

THE OVERLOOKED *OROBANCHE BALSENSIS* (J.A. GUIM.), COMB. NOV., AND SOME REMARKS ON *O. SUBBAETICA* TRIANO & A. PUJADAS

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ABSTRACT: In this paper a neglected taxon of *Orobanche s. str.* is shown to deserve specific rank for combining a set of correlated morphological features and a particular host (*Carlina*). As it had already been validly named at varietal and subvarietal rank by J. A. Guimarães it needn't be validly described, but is here typified, raised to the rank of species, thoroughly described, illustrated with detailed drawings and colour photographs and demonstrated to occur well beyond its *terra classica* not only in Portugal and Spain, but probably also in southern France, Corsica and Sicily. In addition, some morphological, chorological and iconographical additions to the knowledge of the recently described *Orobanche subbaetica* will be done. **Key words:** Orobanchaceae, Mediterranean flora, *Carlina*, parasitic plants, biosystematics, biogeography, evolution.

RESUMEN: La subestimada *Orobanche balseensis* (J.A. Guim.), comb. nov., y algunos comentarios acerca de *O. subbaetica* Triano & A. Pujadas. En este trabajo se dan pruebas de la pertinencia del rango específico para un taxon desatendido de *Orobanche s. str.* en el que coinciden todo un conjunto de caracteres morfológicos y un hospedante propio (*Carlina*). Puesto que J. A. Guimarães ya le había dado nombre válido en los rangos varietal y subvarietal, no es preciso describirlo como nuevo, y aquí tan solo se lo tipifica, se lo eleva al rango de especie, se lo describe en detalle, se lo ilustra con dibujos y fotografías en color y se muestra que su área de distribución rebasa la *terra classica* y se extiende, no solo por España y Portugal, sino muy probablemente por el sur de Francia, Córcega y Sicilia. Además, se hacen algunas adiciones morfológicas, corológicas e iconográficas al conocimiento de la recién descrita *Orobanche subbaetica*. **Palabras clave:** Orobanchaceae, flora mediterránea, *Carlina*, plantas parásitas, biosistemática, biogeografía, evolución.

INTRODUCTION

Both morphology (namely the crenate corolla lip lobes and the deeply divided calyx, with long and narrowly lanceolate, often distally filiform teeth) and, more recently, molecular analysis (SCHNEE-

WEISS & al. 2004) have recognised the existence of a widespread and well-characterised set of species typified by *Orobanche minor* and categorised under several taxonomic ranks –*Orobanche* ser. *Minores* Beck (1882) ["tribus" sensu BECK (1890) = "Grexx" sensu BECK (1930)], *O.*

subsect. *Minores* (Beck) Teryokhin (1993)–. But the internal structure of this group, obscured by the subtlety of morphological divergences as well as by a remarkable molecular homogeneity, has been controversial. Some authors have adopted an extremely synthetic treatment, not admitting but a handful of species to which the rest were synonymised or, at most, infraspecifically subordinated, whereas other have advocated very analytical approaches, with dozens of taxa arranged into complex hierarchical systems.

Such discrepant systematic views are well apparent in the Iberian Peninsula, which represents a remarkable hotspot for this group. The seminal monograph by BECK (1890) inspired the detailed studies by GUIMARÃES (1904), who offered a complex and extremely analytical taxonomic treatment. On the opposite side, lies the synthetic review by FOLEY (2001). PUJADAS (2002) presents a more thorough and balanced review of the Iberian diversity of these plants, also summarising his own noticeable contributions. Important, comprehensive studies about the nature and evolutionary roots of the diversity of the group, partially referred to Iberian plants, are those by THOROGOOD & al. (2008, 2009).

The *Minores* include both broad host range species, namely *O. minor* s. str. (parasite mostly on Asteraceae, Fabaceae and Apiaceae, more rarely on other families like Solanaceae, its real host range having probably been exaggerated in literature as a result of the misidentification of the actual host and confusion among species), and truly specialised, morphologically recognisable and for the most part molecularly supported species like *O. amethystea*, *O. artemisiae-campestris*, *O. ballotae*, *O. hederæ*, *O. picridis* and *O. santolinae* (see FRAJMAN & al., 2013: 6). The evolutionary basis and significance of this duality will be explored in some detail in the discussion section of this paper.

Orobanchë balsensis (J.A. Guim.) Carlón, M. Láinz, Moreno Mor. & Ó. Sánchez, comb. nov.

- ≡ *Orobanchë loricata* var. *synomora* J.A. Guim. subvar. *balsensis* J.A. Guim. in Brotéria 3: 163[–164] (1904) [basonym]. *Ind. loc.*: “β. 2 (*O.*) *balsensis* Guim.”. Portugal, “Algarve: Nas colinas áridas proximo de Tavira (parasita da *Carlina corymbosa* L., *Welwitsch!*)” (cf. Guimarães, 1904: 164). Lectotype [designated here (hic designatus)]: LISU 34658 (Flor. Algarb. N° 780 / *Orobanchë* / ad radices *Carlina hispanicae* parasitic / pr. Tavira in collinis aridis. / ... / maio [1]847).
- ≡ *O. loricata* f. *balsensis* (J.A. Guim.) Beck in Engl., Pflanzenr. 96: 200 (1930).
- = *O. loricata* var. *synomora* J.A. Guim. subvar. *synomora* J.A. Guim. in Brotéria 3: 163[–164] (1904). *Ind. loc.*: “β. 1 (*O.*) *synomora* Guim.”. Portugal, “Algarve: Serra de Monchique: Foia (sobre a *Carlina* sp., *Welwitsch!*); na charneca arenosa do Cabo de S. Vicente (fôrma de transição para a *O. Picridis* Schultz, com as antheras mais curtamente mucronadas, *Welwitsch!*)” (cf. Guimarães, 1904: 164). Lectotype [designated here (hic designatus)]: LISU 34657 [Flor. Algarb. N° 944 / *Orobanchë* / In addition ... Foiae / in *Carlina* ... / ... / 26 Jun (1)847].
- = *O. loricata* f. *synomora* (J.A. Guim.) Beck in Engl., Pflanzenr. 96: 200 (1930).
- = *O. lusitanica* J.A. Guim., nom. nud., in schedis.
- = *O. pseudoloricata* J.A. Guim., nom. nud., in schedis.
- ?= *O. minor* subsp. *neglecta* var. *strangulata* f. *genuina* J.A. Guim. in Brotéria 3: 174 (1904), nom. illeg. *Ind. loc.*: “γ I (*O.*) *strangulata* Guim.”. Portugal, “Centro littoral:—Otta (juncto da *Carlina* sp., *Welwitsch!*) / Algarve:—Estoy (A. Guimarães!)”. Lectotype [designated here (hic designatus)]: LISU 34683 (*Orobanchë* / Tota sordida purpu-/reo – violacea / auf *Carlina* / ... Otta junio [1]848 !)” (cf. Guimarães, 1904: 178).
- ?= *O. minor* subsp. *neglecta* var. *strangulata* subvar. *strangulata* J.A. Guim. Ex Beck in Engl., Pflanzenr. 96: 212 (1930).
- *O. minor* [race / ecotype] “on *Carlina corymbosa*” Thorogood, C.J., Rumsey, F.J., Harris, S.A. & Hiscock, J. in Plant Syst. Evol. 282, Nos. 1–2: 37[–38] f. 4f (2009). *Ind. loc.*: “on Cape St Vincent, Portugal”.
- *O. amethystea* auct., non Thuill.
- *O. artemisiae-campestris* auct., non Vaucher ex Gaudin
- *O. castellana* auct., non Reut.

Plants sharing with other *Minores* the prolonged calyx teeth and the crenate corolla lip margin, but readily distinct by

their slender habit, their lax and short inflorescences (shorter than the rest of the stem) and the markedly patent flowers which are tubular in shape, a bit widened distally and with a mostly straight dorsal line (such a straight, patent, geniculated corolla evokes *O. amethystea*, which is nonetheless a much more robust, thick-stemmed plant with more crowded inflorescences and bracts exceeding the flowers). Parasitic on *Carlina* (Asteraceae).

Description: Stem (14)17-34(37,5) × (0,16)0,30-0,42 cm, simple, usually slender, purplish or creamy (somewhat purple-tinged towards the inflorescence), glandular-hairy throughout (hair density decreasing from the inflorescence towards the base). Leaves 10-15 × 2,3-5 mm, triangular-lanceolate. Inflorescence (3,8) 6,5-11,0(12,5) × (2,8)3,0-3,6(4,4) cm, comparatively short -shorter than the rest of the stem [ratio long. infl. / long. stem = 0,27-0,36(0,41)]-, oblong [ratio width infl. / long. infl. = (0,26)0,33-0,48(0,60)], lax (most of the flowers distant from each other), dense only in the apex [(9)12-26(31) flowers]; bracts (9)10-13,0(14) × (2,9)4-5,0 mm, lanceolate, commonly shorter than the corolla [ratio long. bract / long. corolla = 0,58-0,80(0,93)], purple throughout, more rarely creamy in the base, densely covered with glandular hairs (yellowish gland). Calyx (9)11-12,5(14) × (2,1)2,5-3,5(4) mm, segments free, ± unequally two-toothed with the upper tooth usually longer, pink-purplish (more deeply in the middle nerves of the teeth and in the upper 2/3 of the tube, sometimes ± creamy towards the base), densely covered with glandular hairs (yellowish gland), specially in the teeth, which are (7,0)9,0-9,5(11,5) mm, long, unequal, narrowly lanceolate, acuminate to filiform in the apex and usually much longer than the tube [ratio long. teeth / long. tube = (1,75)2,0-4,0(5,6)]. Corolla (15,0)16-20 mm, ratio long. calyx / long. corolla =

(0,46)0,55-0,73(0,83), patent (forming an angle of 57-75° with the axis of the inflorescence), ± tubular, slightly broadened distally, dorsal line geniculate at the point where the stamens are inserted and then straight; outer surface, specially in the dorsal area, densely covered with glandular hairs (translucent hairs with yellowish gland), whitish with purple nerves, sometimes purplish-spotted distally; upper lip shallowly bilobate, with its lobes variably displayed (erect, bent forward or even a bit deflexed) during the anthesis, ± rounded in shape, with undulated and crenate-denticulate margins; lower lip trilobate, with deflexed, almost overlapping or slightly distant lobes, rounded to subquadrangular in shape and with ± crenate-denticulate margins. Filaments 6,5(8,5)-9,0(10,2) mm, inserted at (2,1)2,5-3,5(4) mm from the base of the corolla, hairy only in their basal half (translucent and rather long glandless hairs), whitish or somewhat yellowish and more or less purple-tinged below the anthers. Anthers 1,5-1,75 × 0,7-0,9 mm (beak c. 0,3 mm), purple or brown-greyish (beak white, conspicuous), glabrous except along the sutures in the basal half. Ovary whitish, glabrous. Style ± pure white and glabrous in the base and increasingly purplish and covered with short glandular hairs towards the apex. Stigma ± deeply purple.

Its only confirmed host is *Carlina corymbosa* L., s.l. (Asteraceae), and its currently known area covers the southwestern corner of the Iberian Peninsula (Portuguese region of Algarve and Spanish provinces of Cádiz and Málaga) at elevations of 0-900 m a.s.l. As explained below, it's possible and even probable that the species occurs as well in other regions around the Mediterranean, where it might be parasitic on other species of *Carlina*.

Studied specimens other than the above cited lectotypes:

POR, Algarve: Faro: 29SNA0197, Vila do Bispo, Laginha, near Cabo de São Vicente, not far from Sagres, 60 m, parasitic on (!) *C. corymbosa* in the clearings of the scrub, on stony soils, 29-IV-2013, *G. Moreno Moral* MM0041/2013 (herb. Sánchez Pedraja 13841); 29SNB9001, Mata do Pontal, near Gambelas, but in the *concelho* of Loulé, 25 m, beside *C. corymbosa* in a grassy wayside, 1-V-2014, *G. Moreno Moral* MM0007/2014 et MM0008/2014 (herb. Sánchez Pedraja 13963 et 13964); 29SNB9102, Mata do Pontal, south from Vale da Venda, above the bed of stream Biogal, 30 m, parasitic on *C. corymbosa* in a shady slope under pine trees, 2-V-2014, *G. Moreno Moral* MM0011/2014 (herb. Sánchez Pedraja 13967).

ESP, Andalucía: *Cádiz: 30STF8315, San Roque, southern slope of Cerro del Águila, Pinar del Rey, near San Roque, 110 m, parasitic on *C. corymbosa* on sandy soils in the clearings of a pine grove, 15-V-2011, *J.A. García Rojas*, *G. Moreno Moral*, *F. Muñoz Secilla* & *G. Velasco Cintrano* MM0033/2011 (herb. Sánchez Pedraja 13668); 30STF8468, Benaocaz, above the Cortijo de la Fuentezuela, near Benaocaz, 860 m, beside *C. corymbosa* on soils shaded by holm oaks by the path to the Tajo del Cabrero, 13-VI-2013, *L. Carlón* & *G. Moreno Moral* MM0094/2013 (herb. Sánchez Pedraja 13882). ***Málaga:** 30STF8741, Gaucín, la Almuña, 400 m, parasitic on *C. corymbosa* in sunny meadows but under the shadow of scattered holm oaks, 23-V-2004, *G. Gómez Casares* & *G. Moreno Moral* MM0097/2004 (herb. Sánchez Pedraja 11852 & 11853).

The molecular analysis by THOROGOOD & al. (2009) (see discussion section of this paper) supports the singularity of this plant, whose morphological distinctiveness, that we had noticed already in 2004, was also neatly outlined there, but without taking the step of proposing its formal systematic recognition. Nevertheless, our bibliographical surveys in search of a name for the species suggested that the first in realizing the existence of this

well characterised *Carlina* parasite was José d'Ascensão Guimarães during his profound review of Portuguese Orobanchaceae. Intentional visits to some of the Portuguese localities cited by Guimarães strengthened that suspicion, which at last could be fully confirmed. As pointed out in the above nomenclatural list, it is unclear whether the type material of the “var. *strangulata*” and that of *balsensis* are taxonomically identical, and thus whether both names are synonyms: the flowers of the “var. *strangulata*” are shorter and with an intense apical tinge. We will try to study the plant in the field as soon as possible, but in the mean time it can't be discarded that it corresponds to a form of the widespread and host-unspecific *O. minor* s. str.

In order to prevent host-based misidentifications, it must be kept in mind that broomrapes other than *O. balsensis* parasitize on *Carlina* around the Mediterranean. *Carlina nebrodensis* and *C. sicula*, for instance, are amongst the short-lived Asteraceae on which *O. canescens* C. Presl is known to grow. But this species described from Sicily differs from *O. balsensis* by its much shorter, erecto-patent and dorsally curved flowers, and is barely distinguished from *O. minor* by the yellowish-tinge in the top of the inflorescence and in the stigma (DOMINA & STEPANEK, 2009).

This doesn't mean necessarily that *O. balsensis* is absent from Sicily herself, from where we have seen pictures of plants presumably parasitic on *Carlina* and showing a strong resemblance to the species [e. g. those taken in Monte Catalano by C. Marcenò, those that A. La Rosa took near Castelvetro, and two pictures taken in Castiglione di Sicilia by F. Russo (viewable, sub *O. crenata*, at www.flickr.com/photos/etnature/)]. The case of Corsica, judging by the pictures taken in La Rondinara by J.-P. Chabert (<http://kalliste.flora.free.fr/>, sub *O. mi-*

nor), results, not surprisingly, analogous, as does that of Southern France attending to the specimen P 04419134 - herb. Grenier (“n.º 2 / Cette [Sète, Hérault] - Sur le *Carlina* / corymbosa / fleur bleu / Godron 1851”); but this notwithstanding, and despite our inability to see any reason why this specialised *Carlina* parasite should be restricted to the small area from which we can so far confirm its occurrence, we prefer to be cautious and wait for sounder proofs and *in vivo* studies before firmly assigning a larger geographical range to *O. balsensis*, and in fig. 1 we show as still uncertain all of the non-Iberian localities.

For the above stated reasons, it appears too soon to evaluate sensibly the

conservation status of *O. balsensis*. Assuming the so far known data in an exercise of ephemeral formalism, an application of the IUCN (2013) criteria would lead to consider the species vulnerable, VU [B1ac(ii, iii,iv)+2ac(ii,iii,iv); D1]. Its habitat is subject to some degree of human impact by means of animal husbandry, silvicultural activities and roadworks, but the species is likely to overcome such pressures by following its abundant host from recently disturbed to abandoned patches, and there is no reason to suspect significant declines. The confirmation of the French and Italian populations would suffice to take the conservation status of the species well into the Least Concern (LC) category.



Fig. 1. Known distribution of *Orobanchе balsensis* (red) and *O. subbaetica* (yellow). Stars indicate not fully confirmed but very plausible records (see text). The map was plotted with QGIS 2.6.0 and uses as base a cross-blended hypsometric tint (www.naturalearthdata.com) corresponding to an area approximately between 30 and 48°N and between 10°W and 20°E. Each side of the grid equals to 6 arc degrees.



Fig. 2. Lectotype of *Orobanche balsensis* (LISU 34658)



Fig. 3. *Orobanche balsensis*: Portugal, Algarve, Faro, Vila do Bispo, Laginha, near Cabo de São Vicente, not far from Sagres, 29-IV-2013, photo by G. Moreno Moral (herb. Sánchez Pedraja 13841). These plants inhabit a very sunny and windy spot, whereas in other localities the species grows in less exposed places under the shade of trees. It is thus conceivable that the paler colour of these plants is purely phenotypical (the marked, diagnostic dark veins of the corolla lobes remain, however, as obviously do all the distinctive morphological features).



Fig. 4. *Orobanche balsensis*: Spain, Cádiz, San Roque, southern slope of Cerro del Águila, Pinar del Rey, near San Roque, 15-V-2011, photo by G. Moreno Moral (herb. Sánchez Pedraja 13688).



Fig. 5. *Orobanche balsensis*: Spain, Málaga, Gaucín, la Almuña, 23-V-2004 by G. Moreno Moral (herb. Sánchez Pedraja 11852 & 11853).

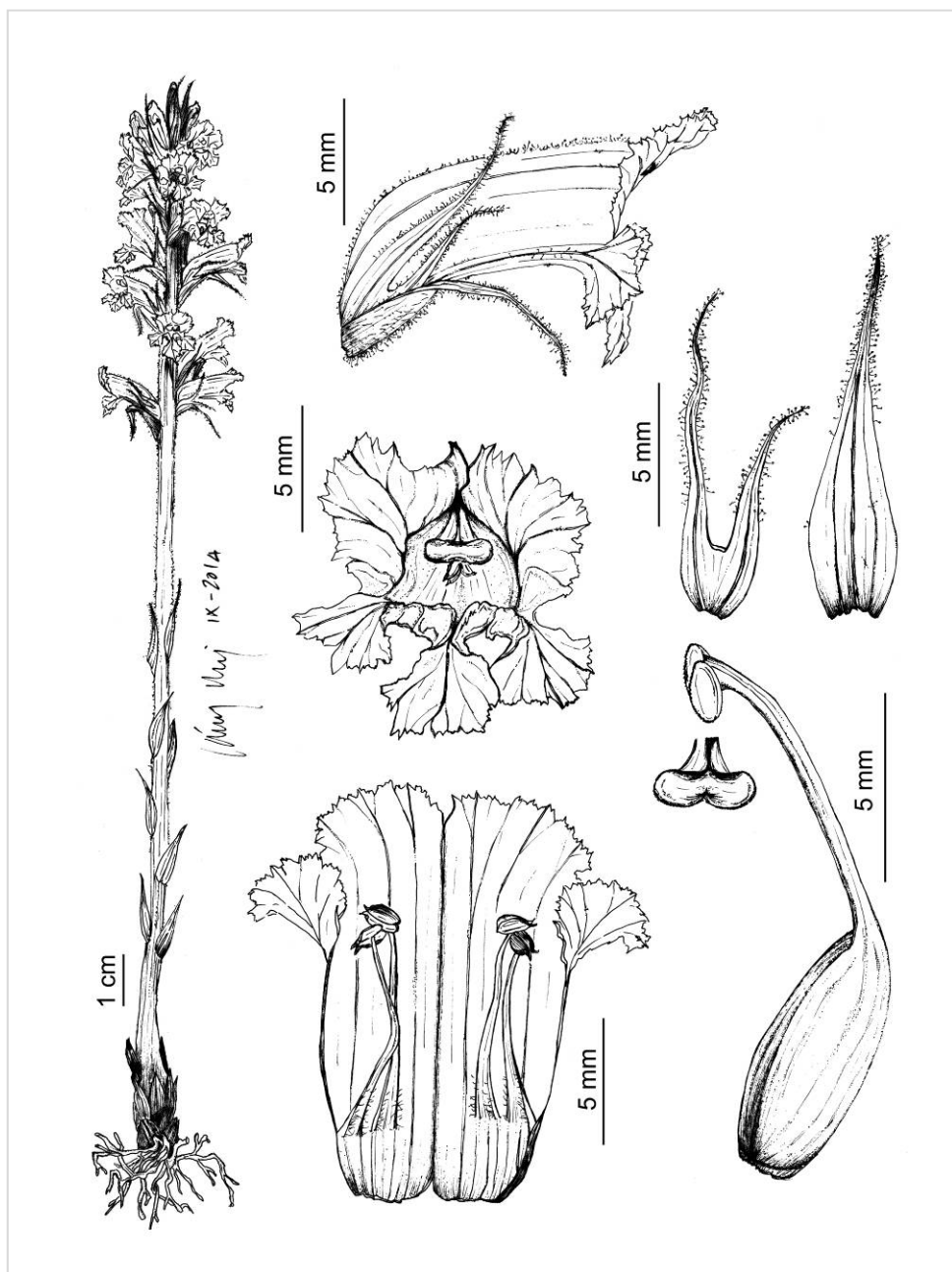


Fig. 6. *Orobanche balsensis*, Ó. Sánchez Pedraja del., coram herb. Sánchez Pedraja 13841: a) habit; b) flower, lateral view; c) corolla, frontal view; d) opened corolla showing stamens (middle lobe of lower lip and its part of tube cut away); e) calyx segment and bract; f) pistil and stigma (this from two different angles).

Orobanche subbaetica Triano & A. Pujadas in Acta Bot. Malacitana 39: 275 (2014)

We will obviously omit our complete description of this recently published and very well characterized species, whose publication as new had to be suppressed from this very paper in the last moment and whose chosen holotype, for which we had even reserved a number in MA, had been drawn in detail by one of us (fig. 7). Such statement must be understood as a way to highlight the soundness of the new species by showing that it was independently recognised in different localities by two groups of researchers. Nevertheless, we still find useful some descriptive, diagnostic remarks and more importantly some distributional additions.

We would summarise and somewhat reinforce the protologue by saying that, in addition to its peculiar host, *O. subbaetica* is defined by the association of a) distinct dorsally purplish-blue and ventrally whitish corollas, b) stigma with distinctive, deep-purple spherical lobes and c) rectangle-shaped, short and divergent lower corolla lip lobes. Other particular features can be cited to distinguish it from other Iberian thick-stemmed *Minores*: from *Orobanche castellana*, specially by the above referred lower corolla lip lobes and stigma and by the purplish instead of brown-reddish pigmentation; from *O. calendulae* also by the denser indumentum of longer hairs, the erecto-patent flowers, the entire or strongly asymmetric calyx and the uniformly curved dorsal line of the corolla; from *O. amethystea* it can be readily distinguished by the erecto-patent non-geniculate flowers and the not so longly filiform calyx teeth; from *O. santolinae*, in addition to the already mentioned traits, by the lack of the pulverulent tomentum (particularly apparent in the bracts of dried plants) and by the glabrescence of ovary, style and staminal filaments; apart from by the unique arrangement of the lower corolla lip and by

the stigma, it is distinguished from *O. picrodis* by the uniformly curved and much more extensively and intensely pigmented corolla, and from *O. artemisiae-campensis* by the lack of a straight segment in the dorsal line of the corolla, the absence of winish tones, the not so filiform calyx teeth and the untwisted apical crown of bracts.

In the populations by us studied (see below) flowers are larger than indicated in the protologue (18-22 mm), and anther filaments are entirely glabrous or subglabrous (fig. 7). However, a comparative glance at the protological pictures and ours (fig. 8) suffices to dispel all doubts about the conspecificity of all these *Antirrhinum* parasites, and don't imply but a somewhat larger morphological variability within *Orobanche subbaetica*.

With regards to the ecology and biogeography of the species, we can add *Antirrhinum australe* Rothm. as a host and improve the knowledge of its distributional area by indicating the following localities, some 140 km to the southwest from the *locus classicus*:

ESP, Andalucía, *Cádiz: 30STF8865, Villaluenga del Rosario, below Casa del Encinar, km 5.900 of the road A-374 between Grazalema and Villaluenga del Rosario, 840 m, parasitic on *A. australe* in a rocky calcareous road bank, G. Moreno Moral MM0020/2012 (herb. Sánchez Pedraja 13751); 30STF8563, Villaluenga del Rosario, base of the rocky, calcareous, sunny slope of the Sierra de la Bandera, above the Manga de Villaluenga, 880 m, close to *A. australe*, 12-VI-2013, L. Carlón & G. Moreno Moral (obs.); 30STF8970, Grazalema, below the town of Grazalema, km 51 of the road A-372, 800 m, parasitic on *A. australe* on limestone boulders at the foot of an east-facing cliff, 12-VI-2013, L. Carlón & G. Moreno Moral, MM0093/2013 (herb. Sánchez Pedraja 13881). ***Málaga:** 30STF9967, Benaolán, between Benaolán and Montejaque, 580 m, parasitic on (!) *A. australe*, 16-V-2011, G. Moreno Moral MM0040/2011 (herb. Sánchez Pedraja 13675); 30SUF0069, Benaolán, near the Puerto de Tavizna pr. Mon-

tejaque, 730 m, parasitic on (!) *A. australe*, 16-V-2011, G. Moreno Moral MM0041/2011 (herb. Sánchez Pedraja 13676); 30SUF0069, Montejaque, near Puerto de Tavizna, between km 4 and 5 of the road MA-505, pr. Montejaque, 750 m, parasitic on *A. australe* in the rocky road bank, 12-VI-2013, L. Carlón & G. Moreno Moral, MM0092/2013 (MA 884663 ex herb. Sánchez Pedraja 13880); 30STF9867, Montejaque, below Cerro Chanchuelo, above the path to the fountain of the Llanos de Líbar, in the outskirts of Montejaque, 730 m, parasitic on *A. australe* in the rocks lying at the foot of the northern slope of the hill, 12-VI-2013, L. Carlón & G. Moreno Moral (obs.).

Attending to the data and comments provided by CARINE & al. (2006: 215) it seems very likely that *O. subbaetica* occurs as well on the other side of the Strait of Gibraltar, in the climatically and biogeographically analogous mountains of the Western Rif, some 200 km to the south (fig. 1). Further findings in the Iberian Peninsula and North Africa, where so many species of the host genus are widespread, are to be expected.

DISCUSSION

The two above considered species are specific parasites of perennial hosts and presumably perennial themselves. Given the plasticity that this crucial feature of the life cycle shows within the subsect. *Minores* of *Orobancha* to which both *O. balsensis* and *O. subbaetica* undoubtedly belong, putting their systematic and evolutionary significance in its proper context requires going to some length to understand the roots of this revealing eco-physiological divergence.

Generalist parasites, germinating in response to unspecific signals, can thrive in diverse, patchy, annual-dominated landscapes, where, being the dispersal of host and parasites independent, the offspring of successful parasites on certain hosts is unlikely to reencounter those hosts. It is probably no coincidence that

the most neatly unspecific Mediterranean broomrapes carry names like *Orobancha minor* and *Phelipanche nana*, their short size minimising their risk of tapping to death any annual host before completing their own cycle. In more stable habitats (like the steep slopes and cliffs where *Carlina* occurs and the rocky outcrops colonised by *Antirrhinum*) perennial, reliably available hosts prevail and tend to induce the appearance of host-specific lineages (THOROGOOD & HISCOCK, 2010).

Population genetic evidence suggests that host-driven diversification of *Orobanchaceae* depends on the comparative resistance of parasites to inbreeding, given that their reduced physiology implies fewer “fragile components” (WICKE & al., 2013). A single mother plant which results successful in a host can even self-pollinate and found a population by producing thousands of seeds inheriting the ability to grow on that kind of host. Any mutation linking the germination to the particular exudates of that host will rapidly prevail by preventing the useless production of seeds attacking unreliable hosts. As a result of their more complex physiology, hosts are more vulnerable to inbreeding depression, which slows down their pace in the coevolutionary arms race in such a way that comparatively resistant strains of the host would spread only after repeated genetic bottlenecks in the parasite have sculpted homogeneous, recognisable species. Gap-prone soils (e.g. gypsum, scree, sand dunes, cracking clay) further catalyse the speciation of broomrapes by facilitating the access of seeds to the often compensatorily extensive root systems of the hosts.

It remains uncertain whether broomrapes were at first unspecific parasites of annuals or grew specifically on a limited number of perennial hosts (SCHNEEWEISS, 2007). However, it appears more likely, given all the above considerations

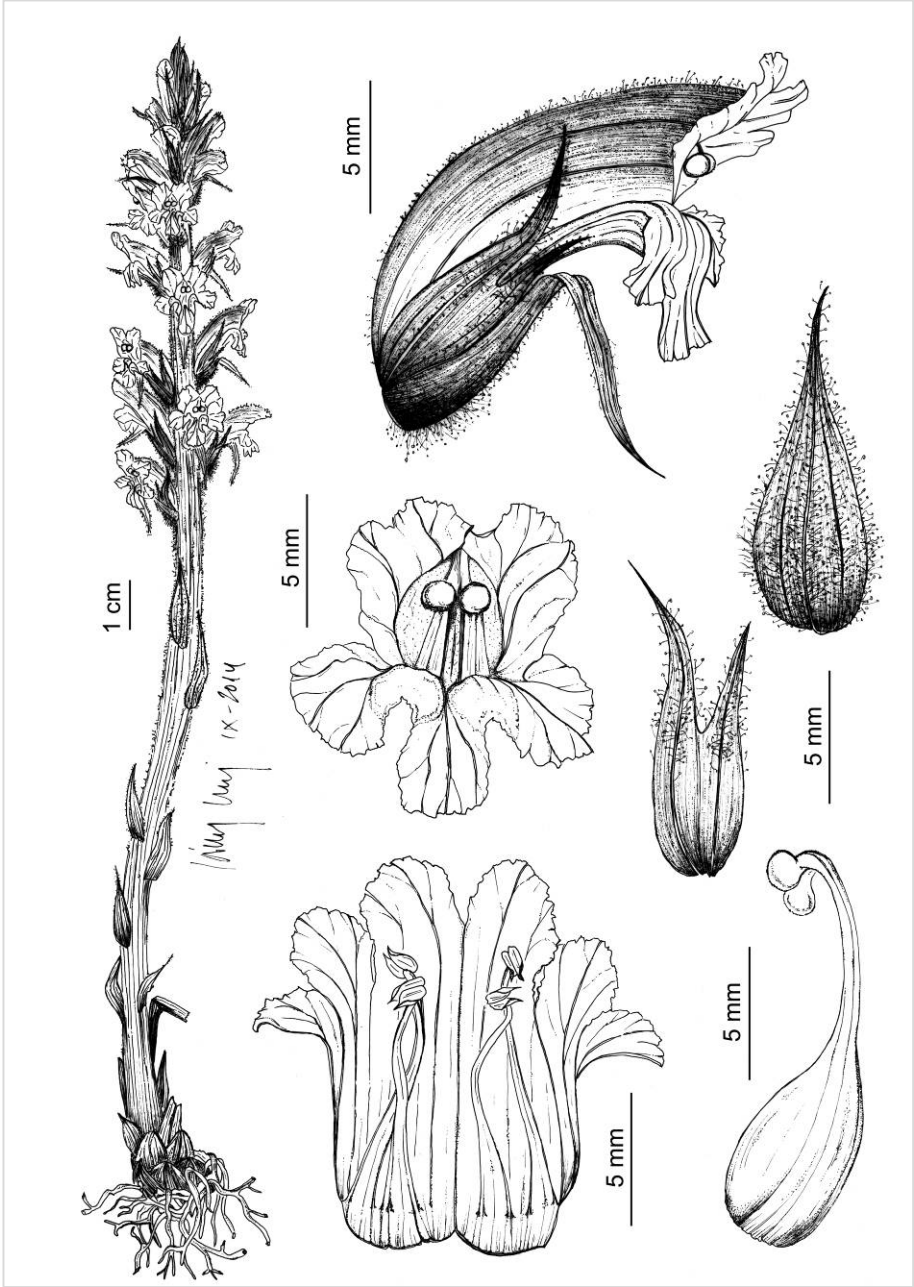


Fig. 7. *Orobanche subbaetica*: Sánchez Pedraja del., coram herb. Sánchez Pedraja 13880: a) habit; b) flower, lateral view; c) corolla, frontal view; d) opened corolla showing stamens; e) calyx segment and bract; f) pistil and stigma.



Fig. 8. *Orobanche subbaetica*: Spain, Málaga, between Benaoján and Montejaque, 16-V-2011, photo by G. Moreno Moral (herb. Sánchez Pedraja 13675).

and the findings on other broadly Irano-Mediterranean lineages (JABBOUR & RENNER, 2011), that the perennial, presumably host-specific condition was first. The two species here considered would thus be two particular members of an older set of specific parasites from some of which the unspecific *O. minor* evolved as a response to the massive annualization of the Mediterranean flora, rather than recent specialised descendants of an annual, widespread lineage. In this case, the lack of molecular divergence within the *Minores*, by comparison with other sections of the genus containing as well species tightly linked to specific hosts, would be a consequence of the introgression with the annual and widespread *O. minor* after this species' range was amplified by human activities (THOROGOOD & al., 2009). Furthermore, annualization and host-range expansion within the *Minores* could arise more than once, and the process of molecular blurring might have been multifront and thus relatively fast.

Were this the case, to their intrinsic biological interest these modest wild species would add a considerable agromonomical interest as snapshots of the evolutionary background of actual or potential pest species like *O. crenata* and *O. minor* itself. In fact, the molecular analysis by THOROGOOD & al. (2009), in agreement with an obvious morphological similarity, places *O. balsensis* in the very core of a widespread generalist *O. minor* lineage, although differentiated from it. Its long branch in the phylogram is interpretable in the light of the above considerations as the result of successive population bottlenecks through the adaptation to a specific host, the homogeneity of *O. minor* and its lesser divergence from their putative common ancestor being attributable to the lack of selective forces combined with larger populations.

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