *Lora* and *Pujadas* (COA 22077). Córdoba, Cortijo del Partido, 2 Jul. 1997, *Pujadas* (COA 23745). Málaga, near Laguna de la Fuente de Piedra, 8 Jun.1995, *Lora* and *Pujadas* (COA 17628). Sevilla, Km 3 from Ecija to Estepa, 1 Jul. 1996, *Pujadas, Lora* and *Jiménez* (COA 22079). Sevilla, El Coronil, 16 Jun. 1986, *García* (COA 13636).

Orobanche densiflora Reut. SPAIN. Cádiz, Rota, Punta Candor, 26 Apr. 1998, *Pujadas* (COA 25299). Cádiz, Chiclana, Sancti-Petri, 14 May 2000, *Pujadas* (COA 29912). Cádiz, Barbate beach, 15 Jun. 2000, *Sánchez* (COA 29586). Cádiz, Tarifa, Bolonia, 15 Jun. 2000, *Plaza*. (COA 29881).

Orobanche elatior Sutton subsp. *icterica* (Pau) A. Pujadas SPAIN. Alicante, Palomaret-Agrost, 17 May 1996, *Pujadas* (COA 29595). Alicante, Castalla, Rambla de Cañoles, 8 Jun. 1996, *Pujadas* (COA 30537).

Orobanche foetida Poir. SPAIN. Granada, Río Trevélez, near Trevélez, 16 Jul. 1990, *Pujadas* and *Poyato* (COA 17375), Granada, Km 2 N Trevélez, near Río Trevélez, 19 Jul. 2000, *Pujadas* and *López* (COA 30538). Huelva, El Conquero, 10 Jun. 1998, *E. Sánchez-Gullón* (COA 28430).

Orobanche gracilis Sm. SPAIN. Cádiz, Sierra del Aljibe, Garganta del Pozo Oscuro, 26 Apr. 1997, *Villamandos* (COA 23746). Málaga, Campillos, Sierra de Peñarrubia, La Herriza, 26 Mar. 1998, *Pujadas*, *Plaza* and *Rubio* (COA 25553). Huelva, Bailones, cumbres de San Bartolomé, 22 Apr. 1998, *López* (COA 25302).

Orobanche haenseleri Reut. SPAIN. Jaén, Sierra Mágina, Almadén, Torres, 16 Jun. 2000, *Román* and *Martínez* (COA 29921). Granada, Sierra Nevada, Barranco de los Alisos near Río Dúrcal, 22 Jul.1997, *Prados*, *Parra* and *Jiménez* (COA 23555). Granada, Trevélez, Km 5 N from Río Trevélez, 19 Jul. 2000, *Pujadas* and *López* (COA 30481). Málaga, Sierra de las Nieves, El Corona-Tolox, 27 Agu. 1997, *Plaza* (COA 25719).

Orobanche hederae Duby SPAIN. Burgos, Munilla, 31 Jul. 1990, *Pujadas* and *Poyato* (COA 17479). Burgos, Villanés, 30 Jul. 1990, *Pujadas* and *Poyato* (COA 17483). Cádiz, P.N. Los Alcornocales, Canuto de la Alcaria, between Sierra La Palma and Sierra Luna, 20 Jun. 1995, *Lora*, *Plaza* and *Escuín* (COA 17469). Córdoba, Cabra, La Nava, 6 Jun. 1995, *Lora* (COA 17665).

Orobanche laserpitii-sileris Jordan FRANCIA, Lescum, Pyr. Atlantiques Le Piquet de Lhurs, 25 Agu. 1999, *Villar* and *Benito* (COA 30541). SPAIN. Lleida, Tredós, Val d'Aran, 29 Jun. 2001, *Pujadas* (COA 31053).

Orobanche latisquama (F.W. Schultz) Batt. in Batt. & Trabut SPAIN. Ciudad Real, Fuencaliente, 20 May 1997, *Carrillo* (COA 28909). Granada, Km 6 from Puebla de Don Fadrique to Santiago de la Espada, 19 Jul.1999, *Pujadas* (COA 28909). Murcia, Totana, ermita Santa Eulalia, 30XG2784, 19 Jun. 1997, *Pujadas* (COA 23752).

Orobanche lavandulacea Reichenb SPAIN. Córdoba, Iznájar, cerro del Azucarón, 2 May 1998 (COA 25304). Girona, Km 2 from Port de la Selva to Cadaqués, 12 May 1998, *Pujadas* (COA 25542). Jaén, Los Cañones, Secos, 1 Jun. 2000, *Román* and *Fiestas* (COA 29501).

Orobanche minor Sm SPAIN. Girona, Cadaqués, Faro de Cap de Creus, 15 May 1998, *Pujadas* (COA 28172). Girona, El Port de la Selva, near Tamariua beach, 15 May 1998, *Pujadas* (COA 28200). Huelva, Km 3 from Linares de la Sierra a Aracena, 07 May 1997, *Lora* and *Pujadas* (COA 30528).

Orobanche montserratii A. Pujadas & D. Gómez SPAIN. Huesca, Fanlo, Cañón de Añisclo, near Ermita San Urbez, 21 Jul. 1997, *Pujadas*, *Montserrat* and *Gómez* (COA 27731). Huesca, Fanlo, San Urbez, Cañón de Añisclo, 2 Agu. 1975, *Montserrat* (COA 24394). Huesca, Fanlo, Cañón de Añisclo, 21 Jul. 1997, *Pujadas*, *Montserrat* and *Gómez* (COA 27730).

Orobanche mutelii F.W. Schultz in Mutel SPAIN. Almería, Santa María de Nieva, Puertecico-Cruce a Los Cabreras de Abajo, 11 May 1994, *Pujadas* (COA 17451). Granada, Cúllar de Baza, Arroyo El Margen, 8 Jun. 2000, *Pujadas* (COA 29503). Huesca, Jaca, near Barbastro, 19 May 1995, *Benito* (COA 13590). Toledo, 2 Km N from Ciruelos, 24 May 1995, *Pujadas* (COA 17452).

Orobanche nana (Reut.) Beck SPAIN. Albacete, Sierra Alcaraz, Puerto Crucetilla, 9 Jun. 1992, *Pujadas*, *Lora* and *Prados* (COA 17461). Córdoba, Alcolea, near Pantano de San Rafael, 16 May 2000, *Pujadas*, *Plaza* and *Román* (COA 29505). Granada, Sierra Parapanda, 28 Jun. 2000, *Pujadas*, *Plaza* and *Román* (COA 29509).

Orobanche olbiensis (Coss.) Nyman SPAIN. Alicante. Pinet beach, Santa Pola, 22 Jun.2000, *Crespo* (COA 29597).

Orobanche purpurea Jacq. SPAIN. Jaén, Sierra Mágina, Torres, El Almadén, 5 Sep.1997, Pujadas and Mazariegos (COA 25416).

Orobanche ramosa L. SPAIN. Granada, El Jau, 21 Sep. 2000, *Pujadas* (COA 30534). Granada, Cullar de Vega, 5 Oct. 1989, *Pujadas* and *Oliveira* (COA 13605). Granada, La Zubia, 27 Agu. 1988, *Oliveira* (COA 13816).

Orobanche rapum-genistae Thuill. SPAIN. Albacete, Sierra Alcaraz, near from Río Mundo, 10 Jun. 1992, *Pujadas*, *Prados* and *Lora* (COA 17594). Granada, Puebla de Don Fadrique, near from Puerta del Pinar, 03 Jun. 2000, *Pujadas* and *López* (COA 29576). Huelva, Parque Natural Doñana, La Rocina, Almonte, 15 Apr. 2000, *Sánchez Gullón* and *Cobos* (COA 29585). Madrid, El Escorial, 23 Jun. 1972, *Hernández* and *Benítez* (COA 13608).

Orobanche reticulata Wallr. subsp. *reticulata* GERMANY. Bayern, Traithen Kar, Östhang, swischen Oberem Sudelfeld und Kleinem Traithen, 3 Agu.1996, *Angerer* and *Pusch* (COA 29393).

Orobanche santolinae Loscos SPAIN. Almería, Tabernas, Venta de los Yesos, 18 May 1996, *Pujadas* (COA 23566). Córdoba, Rute, Sierra Alta, 29 Jun. 1996, *Pujadas* and *Lora* (COA 29460). Granada, Sierra Parapanda, Illora, 07 Jun.2000, *Pujadas* (COA 29929).

Orobanche schultzii Mutel SPAIN. Almería, Puerto de Santa María de Nieva, 30 May 1994, *Pujadas* (COA 17465). Huelva, Casa de la Madrina, Sanlúcar de Guadiana, 15 Jun. 2001, *Sánchez Gullón* (COA 31015).

Orobanche tunetana Beck SPAIN. Alicante, Cabo de Huertas, 17 May 1997, *Pujadas* and *Aguilella* (COA 22550).

Orobanche teucrii Holandre FRANCIA. Laruns, Valle de Ossau, Hourat, Cirque de Pan, 07 Jul. 1999, *Villar et al.* (JACA 97599).