

Unravelling the phylogeny of the root-hemiparasitic genus *Odontites* (tribe Rhinanthaeae, Orobanchaceae): Evidence for five main lineages

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Abstract Despite the recent publication of several phylogenies focused on Rhinanthaeae, which has been expanded to include three Asian endemic genera, few studies so far have dealt with particular genera within the tribe. Here, we focus on *Odontites* and related genera because of the high morphological variability of the group and its unclear generic boundaries. Phylogenetic analyses were performed for nrDNA (ITS) and cpDNA (*trnK* region and *rps16* intron) datasets, using Bayesian and Parsimony analyses. Our results cast doubt on the inclusion of *Pterygiella* and related genera within the Rhinanthaeae and support the paraphyly of *Phtheirospermum*, making it necessary to propose three new combinations to avoid it. *Odontites* is circumscribed to include *Bartsiella*, *Bornmuellerantha*, and *Macrosyringion*, but not *Odontitella*. Within *Odontites*, five distinct lineages are identified. These are distinguishable either by morphological synapomorphies or by a combination of several character states. Most of the *Odontites* species are regarded as monophyletic. In the *O. vernus* and *O. luteus* complexes, some taxonomic changes are made to avoid paraphyly, which results in three new combinations.

Keywords *Odontites* and related genera; *Phtheirospermum*; phylogenetic incongruence; *Pterygiella* complex; Rhinanthaeae; species monophyly

Supplementary Material Electronic Supplement (Appendix S1; Fig. S1) and DNA sequence alignment files are available in the Supplementary Data section of the online version of this article at <http://ingentaconnect.com/content/iapt/tax>

■ INTRODUCTION

Traditionally, all root-parasitic Scrophulariaceae (today considered part of Orobanchaceae; Young & al., 1999; Bennett & Mathews, 2006; McNeal & al., 2013) have been included in tribe Rhinanthaeae. The data available to date show that this tribe is not monophyletic. However, a subgroup of 15–20 genera (depending on different taxonomic treatments) forms a natural group, which includes the type genus *Rhinanthus* L. (“*Bartsia* clade” in Wolfe & al., 2005, or “Clade V” in Bennett & Mathews, 2006 and McNeal & al., 2013). Tribe Rhinanthaeae has recently been redefined as the “least inclusive crown clade that includes: *Pterygiella nigrescens* Oliv. 1896, *Rhinanthus crista-galli* L. 1753, *Melampyrum pratense* L. 1753, and *Tozzia alpina* L. 1753” (McNeal & al., 2013). This tribe has been the focus of four phylogenetic studies. The first two (Těšitel & al., 2010; Scheunert & al., 2012) improved the taxon sampling and filled sampling gaps. They corroborated the monophyly of the tribe, identified major lineages within it, and proposed some taxonomic changes including new nomenclatural combinations.

Later on, Uribe-Convers & Tank (2015) and Gaudeul & al. (2016) investigated the diversification dynamics and biogeography of *Bellardia* All. s.l. (including *Bellardia*, *Parentucellia* Viv., and *Neobartsia* Uribe-Convers & Tank; “*Bellardia* clade” in Scheunert & al., 2012) and *Odontites* Ludw., respectively, and made use of the phylogeny of Rhinanthaeae only as an evolutionary framework. None of these studies included samples of the endemic Chinese genus *Pterygiella* Oliv. or of the related genera *Phtheirospermum* Bunge ex Fisch. & C.A.Mey., *Xizangia* D.Y.Hong and *Pseudobartsia* D.Y.Hong. Apart from investigations at tribal level, there are few molecular studies on particular genera of the Rhinanthaeae (*Euphrasia* L., Gussarova & al., 2008; the “*Pterygiella* complex”, Dong & al., 2013; *Neobartsia*, Uribe-Convers & Tank, 2015; Uribe-Convers & al., 2016).

Figure 1 summarizes the phylogenetic hypotheses of the “core group of Rhinanthaeae” (sensu Scheunert & al., 2012) proposed so far (Těšitel & al., 2010; Scheunert & al., 2012; McNeal & al., 2013; Uribe-Convers & Tank, 2015; Gaudeul & al., 2016). In most of them, *Odontites* (including *Bornmuellerantha* Rothm.) was deemed sister to the *Bellardia* clade in cpDNA and

combined datasets (nrDNA+cpDNA). Only Scheunert & al. (2012) and Gaudeul & al. (2016) included samples of *Bartsia* Bolliger, *Macrosyringion* Rothm. and *Odontitella* Rothm. in their studies. Scheunert & al. (2012) found *Odontitella* to be sister to *Nothobartsia* Bolliger & Molau, supporting its segregation from *Odontites*. In Scheunert & al. (2012) and Gaudeul & al. (2016), *Bartsia* and *Bornmuellerantha* were nested within *Odontites* s.str. (sensu Bolliger, 1996), and both genera were consequently re-included in it. Following Scheunert & al. (2012), the position of *Macrosyringion* remained doubtful due to topological incongruence and low clade support (in the

cpDNA tree). Gaudeul & al. (2016) did not detect the same relationships at the genus level as previous authors did, probably due to limited taxon sampling (*Nothobartsia*, *Neobartsia*, and *Hedbergia* Molau were not included). This latter study found *Macrosyringion* as sister to the clade containing *Bellardia* and *Parentucellia* with high support.

Odontites (with ca. 30 species and 15 subspecies in its traditional and broadest sense, hereafter referred to as *Odontites* s.l.; Bolliger, 1993) is distributed throughout temperate Eurasia, the Mediterranean region (including several islands), and Macaronesia, with a diversification centre in the Western

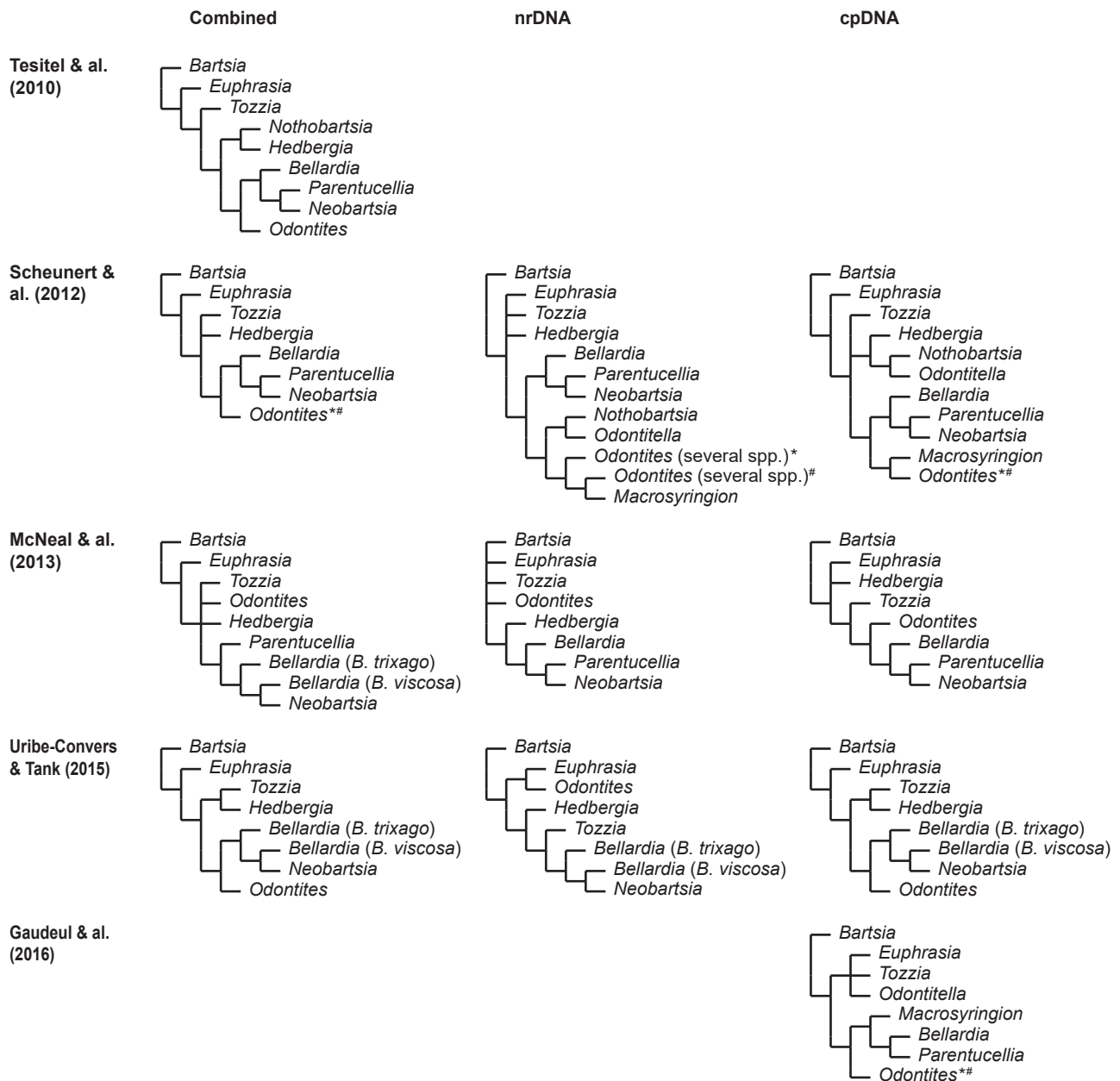


Fig. 1. Summary of the tree topologies obtained from the nrDNA, cpDNA and combined datasets published in the most relevant studies of tribe Rhinanthaeae (redrawn from Těšitel & al., 2010; Scheunert & al., 2012; McNeal & al., 2013; Uribe-Convers & Tank, 2015; and Gaudeul & al., 2016). Trees were pruned to only show the “core group of Rhinanthaeae” (sensu Scheunert & al., 2012), and branches with low support were collapsed into polytomies. Clades containing *Bartsia* and *Bornmuellerantha* samples were marked with * and # respectively.

Mediterranean area. Its taxonomy has long been controversial. Linnaeus (1753) described several species of *Odontites* under *Euphrasia*, and later taxonomists added newly discovered species and proposed several rearrangements (e.g., Don, 1838; Kerner, 1888; Beauverd, 1911). Most recently, Rothmaler (1943) segregated *Bornmuellerantha*, *Macrosyringion*, and *Odontitella* from *Odontites* s.l. The remaining species were divided into three sections based on the morphology of the corolla and stamens (sect. *Dispermothea* (Beauv.) Rothm., sect. *Orthantha* Benth. em. Rothm., sect. *Euodontites* Benth. em. Rothm.). Although this proposal was not considered by Webb & Camarasa (1972), Bolliger (1996) recognized the three small genera segregated by Rothmaler (1943), and even separated an additional genus, *Bartsiella*, based on pollen exine sculpturing and calycinal glandular hairs (Bolliger, 1985; Bolliger & Wick, 1990). Bolliger (1996) included 26 species in *Odontites* s.str. and did not accept sections within the genus, although several species groups were recognized. Most are present in the Iberian Peninsula (Rico, 2009), and recently this area has been postulated as the centre of origin of a clade composed of *Odontites* s.str., *Bartsiella*, and *Bornmuellerantha* (Gaudeul & al., 2016).

Morphologically, *Odontites* s.l. has character states which are intermediate between those of *Euphrasia* and *Bartsia* L. (Bolliger, 1996). Marked morphological variability exists within *Odontites* s.l., especially regarding corolla shape and colour, as well as calyx and corolla indument (Fig. 2). Many vegetative and reproductive characters appear to have undergone parallel, convergent, and reverse evolution (Bolliger, 1993). Furthermore, some morphological characters and phenology are influenced by host plants (Snogerup, 1982), and in some species groups seasonal ecotypes exist (ter Borg, 1985; Bolliger, 1996; Koutecký & al., 2012). Therefore, the delimitation of species and the analysis of species relationships are difficult when based only on morphology.

Hybridization and incomplete lineage sorting (ILS) are the most widely studied processes that might explain gene-tree incongruence (Kubatko, 2009). Hybridization events can also result in allopolyploid speciation; recurrent formation of polyploids in plants has been shown to be the rule rather than the exception (Soltis & Soltis, 1993, 1999). However, other biological processes (e.g., gene duplication and horizontal gene transfer) may also be a source of phylogenetic incongruence. Regarding the members of tribe Rhinanthae, several cases of incongruence between gene trees involving several genera, (e.g., the clade *Odontitella*+*Nothobartsia*; Scheunert & al., 2012), individual genera (e.g., *Tozzia* L. or *Odontites*; Uribe-Convers & Tank, 2015) and species within genera (e.g., *Bartsia* sp.; Scheunert

& al., 2012) have been detected. Polyploidization is not extensive within *Odontites* s.l., although two taxa, *O. jaubertianus* (Boreau) D.Dietr. and *O. vernus* (Bellardi) Dumort. subsp. *vernus*, could be the result of allo- and autopolyploidization, respectively (Bolliger & al., 1990; Bolliger, 1996).

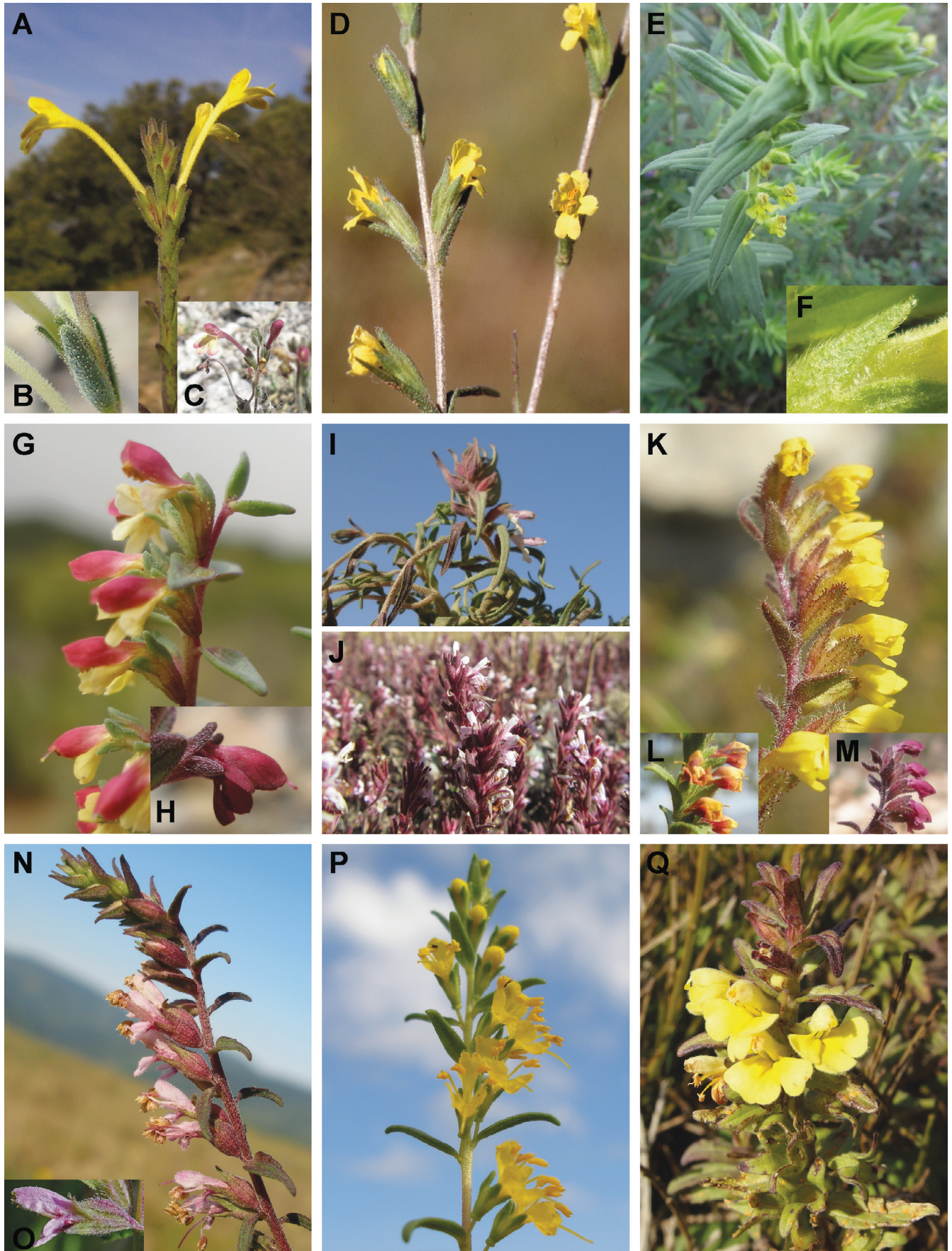
The aims of this study were to: (1) test the monophyly and topological position of *Odontites*, using a complete phylogenetic framework (i.e., all genera included in tribe Rhinanthae sensu McNeal & al., 2013); (2) determine the usefulness of several morphological characters considered relevant in previous taxonomic treatments in delimiting and supporting monophyletic groups, especially in *Odontites* and related genera; and (3) finally, test the monophyly of those species in the *Odontites* clade for which more than one specimen was collected, covering the entire species distribution range.

■ MATERIALS AND METHODS

Plant material. — Taxon sampling covered a representative number of species of all genera included in tribe Rhinanthae (clade V+*Pterygiella* complex; McNeal & al., 2013). A total of 350 ingroup individuals (747 newly generated sequences) were included in the analyses. They represent 86 species of 17 genera. For correct choice of outgroup taxa, the most comprehensive molecular phylogeny of Orobanchaceae to date (McNeal & al., 2013) was followed. One representative species of tribe Buchnereae Benth. (*Striga asiatica* (L.) Kuntze; clade VI) together with three of tribe Pedicularideae Duby (*Seymeria laciniata* (M.Martens & Galeotti) Standl., *Pedicularis groenlandica* Retz. and *Phtheirospermum japonicum* (Thunb.) Kanitz; clade IV) were chosen to root the phylogenetic analyses. All sequences used in the study (from GenBank and newly generated data with voucher information) are listed in Appendix 1. The keys provided by Bolliger (1996) and Rico (2009) were used to identify most of the herbarium vouchers used here. Seven species belonging to *Odontites* s.str., which are narrowly endemic in North Africa (Algeria and Tunisia; 5 spp.), Sicily (1 sp.), and the Near East (Lebanon and Syria; 1 sp.), were not included in this study because it was not possible to obtain good-quality DNA samples.

DNA extraction and amplification. — Total genomic DNA was isolated either from silica-gel-dried tissue (leaves and/or bracts) or from herbarium samples using the modified CTAB method (Doyle & Doyle, 1987) or the NucleoSpin Plant Kit following the protocols of the manufacturer (Macherey-Nagel, Düren, Germany). DNA was diluted in 50 µl of buffer.

Fig. 2. Morphological diversity in *Odontites*. Herbarium number or locality are indicated in parentheses. **A–C**, *Macrosyringion* lineage; **D**, *Bornmuellerantha* lineage; **E & F**, *Pyrenaeus* lineage; **G–M**, *Viscosus* lineage; **N–Q**, *Vernus* lineage. **A**, *O. longiflorum* (Spain, Burgos, Montes Obarenes); **B**, *O. longiflorum* (SALA 135639; detail of calyx and corolla indument); **C**, *O. longiflorum* (SALA 110071; variability in corolla colour); **D**, *O. aucheri* (SALA 120807); **E**, *O. cebennensis* (SALA 156186); **F**, *O. cebennensis* (SALA 135679; detail of calyx and corolla indument); **G**, *O. foliosus* (SALA 134537); **H**, *O. bolligeri* (SALA 142142, detail showing a glabrous corolla); **I**, *O. rameauanus* (MA 746138); **J**, *O. maroccanus* (SALA 156178); **K**, *O. viscosus* (SALA 137360); **L & M**, *O. viscosus* (SALA 110047 and SALA 137373; variability in corolla colour); **N**, *O. vernus* (SALA 135643); **O**, *O. vernus* (Spain, Valladolid, San Miguel del Arroyo; detail of calyx and corolla indument); **P**, *O. luteus* (SALA 135662); **Q**, *O. hollianus* (MA 714540). — Photographs by S. Andrés-Sánchez (A, H, L), D. Pinto-Carrasco (B, C, E, J), E. Rico (D, F, G, I, K, M, N, P, Q) and J. Bobo-Pinilla (O).



Concentration and quality were assessed by spectrophotometry and electrophoresis (1.0% agarose gel), respectively. One nuclear ribosomal region (including the ITS1 and ITS2 spacer regions and the 5.8S rRNA gene) plus two non-coding chloroplast regions (part of the *trnK* region and the *rps16* intron) were chosen for phylogenetic analyses. Reagent concentrations, PCR profiles, and primers followed Scheunert & al. (2012). Most of the markers were sequenced bidirectionally with the same primer pairs as used for amplification, using BigDye chemistry on an ABI 3730XL analyzer at Macrogen Europe or at Ludwig-Maximilians-University sequencing services.

Sequence editing, alignment, and indel-coding. — All newly generated sequences were edited, assembled, and automatically aligned using Geneious v.5.5.8 (Kearse & al., 2012). Online available sequences completing taxon sampling were taken mainly from Těšitel & al. (2010), Scheunert & al. (2012), Dong & al. (2013) and Uribe-Convers & Tank (2015). They were trimmed to fit the length of the newly generated sequences and added to the alignments. Some minor adjustments were made manually after visual inspection, and mononucleotide repeats (≥ 5 bp) were excluded from further analysis. Insertions and deletions (indels) were coded according to the simple indel-coding method (Simmons & Ochoterena, 2000), as implemented in SeqState v.1.4.1 (Müller, 2005). They were added to the data as a binary matrix and, consequently, gaps were treated as missing data.

Datasets and phylogenetic analyses. — Two datasets were analysed independently: (1) nrDNA (ITS) and (2) cpDNA (*trnK* + *rps16*). Since both soft and hard (posterior probabilities [PP] ≥ 0.80 and ≥ 0.95 respectively) topological incongruences between nrDNA and cpDNA trees were detected (see the paragraph “Visualization of topological incongruence” below), analyses using a combined dataset were not performed.

Phylogenetic analyses were conducted using both Bayesian inference (BI) and maximum parsimony (MP). Bayesian analyses were performed with MrBayes v.3.2 for 64-bit systems (Ronquist & al., 2012), using the best substitution model for each sequenced region identified using the BIC criterion as implemented in jModeltest v.2.1.4 (Darriba & al., 2012). The indel partitions were treated as restriction data and analysed using the model settings recommended by Ronquist & al. (2009). Short preliminary runs were carried out with different hot chain temperatures (in the range 0.01–0.2) to check for swapping efficiency among chains. For the final analyses, the temperature parameter was fixed to $\text{temp} = 0.025$. Two Markov chain Monte Carlo (MCMC) runs with four chains each (one cold chain, three hot chains) were started from independent random seeds and computed 10 million generations, with trees sampled every 1000th generation. After discarding a burn-in of 3000 trees (30% of all sampled trees) from each run, a majority-rule consensus tree was calculated. Traces were visually inspected in Tracer v.1.6 (Rambaut & al., 2015) to ensure that the effective sample sizes (ESSs) of all parameters were >200 , as recommended by the authors, and to check the convergence of parameter estimates across runs. Nodes with PP ≥ 0.95 were considered to be strongly supported (Huelsenbeck & Rannala, 2004).

Parsimony analyses were conducted with TNT (Tree analysis using New Technology) v.1.1. (Goloboff & al., 2008), applying the traditional search option (TBR, Tree Bisection-Reconnection branch swapping) with equal character weights. In an initial run, 10,000 random addition sequence replicates were performed, using TBR branch-swapping and saving 10 trees per replicate. Since some replicates reached the maximum number of saveable trees, the trees from the first run were used as starting trees in a second heuristic search. Bootstrap support (BS) was calculated with 1000 replicates, each consisting of 500 random addition sequence replicates using TBR branch-swapping (saving 100 trees per replicate) in PAUP* v.4.0b10 (Swofford, 2002). BS values ≥ 70 were considered to indicate good node support (Hills & Bull, 1993). Consistency index (CI), retention index (RI), and rescaled consistency index (RC) were likewise calculated using PAUP*.

Visualization of topological incongruence. — To represent the differences between trees obtained with differently inherited markers (biparental vs. maternal, i.e., ITS vs. cpDNA) as a network, network building algorithms were run using the corresponding consensus trees. As a means of maintaining only statistically robust nodes, those with PP < 0.80 in majority-rule consensus trees from the Bayesian analysis were collapsed using Mesquite (Maddison & Maddison, 2014). Using this relatively low threshold, soft and hard incongruences can be shown at the same time. Collapsed trees were imported into SplitsTree v.4 (Huson & Bryant, 2006). The SuperNetwork algorithm was run with the Edge Weights option set to none (branch lengths are not taken into account). The network was not rooted in order to avoid graphical distortion.

■ RESULTS

Sequencing and alignments. — For this study, a total of 747 sequences was generated: 248 for ITS, 249 for the *rps16* intron, and 250 for the *trnK* region. As most of the ITS sequences provided unambiguous pherograms (i.e., without any signs of length polymorphisms), no cloning was performed, and, when required, single nucleotide polymorphisms were coded as IUPAC Nucleotide Codes. In addition to the newly generated sequences, 247 sequences were taken from GenBank (<http://www.ncbi.nlm.nih.gov>) to complete the taxon sampling. Table 1 summarizes details of alignment statistics for all markers and datasets including the proportions of parsimony-informative characters and the models of molecular evolution.

The topology of the 50% majority-rule consensus trees from the maximum parsimony and Bayesian analyses proved almost identical and differed only in the topology of some nodes that were poorly supported. As Bayesian trees were generally better resolved and supported, only the Bayesian topologies are shown. Bootstrap support derived from MP analyses were added to these trees.

Major clades in the ITS and cpDNA trees. — The topology of the cpDNA tree was generally similar to that of the ITS tree (Fig. 3; Electr. Suppl.: Fig. S1), but support values were overall slightly lower in the cpDNA tree. All genera were recovered as

well supported clades (in one or both trees), with the exception of *Phtheirospermum*. The generitype species, *Ph. japonicum*, grouped within tribe Pedicularideae (sensu McNeal & al., 2013; clade A; ITS PP = 1; BS = 97, cpDNA PP = 1; BS = 100; Electr. Suppl.: Fig. S1), while the remaining three species formed a clade with *Pterygiella* (ITS PP = 1; BS = 100, cpDNA PP = 1; BS = 86).

Comparing ITS and cpDNA topologies (Fig. 3; Electr. Suppl.: Fig. S1), only two cases (affecting six genera) of phylogenetic incongruence at generic or higher taxonomic levels were detected. These are visualized in a SuperNetwork (see below, Fig. 6A). The first is clade B (ITS PP = 0.93; BS = 86, cpDNA PP = 1; BS = 51; “*Pterygiella* complex II” sensu Dong & al., 2013; i.e., a clade composed of *Pterygiella*, *Pseudobartsia* and *Xizangia*) that was sister to tribe Rhinanthaeae s.str. (clades C–K) in cpDNA but related to tribe Pedicularideae (clade A) in ITS. The second concerns *Euphrasia* (clade H) and a clade that includes *Odontitella* and *Nothobartsia* (clade J). *Euphrasia* was part of a clade containing *Hedbergia* and *Tozzia* in ITS, but it was recovered as sister to clades F–K in cpDNA. On the other hand, clade J (ITS PP = 1; BS = 99, cpDNA PP = 1; BS = 99) was sister to *Hedbergia* (clade F) in the cpDNA tree, but sister to *Odontites* s.l.+*Macrosyringion* (clade K) in the ITS analysis (PP = 0.94; BS < 50).

Tribe Rhinanthaeae s.str. (clades C–K; clade V in McNeal & al., 2013) was strongly supported in both analyses (ITS PP = 1; BS = 97, cpDNA PP = 1; BS = 93). The branching pattern of clade C (*Melampyrum*), clade D (“RRL clade”, composed of *Rhinanthus*, *Lathraea* L. and *Rhynchocorys*) and the “core group of Rhinanthaeae” (clades E–K) was identical to that in Scheunert & al. (2012). *Bartsia alpina* L. (clade E) was the first-branching taxon within the core group of Rhinanthaeae. Leaving aside incongruent clades (clades H and J), the remaining taxa were grouped into two clades in the ITS tree, the first containing *Hedbergia* and *Tozzia* (clades F and G), and the

second grouping together the *Bellardia* and *Odontites* clades (clades I and K, respectively). All samples of *Tozzia* formed a clade (clade G; ITS PP = 1; BS = 100; cpDNA PP = 1; BS = 97). In the cpDNA tree, the position of *Tozzia* remained unresolved, as the branch that connected it with clade I-Bellardia plus clade K-Odontites had low support. Clade I-Bellardia was sister to clade K-Odontites in the cpDNA tree (PP = 0.91; BS = 54). Finally, all species of *Odontites* formed a clade (clade K) in both analyses, but with low support in the cpDNA tree (ITS PP = 1; BS = 95, cpDNA PP = 0.71; BS = 61).

Phylogenetic relationships among species of *Odontites* s.l. (clade K). — In the ITS tree, the clade K.2-Macrosyringion (grouping *O. longiflorus* and *O. glutinosus*) appeared nested within *Odontites*, but was recovered as sister to the remaining *Odontites* in cpDNA (Fig. 4, clade K.2; ITS PP = 1; BS = 100; cpDNA PP = 1; BS = 100). Five main lineages were detected in the ITS analysis, and confirmed in the cpDNA tree (Figs. 4, 5). Relationships among these five lineages remained unclear due to low support and short lengths of some internal branches, especially in the ITS analysis. The two species included in the K.1-Pyrenaeus clade (ITS PP = 1; BS = 100; cpDNA PP = 1; BS = 100), *O. cebennensis* H.J.Coste & Soulié and *O. pyrenaeus* (Bubani) Rothm., were monophyletic according to the ITS tree. However, in the cpDNA tree, only the samples corresponding to the former were recovered as a clade, whereas the later formed a grade. The well-supported K.2-Macrosyringion clade was composed of two species, both recovered as monophyletic. In the K.3-Bornmuellerantha clade (ITS PP = 1; BS = 97; cpDNA PP = 1; BS = 100), it was not possible to test the reciprocal monophyly of its two species as only one sequence of *O. alshehbazianus* (Dönmez & Mutlu) A.Fleischm. & Heubl was analysed. The K.4-Viscosus clade contains a higher number of taxa compared to clades K.1 to K.3. The K.4 clade was monophyletic in the ITS tree (PP = 1; BS = 95), but divided into two subclades in the cpDNA tree, with one being sister to the K.1-Pyrenaeus clade.

Table 1. Summary of sequence characteristics and analysis results for the different regions and datasets.

	ITS	<i>rps16</i>	<i>trnK</i>	cpDNA
Number of individuals	353	308	333	349
Taxon sampling: species (genera)	87 (21)	65 (19)	75 (20)	83 (20)
Length of newly generated sequences in bp (average)	577–734 (695)	524–861 (826)	676–1057 (1038)	–
Aligned length in bp, after trimming	797	952	1128	2080
Number of coded indels	138	85	64	149
% total missing data	6.3	3.3	3.0	10.7
Model of molecular evolution (Bayesian information criterion)	SYM+I+G	TVM+G	TVM+G	–
No. of variable sites (%)	579 (61.9)	–	–	949 (42.6)
No. of parsimony-informative sites (%)	483 (51.7)	–	–	621 (27.9)
Tree length of most parsimonious trees	2123	–	–	1614
Consistency index (CI)	0.4207	–	–	0.7127
CI excluding uninformative sites	0.3931	–	–	0.6347
Retention index (RI)	0.9203	–	–	0.9491
Rescaled consistency index (RC)	0.3872	–	–	0.6764

Fig. 3. Majority-rule consensus trees from the Bayesian analysis of tribe Rhinanthae ITS and cpDNA datasets, with branch support (PP/BS). Main clades are indicated with different letters. Clade names: A, Tribe Pedicularideae, B, Pterygiella Complex II, C, Melampyrum, D, RRL, E, Bartsia s.str., F, Hedbergia, G, Tozzia, H, Euphrasia, I, Bellardia, J, Nothobartsia-Odontitella, K, Odontites. Clades corresponding to genera were collapsed.

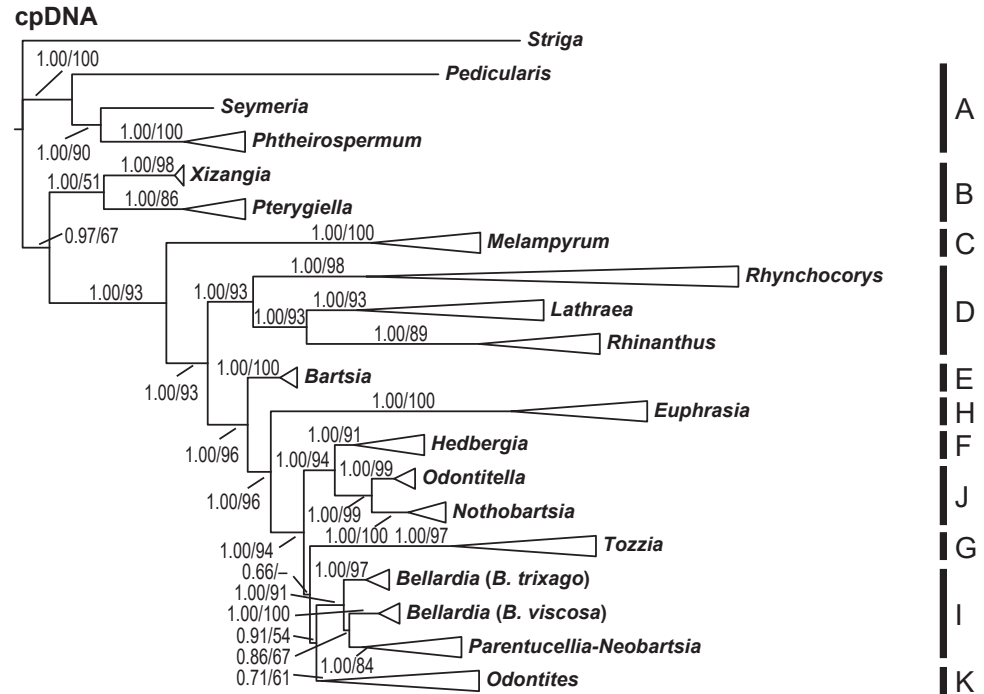
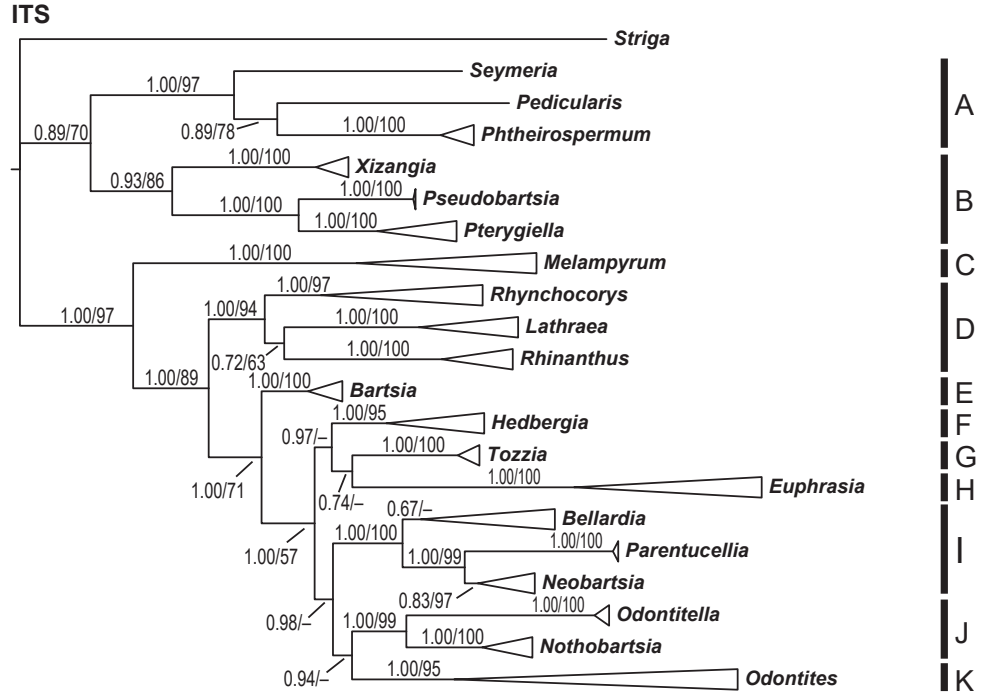
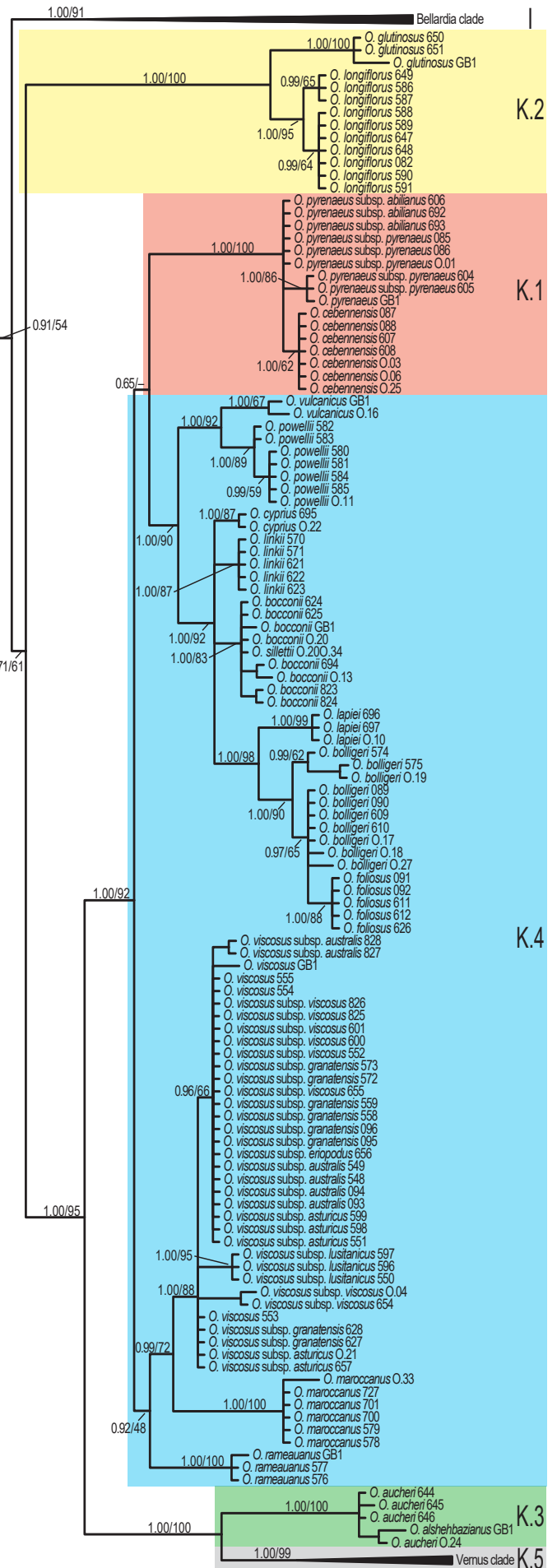
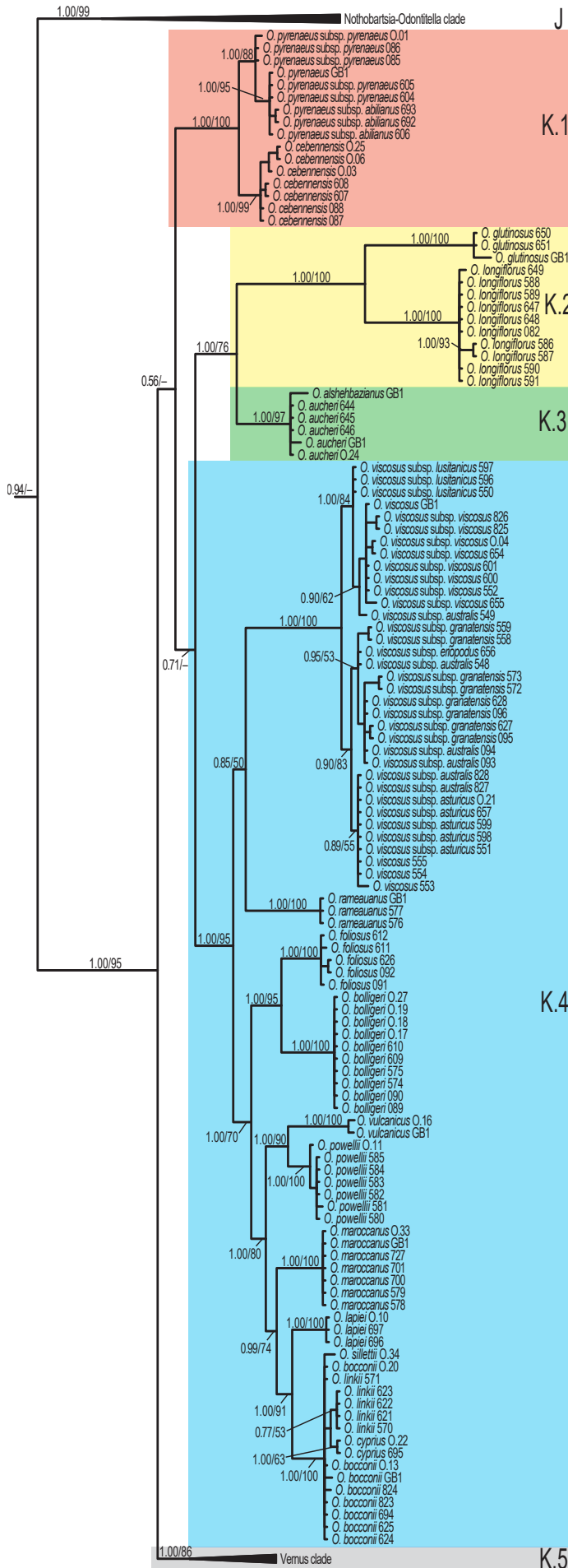


Fig. 4. Majority-rule consensus trees from the Bayesian inference analysis, with branch support (PP/BS), showing the main clades of *Odontites* and sister clades (J-Nothobartsia-Odontitella, I-Bellardia) based on ITS and cpDNA. Main lineages are indicated with different colours and letters. Clade names: K.1-Pyrenaeus, K.2-Macroxyringion, K.3-Bornmuellerantha and K.4-Viscosus. Clade K.5-Vernus was collapsed. Ma., *Macroxyringion*; O., *Odontites*; Synonyms: *O. cyprius* = *O. linkii* subsp. *cyprius*; *O. glutinosus* = *Ma. glutinosum*; *O. longiflorus* = *Ma. longiflorum*.

ITS

cpDNA



However, given that the branch that grouped K.1 with this K.4 subclade had low support (PP = 0.65; BS < 50), the topologies of the two trees showed a soft incongruence and became compatible when a branch collapsing threshold of PP < 0.80 was applied. Most of the species sampled of the K.4-Viscosus clade proved to be monophyletic (with two exceptions; i.e., *O. bolligeri* E.Rico & al. in the cpDNA tree, and the species belonging to the “Bocconii group” sensu Bolliger, 1996). Finally, of the large number of taxa in the K.5-Vernus clade (ITS PP = 1; BS = 86; cpDNA PP = 1; BS = 99), which have been described based on morphology, only four narrowly endemic species formed monophyletic groups: *O. corsicus* (Loisel.) G. Don. (in ITS only), *O. hollianus* (Lowe) Benth., *O. kaliformis* (Pouret. ex Willd.) Pau, and *O. recordonii* Burnat & Barbey.

Several cases of topological incongruence were detected at both the intrageneric and interspecific levels. At the intrageneric level (Fig. 6A), the K.3-Bornmuellerantha clade was sister to the K.2-Macrosyringion clade in the ITS tree (PP = 1; BS = 76), but sister to the K.5-Vernus clade in the cpDNA tree (PP = 1; BS = 100). At the interspecific level, there were two cases of incongruence, both in the K.4-Viscosus clade (Fig. 6B). The first case concerned *O. maroccanus* Bolliger. It was sister to *O. viscosus* (L.) Clairv. in the cpDNA tree (PP = 0.99; BS = 72), but sister to a clade containing *O. lapiei* Batt. and the Bocconii-linkii clade (PP = 0.99; BS = 74) in the ITS tree. The second incongruence concerned a clade that included two species: *O. bolligeri* and *O. foliosus* Pérez Lara. This clade was sister to *O. lapiei* in the cpDNA tree (PP = 1; BS = 98), but part of a clade that included most of the North African and Central to Eastern Mediterranean species (PP = 1; BS = 70) in ITS.

DISCUSSION

Delimitation of tribe Rhinanthae. — Here, the most comprehensive phylogeny of tribe Rhinanthae to date, including two or more samples of all recognized genera, is presented. All major clades revealed in previous ITS phylogenies were confirmed as well as most of the clades recovered in previous cpDNA studies (Scheunert & al., 2012; Dong & al., 2013; McNeal & al., 2013; Uribe-Convers & Tank, 2015; Gaudeul & al., 2016). The monophyly of tribe Rhinanthae (sensu McNeal & al., 2013, i.e., including the East Asian *Pterygiella* complex II) was not supported by our ITS tree, as the *Pterygiella* complex II was recovered as sister to tribe Pedicularideae (Fig. 3A, clades B and A respectively). In the cpDNA analysis, it was sister to Rhinanthae s.str., although both groups were separated by long branches (i.e., large genetic distances). This topological incongruence had previously been detected by McNeal & al. (2013) and Zhou & al. (2014), although they did

not explicitly comment on it. McNeal & al. (2013) even proposed a node-based definition of the Rhinanthae that omitted this finding. The monophyly of the *Pterygiella* complex II has been clearly demonstrated (Dong & al., 2013), and the observed topological incongruence casts its inclusion in tribe Rhinanthae into doubt. Additionally, the members of this complex have at least two morphological characters that differentiate them from those of tribe Rhinanthae s.str. (clade V in McNeal & al., 2013). First, they have a five-toothed instead of a four-toothed calyx as present in the Rhinanthae (Molau, 1988, 1990; Hong & al., 1998; Benedi & al., 2009). Second, all species in the *Pterygiella* complex II have pollen grains of types Ia-1 or IV (with granulate or regularly retipilate exine sculpturing, and a size of <27 µm; Lu & al., 2007), while in tribe Rhinanthae s.str. pollen grains have variable exine surfaces and sizes >27 µm (except in *Tozzia*; İnceoğlu, 1982; Minkin & Eshbaugh, 1989; Bolliger & Wick, 1990; Lu & al., 2007). Further studies are necessary to shed light on the tribal placement of *Pseudobartsia*, *Pterygiella* and *Xizangia*, using an adequate selection of markers and samples.

Our results validate the polyphyly of *Phtheirospermum*, as already suggested by various authors (Dong & al., 2013; McNeal & al., 2013; Zhou & al., 2014). The generitype species, *Ph. japonicum* (= *Ph. chinense* Bunge ex Fisch. & C.A.Mey.), clustered within tribe Pedicularideae (clade A-Pedicularideae), but the other three species of *Phtheirospermum* formed a clade together with *Pterygiella* (clade B-*Pterygiella* complex II; see Fig. S1). As recommended by McNeal & al. (2013), the most conservative option is to include *Ph. muliense* C.Y.Wu & D.D.Tao, *Ph. parishii* Hook.f., and *Ph. tenuisectum* Bureau & Franch. in *Pterygiella*. The following new combinations are therefore required:

Pterygiella muliense (C.Y.Wu & D.D.Tao) Pinto-Carrasco, E.Rico & M.M.Mart.Ort., **comb. nov.** ≡ *Phtheirospermum muliense* C.Y.Wu & D.D.Tao in Acta Bot. Yunnan. 18: 307, fig. 4. 1996.

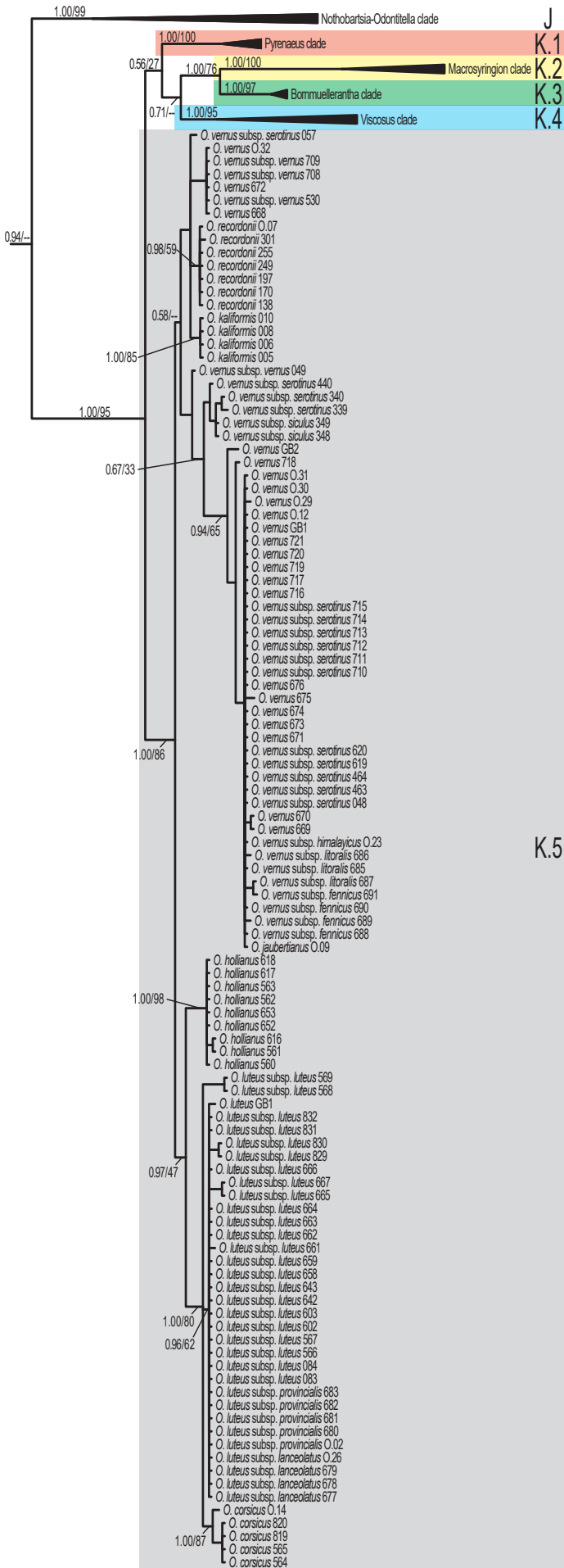
Pterygiella parishii (Hook.f.) Pinto-Carrasco, E.Rico & M.M.Mart.Ort., **comb. nov.** ≡ *Phtheirospermum parishii* Hook.f., Fl. Brit. India 4: 304. 1884.

Pterygiella tenuisecta (Bureau & Franch.) Pinto-Carrasco, E.Rico & M.M.Mart.Ort., **comb. nov.** ≡ *Phtheirospermum tenuisectum* Bureau & Franch. in J. Bot. (Morot) 5: 129. 1891.

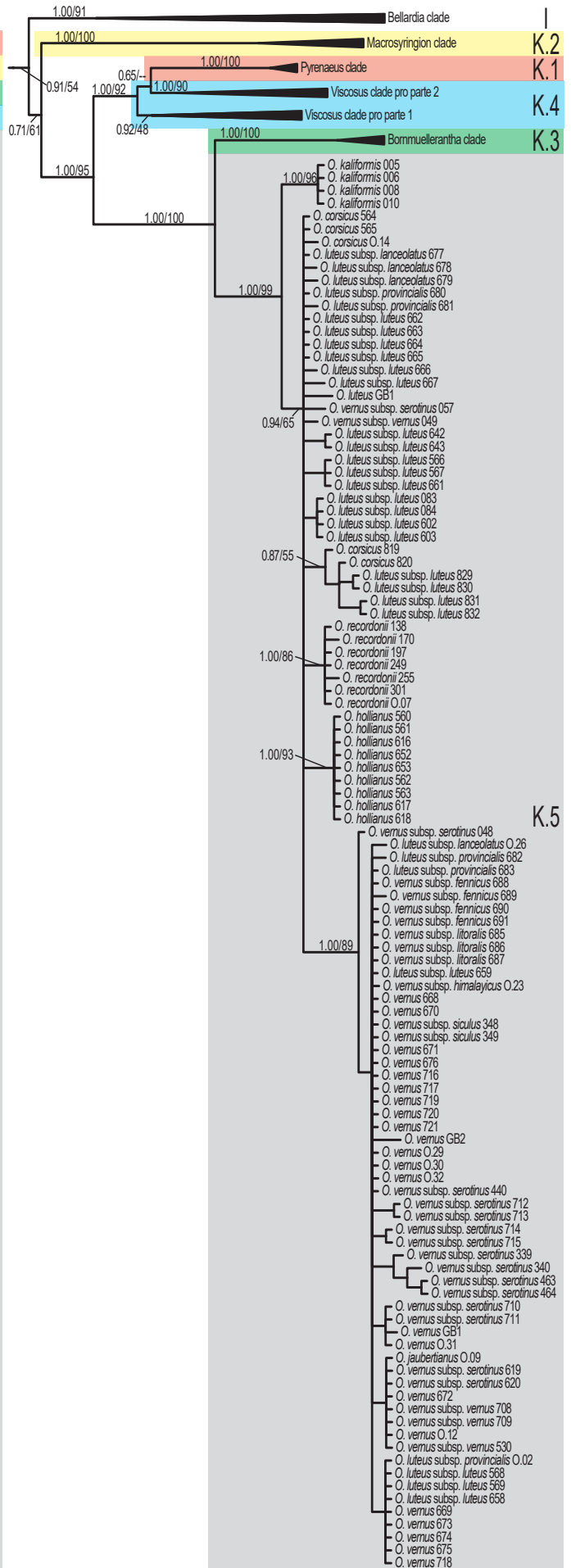
Relationships within tribe Rhinanthae. — Relationships among genera in tribe Rhinanthae s.str. as presented here are very similar to those previously reported. The position of the

Fig. 5. Majority rule consensus trees from the Bayesian inference analysis, with branch support (PP/BS), showing the K.5- Vernus clade based on A) ITS and B) cpDNA. Other clades belonging to *Odontites* (K.1- Pyrenaeus, K.2- Macrosyringion, K.3- Bornmuellerantha and K.4- Viscosus) and sister clades (J- Nothobartsia-Odontitella, I- Bellardia) were collapsed. O. = *Odontites*. Synonyms: *O. luteus* subsp. *lanceolatus* = *O. lanceolatus* subsp. *lanceolatus*; *O. luteus* subsp. *provincialis* = *O. lanceolatus* subsp. *provincialis*; *O. vernus* subsp. *fennicus* = *O. litoralis* subsp. *fennicus*; *O. vernus* subsp. *himalayicus* = *O. vulgaris* subsp. *himalayicus*; *O. vernus* subsp. *litoralis* = *O. litoralis* subsp. *litoralis*; *O. vernus* subsp. *serotinus* = *O. vulgaris* subsp. *vulgaris*; *O. vernus* subsp. *siculus* = *O. vulgaris* subsp. *siculus*.

ITS



cpDNA



most basal clades (clade C-Melampyrum, clade D-RRL and clade E-Bartsia s.str.) seems to be undisputed, as the same topology was recovered with high support in most studies (Těšitel & al., 2010; Scheunert & al., 2012; McNeal & al., 2013, Uribe-Convers & Tank, 2015), with only one exception (Gaudeul & al., 2016), probably due to incorrect outgroup selection. The branching order of the remaining genera is more questionable. The presence of short branches, poorly supported

nodes and incongruence among markers results in discordant evolutionary hypotheses among studies. One of the most controversial points is the position of *Tozzia*. Our study is the first to analyse more than one sample (including *T. alpina* subsp. *carpathica* (Woł.) Pawł. & Jasiewicz = *T. carpathica* Woł.) of *Tozzia*, confirming its monophyly. With respect to this genus, our topologies disagree with three previously published phylogenies (McNeal & al., 2013; Uribe-Convers & Tank 2015;

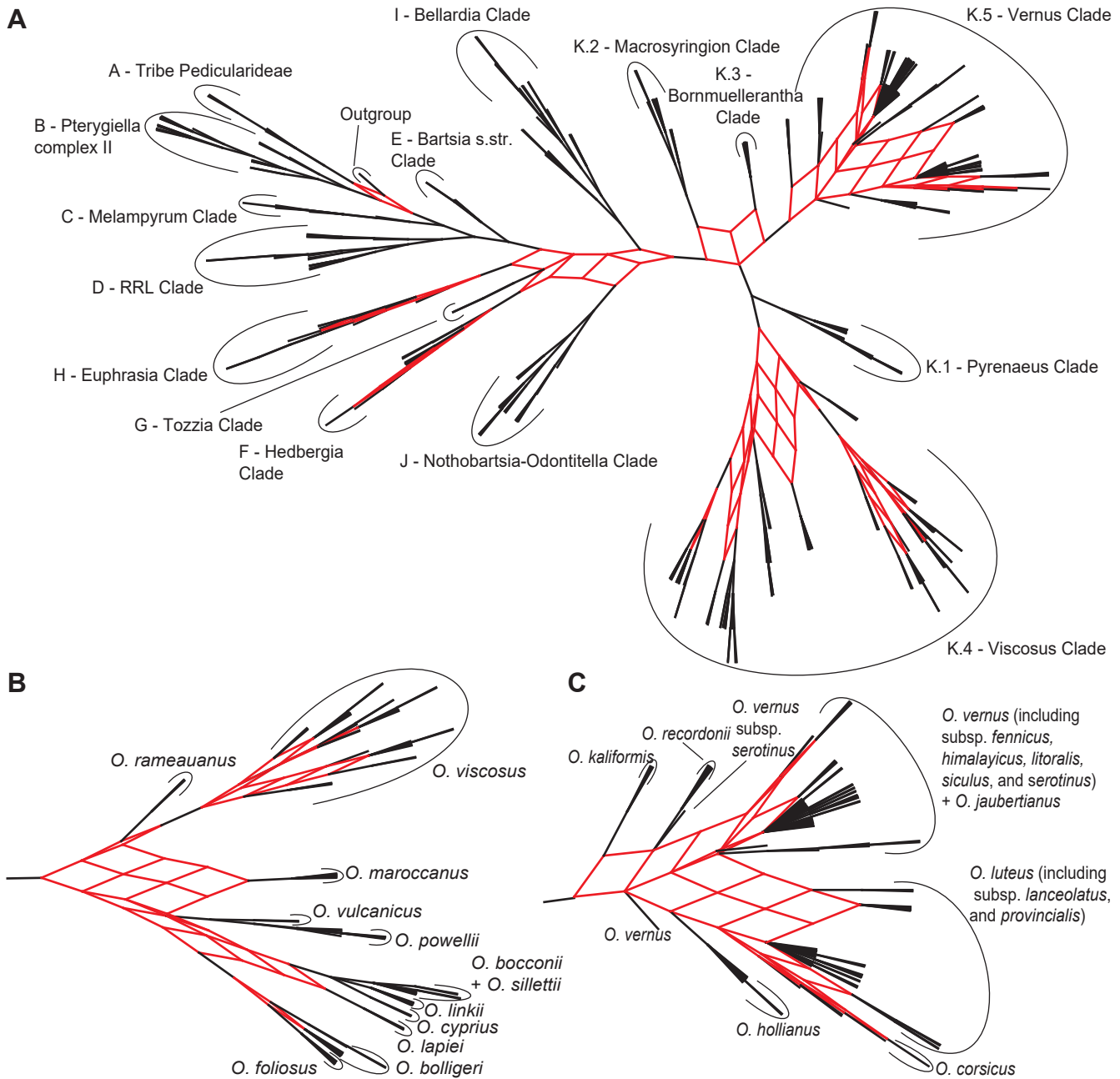


Fig. 6. SuperNetwork obtained from the Bayesian inference trees (branches collapsed at PP < 0.8) illustrating the incongruence between ITS and cpDNA topologies. Branch lengths were not taken into account. Clades are named as in Figs. 2–4. **A**, Tribe Rhinantheae; **B**, K.4-Viscosus clade; **C**, K.5-Vernus clade. Ma., *Macrosyringion*; O. = *Odontites*. Synonyms: *O. cyprius* = *O. linkii* subsp. *cyprius*; *O. luteus* subsp. *lanceolatus* = *O. lanceolatus* subsp. *lanceolatus*; *O. luteus* subsp. *provincialis* = *O. lanceolatus* subsp. *provincialis*; *O. vernus* subsp. *fennicus* = *O. litoralis* subsp. *fennicus*; *O. vernus* subsp. *himalayicus* = *O. vulgaris* subsp. *himalayicus*; *O. vernus* subsp. *litoralis* = *O. litoralis* subsp. *litoralis*; *O. vernus* subsp. *serotinus* = *O. vulgaris* subsp. *vulgaris*; *O. vernus* subsp. *siculus* = *O. vulgaris* subsp. *siculus*.

Gaudeul & al., 2016; Fig. 1), but agree with Scheunert & al. (2012). In all cases, the phylogenetic relationships of *Tozzia* are not statistically supported (in both nrDNA and cpDNA trees). Furthermore, the morphology and life form of *Tozzia* is so different from that of the phylogenetically most closely related genera [e.g., unilocular one-seeded and slightly fleshy indehiscent (sometimes dehiscent by late ripening) fruits vs. bilocular many-seeded dry capsules] that it is not possible to make a suggestion concerning its relationships. The evolutionary history of *Tozzia* needs more thorough study.

Concerning clade J, our results agree with previous phylogenies (Scheunert & al., 2012; Gaudeul & al., 2016) placing the Iberian endemic *Odontitella* as sister to, however clearly differentiated from, the Iberian subendemic *Nothobartsia*. Despite the great number of shared character states between *Odontitella* and *Nothobartsia* (e.g., strongly bilabiate corolla with entire galea, papillose pubescence of stamen filaments, mucronate anthers, retipilate pollen exine sculpturing, long-stalked calycinal glandular hairs absent; Bolliger & Molau, 1992), only a few of them differentiate this clade from *Odontites* (clade K), due to the high morphological variability in the latter genus. Diagnostic characters include the stem indument, which in the members of clade J is composed only of eglandular antrorse (sometimes antrorse to patent) hairs, while this specific type of hair is never present in *Odontites* (Benedí, 2009; Rico, 2009). Additionally, corolla colour darkens during anthesis, from yellow to brownish-red, in *Odontitella virgata* (Link) Rothm. and *N. asperrima* (Link) Benedí & Herrero (not observable in *N. spicata* (Ramond) Bolliger & Molau as its corolla is invariably purple-violet), while it has never been found to change in any species of *Odontites*. On the other hand, there are several characters that separate *Odontitella* and *Nothobartsia*. *Odontitella* is an annual, with entire to few-toothed, linear to narrowly lanceolate leaves, bracts resembling the leaves, corolla tube shorter than (or as long as) the calyx, and style clavate beneath the stigma, while *Nothobartsia* is a perennial, with crenate to dentate, broadly ovate or elliptical leaves, bracts not resembling the leaves, corolla tube longer than calyx, and style not clavate beneath the stigma. The inclusion of *Nothobartsia* in *Odontitella* is therefore not supported by morphological data, and phylogenetic data do not provide direct evidence to merge them. Thus, we propose to maintain them as separate genera.

Delimitation and main lineages of *Odontites* (clade K). —

The delimitation of *Odontites* has long been controversial. The topologies presented here generally agree with those of Scheunert & al. (2012), but disagree with the cpDNA tree obtained by Gaudeul & al. (2016). In the latter study, *Macrosyringion* was recovered as sister to a clade composed by *Bellardia* and *Parentucellia*, with high support. However, based on our results, and in contrast to the taxonomy used by these authors, we propose that *M. longiflorum* (Lam.) Rothm. and *M. glutinosum* (M.Bieb.) Rothm. should be transferred back to *Odontites*. Consequently, our clade-based definition of *Odontites* is: the least inclusive crown clade containing *O. pyrenaicus* (Bubani) Rothm., *O. longiflorus* (Lam.) G.Don., *O. aucheri* Boiss., *O. viscosus* (L.) Clairv., and *O. vernus* (Bellardi) Dumort. (= *Euphrasia odontites* L.; type of the genus name).

The reinclusion of *Macrosyringion* in *Odontites* does not involve any nomenclatural changes, as validly published combinations already exist for these taxa: *O. longiflorus* (Lam.) G.Don and *O. glutinosus* (M.Bieb.) Benth. Furthermore, as samples of *O. longiflorus* subsp. *lateritius* (Charpin & Fern. Casas) Sánchez-Gómez and *O. longiflorus* var. *roseus* A.Segura did not genetically differ from other samples of *O. longiflorus*, and morphological differences among them are superficial, we do not consider them separate taxonomic entities.

The five main lineages of *Odontites* can be distinguished morphologically using characters related mainly to the flower and inflorescence (Fig. 2). Table 2 summarizes the states of several morphological traits present in the species of the respective lineages. The morphological characterization of these five lineages is based on the comparison of the extensive descriptions found in the monograph by Bolliger (1996), *Flora iberica* (Rico, 2009), as well as in the papers where new taxa were described (Dönmez & Mutlu, 2010; Brullo & al., 2015). The morphologically most distinct lineages are clade K.2-Macrosyringion and clade K.3-Bornmuellerantha, which have at least five and three morphological synapomorphies, respectively; by contrast, the taxa belonging to clade K.4-Viscosus have only one (and a second character state is almost synapomorphic). The K.1-Pyrenaicus and K.5-Vernus lineages share at least nine character states that, despite not being unique, are useful in combination to distinguish these from the remaining lineages. However, in our opinion, the only characters which unambiguously differentiate those two lineages from each other are cell number, orientation of cellular divisions, and outline of the head of the calycinal glandular hairs. In the Lanceolata and Kaliformis-types (present in only some species of the K.5-Vernus clade) of long-stalked glands (Bolliger, 1985), the general arrangement of the glandular head (sphaerical, with two to 16 cells, derived mainly from longitudinal divisions) is almost identical to that of the typical short-stalked glandular hairs differing only in length. In our view, the Lanceolata and Kaliformis-type glands should be reclassified to be included into the variability of the short-stalked glands. Therefore, all members of the K.5-Vernus clade lack long-stalked calycinal glands, while those belonging to the K.1-Pyrenaicus clade show Pyrenaica-type glands (ellipsoid to sphaerical and composed of a much higher number of cells [30–200], which derive from both transversal and longitudinal divisions).

A widely used character, at least in dichotomous keys (e.g., Webb & Camarasa, 1972; Bolliger, 1996), is corolla colour. However, its usefulness is dubious. Fixed colours are found only in the K.3-Bornmuellerantha and K.1-Pyrenaicus lineages, which consistently have yellow corollas. Nevertheless, there exist species in all other lineages sharing this character state (Fig. 2). Within lineages, corolla colour is useful in K.5-Vernus as stated below. At the species level, corolla colour is almost constant in most cases. In *O. longiflorus*, *O. jaubertianus*, and *O. viscosus*, however, this character is polymorphic (yellow and pink in the first two species, and a gradient from yellow to dark red in the latter; Fig. 2). Taking into account these facts, corolla colour can be useful as the main character to differentiate groups of species only in particular cases (e.g., K.5-Vernus clade).

Although it was not possible to include samples of several narrowly endemic species from North Africa, Sicily, and the Near East in our study, we can place them preliminarily into our lineages, using the cpDNA data from Gaudeul & al. (2016). *Odontites hispidulus* (Boiss.) Bolliger, endemic to Lebanon and Syria, is morphologically very similar to *O. luteus* (L.) Clairv. (Bolliger, 1996). The species was recovered within clade B2 by Gaudeul & al. (2016), which is part of our K.5-Vernus lineage. Based on this evidence, we tentatively consider *O. hispidulus* to be a member of the K.5-Vernus clade. All but one North African species (i.e., *O. discolor* Pomel, *O. purpureus* (Desf.) G. Don, *O. triboutii* Gren. & Paill. and *O. violaceus* Pomel), and the Sicilian *O. rigidifolius* (Biv.) Benth., which were not sampled here, in Gaudeul & al. (2016) were part of a highly supported clade with *O. vulcanicus* Bolliger, *O. powellii* Maire, *O. linkii* Heldr. & Sart. ex Boiss.,

O. bocconii (Guss.) Walp. and *O. lapiei*. All of these taxa are found within our K.4-Viscosus lineage; thus, the unsampled species are likely to be part of K.4-Viscosus as well. The only North African species for which phylogenetic affinities remain unknown is the Tunisian endemic *O. citrinus* Bolliger. The morphologically most similar and geographically nearest species is *O. triboutii* (endemic from NE Algeria and Tunisia), and together they form the Triboutii-group (Bolliger, 1996). Therefore, we tentatively include *O. citrinus* in our K.4-Viscosus lineage. A list of taxa included in each lineage is provided in Table 3.

Species monophyly, hybridization, and ILS: Assessing taxonomic boundaries within *Odontites*. — By including at least two samples per species, we were able to test the monophyly of the vast majority of species studied. Within *Odontites*, only three species (*O. alshehbazianus*, *O. jaubertianus* and

Table 2. Morphological characters for differentiation of lineages or groups of species.

	Lineage				
	K.2-Macrocyringion	K.3-Bornmuellerantha	K.4-Viscosus	K.1-Pyrenaeus	K.5-Vernus
Glandular hairs at base of stem	present (0.2–0.3 mm)	absent	absent (present – 0.5 to 3.0 mm – in <i>O. viscosus</i> *)		absent
Long-stalked glands on calyx	present (longiflora type)	present (pyrenaea type)	present (rameauana, pyrenaea and viscosa types) or absent	present (pyrenaea type)	absent
Corolla shape	strongly bilabiate	subrotate	strongly bilabiate		strongly bilabiate
Corolla hairs	glandular plus eglandular	eglandular (restricted to lips)	absent or almost absent (tube with eglandular hairs in <i>O. rameauanus</i>)		eglandular
Corolla tube	long (2–5 times longer than calyx)	short (slightly shorter or longer than calyx)	short (slightly shorter or longer than calyx)		short (slightly shorter or longer than calyx)
Corolla upper lip	straight	-	folded downwards	straight	straight or folded upwards*
Theca base	mucronate	obtuse	mucronate		mucronate
Pollen exine	retipilate	retirugulate	microreticulate or retipilate		microreticulate
Stigma shape	bilobate	entire	entire		entire
Habit	annual	annual	annual or perennial*		annual
Growth form	erect	erect	erect or prostrate	erect	erect or prostrate
Inflorescence type	acropetal	acropetal	acropetal or basipetal*		acropetal
Toothed bracts	no	no	no		yes or no
Corolla colour	yellow or very rarely pink	yellow	yellow, pink, dark red* or bicoloured*	yellow	yellow or pink
Stamen filament pubescence	papillose	glabrous	papillose or glabrous	papillose	papillose or pilose* (glabrous in <i>O. corsicus</i>)
Seed number	17–40	10–12	4*–20	8–14	12–40
Chromosome number	22–24–26	24	20–22–24–26	24	18*–20–22–24–26–40*

Synapomorphies for each lineage are in bold.

* Character state present in only one lineage, but not shared by all species.

O. sillettii Brullo & al.) were represented by a single sequence, and the monophyly of them thus remains undemonstrated. Of the remaining 23 species (78%), 18 were monophyletic and were recovered as well-supported clades in at least one dataset (most of them in both datasets). All of them are recognized here as valid species (Table 3). The monophyly of *O. linkii* (as circumscribed by Bolliger, 1996, i.e., including *O. cyprius* Boiss. and *O. creticus* Boiss.) was not supported. In the cpDNA analysis, these sequences formed two clades that corresponded to the samples collected in Cyprus and the Peloponnese, respectively. Additionally, the samples from Cyprus were also recovered as monophyletic in the ITS tree, which encourages us to recognize the taxon as a separate species under the resurrected name *O. cyprius*. The taxonomic status of *O. creticus* remains unknown.

Regarding *Odontites hollianus*, the samples from Madeira Island (Madeira Archipelago) were molecularly indistinguishable from those collected in La Palma Island (Canary Islands). Morphologically, the Canary Islands plants are very similar to those from Madeira, but there is a slight difference in stamen morphology that has been considered taxonomically useful (i.e., Rothmaler, 1943; Bolliger, 1996). The papillae on the stamen filaments are ca. 45 µm long in the Canary Island samples, instead of ca. 30 µm in the Madeiran material. Despite their clear isolation by distance (ca. 500 km), the incipient morphological differentiation is not sufficient to segregate the Canary Island populations in a new taxon (subspecies or species). Further studies using adequate molecular tools (e.g., microsatellites; Pinto-Carrasco & al., 2016) are necessary to investigate its genetic isolation and re-evaluate our conservative taxonomic treatment.

By comparing the trees obtained from the ITS and cpDNA datasets, we detected incongruences at three levels (lineages, species, and individuals). The backbones of the ITS and cpDNA trees show short branches and low support (Figs. 3 and 4). This situation is consistent with a scenario where several lineages evolved in a short time (Wortley & al., 2005). The soft incongruence affecting the K.1-Pyrenaeus and K.4-Viscosus clades could be the result of such a scenario, since each genetic

Table 3. Taxa assigned to particular phylogenetic lineages.

Lineage	Species and subspecies of <i>Odontites</i> Ludw.
K.1-Pyrenaeus	<i>O. cebennensis</i> H.J.Coste & Soulié <i>O. pyrenaeus</i> (Bubani) Rothm. subsp. <i>pyrenaeus</i> <i>O. pyrenaeus</i> subsp. <i>abilianus</i> P.Monts.
K.2-Macrosyringion	<i>O. glutinosus</i> (M.Bieb.) Benth. <i>O. longiflorus</i> (Lam.) G.Don
K.3-Bornmuellerantha	<i>O. alshehbazianus</i> (Dönmez & Mutlu) A.Fleischm. & Heubl <i>O. aucheri</i> Boiss.
K.4-Viscosus	<i>O. bocconii</i> (Guss.) Walp. <i>O. bolligeri</i> E.Rico & al. * <i>O. citrinus</i> Bolliger <i>O. cyprius</i> Boiss. * <i>O. discolor</i> subsp. <i>ciliatus</i> (Pomel) Bolliger * <i>O. discolor</i> Pomel subsp. <i>discolor</i> <i>O. foliosus</i> Pérez Lara <i>O. lapiei</i> Batt. <i>O. linkii</i> Heldr. & Sart. ex Boiss. <i>O. maroccanus</i> Bolliger <i>O. powellii</i> Maire * <i>O. purpureus</i> (Desf.) G.Don <i>O. rameauanus</i> Emb. * <i>O. rigidifolius</i> (Biv.) Benth. <i>O. sillettii</i> Brullo & al. * <i>O. triboutii</i> Gren. & Paill. * <i>O. violaceus</i> Pomel <i>O. viscosus</i> subsp. <i>asturicus</i> M.Lainz <i>O. viscosus</i> subsp. <i>australis</i> (Boiss.) Jahand. & Maire <i>O. viscosus</i> subsp. <i>eriopodus</i> Litard. & Maire <i>O. viscosus</i> subsp. <i>granatensis</i> (Boiss.) Bolliger <i>O. viscosus</i> subsp. <i>lusitanicus</i> Bolliger <i>O. viscosus</i> (L.) Clairv. subsp. <i>viscosus</i> <i>O. vulcanicus</i> Bolliger
K.5-Vernus	<i>O. corsicus</i> (Loisel.) G.Don. * <i>O. hispidulus</i> (Boiss.) Bolliger <i>O. hollianus</i> (Lowe) Benth. <i>O. jaubertianus</i> (Boreau) D.Dietr. <i>O. kaliformis</i> (Pourr. ex Willd.) Pau <i>O. luteus</i> subsp. <i>lanceolatus</i> (Gaudin) P.Fourn. <i>O. luteus</i> (L.) Clairv. subsp. <i>luteus</i> <i>O. luteus</i> subsp. <i>provincialis</i> (Bolliger) J.-M.Tison <i>O. recordonii</i> Burnat & Barbey <i>O. vernus</i> subsp. <i>fennicus</i> (Markl.) Pinto-Carrasco & al. <i>O. vernus</i> subsp. <i>himalayicus</i> (Pennell) Pinto-Carrasco & al. <i>O. vernus</i> subsp. <i>litoralis</i> (Fr.) Nyman * <i>O. vernus</i> subsp. <i>mesatlanticus</i> (Emb. & Maire) Pinto-Carrasco & al. <i>O. vernus</i> subsp. <i>serotinus</i> Corb. <i>O. vernus</i> subsp. <i>siculus</i> (Guss.) Sell <i>O. vernus</i> (Bellardi) Dumort. subsp. <i>vernus</i>

* Not included in our molecular analysis. Inclusion in its lineage based on morphological similarity and/or results by Gaudeul & al. (2016).

marker could reveal a slightly different evolutionary history. Concerning the phylogenetic relationships among the clades K.3-Bornmuellerantha, K.5-Vernus, and K.2-Macrosyringion observed in the trees, two alternative hypotheses involving ancient homoploid hybridization could be postulated: (A) ancestors of the K.5-Vernus and K.2-Macrosyringion clades hybridized to generate the K.3-Bornmuellerantha clade; or (B) the K.2-Macrosyringion clade was the result of an interspecific cross between the ancestor of the K.3-Bornmuellerantha clade and a currently extinct taxon that would be the ancestor of the extant *Odontites*. Supporting the first option, species belonging to clades K.5 and K.2 are present where the taxa of K.3 grow today (Near East, from Turkey to the Caspian Sea; Bolliger, 1993, 1996). On the other hand, the low support for the sister relationship of clade K.2 and the remaining clades (K.1, K.3–5) in the cpDNA tree are in agreement with the second hypothesis as this could be the result of not sampling its extinct maternal parent. Morphologically, K.3-Bornmuellerantha and K.2-Macrosyringion are the two most divergent clades (three and five synapomorphies, respectively; Table 2), which blurs their phylogenetic relationships. The choice of either hypothesis would be merely speculative; further studies are needed to clarify this issue. In case reticulate evolutionary processes should have led to the formation of *O. maroccanus* and *O. bolligeri*–*O. foliosus* (and thus would have caused the observed incongruence between nuclear and plastid trees), they might have occurred more recently than those of the Bornmuellerantha/Macrosyringion clades, as the presumed parents should have been members of the K.4-Viscosus clade. The node ages recently published by Gaudeul & al. (2016) corroborate our findings. According to these authors, the K.3-Bornmuellerantha clade diverged from the K.5-Vernus clade around 10.3 million years ago (mya), while *O. maroccanus* diverged from *O. viscosus*, and *O. bolligeri*–*O. foliosus* (included under the nomen nudum *O. squarrosus*; Rico & al., 2008) from *O. lapiei* around 4.8 and 2.9 mya, respectively.

Regarding the highly polymorphic *O. viscosus*, not all morphological subspecies constituted molecular clades (Fig. 4). However, the samples were to some extent structured by geography in the ITS tree. This situation might be due to a scenario of recent and/or current gene flow between subspecies in contact zones; this was also postulated using morphological data (gradation in some characters in contact zones; Bolliger, 1996; Rico, 2009). *Odontites viscosus* subsp. *asturicus* M.Laínz and *O. viscosus* subsp. *granatensis* (Boiss.) Bolliger are morphologically and ecologically similar (small few-branched orophytes), but phylogenetically indistinguishable from *O. viscosus* subsp. *australis* (Boiss.) Jahand. & Maire and *O. viscosus* subsp. *eriododus* Litard. & Maire. Finally, the samples of *O. viscosus* subsp. *lusitanicus* Bolliger group together in both analyses. Despite Rico (2009) considering this subspecies to be part of the huge variability of *O. viscosus* subsp. *australis*, we temporarily reinstate *O. viscosus* subsp. *lusitanicus* until further studies shed light on the validity and the distribution range of all subspecies.

The molecular delimitation of the K.5-Vernus clade as a whole was unambiguous (Fig. 5), but species delimitation

within this group was more problematic, likely due to extensive phylogenetic incongruence (Fig. 6C). Only four species within the complex were recovered as monophyletic and are therefore accepted here (*O. corsicus*, *O. hollianus*, *O. kaliformis*, and *O. recordonii*). The remaining three species (i.e., *Odontites vernus* s.l., *O. luteus* s.l., *O. jaubertianus*) were completely intermixed in the cpDNA tree. They form two morphological groups of taxa with different corolla colour and floral morphology (*O. vernus* and *O. luteus* groups; Bolliger, 1996), with *O. jaubertianus* being morphologically intermediate between them due to its allopolyploid origin (Bolliger & al., 1990). In the ITS analyses, relationships among taxa were somewhat clearer, and the K.5-Vernus clade was divided into two subclades associated with corolla colour (yellow in *O. corsicus*, *O. hollianus*, and *O. luteus* s.l., and pink in *O. kaliformis*, *O. recordonii*, *O. jaubertianus* var. *jaubertianus*, and *O. vernus* s.l.). However, two species recognized by Bolliger (1996), *O. litoralis* (Fr.) Fr. (with two subspecies), and *O. vulgaris* Moench. (with four subspecies) remain indistinguishable from *O. vernus*, and the same applies to *O. lanceolatus* (Gaudin) Reichenb. (with two subspecies), which cannot be distinguished from *O. luteus*. That situation could be the result of ILS, and / or recent or current hybridization events. Despite the fact that the already stabilized *O. jaubertianus* is derived from hybridization between *O. vernus* and *O. luteus* (Bolliger & al., 1990), the two latter species are almost completely isolated reproductively. They grow sympatrically in vast areas, but individuals of presumed hybrid origin (intermediate morphology) have very scarcely been reported. No crossing experiments among taxa of the *O. luteus* complex (i.e., subsp. *luteus*, subsp. *lanceolatus* (Gaudin) P. Fourn. and subsp. *provincialis* (Bolliger) J.-M. Tison) have been made. Nevertheless, there is a morphological gradient between the three subspecies (local adaptation to environmental conditions; Tison & al., 2010) and interbreeding could be extensive as they grow in partial sympatry and they have the same chromosome number ($2n = 20$, Bolliger, 1996). Taking into account the high genetic and morphological similarity between the taxa formerly called *O. lanceolatus* subsp. *lanceolatus* and *O. lanceolatus* subsp. *provincialis* Bolliger, we consider that the most conservative taxonomic solution is to include them in *O. luteus*.

Regarding the *O. vernus* complex, the situation is more intricate than in the case of the *O. luteus* complex, as seven taxa (species and subspecies; Bolliger, 1996), two ploidy levels (di- and tetraploid) and two basic chromosome numbers ($x = 9$ and $x = 10$; Delgado & al., 2015) are involved. The only study of intraspecific hybridization in this group (Snogerup, 1983) was performed using diploids (*O. vernus* subsp. *fennicus* (Markl.) Pinto-Carrasco & al., subsp. *litoralis* (Fr.) Nyman and subsp. *serotinus* Corb.; unknown chromosome base number but probably $x = 9$) and tetraploids (*O. vernus* subsp. *vernus*; $x = 10$). Diploids are reproductively compatible (within and between subspecies), but almost complete incompatibility occurs between different ploidy levels. Morphologically, the extremes of the variability range are clearly distinguishable, but the wide variation in both vegetative and reproductive characters hampers the attribution to subspecies of a great number

of individuals (Bolliger, 1996; Rico, 2009). Considering the changes in morphology due to different host plants (Snogerup, 1982), the presence of ecotypes linked to cytotypes (Koutecký & al., 2012), and the probability of recurrent autopolyploidization (Pinto-Carrasco & al., in prep.), we recommend cautious taxonomic treatment, i.e., to include *O. litoralis* and *O. vulgaris* (sensu Bolliger, 1996) in *O. vernus*. In this way, paraphyly could be avoided to some extent as most of the *O. vernus* s.l. samples form one group in the ITS tree. Further studies, using more variable markers, are needed to shed light on the validity of all subspecies that are now included in this complex.

For *O. litoralis* and *O. vulgaris* to be included in the variability of *O. vernus*, the following new combinations are required:

Odontites vernus subsp. *fennicus* (Markl.) Pinto-Carrasco, E.Rico & M.M.Mart.Ort., **comb. nov.** ≡ *Odontites litoralis* subsp. *fennicus* Markl. in Acta Soc. Fauna Fl. Fenn. 72(16): 5. 1955 (“*fennica*”).

Odontites vernus subsp. *himalayicus* (Pennell) Pinto-Carrasco, E.Rico & M.M.Mart.Ort., **comb. nov.** ≡ *Odontites vulgaris* subsp. *himalayicus* (Pennell) Bolliger in Willdenowia 26: 113. 1996 ≡ *Odontites himalayicus* Pennell, Scroph. W. Himal. (Monogr. Acad. Nat. Sci. Philadelphia 5): 98. 1943.

Odontites vernus subsp. *mesatlanticus* (Emb. & Maire) Pinto-Carrasco, E.Rico & M.M.Mart.Ort., **comb. nov.** ≡ *Odontites vulgaris* subsp. *mesatlanticus* (Emb. & Maire) Bolliger in Willdenowia 26: 111. 1996 ≡ *Odontites mesatlanticus* Emb. & Maire in Bull. Soc. Hist. Nat. Afrique N. 22: 58.1931.

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■ LITERATURE CITED

Beauverd, G. 1911. Plantes nouvelles ou critiques de la flore du Bassin supérieur du Rhône [New or critical plants from the Flora of the Superior basin of the Rhône river]. *Bull. Soc. Bot. Genève*, sér. 2, 3: 297–339.

Benedí, C. 2009. *Nothobartsia* Bolliger & Molau. Pp. 473–501 in: Benedí, C., Rico, E., Güemes, J. & Herrero, A. (eds.), *Flora iberica*,

vol. 13, *Plantaginaceae–Scrophulariaceae*. Madrid: Real Jardín Botánico, CSIC.

- Benedí, C., Rico, E., Güemes, J. & Herrero, A.** 2009. Scrophulariaceae. Pp. 44–539 in: Benedí, C., Rico, E., Güemes, J. & Herrero, A. (eds.), *Flora iberica*, vol. 13, *Plantaginaceae–Scrophulariaceae*. Madrid: Real Jardín Botánico, CSIC.
- Bennett, J.R. & Mathews, S.** 2006. Phylogeny of the parasitic plant family Orobanchaceae inferred from phytochrome A. *Amer. J. Bot.* 93: 1039–1051. <https://doi.org/10.3732/ajb.93.7.1039>
- Bolliger, M.** 1985. Die Drüsenhaare der Gattung *Odontites* Ludwig (Scrophulariaceae) und ihre systematische Bedeutung [The glandular hairs of the genus *Odontites* Ludwig (Scrophulariaceae) and their systematic significance]. *Bot. Jahrb. Syst.* 107: 153–175
- Bolliger, M.** 1993. Systematik und Chorologie der Gattung *Odontites* Ludwig s.l. (Scrophulariaceae) [Systematics and chorology of the genus *Odontites* Ludwig s.l. (Scrophulariaceae)]. *Flora, Morphol. Geobot. Ecophysiol.* 188: 345–365
- Bolliger, M.** 1996. Monographie der Gattung *Odontites* (Scrophulariaceae) sowie der verwandten Gattungen *Macrosyringion*, *Odontitella*, *Bornmuellerantha* und *Bartsietta* [Monograph of the genus *Odontites* (Scrophulariaceae) and the related genera *Macrosyringion*, *Odontitella*, *Bornmuellerantha* and *Bartsietta*]. *Willdenowia* 26: 37–168. <https://doi.org/10.3372/wi.26.2603>
- Bolliger, M. & Molau, U.** 1992. *Nothobartsia*, a new genus of Scrophulariaceae from south-west Europe. *Pl. Syst. Evol.* 179: 59–71. <https://doi.org/10.1007/BF00938019>
- Bolliger, M. & Wick, L.** 1990. The pollen morphology of *Odontites* (Scrophulariaceae) and its taxonomic significance. *Pl. Syst. Evol.* 173: 159–178. <https://doi.org/10.1007/BF00940860>
- Bolliger, M., Terrisse, J. & Heubl, G.** 1990. On the allopolyploid origin and the distribution of *Odontites jaubertianus* (Bor.) D. Dietr. *Bot. Jahrb. Syst.* 112: 1–27.
- Brullo, S., Tomaselli, V. & Wagensommer, R.P.** 2015. A new species of *Odontites* (Orobanchaceae) from southern Italy. *Phytotaxa* 213: 271–281. <https://doi.org/10.11646/phytotaxa.213.3.7>
- Darriba, D., Taboada, G.L., Doallo, R. & Posada, D.** 2012. jModel-Test 2: More models, new heuristics and parallel computing. *Nature, Meth.* 9: 772. <https://doi.org/10.1038/nmeth.2109>
- Delgado, L., Pinto-Carrasco, D., Gallego Martín, F. & Rico, E.** 2015. Contribution to the karyological knowledge of *Odontites* s.l. (Orobanchaceae) on the Iberian Peninsula and in Morocco. *Folia Geobot.* 50: 63–74. <https://doi.org/10.1007/s12224-015-9201-4>
- Don, G.** 1838. *A general history of the dichlamydeous plants*, vol. 4, *Corolliflorae*. London: print for J.G. and F. Rivington, etc. <https://doi.org/10.5962/bhl.title.502>
- Dong, L.-N., Wang, H., Wortley, A.H., Lu, L. & Li, D.-Z.** 2013. Phylogenetic relationships in the *Pterygiella* complex (Orobanchaceae) inferred from molecular and morphological evidence. *Bot. J. Linn. Soc.* 171: 491–507. <https://doi.org/10.1111/j.1095-8339.2012.01326.x>
- Dönmez, A.A. & Mutlu, B.** 2010. *Bornmuellerantha alshehbaziana* (Orobanchaceae), a new species from Turkey. *Novon* 20: 265–267. <https://doi.org/10.3417/2008110>
- Doyle, J.J. & Doyle, J.L.** 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochem. Bull. Bot. Soc. Amer.* 19: 11–15.
- Gaudeul, M., Véla, E. & Rouhan, G.** 2016. Eastward colonization of the Mediterranean Basin by two geographically structured clades: The case of *Odontites* Ludw. (Orobanchaceae). *Molec. Phylog. Evol.* 96: 140–149. <https://doi.org/10.1016/j.ympev.2015.12.008>
- Goloboff, P.A., Farris, J.S. & Nixon, K.C.** 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24: 774–786. <https://doi.org/10.1111/j.1096-0031.2008.00217.x>
- Gussarova, G., Popp, M., Vitek, E. & Brochmann, C.** 2008. Molecular phylogeny and biogeography of the bipolar *Euphrasia* (Orobanchaceae): Recent radiations in an old genus. *Molec. Phylog. Evol.* 48: 444–460. <https://doi.org/10.1016/j.ympev.2008.05.002>

- Hills, D.M. & Bull, J.J. 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Syst. Biol.* 42: 182–192. <https://doi.org/10.1093/sysbio/42.2.182>
- Hong, D.Y., Yang, H., Jin, C. & Holmgren, N.H. 1998. Scrophulariaceae. Pp. 1–212 in: Wu, Z.Y. & Raven, P.H. (eds.), *Flora of China*, vol. 18. Beijing: Science Press; St. Louis: Missouri Botanical Garden Press.
- Huelsenbeck, J.P. & Rannala, B. 2004. Frequentist properties of bayesian posterior probabilities of phylogenetic trees under simple and complex substitution models. *Syst. Biol.* 53: 904–913. <https://doi.org/10.1080/10635150490522629>
- Huson, D.H. & Bryant D. 2006. Application of phylogenetic networks in evolutionary studies. *Molec. Biol. Evol.* 23: 254–267. <https://doi.org/10.1093/molbev/msj030>
- İnceoğlu, Ö. 1982. Pollen grains in some Turkish Rhinanthaeae (Scrophulariaceae). *Grana* 21: 83–96. <https://doi.org/10.1080/00173138209427684>
- Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Mentjies, P. & Drummond, A. 2012. Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28: 1647–1649. <https://doi.org/10.1093/bioinformatics/bts199>
- Kerner, A. 1888. Ueber die Bestäubungseinrichtungen der Euphrasieen [About the pollination features of *Euphrasia*]. *Verh. Zool.-Bot. Ges. Wien* 38: 563–566.
- Koutecký, P., Tuleu, G., Badurová, T., Košnar, J., Štech, M. & Těšitel, J. 2012. Distribution of cytotypes and seasonal variation in the *Odontites vernus* group in central Europe. *Preslia* 84: 887–904.
- Kubatko, L.S. 2009. Identifying hybridization events in the presence of coalescence via model selection. *Syst. Biol.* 58: 478–88. <https://doi.org/10.1093/sysbio/syp055>
- Linnaeus, C. 1753. *Species plantarum*, 2. vols. Holmiae [Stockholm]: impensis Laurentii Salvii. <https://doi.org/10.5962/bhl.title.669>
- Lu, L., Wang, H., Blackmore, S., Li, D.Z., & Dong, L.-N. 2007. Pollen morphology of the tribe Rhinanthaeae (Orobanchaceae) and its systematic significances. *Pl. Syst. Evol.* 268: 177–198. <https://doi.org/10.1007/s00606-007-0562-x>
- Maddison, W.P. & Maddison, D.R. 2014. Mesquite: A modular system for evolutionary analysis, version 3.01. <http://mesquiteproject.org/>
- McNeal, J.R., Bennett, J.R., Wolfe, A.D. & Mathews, S. 2013. Phylogeny and origins of holoparasitism in Orobanchaceae. *Amer. J. Bot.* 100: 971–983. <https://doi.org/10.3732/ajb.1200448>
- Minkin, J.P. & Eshbaugh, W.H. 1989. Pollen morphology of the Orobanchaceae and rhinanthoid Scrophulariaceae. *Grana* 28: 1–18. <https://doi.org/10.1080/00173138909431007>
- Molau, U. 1988. *Hedbergia*, a new genus of Scrophulariaceae from Africa. *Nordic J. Bot.* 8: 193–195. <https://doi.org/10.1111/j.1756-1051.1988.tb00500.x>
- Molau, U. 1990. The genus *Bartsia* (Scrophulariaceae-Rhinanthoideae). *Opera Bot.* 102: 1–99.
- Müller, K.F. 2005. SeqState: Primer design and sequence statistics for phylogenetic DNA datasets. *Appl. Bioinf.* 4: 65–69. <https://doi.org/10.2165/00822942-200504010-00008>
- Pinto-Carrasco, D., Košnar, J., López-González, N., Koutecký, P., Těšitel, J., Rico, E. & Martínez-Ortega, M.M. 2016. Development of 14 microsatellite markers in *Odontites vernus* s.l. (Orobanchaceae) and cross-amplification in related taxa. *Appl. Pl. Sci.* 4: 1500111. <https://doi.org/10.3732/apps.1500111>
- Rambaut, A., Suchard, M.A., Xie, D. & Drummond, A.J. 2015. Tracer, version 1.6. <http://beast.bio.ed.ac.uk/Tracer>
- Rico, E. 2009. *Odontites* Ludw.; *Odontitella* Rothm.; *Macrosyringion* Rothm. Pp. 473–501 in: Benedí, C., Rico, E., Güemes, J. & Herrero, A. (eds.), *Flora iberica*, vol. 13, *Plantaginaceae–Scrophulariaceae*. Madrid: Real Jardín Botánico, CSIC.
- Rico, E., Delgado, L. & Herrero, A. 2008. Reassessing the *Odontites purpureus* group (Orobanchaceae) from south-east Spain and north-west Africa. *Bot. J. Linn. Soc.* 158: 701–708. <https://doi.org/10.1111/j.1095-8339.2008.00892.x>
- Ronquist, F., Huelsenbeck, J.P. & Van der Mark, P. 2009. Bayesian phylogenetic analysis using MrBayes. Pp. 210–265 in: Lemey, P., Salemi, M. & Vandamme, A. (eds.), *The phylogenetic handbook: A practical approach to phylogenetic analysis and hypothesis testing*, ed. 2. Cambridge: Cambridge University Press. <https://doi.org/10.1017/CBO9780511819049.009>
- Ronquist, F., Teslenko, M., Van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* 61: 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Rothmaler, W. 1943. Die Aufspaltung von *Odontites* Hall. ex Zinn. [The splitting of *Odontites* Hall. ex Zinn.]. *Mitth. Thüring. Bot. Vereins* 50: 224–230.
- Scheunert, A., Fleischmann, A., Olano-Marín, C., Bräuchler, C. & Heubl, G. 2012. Phylogeny of tribe Rhinanthaeae (Orobanchaceae) with a focus on biogeography, cytology and re-examination of generic concepts. *Taxon* 61: 1269–1285.
- Simmons, M.P. & Ochoterena, H. 2000. Gaps as characters in sequence-based phylogenetic analyses. *Syst. Biol.* 49: 369–381. <https://doi.org/10.1093/sysbio/49.2.369>
- Snogerup, B. 1982. Host influence on northwest European taxa of *Odontites* (Scrophulariaceae). *Ann. Bot. Fenn.* 19: 17–30.
- Snogerup, B. 1983. Northwest European taxa of *Odontites* (Scrophulariaceae). *Acta Bot. Fenn.* 124: 1–62.
- Soltis, D.E. & Soltis, P.S. 1993. Molecular data and the dynamic nature of polyploidy. *Crit. Rev. Pl. Sci.* 12: 243–273. <https://doi.org/10.1080/07352689309701903>
- Soltis, D.E. & Soltis, P.S. 1999. Polyploidy: Recurrent formation and genome evolution. *Trends Ecol. Evol.* 14: 348–352. [https://doi.org/10.1016/S0169-5347\(99\)01638-9](https://doi.org/10.1016/S0169-5347(99)01638-9)
- Swofford, D.L. 2002. PAUP*: Phylogenetic analysis using parsimony (*and other methods). Sunderland, Massachusetts: Sinauer.
- Ter Borg, S.J. 1985. Population biology and habitat relations of some hemiparasitic Scrophulariaceae. Pp. 463–487 in: White J. (ed.), *The population structure of vegetation*. Dordrecht: Junk. https://doi.org/10.1007/978-94-009-5500-4_19
- Těšitel, J., Říha, P., Svobodová, Š., Malinová, T. & Štech, M. 2010. Phylogeny, life history evolution and biogeography of the Rhinanthoid Orobanchaceae. *Folia Geobot.* 45: 347–367. <https://doi.org/10.1007/s12224-010-9089-y>
- Tison, J.M., Jauzein, P., Girod, C. & Espeut, M. 2010. Combinaisons et statuts nouveaux proposés dans la “Flore de la France Méditerranéenne continentale” [New combinations and status proposed in “Flore de la France Méditerranéenne continentale”]. *Biocosme Méditerranéen* 27: 109–133
- Uribe-Convers, S. & Tank, D.C. 2015. Shifts in diversification rates linked to biogeographic movement into new areas: An example of a recent radiation in the Andes. *Amer. J. Bot.* 102: 1854–1869. <https://doi.org/10.3732/ajb.1500229>
- Uribe-Convers, S., Settles, M.L. & Tank, D.C. 2016. A phylogenomic approach based on PCR target enrichment and high throughput sequencing: Resolving the diversity within the South American species of *Bartsia* L. (Orobanchaceae). *PLoS ONE* 11: e0148203. <https://doi.org/10.1371/journal.pone.0148203>
- Webb, D.A. & Camarasa, J.M. 1972. *Odontites* Ludwig. Pp. 266–269 in: Tutin, T.G., Heywood, V.H., Burges, N.A., Moore, D.M., Valentine, D.H., Walters, S.M. & Webb, D.A. (eds.), *Flora Europaea*, vol. 3. Cambridge: Cambridge University Press.
- Wolfe, A.D., Randle, C.P., Liu, L. & Steiner, K.E. 2005. Phylogeny and biogeography of Orobanchaceae. *Folia Geobot.* 40: 115–134. <https://doi.org/10.1007/BF02803229>
- Wortley, A.H., Rudall, P.J., Harris, D.J. & Scotland, R.W. 2005.

How much data are needed to resolve a difficult phylogeny? Case study in Lamiales. *Syst. Biol.* 54: 697–709.

<https://doi.org/10.1080/10635150500221028>

Young, N.D., Steiner, K.E. & dePamphilis, C.W. 1999. The evolution of parasitism in Scrophulariaceae/Orobanchaceae: Plastid gene

sequences refute an evolutionary transition series. *Ann. Missouri Bot. Gard.* 86: 876–893. <https://doi.org/10.2307/2666173>

Zhou, Q.-M., Jensen, S.R., Liu, G.-L., Wang, S. & Li, H.-Q. 2014. Familial placement of *Wightia* (Lamiales). *Pl. Syst. Evol.* 300: 2009–2017. <https://doi.org/10.1007/s00606-014-1029-5>

Appendix 1. Details of sequences (1) newly generated in this study and (2) obtained from GenBank. For newly generated data, we give information about taxon, ID, DNA source, locality, longitude, latitude, collectors, collection number (and/or exsiccatae number), herbarium voucher, and NCBI accession numbers. For sequences obtained from GenBank, we give taxon, ID, NCBI accession numbers and references where they were originally published (see end of Appendix). In both cases accession numbers are shown in the following order: ITS, *trnK* and *rps16*. Unavailable sequences are indicated by a dash (–). The taxon names previous to the taxonomic changes proposed in this paper are shown in brackets. DNA source was silica gel-dried material (s) and herbarium specimens (h). * Coordinates assignment based on locality description; ** silica gel-dried material and voucher specimens were collected in the same location but on different dates.

(1) Sequences produced for this study

Bellardia trixago (L.) All., 629, s, Spain, Cáceres, Poblado del embalse de Gabriel y Galán, –6.12514, 40.22047, *M. Martínez Ortega & X. Giráldez Fernández*, MO 6020 (SALA 142078), KX958618, KX959115, KX958866; *Bellardia trixago*, 630, s, Spain, Cáceres, Poblado del embalse de Gabriel y Galán, –6.12514, 40.22047, *M. Martínez Ortega & X. Giráldez Fernández*, MO 6020 (SALA 142078), KX958619, KX959116, KX958867; *Bellardia trixago*, 698, s, Spain, Burgos, Castrillo de la Vega, –3.78344, 41.65452, *D. Pinto Carrasco*, DP 918 (SALA 142076), KX958685, KX959182, KX958933; *Bellardia trixago*, 699, s, Spain, Burgos, Castrillo de la Vega, –3.78344, 41.65452, *D. Pinto Carrasco*, DP 918 (SALA 142076), KX958686, KX959183, KX958874; *Bellardia viscosa* (L.) Fisch. & C.A.Mey., 633, s, Spain, Cáceres, between Guijo de Granadilla and Mohedas de Granadilla, –6.18073, 40.22402, *M. Martínez Ortega & X. Giráldez Fernández*, MO 6021 (SALA 142079), KX958622, KX959119, KX958870; *Bellardia viscosa*, 634, s, Spain, Cáceres, between Guijo de Granadilla and Mohedas de Granadilla, –6.18073, 40.22402, *M. Martínez Ortega & X. Giráldez Fernández*, MO 6021 (SALA 142079), KX958623, KX959120, KX958871; *Euphrasia hirtella* Jord. ex Reut., 702, s, Spain, Ávila, San Martín de la Vega del Alberche, –5.150, 40.431, *E. Rico & V. Lucía*, ER 8041 (SALA 142118), KX958689, KX959186, KX958937; *Euphrasia hirtella*, 703, s, Spain, Ávila, San Martín de la Vega del Alberche, –5.150, 40.431, *E. Rico & V. Lucía*, ER 8041 (SALA 142118), KX958690, KX959187, KX958938; *Nothobartsia asperrima* (Link) Benedí & Herrero, 615, s, Portugal, Setúbal, Sesimbra, Cabo Espichel, –9.2108, 38.4142, *M. Santos Vicente & al.*, MS 960 (SALA 123311), KX958604, KX959101, KX958852; *Nothobartsia asperrima*, 637, s, Portugal, Santarem, Tomar, Algarvias, –8.431, 39.594, *E. Rico*, ER 7909 (SALA 123313), KX958626, KX959123, KX958874; *Nothobartsia asperrima*, 638, s, Portugal, Santarem, Tomar, Algarvias, –8.431, 39.594, *E. Rico*, ER 7909 (SALA 123313), KX958627, KX959124, KX958875; *Nothobartsia asperrima*, 639, s, Portugal, Setúbal, Sesimbra, Cabo Espichel, –9.2108, 38.4142, *M. Santos Vicente & al.*, MS 960 (SALA 123311), KX958628, KX959125, KX958876; *Nothobartsia asperrima*, 640, s, Portugal, Setúbal, Vendas de Azeitão, –8.9843, 38.5284, *M. Santos Vicente & al.*, MS 958 (SALA 123310), KX958629, KX959126, KX958877; *Nothobartsia asperrima*, 641, s, Portugal, Setúbal, Vendas de Azeitão, –8.9843, 38.5284, *M. Santos Vicente & al.*, MS 958 (SALA 123310), KX958630, KX959127, KX958878; *Nothobartsia asperrima*, 821, s, Morocco, Tanger-Tétouan, between Sidi Jel and Beni Bouker, –5.12731, 35.18902, *D. Pinto Carrasco & al.*, DP 1062 (SALA 156176), KX958708, KX959205, KX958956; *Nothobartsia asperrima*, 822, s, Morocco, Tanger-Tétouan, between Sidi Jel and Beni Bouker, –5.12731, 35.18902, *D. Pinto Carrasco & al.*, DP 1062 (SALA 156176), KX958709, KX959206, KX958957; *Nothobartsia spicata* (Ramond) Bolliger & Molau, 613, s, Spain, Santander, Peñarrubia, La Hermida, –4.64, 43.26, *E. Rico*, ER 7921 (SALA 125801), KX958602, KX959099, KX958850; *Nothobartsia spicata*, 614, s, Spain, Santander, Peñarrubia, La Hermida, –4.64, 43.26, *E. Rico*, ER 7921 (SALA 125801), KX958603, KX959100, KX958851; *Nothobartsia spicata*, 635, s, Spain, Oviedo, Ribadesella, –5.03, 43.43, *E. Rico*, ER 7920 (SALA 125802), KX958624, KX959121, KX958872; *Nothobartsia spicata*, 636, s, Spain, Oviedo, Ribadesella, –5.03, 43.43, *E. Rico*, ER 7920 (SALA 125802), KX958625, KX959122, KX958873; *Odontitella virgata* (Link) Rothm., 81, s, Spain, Burgos, Castrillo de la Vega, –3.75889, 41.64505, *D. Pinto Carrasco*, DP 14 (SALA 135636), KX958509, KX959006, KX958757; *Odontitella virgata*, 592, s, Spain, Cádiz, Los Barrios, –5.59, 36.22, *E. Rico*, ER 7959 (SALA 136278), KX958581, KX959078, KX958829; *Odontitella virgata*, 593, s, Spain, Cádiz, Los Barrios, –5.59, 36.22, *E. Rico*, ER 7959 (SALA 136278), KX958582, KX959079, KX958830; *Odontitella virgata*, 594, s, Spain, A Coruña, Santiso, Barazón, –8.00755, 42.85990, *L. Delgado Sánchez & al.*, LD 1069 (SALA 136280), KX958583, KX959080, KX958831; *Odontitella virgata*, 595, s, Spain, A Coruña, Santiso, Barazón, –8.00755, 42.85990, *L. Delgado Sánchez & al.*, LD 1069 (SALA 136280), KX958584, KX959081, KX958832; *Odontites aucheri* Boiss., 644, h, Turkey, Erzincan, Sakaltutan Geçidi, 39.12, 39.87, *J. Aldasoro & al.*, A-2691 (SALA 120807), KX958633, KX959130, KX958881; *Odontites aucheri*, 645, h, Turkey, Sivas, Dogançal, 38.03, 39.88, *J. Aldasoro & al.*, A-2783 (SALA 121447), KX958634, KX959131, KX958882; *Odontites aucheri*, 646, h, Armenia, Ararat, Lusashogh, 44.9653, 39.8597, *M. Oganessian & al.*, 03-1575 (MA 742689), KX958635, KX959132, KX958883; *Odontites aucheri*, O.24, h, Armenia, Ararat, Lusashogh, 44.9653, 39.8597, *M. Oganessian & al.*, 03-1575 (MSB 123864), KX958740, KX959237, KX958988; *Odontites bocconii* (Guss.) Walp., 624, s, Italy, Sicily, San Martino delle Scale, 13.2581, 38.0861, *G. Domina*, s.n. (PAL 90581), KX958613, KX959110, KX958861; *Odontites bocconii*, 625, s, Italy, Sicily, San Martino delle Scale, 13.2581, 38.0861, *G. Domina*, s.n. (PAL 90581), KX958614, KX959111, KX958862; *Odontites bocconii*, 694, h, Italy, Sicily, Chiusa Sclafani, 13.28698, 37.66516, *G. Certa*, Soc. Éch. Pl. Vasc. Eur. Occid. Médit. nr. 18421 (SALA 118685), KX958681, KX959178, KX958929; *Odontites bocconii*, 823, s, Italy, Sicily, Le Madonie National Park, near Monte Scalone, 14.02147, 37.84662, *J. Peñas de Giles & al.*, JPG-11-03 (SALA 142125), KX958710, KX959207, KX958958; *Odontites bocconii*, 824, s, Italy, Sicily, Le Madonie National Park, near Monte Scalone, 14.02147, 37.84662, *J. Peñas de Giles & al.*, JPG-11-03 (SALA 142125), KX958711, KX959208, KX958959; *Odontites bocconii*, O.13, h, Italy, Sicily, Chiusa Sclafani, 13.28698, 37.66516, *G. Certa*, Soc. Éch. Pl. Vasc. Eur. Occid. Médit. nr. 18421 (M), KX958730, KX959227, KX958978; *Odontites bocconii*, O.20, h, Italy, Sicily, 9 km N of Polizzi Generosa, 14.01, 37.84, *J.R. Akeroyd & al.*, 3664 (B 10 0050066), KX958736, KX959233, KX958984; *Odontites bolligeri* E.Rico, L. Delgado & Herrero, 89, s, Spain, Granada, Restábal, –3.57582, 36.92045, *M. Martínez Ortega & al.*, MO 4566 (SALA 135619), KX958517, KX959014, KX958765; *Odontites bolligeri*, 90, s, Spain, Granada, Restábal, –3.57582, 36.92045, *M. Martínez Ortega & al.*, MO 4566 (SALA 135619), KX958518, KX959015, KX958766; *Odontites bolligeri*, 574, s, Morocco, Oriental, Béni Snassen Natural Park, –2.37950, 34.80917, *A. Quintanar & al.*, AQ 2812 (SALA 142142), KX958563, KX959060, KX958811; *Odontites bolligeri*, 575, s, Morocco, Oriental, Béni Snassen Natural Park, –2.37950, 34.80917, *A. Quintanar & al.*, AQ 2812 (SALA 142142), KX958564, KX959061, KX958812; *Odontites bolligeri*, 609, s, Spain, Málaga, Frigiliana, –3.89672, 36.77680, *D. Pinto Carrasco & V. Lucía*, DP 832 (SALA 136804), KX958598, KX959095, KX958846; *Odontites bolligeri*, 610, s, Spain, Málaga, Frigiliana, –3.89672, 36.77680, *D. Pinto Carrasco & V. Lucía*, DP 832 (SALA 136804), KX958599, KX959096, KX958847; *Odontites bolligeri*, O.17, h, Spain, Almería, Laujar de Andarax, –2.87629, 37.00067, *L. Posadas & al.*, s.n. (MA 861304), KX958733, KX959230, KX958981; *Odontites bolligeri*, O.18, h, Morocco, Oriental, Béni Snassen Natural Park, –2.37500, 34.81983, *A. Quintanar & al.*, AQ 2816 (MA 782726), KX958734, KX959231, KX958982; *Odontites bolligeri*, O.19, h, Morocco, Oriental, Béni Snassen Natural Park, –2.37950, 34.80917, *A. Quintanar & al.*, AQ 2812 (MA 782731), KX958735, KX959232, KX958983; *Odontites bolligeri*, O.27, h, Spain, Granada, Orjiva, Sierra de Lújar, –3.4, 36.9*, *H. Merxmüller & W. Gleißner*, 29171 (M), KX958743, KX959240, KX958991; *Odontites cebennensis* H.J.Coste & Soulié, 87, s, Spain, Barcelona, La Poble de Lillet, 2.01349, 42.24492, *D. Pinto Carrasco & al.*, DP 628 (SALA 135679), KX958515, KX959012, KX958763; *Odontites cebennensis*, 88, s, Spain, Barcelona, La Poble de Lillet, 2.01349, 42.24492, *D. Pinto Carrasco & al.*, DP 628 (SALA 135679), KX958516, KX959013, KX958764; *Odontites cebennensis*, 607, s, Spain, Barcelona, Cercs, 1.86497, 42.14434, *D. Pinto Carrasco & al.*, DP 632 (SALA 135683), KX958596, KX959093, KX958844; *Odontites cebennensis*, 608, s, Spain, Barcelona, Cercs, 1.86497, 42.14434, *D. Pinto Carrasco & al.*, DP 632 (SALA 135683), KX958597, KX959094, KX958845;

Appendix 1. Continued.

Odontites cebennensis, O.03, h, Spain, Barcelona, between Sant Quirze de Besora and Ripoll, 2.2, 42.1*, *M. Bolliger*, 0-23 (M), KX958722, KX959219, KX958970; *Odontites cebennensis*, O.06, h, Spain, Gerona, between Campdevanòl and La Pobra de Lillet, 2.1, 42.2*, *M. Bolliger*, 0-45 (M), KX958724, KX959221, KX958972; *Odontites cebennensis*, O.25, h, Spain, Gerona, Ripoll, 2.2, 42.2*, *F. Sennen*, s.n. (M), KX958741, KX959238, KX958989; *Odontites corsicus* (Loisel.) G.Don., 564, s, France, Corsica, Olmeta-di-Capocorso, Bocca di San Ghjacintu, 9.3842, 42.7489, *A. Tribsch*, s.n. (SALA 137639), KX958553, KX959050, KX958801; *Odontites corsicus*, 565, s, France, Corsica, Olmeta-di-Capocorso, Bocca di San Ghjacintu, 9.3842, 42.7489, *A. Tribsch*, s.n. (SALA 137639), KX958554, KX959051, KX958802; *Odontites corsicus*, 819, s, France, Corsica, Olmeta-di-Capocorso, Bocca di San Ghjacintu, 9.3842, 42.7489, *A. Tribsch*, s.n. (SALA 137639), KX958706, KX959203, KX958954; *Odontites corsicus*, 820, s, France, Corsica, Olmeta-di-Capocorso, Bocca di San Ghjacintu, 9.3842, 42.7489, *A. Tribsch*, s.n. (SALA 137639), KX958707, KX959204, KX958955; *Odontites corsicus*, O.14, h, France, Corsica, Col de Vergio, 8.9, 42.3*, *J. Lambinon*, 98/765 Soc. Éch. Pl. Vasc. Eur. Occid. Médit. nr. 19537 (M), KX958731, KX959228, KX958979; *Odontites cyprius* Boiss. [*Odontites linkii* subsp. *cyprius*] (Boiss.) Bolliger], 695, h, Cyprus, Larnaka, Páno Léfkara, 33.3, 34.9*, *Alziar & al.*, *Iter Med. IV nr. 0762* (MA 495442), KX958682, KX959179, KX958930; *Odontites cyprius* [*Odontites linkii* subsp. *cyprius*], O.22, h, Cyprus, Kirenia, Saint Hilarion, 33.2547, 35.3078, *E. Vitek*, 04-1961 (M), KX958738, KX959235, KX958986; *Odontites foliosus* Pérez Lara, 91, s, Spain, Cádiz, Puerto Real, -6.14, 36.51, *E. Rico & al.*, *ER 7939* (SALA 134536), KX958519, KX959016, KX958767; *Odontites foliosus*, 92, s, Spain, Cádiz, Puerto Real, -6.14, 36.51, *E. Rico & al.*, *ER 7939* (SALA 134536), KX958520, KX959017, KX958768; *Odontites foliosus*, 611, s, Spain, Málaga, Manilva, -5.26139, 36.34094, *D. Pinto Carrasco & al.*, *DP 821* (SALA 156297), KX958600, KX959097, KX958848; *Odontites foliosus*, 612, s, Spain, Málaga, Manilva, -5.26139, 36.34094, *D. Pinto Carrasco & al.*, *DP 821* (SALA 156297), KX958601, KX959098, KX958849; *Odontites foliosus*, 626, s, Spain, Cádiz, Barbate, Los Caños de Meca, -5.958, 36.182, *E. Rico*, *ER 7903* (**SALA 103775), KX958615, KX959112, KX958863; *Odontites glutinosus* (M.Bieb.) Benth. [*Macrosyringion glutinosum* (M.Bieb.) Rothm.], 650, h, Bulgaria, Pernik, Golo Búrdó, 23.1, 42.6*, *H. Kocev & N. Vihodcevsy*, *Pl. Bu. Ex., Cent. VI nr. 586* (MA 183144), KX958639, KX959136, KX958887; *Odontites glutinosus* [*Macrosyringion glutinosum*], 651, h, Turkey, Erzincan, Sakaltutan Geçidi, 39.12, 39.87, *J. Aldasoro & al.*, *A-2687* (MA 689821), KX958640, KX959137, KX958888; *Odontites hollianus* (Lowe) Benth., 560, s, Portugal, Madeira, between O Ninho da Manta and O Pico Cidrão, -16.94415, 32.74116, *M. Sequeira & al.*, *MS 5056* (SALA 125030), KX958549, KX959046, KX958797; *Odontites hollianus*, 561, s, Portugal, Madeira, between O Ninho da Manta and O Pico Cidrão, -16.94415, 32.74116, *M. Sequeira & al.*, *MS 5056* (SALA 125030), KX958550, KX959047, KX958798; *Odontites hollianus*, 562, s, Spain, Isla de La Palma, Tijarafe, -17.92329, 28.73860, *M. Diaz & al.*, *PALMA 240610* (SALA 156496), KX958551, KX959048, KX958799; *Odontites hollianus*, 563, s, Spain, Isla de La Palma, Tijarafe, -17.92329, 28.73860, *M. Diaz & al.*, *PALMA 240610* (SALA 156496), KX958552, KX959049, KX958800; *Odontites hollianus*, 616, s, Portugal, Madeira, between Pico do Arieiro and Pico Ruivo, -16.94, 32.73, *S. Castroviejo & al.*, *SC 17379* (MA 714540), KX958605, KX959102, KX958853; *Odontites hollianus*, 617, s, Spain, Isla de La Palma, Tijarafe, -17.92329, 28.73860, *M. Diaz & al.*, *PALMA 240610* (SALA 156496), KX958606, KX959103, KX958854; *Odontites hollianus*, 618, s, Spain, Isla de La Palma, Tijarafe, -17.92329, 28.73860, *M. Diaz & al.*, *PALMA 240610* (SALA 156496), KX958607, KX959104, KX958855; *Odontites hollianus*, 652, h, Portugal, Madeira, Encumeada, -17.0, 32.8*, *M. Velayos*, 9717 (MA 655312), KX958641, KX959138, KX958889; *Odontites hollianus*, 653, h, Portugal, Madeira, between Ribeiro Frio and Os Balcoes, -16.9, 32.7*, *J. Malato Beliz*, 1698 (MA 303197), KX958642, KX959139, KX958890; *Odontites jaubertianus* (Boreau) D.Dietr., O.09, h, France, Charente, Saint-Angeau, 0.3, 45.8*, *A. Terrisse*, 0-151 (M), KX958726, KX959223, KX958974; *Odontites kaliformis* (Pourr. ex Willd.) Pau, 5, s, Spain, Valencia, Sagunto, -0.25, 39.63, *E. Rico & al.*, *ER 7913* (SALA 124706), KX958502, KX958999, KX958750; *Odontites kaliformis*, 6, s, Spain, Valencia, Sagunto, -0.25, 39.63, *E. Rico & al.*, *ER 7913* (SALA 124706), KX958503, KX959000, KX958751; *Odontites kaliformis*, 8, s, Spain, Castellón, Cabanes, 0.18, 40.18, *E. Rico & al.*, *ER 7914* (SALA 124707), KX958504, KX959001, KX958752; *Odontites kaliformis*, 10, s, Spain, Castellón, Cabanes, 0.18, 40.18, *E. Rico & al.*, *ER 7914* (SALA 124707), KX958505, KX959002, KX958753; *Odontites lapiei* Batt., 696, h, Algeria, Tizi Ouzou, Djurdjura National Park, Djebel Heïdzer, 4.0, 36.5*, *A. Dubuis & al.*, *Soc. Éch. Pl. Vasc. Eur. Occid. Médit. nr. 18423* (SALA 118683), KX958684, KX959181, KX958932; *Odontites lapiei*, O.10, h, Algeria, Tizi Ouzou, Djurdjura National Park, Djebel Heïdzer, 4.0, 36.5*, *A. Dubuis & al.*, *Soc. Éch. Pl. Vasc. Eur. Occid. Médit. nr. 18423* (MSB), KX958727, KX959224, KX958975; *Odontites linkii* Heldr. & Sart. ex Boiss., 570, s, Greece, Corinthia, Trikala, 22.4639, 37.9832, *A. Herrero & al.*, *AH 3480* (SALA 140486), KX958559, KX959056, KX958807; *Odontites linkii*, 571, s, Greece, Corinthia, Trikala, 22.4639, 37.9832, *A. Herrero & al.*, *AH 3480* (SALA 140486), KX958560, KX959057, KX958808; *Odontites linkii*, 621, s, Greece, Achaia, between Kalávríta and Kalivítis, 22.1708, 38.0807, *A. Herrero & al.*, *AH 3359* (SALA 140386), KX958610, KX959107, KX958858; *Odontites linkii*, 622, s, Greece, Lakonia, Lagadha gorge, 22.3355, 37.0940, *C. Aedo*, *CA 14257* (SALA 140800), KX958611, KX959108, KX958859; *Odontites linkii*, 623, s, Greece, Lakonia, Lagadha gorge, 22.3355, 37.0940, *C. Aedo*, *CA 14257* (SALA 140800), KX958612, KX959109, KX958860; *Odontites longiflorus* (Lam.) G.Don. [*Macrosyringion longiflorum* (Lam.) Rothm.], 82, s, Spain, Burgos, Castrillo de la Vega, -3.77922, 41.62688, *D. Pinto Carrasco*, *DP 11* (SALA 135639), KX958510, KX959007, KX958758; *Odontites longiflorus* [*Macrosyringion longiflorum*], 586, s, Morocco, Tanger-Tétouan, Jbel L'akraa, -5.1423, 35.1366, *V. Lucia & al.*, *VL 82* (SALA 137638), KX958575, KX959072, KX958823; *Odontites longiflorus* [*Macrosyringion longiflorum*], 587, s, Morocco, Tanger-Tétouan, Jbel L'akraa, -5.1423, 35.1366, *V. Lucia & al.*, *VL 82* (SALA 137638), KX958576, KX959073, KX958824; *Odontites longiflorus* [*Macrosyringion longiflorum*], 588, s, Spain, Soria, Aldehuela de Periañez, -2.34517, 41.81283, *D. Pinto Carrasco*, *DP 851* (SALA 137313), KX958577, KX959074, KX958825; *Odontites longiflorus* [*Macrosyringion longiflorum*], 589, s, Spain, Soria, Aldehuela de Periañez, -2.34517, 41.81283, *D. Pinto Carrasco*, *DP 851* (SALA 137313), KX958578, KX959075, KX958826; *Odontites longiflorus* [*Macrosyringion longiflorum*], 590, s, Spain, Segovia, Ayllón, Grado del Pico, -3.23325, 41.31703, *D. Pinto Carrasco*, *DP 898* (SALA 137290), KX958579, KX959076, KX958827; *Odontites longiflorus* [*Macrosyringion longiflorum*], 591, s, Spain, Segovia, Ayllón, Grado del Pico, -3.23325, 41.31703, *D. Pinto Carrasco*, *DP 898* (SALA 137290), KX958580, KX959077, KX958828; *Odontites longiflorus* [*Odontites longiflorus* var. *roseus* A.Segura], 647, h, Spain, Soria, between Renieblas and Torretartajo, -2.4, 41.8*, *A. Segura Zubizarreta*, 10421, *Soc. Éch. Pl. Vasc. Eur. Occid. Médit. nr. 9646* (SALA 63086), KX958636, KX959133, KX958884; *Odontites longiflorus* [*Odontites longiflorus* var. *roseus*], 648, h, Spain, Soria, between Renieblas and Torretartajo, -2.4, 41.8*, *A. Segura Zubizarreta*, 10421, *Soc. Éch. Pl. Vasc. Eur. Occid. Médit. nr. 9646* (SALA 63086), KX958637, KX959134, KX958885; *Odontites longiflorus* [*Odontites longiflorus* subsp. *lateritius* (Charpin & Fern.Casas) Sánchez-Gómez], 649, h, Spain, Murcia, Moratalla, pico Revolcadores, -2.27, 38.07, *A. Aparicio & al.*, 8807 (MA 594052), KX958638, KX959135, KX958886; *Odontites luteus* subsp. *lancoelatus* (Gaudin) P.Fourn. [*Odontites lanceolatus* (Gaudin) Rchb. subsp. *lancoelatus*], 677, h, France, Hautes-Alpes, Saint-Crépin, 6.6, 44.7*, *G. Dudartre*, *Soc. Éch. Pl. Vasc. Eur. Occid. Médit. nr. 18422* (SALA 118684), KX958665, KX959162, KX958913; *Odontites luteus* subsp. *lancoelatus* [*Odontites lanceolatus* subsp. *lancoelatus*], 678, h, Italy, Piedmont, between Col de Tende and Coni, 7.6, 44.2*, *M. Bolliger*, 0-72 (MA 538540), KX958666, KX959163, KX958914; *Odontites luteus* subsp. *lancoelatus* [*Odontites lanceolatus* subsp. *lancoelatus*], 679, h, France, Hautes-Alpes, Col du Lautaret, 6.3, 45.0*, *M. Bolliger & R. Bolliger*, 0-16 (MA 538542), KX958667, KX959164, KX958915; *Odontites luteus* subsp. *lancoelatus* [*Odontites lanceolatus* subsp. *lancoelatus*], O.26, h, France, Isère, Les Ougiers, 6.1, 45.0*, *O. Angerer*, s.n. (M), KX958742, KX959239, KX958990; *Odontites luteus* (L.) Clairv. subsp. *luteus*, 83, s, Spain, Lerida, between Puente de Montañana and Tremp, 0.77634, 42.16084, *E. Rico*, *ER 7852* (SALA 136275), KX958511, KX959008, KX958759; *Odontites luteus* subsp. *luteus*, 84, s, Spain, Lerida, between Puente de Montañana and Tremp, 0.77634, 42.16084, *E. Rico*, *ER 7852* (SALA 136275), KX958512, KX959009, KX958760; *Odontites luteus* subsp. *luteus*, 566, s, France, Corsica, Olmeta-di-Capocorso, between Celle and Bocca di San Ghjacintu, 9.3822, 42.7544, *A. Tribsch*, s.n. (SALA 137640), KX958555, KX959052, KX958803; *Odontites luteus* subsp. *luteus*, 567, s, France, Corsica, Olmeta-di-Capocorso, between Celle and Bocca di San Ghjacintu, 9.3822, 42.7544, *A. Tribsch*, s.n. (SALA 137640), KX958556, KX959053, KX958804; *Odontites luteus* subsp. *luteus*, 568, s, Croatia, Splitsko-Dalmatinska, between Brela and Gornja Brela, 16.89363, 43.40381, *M. Martínez Ortega & al.*, *MO 5538* (SALA 137346), KX958557, KX959054, KX958805; *Odontites luteus* subsp. *luteus*, 569, s, Croatia, Splitsko-Dalmatinska, between Brela and Gornja Brela, 16.89363, 43.40381, *M. Martínez Ortega & al.*, *MO 5538* (SALA 137346), KX958558, KX959055, KX958806; *Odontites luteus* subsp. *luteus*, 602, s, Spain, Teruel, Arbolí, 0.94110, 41.22580, *D. Pinto Carrasco & al.*, *DP 641* (SALA 135692), KX958591, KX959088, KX958839; *Odontites luteus* subsp. *luteus*, 603, s, Spain, Teruel, Arbolí, 0.94110, 41.22580, *D. Pinto*

Appendix 1. Continued.

Carrasco & al., *DP 641* (SALA 135692), KX958592, KX959089, KX958840; *Odontites luteus* subsp. *luteus*, 642, s, Spain, Albacete, Riópar, –2.39010, 38.49901, *D. Pinto Carrasco & al., DP 763* (SALA 137330), KX958631, KX959128, KX958879; *Odontites luteus* subsp. *luteus*, 643, s, Spain, Albacete, Riópar, –2.39010, 38.49901, *D. Pinto Carrasco & al., DP 763* (SALA 137330), KX958632, KX959129, KX958880; *Odontites luteus* subsp. *luteus*, 658, h, France, Var, between Riez and Sainte-Croix-du-Verdon, 6.1, 43.8*, *M. Bolliger, 0-60* (MA 538314), KX958647, KX959144, KX958895; *Odontites luteus* subsp. *luteus*, 659, h, France, Var, between Moustiers-Sainte-Marie and La Palud-sur-Verdon, 6.2, 43.8*, *M. Bolliger, 0-59* (MA 538312), KX958648, KX959145, KX958896; *Odontites luteus* subsp. *luteus*, 661, h, France, Var, La Garde-Freinet, 6.5, 43.3*, *M. Bolliger & R. Bolliger, 0-145* (MA 538310), KX958649, KX959146, KX958897; *Odontites luteus* subsp. *luteus*, 662, h, France, Alpes-Maritimes, Roussillon, 5.3, 43.9*, *M. Bolliger, 0-68* (MA 538307), KX958650, KX959147, KX958898; *Odontites luteus* subsp. *luteus*, 663, h, France, Bouches-du-Rhône, Allauch, 5.5, 43.3*, *P. Martin, Soc. Éch. Pl. Vasc. Eur. Occid. Médit. nr. 6868* (MA 303024), KX958651, KX959148, KX958899; *Odontites luteus* subsp. *luteus*, 664, h, Italy, Sardinia, Badesi, 8.9114, 41.0306, *C. Aedo & al., 9108* (MA 708621), KX958652, KX959149, KX958900; *Odontites luteus* subsp. *luteus*, 665, h, France, Corrèze, between Noailles and Cressensac, 1.5, 45.1*, *M. Bolliger & R. Bolliger, 0-7* (MA 538313), KX958653, KX959150, KX958901; *Odontites luteus* subsp. *luteus*, 666, h, Italy, Umbria, Norcia, 13.1, 42.8*, *A. Pavesi, Soc. Éch. Pl. Vasc. Eur. Occid. Médit. nr. 13551* (SALA 82871), KX958654, KX959151, KX958902; *Odontites luteus* subsp. *luteus*, 667, h, Germany, Bavaria, Landkreis Neumarkt, Buchenberg, 11.7, 49.2*, *N. Meyer, Soc. Éch. Pl. Vasc. Eur. Occid. Médit. nr. 19539* (SALA 119350), KX958655, KX959152, KX958903; *Odontites luteus* subsp. *luteus*, 829, s, Spain, Valladolid, Santibañez de Valcorba, –4.44673, 41.57944, *D. Pinto Carrasco, DP 1018* (SALA 110042), KX958716, KX959213, KX958964; *Odontites luteus* subsp. *luteus*, 830, s, Spain, Valladolid, Santibañez de Valcorba, –4.44673, 41.57944, *D. Pinto Carrasco, DP 1018* (SALA 110042), KX958717, KX959214, KX958965; *Odontites luteus* subsp. *luteus*, 831, s, Czech Republic, South Moravia, between Klentnice and Mikulov, 16.64113, 48.83663, *B. Rojas-Andrés & al., BR 187* (SALA 142123), KX958718, KX959215, KX958966; *Odontites luteus* subsp. *luteus*, 832, s, Czech Republic, South Moravia, between Klentnice and Mikulov, 16.64113, 48.83663, *B. Rojas-Andrés & al., BR 187* (SALA 142123), KX958719, KX959216, KX958967; *Odontites luteus* subsp. *provincialis* (Bolliger) J.-M.Tison. [*Odontites lanceolatus* subsp. *provincialis* Bolliger], 680, h, France, Alpes-Maritimes, Col de Ferrier, 6.9, 43.7*, *M. Bolliger & R. Bolliger, 0-13* (MA 538451), KX958668, KX959165, KX958916; *Odontites luteus* subsp. *provincialis* [*Odontites lanceolatus* subsp. *provincialis*], 681, h, France, Var, between Castellane and La Palud-sur-Verdon, 6.4, 43.8*, *M. Bolliger, 0-57* (MA 538452), KX958669, KX959166, KX958917; *Odontites luteus* subsp. *provincialis* [*Odontites lanceolatus* subsp. *provincialis*], 682, h, France, Alpes-Maritimes, La Penne, 6.9, 43.9*, *M. Bolliger, 0-65* (MA 538453), KX958670, KX959167, KX958918; *Odontites luteus* subsp. *provincialis* [*Odontites lanceolatus* subsp. *provincialis*], 683, h, France, Alpes-Maritimes, Col de Braus, 7.4, 43.9*, *M. Bolliger, 0-70* (MA 538459), KX958671, KX959168, KX958919; *Odontites luteus* subsp. *provincialis* [*Odontites lanceolatus* subsp. *provincialis*], 0.02, h, France, Alpes-Maritimes, Tinée Valley, 7.2, 43.9*, *M. Bolliger, 0-69* (M), KX958721, KX959218, KX958969; *Odontites maroccanus* Bolliger, 578, s, Morocco, Meknès-Tafilalet, Tizi-n-Tretten, –5.03801, 33.45669, *D. Pinto Carrasco & al., DP 785* (SALA 156299), KX958567, KX959064, KX958815; *Odontites maroccanus*, 579, s, Morocco, Meknès-Tafilalet, Tizi-n-Tretten, –5.03801, 33.45669, *D. Pinto Carrasco & al., DP 785* (SALA 156299), KX958568, KX959065, KX958816; *Odontites maroccanus*, 700, h, Morocco, Meknès-Tafilalet, Ifrane, Oued Tizguit, –5.1167, 33.5528, *Crespo & al., s.n.* (ABH 33424), KX958687, KX959184, KX958935; *Odontites maroccanus*, 701, h, Morocco, Meknès-Tafilalet, Ifrane, Oued Tizguit, –5.1167, 33.5528, *Crespo & al., s.n.* (ABH 33424), KX958688, KX959185, KX958936; *Odontites maroccanus*, 727, h, Morocco, Meknès-Tafilalet, near Jebel Hebri, –5.15, 33.36, *M.A. Mateos & al., 4396/94* (BC 852667), KX958705, KX959202, KX958953; *Odontites maroccanus*, O.33, h, Morocco, Meknès-Tafilalet, Timhadit, –5.1, 33.2*, *E. Jahandiez, 881* (M), KX958748, KX959245, KX958996; *Odontites powellii* Maire, 580, s, Morocco, Meknès-Tafilalet, Tizi-n-Tretten, –5.03961, 33.45582, *D. Pinto Carrasco & al., DP 786* (SALA 156298), KX958569, KX959066, KX958817; *Odontites powellii*, 581, s, Morocco, Meknès-Tafilalet, Tizi-n-Tretten, –5.03961, 33.45582, *D. Pinto Carrasco & al., DP 786* (SALA 156298), KX958570, KX959067, KX958818; *Odontites powellii*, 582, s, Morocco, Tanger-Tétouan, Jbel L'akraa, –5.14364, 35.13683, *V. Lucia & al., VL 83* (SALA 156300), KX958571, KX959068, KX958819; *Odontites powellii*, 583, s, Morocco, Tanger-Tétouan, Jbel L'akraa, –5.14364, 35.13683, *V. Lucia & al., VL 83* (SALA 156300), KX958572, KX959069, KX958820; *Odontites powellii*, 584, s, Morocco, Tadmra-Azilal, Tizi Ait Ouirrah, –6.0186, 32.5208, *A. Quintanar & al., AQ 2119* (MA 746128), KX958573, KX959070, KX958821; *Odontites powellii*, 585, s, Morocco, Tadmra-Azilal, Tizi Ait Ouirrah, –6.0186, 32.5208, *A. Quintanar & al., AQ 2119* (MA 746128), KX958574, KX959071, KX958822; *Odontites powellii*, O.11, h, Morocco, Meknès-Tafilalet, between Ifrane and Zaouia d'Ifrane, –5.1, 33.6*, *M. Bolliger & D. Moser, 0-163* (M), KX958728, KX959225, KX958976; *Odontites pyrenaicus* subsp. *abilianus* P.Monts., 606, s, Spain, Huesca, Jaca, Bernués, –0.60, 42.49, *E. Rico, ER 7746* (SALA 103068), KX958595, KX959092, KX958843; *Odontites pyrenaicus* subsp. *abilianus*, 692, h, Spain, Huesca, Jaca, monte de Larbesa, –0.55, 42.54, *G. Montserrat, s.n.* (SALA 23738), KX958679, KX959176, KX958927; *Odontites pyrenaicus* subsp. *abilianus*, 693, h, Spain, Huesca, Jaca, Casa de Valpregona, –0.58, 42.48, *E. Rico, ER 7745* (SALA 103067), KX958680, KX959177, KX958928; *Odontites pyrenaicus* (Bubani) Rothm. subsp. *pyrenaicus*, 85, s, Spain, Lerida, Sarroca de Bellera, 0.86660, 42.36414, *D. Pinto Carrasco & al., DP 615* (SALA 135664), KX958513, KX959010, KX958761; *Odontites pyrenaicus* subsp. *pyrenaicus*, 86, s, Spain, Lerida, Sarroca de Bellera, 0.86660, 42.36414, *D. Pinto Carrasco & al., DP 615* (SALA 135664), KX958514, KX959011, KX958762; *Odontites pyrenaicus* subsp. *pyrenaicus*, 604, s, Spain, Huesca, Plan, Saravillo, 0.26438, 42.55771, *E. Rico, ER 7845* (SALA 136276), KX958593, KX959090, KX958841; *Odontites pyrenaicus* subsp. *pyrenaicus*, 605, s, Spain, Huesca, Plan, Saravillo, 0.26438, 42.55771, *E. Rico, ER 7845* (SALA 136276), KX958594, KX959091, KX958842; *Odontites pyrenaicus* subsp. *pyrenaicus*, O.01, h, Spain, Lerida, between El Pont de Suert and Sarroca de Bellera, 0.8, 42.4*, *M. Bolliger, 0-38* (M), KX958720, KX959217, KX958968; *Odontites rameuanus* Emb., 576, s, Morocco, Tadmra-Azilal, Jebel Tarkeddid, –6.5069, 31.5464, *A. Quintanar & al., AQ 2129* (MA 746138), KX958565, KX959062, KX958813; *Odontites rameuanus*, 577, s, Morocco, Tadmra-Azilal, Jebel Tarkeddid, –6.5069, 31.5464, *A. Quintanar & al., AQ 2129* (MA 746138), KX958566, KX959063, KX958814; *Odontites recordonii* Burnat & Barbey, 138, s, Spain, Alava, Bachicabo, –3.06771, 42.77934, *M. Martínez Ortega, MO 4526* (SALA 135620), KX958525, KX959022, KX958773; *Odontites recordonii*, 170, s, Spain, Teruel, Formiche Alto, Formiche Bajo, –0.88, 40.29, *L. Delgado Sánchez & al., LD 1020* (SALA 135630), KX958526, KX959023, KX958774; *Odontites recordonii*, 197, s, Spain, Valencia, El Saler, –0.32096, 39.36067, *D. Pinto Carrasco & al., DP 676* (SALA 135726), KX958527, KX959024, KX958775; *Odontites recordonii*, 249, s, Spain, Teruel, Arboli, 0.96434, 41.23127, *D. Pinto Carrasco & al., DP 642* (SALA 135693), KX958528, KX959025, KX958776; *Odontites recordonii*, 255, s, Spain, Zaragoza, Paracuellos de Jiloca, –1.61225, 41.32468, *D. Pinto Carrasco & al., DP 653* (SALA 135704), KX958529, KX959026, KX958777; *Odontites recordonii*, 301, s, Spain, Guadalajara, Fuentelviejo, –2.98810, 40.51173, *D. Pinto Carrasco & al., DP 692* (SALA 135742), KX958530, KX959027, KX958778; *Odontites recordonii*, O.07, h, Spain, Zaragoza, between Urriés and Ruesta, –1.1, 42.6*, *M. Bolliger, 0-30* (M), KX958725, KX959222, KX958973; *Odontites silletii* Brullo, Tomaselli & Wagens., O.34, h, Italy, Apulia, Santeramo in Colle, 16.8, 40.8*, *G.N. Silletti & V. Tomaselli, s.n.* (MSB), KX958749, KX959246, KX958997; *Odontites vernus* (Bellardi) Dumort., 668, h, Denmark, Zealand, Hundige, 12.3, 55.6*, *A. Hansen, Soc. Éch. Pl. Vasc. Eur. Occid. Médit. nr. 13552* (SALA 82870), KX958656, KX959153, KX958904; *Odontites vernus*, 669, h, Germany, Schleswig-Holstein, Leck, Büllsbüll, 9.0, 54.8*, *P. Pedersen & al., Fl. Ger. Ex., Schl.-Hols. nr. 166* (MA 327862), KX958657, KX959154, KX958905; *Odontites vernus*, 670, h, Denmark, Island Fur in Limfjorden, Faerker Hede, 9.0, 56.8*, *K. Larsen & S.S. Larsen, 40738*, *Soc. Éch. Pl. Vasc. Eur. Occid. Médit. nr. 15514* (MA 532164), KX958658, KX959155, KX958906; *Odontites vernus*, 671, h, Russia, Moscow, Abramtsevo, 38.0, 56.2*, *E.E. Gogina, s.n.* (MA 303021), KX958659, KX958907; *Odontites vernus*, 672, h, Belgium, Wallonia, Tihange (Huy), 5.3, 50.5*, *M. Reekmans, 11345*, *Soc. Éch. Pl. Vasc. Eur. Occid. Médit. nr. 11665* (SALA 75333), KX958660, KX959157, KX958908; *Odontites vernus*, 673, h, France, Bas-Rhin, Auenheim, 8.0, 48.8*, *A. Schneider, Soc. Éch. Pl. Vasc. Eur. Occid. Médit. nr. 9650* (SALA 63091), KX958661, KX959158, KX958909; *Odontites vernus*, 674, h, France, motorway Nîmes-Lyon km 111, 4.8, 44.6*, *unknown, 733PV* (MA 443277), KX958662, KX959159, KX958910; *Odontites vernus*, 675, h, Italy, Veneto, Caorle, 12.9, 45.6*, *F. Cernoch, 53749 FC*, *Soc. Éch. Pl. Vasc. Eur. Occid. Médit. nr. 16440* (SALA 88671), KX958663, KX959160, KX958911; *Odontites vernus*, 676, h, Great Britain, Hampshire, Winchester, near Itchen Down Farm, –1.2, 51.1*, *S.L. Lury, Soc. Éch. Pl. Vasc. Eur. Occid. Médit. nr. 15519* (SALA 88476), KX958664, KX959161, KX958912; *Odontites vernus*, 716, h, Russia, Altai Krai, Kadnikovo, 81.88878, 52.87285, *S.I. Molokanov & A.P. Schalimov, s.n.* (ALTB), KX958699, KX959196, KX958947; *Odontites vernus*, 717, h, Russia, Khakassia, foot of a ridge Alan, 91.08460, 52.80173, *A.P. Shalimov & A.D. Djagilev, s.n.* (ALTB), KX958700, KX959197, KX958948; *Odontites vernus*, 718, h, Russia, Altai Krai,

Appendix 1. Continued.

Mikhailovka, east coast of lake Kulundinskoe, 79.8, 53.0*, *D.A. German & D.A. Durnikin, s.n.* (ALTB), KX958701, KX959198, KX958949; ***Odontites vernus***, 719, h, Russia, Altai Republic, near settlement Aktal, 88.87, 49.92, *R.V. Kamelin & al., ADSCH 2328* (ALTB), KX958702, KX959199, KX958950; ***Odontites vernus***, 720, h, Mongolia, Kobdosskii, 10 km at South from Bulgan, 91.5, 46.0*, *D.L. Belkin & A.P. Shalimov, s.n.* (ALTB), KX958703, KX959200, KX958951; ***Odontites vernus***, 721, h, Russia, Altai Krai, between Gonokhovo and Dobraja Volya, 81.24068, 52.92590, *A.I. Shmakov & al., s.n.* (ALTB), KX958704, KX959201, KX958952; ***Odontites vernus***, O.12, h, Germany, Bavaria, Neustadt an der Waldnaab, 12.2, 49.7*, *W. Lippert, 27604* (M), KX958729, KX959226, KX958977; ***Odontites vernus***, O.29, h, USA, Maine, Aroostook County, –68.3397, 46.1247, *D. Atha & M. Lee, 2235* (M), KX958744, KX959241, KX958992; ***Odontites vernus***, O.30, h, China, Xinjiang, Atojinagh Valley, 75.17, 38.95, *U. Wündisch, 748* (MSB 147298), KX958745, KX959242, KX958993; ***Odontites vernus***, O.31, h, Finland, Hämeenlinna, 750m SW of Vanaja church, 24.5, 61.0*, *R. Lampinen, 10379* (M), KX958746, KX959243, KX958994; ***Odontites vernus***, O.32, h, Germany, Bavaria, Landkreis Freising, Eching, 11.6, 48.3*, *Plachter, s.n.* (M 0248419), KX958747, KX959244, KX958995; ***Odontites vernus*** subsp. ***fennicus*** (Markl.) Pinto-Carrasco, E.Rico & M.M.Mart.Ort. [***Odontites litoralis*** subsp. ***fennicus*** Markl.], 688, h, Finland, Uusimaa, Porvoon mlk, Sundby, Karilamalm, 25.87, 60.27, *U. Laine & al., s.n.* (SALA 50565), KX958675, KX959172, KX958923; ***Odontites vernus*** subsp. ***fennicus*** [***Odontites litoralis*** subsp. ***fennicus***], 689, h, Finland, Uusimaa, Ruotsinpyhtää, Söderby, Ropannuden, 26.53, 60.33, *U. Laine & al., s.n.* (SALA 50566), KX958676, KX959173, KX958924; ***Odontites vernus*** subsp. ***fennicus*** [***Odontites litoralis*** subsp. ***fennicus***], 690, h, Finland, Uusimaa, Storpellingne island, isthmus between Koräs and Cape Sandholmen, 25.9, 60.2*, *R. Lampinen, 9302, Soc. Éch. Pl. Vasc. Eur. Occid. Médit. nr. 15511* (SALA 88468), KX958677, KX959174, KX958925; ***Odontites vernus*** subsp. ***fennicus*** [***Odontites litoralis*** subsp. ***fennicus***], 691, h, Finland, Varsinais-Suomi, Nauvo, Västergård, 22.0, 60.2*, *R. Murto & M. Koistinen, 3833, Soc. Éch. Pl. Vasc. Eur. Occid. Médit. nr. 15515* (SALA 88472), KX958678, KX959175, KX958926; ***Odontites vernus*** subsp. ***himalayicus*** (Pennell) Pinto-Carrasco, E.Rico & M.M.Mart.Ort. [***Odontites vulgaris*** subsp. ***himalayicus*** (Pennell) Bolliger], O.23, h, Pakistan, Kashmir, Hushe River, 76.4, 35.3*, *G.L. Webster & E. Nasir, 6290* (M), KX958739, KX959236, KX958987; ***Odontites vernus*** subsp. ***litoralis*** (Fr.) Nyman [***Odontites litoralis*** (Fr.) Fr. subsp. ***litoralis***], 685, h, Finland, Varsinais-Suomi, Lokalahti, 21.27, 60.72, *S. Hinneri, s.n.* (SALA 29309), KX958672, KX959169, KX958920; ***Odontites vernus*** subsp. ***litoralis*** [***Odontites litoralis*** subsp. ***litoralis***], 686, h, Finland, Varsinais-Suomi, Jungfruskär island, 21.08, 60.13, *K. Alho & al., s.n.* (SALA 50567), KX958673, KX959170, KX958921; ***Odontites vernus*** subsp. ***litoralis*** [***Odontites litoralis*** subsp. ***litoralis***], 687, h, Finland, Varsinais-Suomi, Korppoo, Kälö Island, 21.38, 60.08, *U. Laine & al., s.n.* (SALA 50445), KX958674, KX959171, KX958922; ***Odontites vernus*** subsp. ***serotinus*** Corb. [***Odontites vulgaris*** Moench. subsp. ***vulgaris***], 48, s, Spain, Valladolid, Aldeamayor de San Martín, –4.61, 41.52, *L. Delgado Sánchez & M. Santos Vicente, LD 908* (**SALA 110700), KX958506, KX959003, KX958754; ***Odontites vernus*** subsp. ***serotinus*** [***Odontites vulgaris*** subsp. ***vulgaris***], 57, s, Spain, Lugo, Samos, Renche, –7.22, 42.72, *E. Rico, ER 7890* (SALA 110730), KX958508, KX959005, KX958756; ***Odontites vernus*** subsp. ***serotinus*** [***Odontites vulgaris*** subsp. ***vulgaris***], 339, s, Greece, Arcadia, between Tripoli and Nestáni, 22.4236, 37.5834, *L. Medina & al., LM 4132* (MA 762104), KX958531, KX959028, KX958779; ***Odontites vernus*** subsp. ***serotinus*** [***Odontites vulgaris*** subsp. ***vulgaris***], 340, s, Greece, Arcadia, between Tripoli and Nestáni, 22.4236, 37.5834, *L. Medina & al., LM 4132* (MA 762104), KX958532, KX959029, KX958780; ***Odontites vernus*** subsp. ***serotinus*** [***Odontites vulgaris*** subsp. ***vulgaris***], 440, s, Turkey, Kırklareli, Dereköy, 27.35305, 41.93761, *B. Rojas-Andrés & al., BR 39* (SALA 135613), KX958535, KX959032, KX958783; ***Odontites vernus*** subsp. ***serotinus*** [***Odontites vulgaris*** subsp. ***vulgaris***], 463, s, Spain, Granada, Quéntar, –3.40546, 37.23347, *D. Pinto Carrasco & al., DP 663* (SALA 135713), KX958536, KX959033, KX958784; ***Odontites vernus*** subsp. ***serotinus*** [***Odontites vulgaris*** subsp. ***vulgaris***], 464, s, Spain, Granada, Quéntar, –3.40546, 37.23347, *D. Pinto Carrasco & al., DP 663* (SALA 135713), KX958537, KX959034, KX958785; ***Odontites vernus*** subsp. ***serotinus*** [***Odontites vulgaris*** subsp. ***vulgaris***], 619, s, Ireland, County Longford, Cashel Nature Reserve, opposite to Cow Island, –7.98694, 53.58889, *D. Doogue, s.n.* (no voucher), KX958608, KX959105, KX958856; ***Odontites vernus*** subsp. ***serotinus*** [***Odontites vulgaris*** subsp. ***vulgaris***], 620, s, Ireland, County Down, North of the lighthouse at St. John's Point, –5.65722, 54.22944, *D. Doogue, s.n.* (no voucher), KX958609, KX959106, KX958857; ***Odontites vernus*** subsp. ***serotinus*** [***Odontites vulgaris*** subsp. ***vulgaris***], 710, s, France, Aisne, Beaurieux, 3.74058, 49.39850, *M. Martínez Ortega & al., MO 6024* (SALA 142126), KX958693, KX959190, KX958941; ***Odontites vernus*** subsp. ***serotinus*** [***Odontites vulgaris*** subsp. ***vulgaris***], 711, s, France, Aisne, Beaurieux, 3.74058, 49.39850, *M. Martínez Ortega & al., MO 6024* (SALA 142126), KX958694, KX959191, KX958942; ***Odontites vernus*** subsp. ***serotinus*** [***Odontites vulgaris*** subsp. ***vulgaris***], 712, s, Germany, Rheinland-Pfalz, near Landau, 8.13750, 49.17658, *M. Martínez Ortega & al., MO 6027* (SALA 142127), KX958695, KX959192, KX958943; ***Odontites vernus*** subsp. ***serotinus*** [***Odontites vulgaris*** subsp. ***vulgaris***], 713, s, Germany, Rheinland-Pfalz, near Landau, 8.13750, 49.17658, *M. Martínez Ortega & al., MO 6027* (SALA 142127), KX958696, KX959193, KX958944; ***Odontites vernus*** subsp. ***serotinus*** [***Odontites vulgaris*** subsp. ***vulgaris***], 714, s, France, Haut-Rhin, Bergheim, 7.35202, 48.21186, *M. Martínez Ortega & al., MO 6031* (SALA 142128), KX958697, KX959194, KX958945; ***Odontites vernus*** subsp. ***serotinus*** [***Odontites vulgaris*** subsp. ***vulgaris***], 715, s, France, Haut-Rhin, Bergheim, 7.35202, 48.21186, *M. Martínez Ortega & al., MO 6031* (SALA 142128), KX958698, KX959195, KX958946; ***Odontites vernus*** subsp. ***siculus*** (Guss.) Sell [***Odontites vulgaris*** subsp. ***siculus*** (Guss.) Bolliger], 348, s, Italy, Sicily, Geraci Siculo, 14.1539, 37.8803, *G. Domina, s.n.* (PAL 88463), KX958533, KX959030, KX958781; ***Odontites vernus*** subsp. ***siculus*** [***Odontites vulgaris*** subsp. ***siculus***], 349, s, Italy, Sicily, Geraci Siculo, 14.1539, 37.8803, *G. Domina, s.n.* (PAL 88463), KX958534, KX959031, KX958782; ***Odontites vernus*** (Bellardi) Dumort. subsp. ***vernus***, 49, s, Spain, Segovia, Valle de Tabladillo, –3.84, 41.36, *L. Delgado Sánchez & M. Santos Vicente, LD 976* (SALA 128800), KX958507, KX959004, KX958755; ***Odontites vernus*** subsp. ***vernus***, 530, s, Croatia, Ličko-Senjska, between Prijeboj and Ličko Petrovo Selo, 15.68401, 44.84572, *M. Martínez Ortega & al., MO 5531* (SALA 137348), KX958538, KX959035, KX958786; ***Odontites vernus*** subsp. ***vernus***, 708, s, France, Eure, Evreux, 1.10769, 49.01655, *B. Rojas-Andrés & al., BR 158* (SALA 142120), KX958691, KX959188, KX958939; ***Odontites vernus*** subsp. ***vernus***, 709, s, France, Eure, Evreux, 1.10769, 49.01655, *B. Rojas-Andrés & al., BR 158* (SALA 142120), KX958692, KX959189, KX958940; ***Odontites viscosus*** subsp. ***asturicus*** M.Laínz, 551, s, Spain, León, Puebla de Lillo, Isoba, –5.36313, 43.09460, *D. Pinto Carrasco & E. Rico, DP 874* (SALA 137373), KX958542, KX959039, KX958790; ***Odontites viscosus*** subsp. ***asturicus***, 598, s, Spain, León, Puebla de Lillo, Isoba, –5.36313, 43.09460, *D. Pinto Carrasco & E. Rico, DP 874* (SALA 137373), KX958587, KX959084, KX958835; ***Odontites viscosus*** subsp. ***asturicus***, 599, s, Spain, León, Puebla de Lillo, Isoba, –5.36313, 43.09460, *D. Pinto Carrasco & E. Rico, DP 874* (SALA 137373), KX958588, KX959085, KX958836; ***Odontites viscosus*** subsp. ***asturicus***, 657, h, Spain, Oviedo, Lena, Tuizua de Arriba, Peña Cerreos, –5.9372, 43.0164, *J. Calvo, JC 4008* (MA 790195), KX958646, KX959143, KX958894; ***Odontites viscosus*** subsp. ***asturicus***, O.21, h, Spain, Oviedo, Lena, east of Peña Vera, –5.9, 43.0*, *H. Merxmüller & W. Lippert, 29754, Herb. Lipp. nr. 15383* (M), KX958737, KX959234, KX958985; ***Odontites viscosus*** subsp. ***australis*** (Boiss.) Jahand. & Maire, 93, s, Spain, Granada, Güéjar Sierra, Canales, –3.47717, 37.15449, *D. Pinto Carrasco & B.N. Ariza, DP 566* (SALA 136267), KX958521, KX959018, KX958769; ***Odontites viscosus*** subsp. ***australis***, 94, s, Spain, Granada, Güéjar Sierra, Canales, –3.47717, 37.15449, *D. Pinto Carrasco & B.N. Ariza, DP 566* (SALA 136267), KX958522, KX959019, KX958770; ***Odontites viscosus*** subsp. ***australis***, 548, s, Morocco, Tanger-Tétouan, Jbel L'akraa, –5.14364, 35.13683, *V. Lucia & al., VL 91* (SALA 156301), KX958539, KX959036, KX958787; ***Odontites viscosus*** subsp. ***australis***, 549, s, Spain, Toledo, Orgaz, between Marjaliza and Arisgotas, –3.92741, 39.58057, *V. Lucia & al., VL 30* (SALA 137339), KX958540, KX959037, KX958788; ***Odontites viscosus*** subsp. ***australis***, 827, s, Spain, Zamora, Corrales del Vino, –5.71, 41.34, *E. Rico, ER 7974* (SALA 135647), KX958714, KX959211, KX958962; ***Odontites viscosus*** subsp. ***australis***, 828, s, Spain, Zamora, Corrales del Vino, –5.71, 41.34, *E. Rico, ER 7974* (SALA 135647), KX958715, KX959212, KX958963; ***Odontites viscosus*** subsp. ***eriopodus*** Litard. & Maire, 656, h, Morocco, Meknès-Tafilalet, between Ifrane and Zaouïa d'Ifrane, –5.1, 33.6*, *M. Bolliger & D. Moser, 0-164* (MA 538475), KX958645, KX959142, KX958893; ***Odontites viscosus*** subsp. ***granatensis*** (Boiss.) Bolliger, 95, s, Spain, Granada, Sierra Nevada, Collado de Las Sabinas, –3.42448, 37.11694, *J. Peñas de Giles, ODOGRA-G01* (**SALA 135386), KX958523, KX959020, KX958771; ***Odontites viscosus*** subsp. ***granatensis***, 96, s, Spain, Granada, Sierra Nevada, Collado de Las Sabinas, –3.42448, 37.11694, *J. Peñas de Giles, ODOGRA-G01* (**SALA 135386), KX958524, KX959021, KX958772; ***Odontites viscosus*** subsp. ***granatensis***, 558, s, Spain, Granada, Sierra Nevada, barranco del Guarnón, –3.36, 37.08, *D. Pinto Carrasco & al., DP 893* (SALA 157687), KX958547, KX959044, KX958795; ***Odontites viscosus*** subsp. ***granatensis***, 559, s, Spain, Granada, Sierra Nevada, barranco del Guarnón, –3.36, 37.08, *D. Pinto Carrasco & al., DP 893* (SALA 157688), KX958548, KX959045, KX958796; ***Odontites viscosus*** subsp. ***granatensis***, 572, s, Spain, Granada, Sierra Nevada, barranco de Río Seco, –3.34, 37.03, *J. Fuentes, s.n.* (GDA 61399), KX958561, KX959058, KX958809; ***Odontites viscosus*** subsp. ***granatensis***, 573, s, Spain, Granada, Sierra Nevada,

Appendix 1. Continued.

tenuisecta (Bureau & Franch.) Pinto-Carrasco, E.Rico & M.M.Mart.Ort. [*Phtheirospermum tenuisectum* Bureau & Franch.], GB1, JF746383.1², –, –, *Rhinanthus alectorolophus* (Scop.) Pollich, GB1, JF900501.1¹⁰, JF900566.1¹⁰, JF900534.1¹⁰; *Rhinanthus crista-galli* L., GB1, KM408210.1¹⁴, –, KM408313.1¹⁴; *Rhinanthus freynii* (A.Kern. ex Sterneck) Fiori, GB1, GU445319.1², KC542180.1⁶, KM408310.1¹⁴; *Rhinanthus glaciarius* Person., GB1, FJ790041.1¹², FJ790101.1¹², –, *Rhinanthus kyrollae* Chabert, GB1, KM408209.1¹⁴, –, KM408312.1¹⁴; *Rhinanthus minor* L., GB1, FJ790040.1¹², FJ790100.1¹², –, *Rhinanthus rumelicus* Velen., GB1, FJ790043.1¹², FJ790103.1¹², –, *Rhinanthus serotinus* (Schönh.) Oborný, GB1, KM408211.1¹⁴, –, KM408311.1¹⁴; *Rhynchosorys elephas* (L.) Griseb., GB1, FJ790055.1¹², FJ790115.1¹², –, *Rhynchosorys kurdica* Nábělek, GB1, JF900499.1¹⁰, JF900564.1¹⁰, JF900532.1¹⁰; *Rhynchosorys maxima* C.Richter, GB1, FJ790036.1¹², FJ790096.1¹², –, *Rhynchosorys odonthophylla* Burbidge & Richardson, GB1, FJ790034.1¹², FJ790094.1¹², –, *Rhynchosorys orientalis* Benth., GB1, JF900498.1¹⁰, JF900563.1¹⁰, JF900531.1¹⁰; *Rhynchosorys stricta* (C.Koch) Albov, GB1, FJ790056.1¹², FJ790116.1¹², –, *Seymeria laciniata* (M.Martens & Galeotti) Standl., GB1, EF103742.1¹¹, KC542183.1⁶, EF103820.1¹¹; *Striga asiatica* (L.) Kuntze, GB1, EU253604.1⁷, AF052000.1¹⁷, KJ563206.1¹⁸; *Tozzia alpina* subsp. *carpatica* Dostál, GB1, FJ790058.1¹², FJ790118.1¹², –, *Tozzia alpina* L., GB1, JF900512.1¹⁰, JF900576.1¹⁰, JF900544.1¹⁰; *Tozzia alpina*, GB2, EU259251.1⁸, AF052001.1¹⁷, KM408280.1¹⁴; *Xizangia bartschioides* (Hand.-Mazz.) C.Y.Wu & D.D.Tao, GB1, JF746403.1², JF746423.1², –, *Xizangia bartschioides*, GB2, JF746405.1², JF746424.1², –, *Xizangia bartschioides*, GB3, JF979021.1², JF956810.1², –.

- Dong, L.-N., Wortley, A.H., Wang, H., Lu, L. & Li, D.-Z. Unpublished.
- Dong, L.-N., Wortley, A.H., Wang, H., Li, D.-Z. & Lu, L. 2011. Efficiency of DNA barcodes for species delimitation: A case in *Pterygiella* Oliv. (Orobanchaceae). *J. Syst. Evol.* 49: 189–202. <https://doi.org/10.1111/j.1759-6831.2011.00124.x>
- Dong, L.-N., Wang, H., Wortley, A.H., Lu, L. & Li, D. 2013. Phylogenetic relationships in the *Pterygiella* complex (Orobanchaceae) inferred from molecular and morphological evidence. *Bot. J. Linn. Soc.* 171: 491–507. <https://doi.org/10.1111/j.1095-8339.2012.01326.x>
- Li, M., Wunder, J., Bissoli, G., Scarponi, E., Gazzani, S., Barbaro, E., Saedler, H. & Varotto, C. 2008. Development of COS genes as universally amplifiable markers for phylogenetic reconstructions of closely related plant species. *Cladistics* 24: 727–745. <https://doi.org/10.1111/j.1096-0031.2008.00207.x>
- Li, D.-Z., Gao, L.-M., Li, H.-T., Wang, H., Ge, X.-J., Liu, J.-Q., Chen, Z.-D., Zhou, S.-L., Chen, S.-L., Yang, J.-B., Fu, C.-X., Zeng, C.-X., Yan, H.-F., Zhu, Y.-J., Sun, Y.-Sh., Chen, S.-Y., Zhao, L., Wang, K., Yang, T. & Duan, G.-W. 2011. Comparative analysis of a large dataset indicates that internal transcribed spacer (ITS) should be incorporated into the core barcode for seed plants. *Proc. Natl. Acad. Sci. U.S.A.* 108: 19641–19646. <https://doi.org/10.1073/pnas.1104551108>
- McNeal, J.R., Bennett, J.R., Wolfe, A.D. & Mathews, S. 2013. Phylogeny and origins of holoparasitism in Orobanchaceae. *Amer. J. Bot.* 100: 971–983. <https://doi.org/10.3732/ajb.1200448>
- Morawetz, J.J. & Wolfe, A.D. 2009. Assessing the Monophyly of *Alectra* and Its Relationship to *Melasma* (Orobanchaceae). *Syst. Bot.* 34: 561–569. <https://doi.org/10.1600/036364409789271281>
- Morawetz, J.J., Randle, C.P. & Wolfe, A.D. 2010. Phylogenetic relationships within the tropical clade of Orobanchaceae. *Taxon* 59: 416–426.
- Refulio-Rodríguez, N.F. & Olmstead, R.G. 2014. Phylogeny of Lamiidae. *Amer. J. Bot.* 101: 287–299. <https://doi.org/10.3732/ajb.1300394>
- Scheunert, A., Fleischmann, A., Olano-Marin, C., Bräuchler, C. & Heubl, G. 2012. Phylogeny of tribe Rhinanthae (Orobanchaceae) with a focus on biogeography, cytology and re-examination of generic concepts. *Taxon* 61: 1269–1285.
- Tank, D.C. & Olmstead, R.G. 2008. From annuals to perennials: Phylogeny of subtribe Castillejinae (Orobanchaceae). *Amer. J. Bot.* 95: 608–625. <https://doi.org/10.3732/ajb.2007346>
- Těšitel, J., Říha, P., Svobodová, Š., Malinová, T. & Štech, M. 2010. Phylogeny, life history evolution and biogeography of the Rhinanthoid Orobanchaceae. *Folia Geobot.* 45: 347–367. <https://doi.org/10.1007/s12224-010-9089-y>
- Tkach, N., Ree, R.H., Kuss, P., Röser, M. & Hoffmann, M.H. 2014. High mountain origin, phylogenetics, evolution, and niche conservatism of arctic lineages in the hemiparasitic genus *Pedicularis* (Orobanchaceae). *Molec. Phylogen. Evol.* 76: 75–92. <https://doi.org/10.1016/j.ympev.2014.03.004>
- Uribe-Convers, S. & Tank, D.C. 2015. Shifts in diversification rates linked to biogeographic movement into new areas: An example of a recent radiation in the Andes. *Amer. J. Bot.* 102: 1854–1869. <https://doi.org/10.3732/ajb.1500229>
- Wolfe, A.D., Randle, C.P., Liu, L. & Steiner, K.E. 2005. Phylogeny and biogeography of Orobanchaceae. *Folia Geobot.* 40: 115–134. <https://doi.org/10.1007/BF02803229>
- Young, N.D. & dePamphilis, C.W. 2005. Rate variation in parasitic plants: Correlated and uncorrelated patterns among plastid genes of different function. *B. M. C. Evol. Biol.* 5: 16. <https://doi.org/10.1186/1471-2148-5-16>
- Young, N.D., Steiner, K.E. & dePamphilis, C.W. 1999. The evolution of parasitism in Scrophulariaceae/Orobanchaceae: Plastid gene sequences refute an evolutionary transition series. *Ann. Missouri Bot. Gard.* 86: 876–893. <https://doi.org/10.2307/2666173>
- Zhou, Q.-M., Jensen, S.R., Liu, G.-L., Wang, S. & Li H.-Q. 2014. Familial placement of *Wightia* (Lamiales). *Pl. Syst. Evol.* 300: 2009–2017. <https://doi.org/10.1007/s00606-014-1029-5>