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Phylogenetic revision of the genus *Bartsia* (Orobanchaceae): disjunct distributions correlate to independent lineages

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Abstract—We propose a new classification for the South American species of the genus *Bartsia* L. and relatives recently included in an expanded treatment of the genus *Bellardia* (L.) All. This new classification reflects their evolutionary history, and is based on morphological and molecular evidence, biogeographic hypotheses, and rates of diversification for these species. Additionally, we rearranged the current taxonomic classification of close relatives so that the current circumscriptions encompass only monophyletic groups. Some of these changes include the creation of a new genus, *Neobartsia* Uribe-Convers and Tank (47 spp.), as well as the reclassification of *Bellardia latifolia* (L.) Cuatrec. back to *Parentucellia latifolia* (L.) Caruel. These taxonomic changes are important for proper communication within the large Rhinanthaeae clade of Orobanchaceae, and for the interpretation of biogeographic patterns and diversification processes of these species.

Keywords—Andes, *Bellardia*, Neotropics, Páramo, *Parentucellia*, Rhinanthaeae.

A great number of molecular phylogenetic studies have made it evident that some well-established morphological classifications are the result of taxa that are not each other's closest relatives (e.g. Olmstead et al. 2001; Angiosperm Phylogeny Group 2009). Systematists are now able to approach classifications from an evolutionary and phylogenetic perspective, allowing them to erect or update classifications so that they reflect the evolutionary history of the groups they work on, as well as generating hypotheses about times of divergence among taxa (e.g. Swenson et al. 2012), historical biogeography (e.g. Olmstead et al. 2001; Angiosperm Phylogeny Group 2009; Beaulieu et al. 2013), and hybridization (e.g. Swenson et al. 2012; Clay et al. 2012). This is the case with *Bartsia* L., a genus historically of ca. 49 species in the family Orobanchaceae that has recently been included in several family-wide phylogenetic studies (Wolfe et al. 2005; Bennett and Mathews 2006; Těšitel et al. 2010; Scheunert et al. 2012). *Bartsia* was the subject of a detailed taxonomic treatment in which the major sections and taxa were revised, and a few new species were described (Molau 1990). In this treatment, Molau (1990) divided *Bartsia* into seven sections based on morphological characters and geographic distributions. Section *Bartsia* included the type species *B. alpina* L. that is distributed in the Alps, Scandinavia, Greenland, and the Hudson Bay region of northeastern North America. Section *Longiflorae* contained two species (*B. decurva* Benth. and *B. longiflora* Benth.) restricted to the mountains of northeastern Africa, while section *Bellardia* comprised a single species (*B. trixago* L.) with a Mediterranean origin, but with an introduced, and somewhat weedy, distribution in subtropical dry areas, e.g. coastal western North America, especially in the Californian Chaparral, Australia, and Chilean lowlands. Finally, four different sections (*Strictae*, *Orthocarpiflorae*, *Laxae*, and *Diffusae*) formed the largest group in the genus, with ca. 45 species distributed throughout the high elevation páramo ecosystem in the Andes (Fig. 1).

An Orobanchaceae-wide study (Bennett and Mathews 2006) had hinted that *Bartsia*, as circumscribed at the time, may not be monophyletic, but their sampling of only three species was too limited to confidently conclude anything. Těšitel et al. (2010) expanded the sampling of the genus, including five

species in a study of the Rhinanthaeae clade (sensu McNeal et al. 2013), but Scheunert et al. (2012) were the first to include species from all morphological sections, including the complete geographic range of the genus. Their molecular results showed that *Bartsia* was indeed polyphyletic and that it was comprised of four distinct lineages, each corresponding to its geographic distribution, i.e. Europe, the Mediterranean, northeastern Africa, and Andean South America. Based on their phylogenetic results, various taxonomic rearrangements were made to better reflect the evolutionary history of the taxa. The European species *B. alpina* was conserved as the generic type, while the two African species were included in the African genus *Hedbergia* Molau, which was shown to be their closest relative. The Mediterranean species *B. trixago* was found to form a well-supported clade with the two South American species included in their study, as well as with the two species of the genus *Parentucellia* Viv. (*P. latifolia* (L.) Caruel and *P. viscosa* (L.) Caruel). However, the relationships between *P. viscosa*, *B. trixago*, and a well-supported clade containing *P. latifolia* as the sister group to the two South American species was unresolved (Fig. 2). Both *Parentucellia* species have a Mediterranean origin and the same current introduced distribution of *B. trixago*. *Bartsia trixago* has been classified in its own genus in various European floras as *Bellardia trixago* (L.) All. (e.g. Allioni 1785; Tutin 1973), and thus, Scheunert et al. (2012) decided to expand the circumscription of *Bellardia* All. to include the two species of *Parentucellia* and the two South American *Bartsia* species they had sampled; they purposefully avoided reclassifying the remaining 43 South American species due to their poor sampling of the Andean taxa. However, we believe that this taxonomic rearrangement makes little sense, as it leaves ca. 45 South American species classified in a large paraphyletic genus along with the European type species *B. alpina*.

In this study, we update the taxonomic classification of these taxa making use of the results of a recent study on the Rhinanthaeae clade that focused on the diversification of the South American *Bartsia* clade in the context of its mostly European relatives (Uribe-Convers and Tank 2015). In addition, we present a phylogenetic analysis of ~25,000 bp of



FIG. 1. Representative species of *Neobartsia* and its four morphological sections. First row; section *Orthocarpiflorae* from left to right: *N. santolinifolia*, leaf with crenate margin, *N. orthocarpiflora*, *N. laniflora*. Second row; section *Strictae* from left to right: *N. stricta*, *N. pedicularoides* (habit), *N. pedicularoides*, *N. glandulifera*. Third row; section *Laxae* from left to right: *N. camporum*, *N. inaequalis* subsp. *brachyantha*, *N. bartsioides*, *N. weberbaueri*. Fourth row; section *Diffusae* from left to right: *N. fiebrigii* (inflorescence), *N. crenoloba*, *N. serrata*, *N. fiebrigii*.

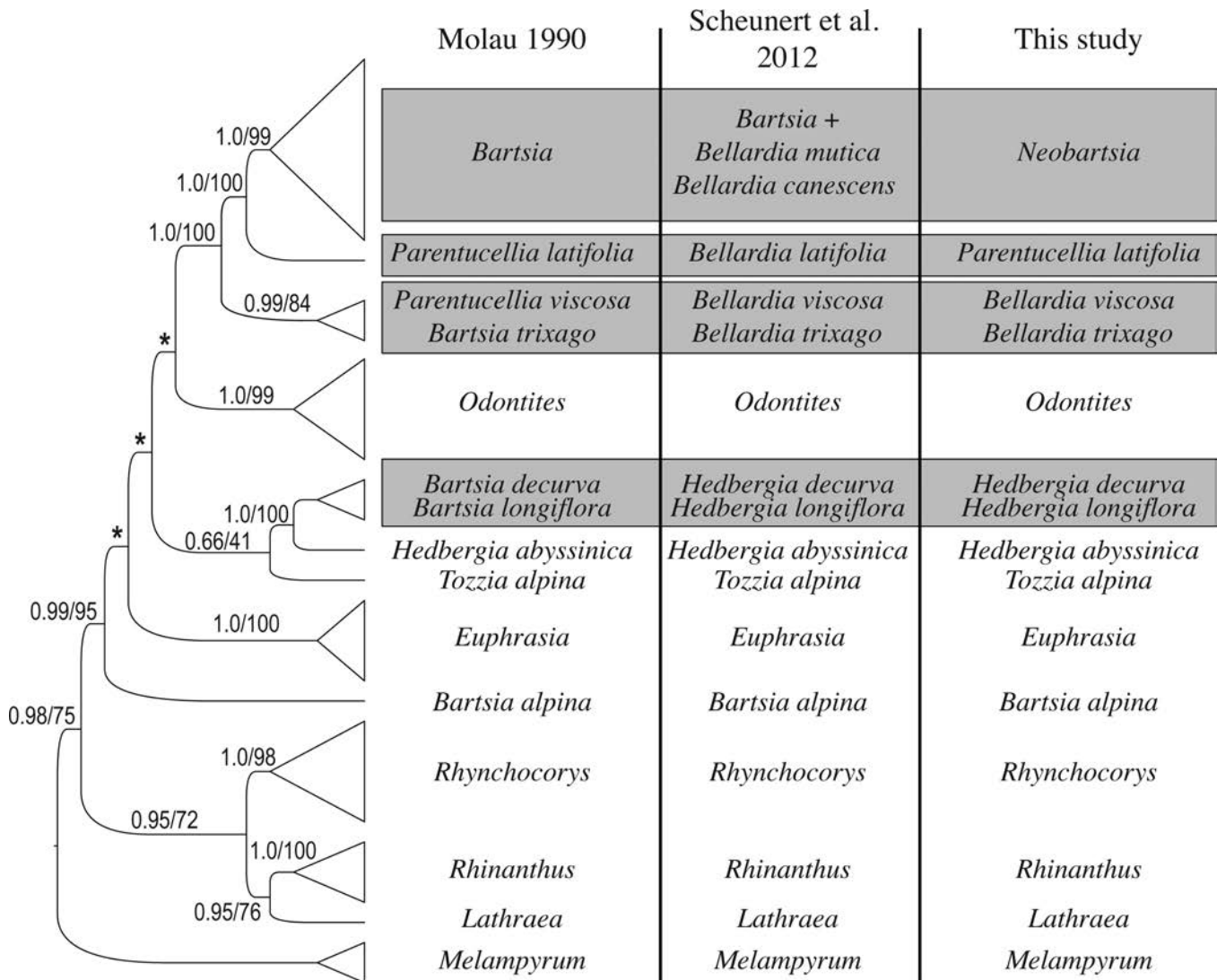


FIG. 2. Summary of the phylogenetic hypotheses for the Rhinanthaeae clade of Orobanchaceae based on taxonomic (Molau 1990) and molecular phylogenetic data (Scheunert et al. 2012; Uribe-Convers and Tank 2015). The size of each triangle corresponds to the sampling proportion in the Sanger dataset. The grey horizontal boxes highlight the recent taxonomic rearrangements in the clade with Molau's (1990) classification in the left column, Scheunert et al. (2012) in the middle column, and this paper's in the right column. Values above the branches represent Bayesian posterior probabilities (PP) and maximum likelihood bootstrap support (BS). The asterisk above the branches represents places where our Sanger dataset is incongruent with previous studies. These incongruences have been shown not to be statistically significant using the approximately unbiased test (Shimodaira 2002), and do not affect the taxonomic conclusions made here. See text and Uribe-Convers and Tank (2015) for more details.

chloroplast DNA sequence data (Uribe-Convers et al. 2016) that includes 43 of the 47 described species of South American *Bartsia* (sensu Molau 1990; Cabrera and Botta 1992; Sylvester 2014). These two scales of phylogeny estimation clarify the relationships between lineages of the Rhinanthaeae clade, and confirm the monophyly of the South American clade. Finally, based on biogeographic analyses, analyses of diversification rates across the clade, morphological differences, and phylogenetic results, we propose a new generic classification for the South American species of *Bartsia* and closely related taxa.

MATERIALS AND METHODS

Sampling—A total of 77 taxa were included in this study based on the sampling of two previous studies (Uribe-Convers and Tank 2015; Uribe-Convers et al. 2016). Because we wanted to both place the South American diversity in the context of the Rhinanthaeae clade and confirm the monophyly of the South American taxa, this sampling included representatives from all of the major lineages that comprise the clade, as well

as 43 of the 47 South American *Bartsia* species (sensu Molau 1990; Cabrera and Botta 1992; Sylvester 2014).

Molecular datasets—This study is based on two different datasets: i) a representative sampling of the Rhinanthaeae clade using Sanger sequences of the Internal and External Transcribed Spacer regions of the nuclear ribosomal repeat (ITS and ETS, respectively) (Uribe-Convers and Tank 2015), which we will refer to as the Sanger dataset henceforth, and ii) a comprehensive sampling of the South American species diversity and close Mediterranean relatives based on ~25,000 base pairs of chloroplast data from a single individual of each species generated via high-throughput sequencing (HTS) (Uribe-Convers et al. 2016), referred to as the HTS dataset. Because the Sanger dataset from Uribe-Convers and Tank (2015) did not include sequences of *Bellardia latifolia*, we complemented it with data for these two regions obtained via HTS (Uribe-Convers et al. 2016). We used these two different datasets to answer phylogenetic questions in this group at different scales and with different foci. The Sanger dataset was compiled to place the South American diversity within the large Rhinanthaeae clade, whereas the HTS dataset was used to confirm the monophyly of the South American taxa, and provide an initial estimate of interspecific relationships in this clade.

Phylogenetic analyses—Both the sequences from the Sanger dataset, including the added sequences for *Bellardia latifolia*, and the HTS dataset

were aligned independently using MUSCLE v3.8.31 in its default settings (Edgar 2004), and the alignments were visually inspected in Geneious R7 v.7.1.9 (Biomatters, Auckland, New Zealand). Model selection of sequence evolution and partition schemes followed Uribe-Convers and Tank (2015) and Uribe-Convers et al. (2016) for the Sanger and HTS datasets, respectively. Each dataset was analyzed in a maximum likelihood (ML) framework in the program RAxML v.8.0.3 (Stamatakis 2014). Clade support was assessed with 1,000 replicates of nonparametric bootstrapping using the rapid bootstrap algorithm (Stamatakis et al. 2008). Additionally, we conducted Bayesian analyses on the Sanger dataset in the program MrBayes v.3.2.2 (Ronquist et al. 2012) with the individual parameters unlinked across the data partitions. These analyses consisted of two independent runs with four Markov chains using default priors and heating values. Each independent run was started from a randomly generated tree, was sampled every 1,000 generations, and consisted of 15 million generations. Convergence of the chains was determined by analyzing the plots of all parameters and the $-\ln L$ using Tracer v.1.5 (Rambaut and Drummond 2004). Stationarity was assumed when all parameters values and the $-\ln L$ had stabilized; the likelihoods of independent runs were considered indistinguishable when the average standard deviation of split frequencies was < 0.001 . A consensus tree was generated after 25% of the trees had been discarded as burn-in using the `sumt` command in MrBayes.

RESULTS AND DISCUSSION

The topologies recovered from both the ML and Bayesian analyses of the Sanger dataset were identical with respect to the relationships among the major lineages of Rhinanthaeae. A summary of the current evolutionary hypothesis of the Rhinanthaeae clade based on the Sanger dataset is given in Fig. 2. In short, our results were concordant with those of previous studies (Těšitel et al. 2010; Scheunert et al. 2012; McNeal et al. 2013), except for the relationship between *Odontites* Ludw. and *Euphrasia* L., which in these analyses were recovered as sister groups. Uribe-Convers and Tank (2015) obtained this same result when only analyzing nuclear ribosomal DNA sequence data (as was used here), but not when they used data from the chloroplast genome. They investigated the incongruencies between these two topologies using the approximately unbiased test (AU test) (Shimodaira 2002), as implemented in the program Consel (Shimodaira and Hasegawa 2001), and showed that these discordant relationships were not statistically significant.

With the addition of *Bellardia latifolia* to the dataset of Uribe-Convers and Tank (2015), our results largely agree with these earlier phylogenetic studies of Rhinanthaeae (Těšitel et al. 2010; Scheunert et al. 2012; McNeal et al. 2013; Uribe-Convers and Tank 2015), including the polyphyletic nature of the former genus *Bartsia*. *Bartsia alpina* was recovered as sister to the rest of the core Rhinanthaeae (sensu Scheunert et al. 2012) with high posterior probability (PP) and bootstrap support (BS) (0.99 PP, 95 BS). The two African species (*B. decurva* and *B. longiflora*) form a clade with the African genus *Hedbergia* (1.0 PP, 100 BS), and this clade was resolved as sister to the European species *Tozzia alpina* L. (0.66 PP, 41 BS). *Odontites* forms a clade (1.0 PP, 99 BS) that is sister to a clade comprised by the current species of *Bellardia* (sensu Scheunert et al. 2012) and the South American *Bartsia* species. Within the latter clade, *Bellardia trixago* was placed sister to *Bellardia viscosa* (L.) Fisch. & C.A. Mey (0.99 PP, 84 BS), with this clade sister to a clade comprised of *Bellardia latifolia* (L.) Cuatrec. and the South American species (1.0 PP, 100 BS). Finally, *Bellardia latifolia* was resolved as the sister group to the South American clade (1.0 PP, 100 BS), which was recovered as monophyletic with strong support (1.0 PP, 99 BS).

The HTS dataset represents the first truly comprehensive sampling for the former genus *Bartsia*, including 43 South American species, the three closely related Mediterranean species of *Bellardia*, and *Bartsia alpina* as the outgroup. The resulting ML phylogeny was congruent with the Sanger dataset with respect to relationships between *Bellardia* and the South American species (Fig. 3). Briefly, *Bellardia trixago* and *Bellardia viscosa* formed a clade (95 BS) sister to a clade of *Bellardia latifolia* and the South American species (97 BS). Finally, the South American species were recovered as monophyletic with strong support (100 BS). It is noteworthy that depending on the data used, the position of *Bellardia latifolia* has not been stable in previous studies (e.g. Těšitel et al. 2010), being sister either to the South American clade or to a clade formed by *Bellardia viscosa* and the new world taxa; in the present study, the position of *Bellardia latifolia* was consistent and robust using both the nuclear and chloroplast datasets.

Within the South American clade, the initial split is between a clade that is mostly comprised of species in section *Diffusae* (Fig. 3, clade A), and a clade mostly comprised of taxa from the other three sections, i.e. *Orthocarpiflorae*, *Strictae*, and *Laxae* (Fig. 3, clade B). Although not highly supported (clade A, 20 BS; clade B, 29 BS), this split is interesting, as it can be associated with the considerably different corolla morphologies between the sections. Species in section *Diffusae* are all characterized by having a deflected lower corolla lip, as opposed to the straight corolla lip found in the other three sections (Fig. 1). The shape of the lip has been hypothesized to be of evolutionary importance with respect to the type of pollinator that visits the flowers. A deflected lip provides a landing site for insect pollinators, in particular bees, whereas a straight corolla lip suggests pollination by hummingbirds (Molau 1990). Support for other groups within the South American clade is sparse, and may likely be attributed to the relatively slow mutation rate of the chloroplast genome, the young age of the group, and the rapid radiation of this clade (Uribe-Convers and Tank 2015; Uribe-Convers et al. 2016). Nevertheless, there are some interesting results that are worth mentioning. For example, one of the few well-supported clades (78 BS) within clade A (clade A', Fig. 3) comprises species collected in the dry, high elevation Jalca habitats in Peru, while clade B' (100 BS) comprises species distributed in the páramo habitats of the northern Andes in Colombia and Ecuador, which are considerably wetter. However, to fully elucidate relationships between the South American species, it will be necessary to include multiple independent nuclear loci that will aid in teasing apart evolutionary processes such as coalescent stochasticity and introgressive hybridization, which are likely playing a large role in the diversification of this group.

TAXONOMIC TREATMENT

South American Species—One of the main goals in systematics is to create robust and well-supported classifications that are stable and long lasting, reflecting the evolutionary history of the species they encompass. In the past, classifications were largely authority-based, classified by morphological similarity, often without taking evolutionary processes like morphological convergence into consideration, and resulting in the erection of unnatural assemblages of species (i.e. non-monophyletic) (e.g. Olmstead et al. 2001).

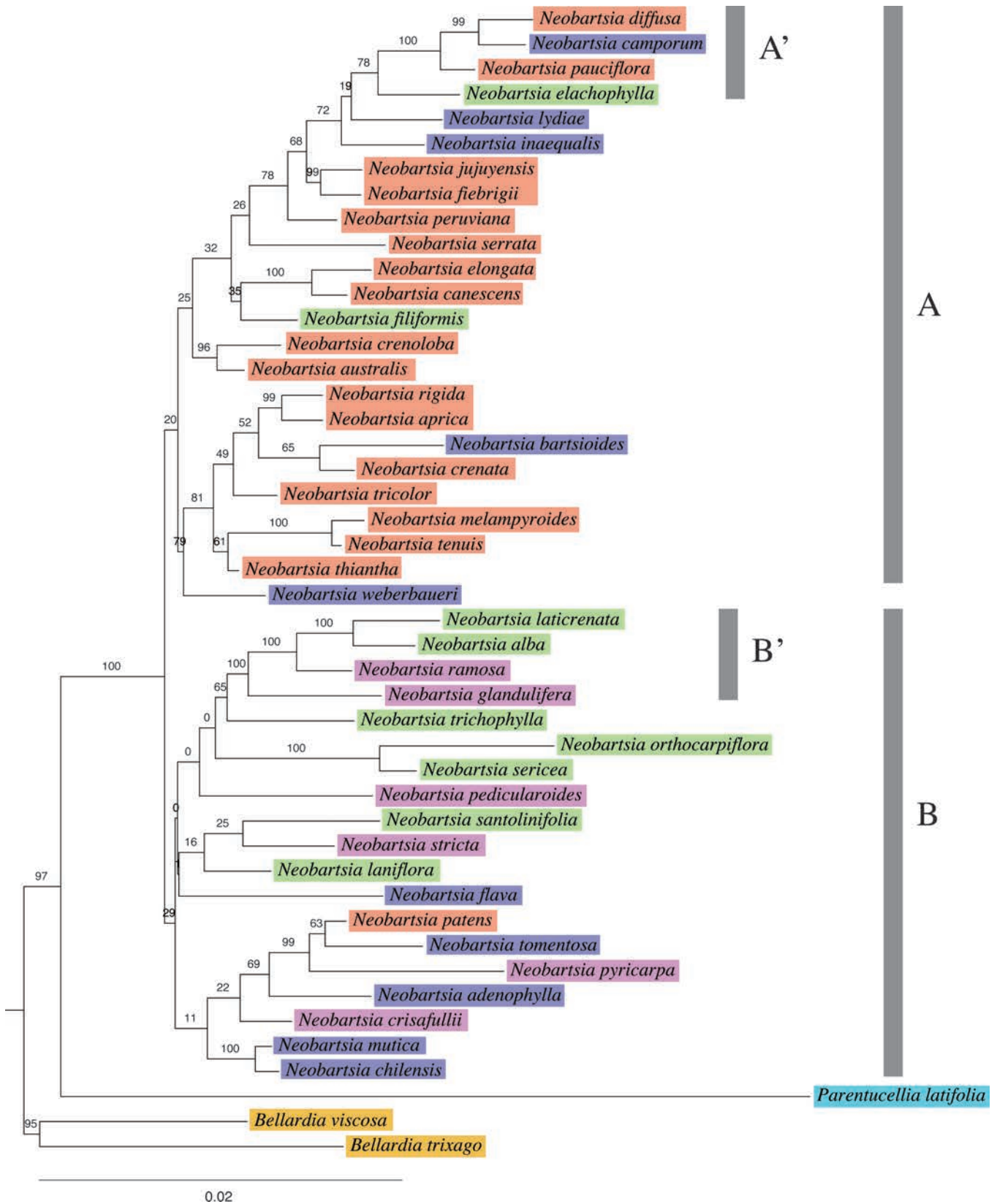


FIG. 3. Current phylogenetic hypothesis based on a maximum likelihood analysis of the South American clade and its close Mediterranean relatives using the high-throughput sequence dataset. Clade A is comprised of species mostly in section *Diffusae* (colored in red), while clade B is comprised mostly of species in the other three sections, i.e. *Laxae* colored in blue, *Orthocarpiflorae* in green, and *Strictae* in purple. Clade A' is comprised of species collected in dry environments in Peru, while clade B' is comprised of species that are distributed in the northern and wetter parts of the Andes in Colombia and Ecuador. Species in the genus *Bellardia* are colored in dark yellow, whereas *Parentucellia latifolia* is colored in teal. Branch lengths are proportional to the number of substitutions per site as measured by the scale bar. Values above the branches represent maximum likelihood bootstrap support (BS). The outgroup, *Bartsia alpina* L., was removed for better visualization.

The major phylogenetic relationships of the Rhinanthaeae clade shown here are consistent with previous Orobanchaceae-wide (Wolfe et al. 2005; Bennett and Mathews 2006; McNeal et al. 2013) and Rhinanthaeae-specific studies (Těšitel et al. 2010; Scheunert et al. 2012; Uribe-Convers and Tank 2015). Although previously implied (Těšitel et al. 2010; Scheunert et al. 2012), this is the first time that the monophyly of the South American taxa has been recovered in a study that incorporates a nearly complete sampling of the species richness of the clade, and not just a few species. The members of this clade are the only species with a South American origin in the Rhinanthaeae clade, as shown in a recent biogeographic study of the group (Uribe-Convers and Tank 2015). In that study, the authors proposed two hypotheses for how the ancestor of the South American species may have colonized the Andes from the Mediterranean region of Europe/north Africa. The first hypothesis relies on a stepwise migration, either via the North American Land Bridge (NALB), a connection that was available between northeastern North America and western Europe between ca. 60–12 million years ago (Ma) (Tiffney 1985), with recent palynological evidence extending the connection to up to ca. 8 Ma (Denk et al. 2010; 2011), or from Eurasia to North America via the Bering Land Bridge, which was available between the late Paleocene and the early to mid-Pliocene, ca. 58–3.5 Ma (Hopkins 1967; Tiffney and Manchester 2001; Tiffney 2008). After colonization of North America via either of these stepwise migration routes, the ancestral lineage would follow a migration into South America over the forming Isthmus of Panama and/or island chains in the mid- to late Pliocene ca. 4.5 Ma (Coates et al. 2004; Kirby and MacFadden 2005; Retallack and Kirby 2007), although new evidence suggests that the closing of the Panama Isthmus may have been a significantly earlier event (Montes et al. 2015; Bacon et al. 2015). Importantly, with either route, a stepwise migration hypothesis implies that the ancestral lineage (and any of its descendants) would have gone extinct thereafter in North America (and in eastern Asia if migration occurred via the Bering Land Bridge route). Both of these routes have been used to describe possible migrations and current distributions of large groups, e.g. Malpighiales (Davis et al. 2002) and Valerianaceae (Moore and Donoghue 2007), and both hypothesized routes fit well with the divergence times reconstructed for the Rhinanthaeae clade by Uribe-Convers and Tank (2015); the crown node for South America has a median age of 2.59 Ma (1.51–4.08 Ma 95% highest posterior density [HPD]) and the divergence between the New World species and the Old World *Bellardia viscosa* was estimated to have a median date of 7.39 Ma (4.21–11.24 Ma 95% HPD). However, in cases like Valerianaceae and Malpighiales there is either current North American diversity (Valerianaceae) or a fossil record in North America (Malpighiales) that corroborates the biogeographic scenario; we have neither with respect to the South American *Bartsia* clade. Lastly, the divergence of *Bellardia trixago* from *Bellardia viscosa* and the South American clade was estimated to have a mean age of 8.73 Ma (5.12–12.76 Ma 95% HPD). The reconstructed dates for these splits allow for an approximately nine million year window for the South American ancestor to reach the then uplifting Andes, and fit well with the proposed ages for both land bridges.

The second hypothesis for the movement of this lineage from Mediterranean Europe/north Africa to the Andes is via long-distance dispersal. Although the seeds of the South American *Bartsia* species are not particularly adapted for flying, they do have short wings and ridges that adhere to surfaces

when wet. Furthermore, each capsule produces ~200 seeds that are each between 0.3–2.0 mm (Molau 1990). It has been shown recently that there is a nearly constant storm track from western Africa (including the northwestern African Mediterranean climatic region) that crosses the Atlantic Ocean into the Caribbean and the Americas, and large influxes of African dust have been found in southern North America, northeastern South America, and the Caribbean basin (Prospero and Mayol-Bracero 2013; Bozlaker et al. 2013; Prospero et al. 2014). This opens the possibility for seeds of a Mediterranean ancestor—even if just one seed in a period of nine million years—to have been picked up and carried over to the New World. Unfortunately, Uribe-Convers and Tank (2015) were not able to accept or reject any of these competing hypotheses.

Moore and Donoghue (2007) demonstrated that upticks in the rate of net diversification (speciation minus extinction) in the plant families Adoxaceae and Valerianaceae were associated not with the appearance of a new key morphological character, but rather to the movement of a lineage to a new geographic area, a process they referred to as “dispersification” (dispersal and diversification). Uribe-Convers and Tank (2015) demonstrated that the same might be true for the Andean species of Rhinanthaeae, as they found elevated rates of net diversification in this clade when compared to the background rate of the tree associated with the biogeographic movement into the Andes. Other young groups of Andean plants have been shown to have elevated rates of diversification in the páramos, e.g. *Lupinus* L. (Hughes and Eastwood 2006), and processes like “dispersification” may be associated with the great diversity that we see today in these rapid radiations. This could be especially relevant when the lineage filling the newly emerging environment already has the relevant morphological and/or physiological adaptations in place, which is concordant with the exaptation-based hypothesis that in circumstances like these, it may be easier for a lineage to track its climatic niche than to evolve adaptations to the novel environment in situ (Donoghue 2008).

All of the evidence gathered for the Andean *Bartsia* clade, i.e. its unique geographic distribution and biogeographic history, the long divergence times from their Mediterranean relatives (~7.39 Ma), and the elevated diversification rates (47 species in ~2.5 Myr), point to the distinctiveness of this group of New World taxa. Not only are they distinct in terms of their evolutionary history, they are different in their reproductive and vegetative morphologies, and possibly their pollination syndromes. The Mediterranean *Bellardia* have a large deflected lower corolla lip, thought to aid in pollination by bees (Molau 1990), and pronounced dorsal gibbae. While the Andean species in section *Diffusae* have a similar morphology of the lower corolla lip, which may be ancestral in Rhinanthaeae, the ca. 26 species in the other three sections (i.e. *Strictae*, *Orthocarpiflorae*, and *Laxae*) have an erect lower lip that contributes to a largely tubular corolla associated with hummingbird pollination (Molau 1990). Additionally, the Mediterranean species of *Bellardia* have coarsely dentate leaves, whereas the South American *Bartsia* species have leaves with tightly crenate, or more rarely, serrate margins. Moreover, the two groups differ substantially in their ecologies; the Mediterranean species grow at low elevations (0–500 m above sea level) in subtropical environments characterized by dry summers and mild, wet winters. On the other hand, the South American taxa are found exclusively at high elevations (2800–4500 m above sea level) in the Andean páramo, jalca, and puna ecosystems, which are

characterized by dramatic daily temperature changes that may range from near freezing at night to over 20°C on a sunny day. Thus, given the evolutionary distinctiveness of the Andean species, we propose here that the South American species of *Bartsia* be classified in the new genus *Neobartsia* Uribe-Convers and Tank, and offer the following taxonomic rearrangements based on the species delimitations designated by Molau (1990). Our revised classification of *Bartsia* and relatives is summarized in Table 1.

Neobartsia Uribe-Convers & Tank, gen. nov.—TYPE: *Neobartsia santolinifolia* (Kunth) Uribe-Convers & Tank. Basionym: *Euphrasia santolinaefolia* Kunth in Humboldt, Bonpland & Kunth, Nov. gen. sp. 2: 333. 1818.

Annual or perennial hemiparasitic herbs or subshrubs, usually pubescent and often glandular; stems prostrate, scandent, or erect, branched mainly in the proximal parts. Leaves decussate, sessile, the blades herbaceous or subcoriaceous with dentate, serrate, crenate, or entire margins, deflexed or revolute. Inflorescences loose to rather dense, often spicate to subspicate. Bracts not or slightly modified, resembling foliage leaves and gradually smaller upwards. Calyx unequally or equally cleft, if the latter, the median clefts usually much deeper than the lateral ones, the dorsal cleft deepest, usually sinuate and widened at base. Calyx lobes straight to reflexed (section *Laxae*). Corolla pubescent, yellow, red, purple, or lavender with the lobes equal to unequal (section *Orthocarpiflorae*). The lower lip straight and flattened to deflect and with dorsal gibbæ (section *Diffusae*). Anthers included, glabrous to pilose, blunt or mucronate. Style included to exposed and in some cases exerted (section *Laxae*). Stigma bilobate, fusiform, or almost capitate. Capsule pilose or setose, rarely glabrous. Seeds 0.3–2.0 mm long, longitudinally winged with the wings finely cross-striate. Distribution: Andean South America.

Neobartsia new clade name. Definition (node-based, branch-modified): the least inclusive clade containing *Neobartsia santolinifolia* (Kunth) Uribe-Convers & Tank 2016 and *Neobartsia canescens* (Wedd.) Uribe-Convers and Tank 2016, but not *Bellardia trixago* (L.) All. 1785, *Parentucellia latifolia* (L.) Caruel 1885, or *Bellardia viscosa* (L.) Fisch. & C.A. Mey 1836. There is no preexisting scientific name for this clade.

Etymology—To alleviate confusion with the new name, we have chosen to conserve part of the previous name of the group (i.e. *Bartsia*), but at the same time incorporating information about its New World distribution (i.e. *Neo*). We believe

that the name *Neobartsia* will facilitate communication between botanists who work in the high Andes, where these taxa are very common.

Justification—Our phylogenetic analyses of both the Sanger and the HTS datasets show that every species found in South America is part of a well-supported clade. The monophyly of these species has been suggested previously, but this is the first time that it has been recovered by a phylogenetic analysis including more than three South American species (e.g. Těšitel et al. 2010, Scheunert et al. 2012). Importantly, by formally treating the forty-plus South American species that were left orphaned by Scheunert et al. (2012), this new classification finally resolves the paraphyly of *Bartsia*, and accurately reflects the unique biogeographic history and diversification dynamics of the clade.

Neobartsia adenophylla (Molau) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia adenophylla* Molau, Opera Bot. 102: 76. 1990. TYPE: PERU. Cajamarca: Prov. Hualgayoc, 8 km from Bambamarca on road to Hualgayoc, 2850 m, 26 Mar 1985, Molau, Öhman & Sánchez Vega 7725 (Holotype: GB; Isotypes: CPUN, HUT).

Neobartsia alba (Molau) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia alba* Molau, Opera Bot. 102: 76. 1990. TYPE: ECUADOR. Chimborazo: Cordillera Occidental, 34 km from Riobamba on road to El Triunfo, summit area, 3850 m, 18 Feb 1985, Molau, Öhman, Arvidsson, Lindqvist & Lindstrom 1327 (Holotype: GB; Isotype: QCA).

Neobartsia aprica (Diels) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia aprica* Diels, Bot. Jahrb. Syst. 37: 430. 1906. TYPE: PERU. Junín: Prov. Tarma, above Tarma, 3300–3700 m, Feb 1903, Weberbauer 2399 (Holotype: B, destroyed; no isotypes found). NEOTYPE: PERU. Junín: Prov. Tarma, 20 km W of (above) Tarma, 4000 m, 9 Apr 1952, Hutchison 640 (Neotype: UC [designated by Molau in Opera Bot. 102: 76. 1990]; Isotype: US).

Euphrasia bicolor Ruiz & Pavón ex A. López, Anal. Inst. bot. Cavanilles 17: 454. 1959 (not validly published, nomenclatural type not designated).

Euphrasia dentata Ruiz & Pavón ex A. López, Anal. Inst. bot. Cavanilles 17: 456. 1959 (not validly published, nomenclatural type not designated).

Neobartsia australis (Molau) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia australis* Molau, Opera Bot. 102: 76. 1990. TYPE: ARGENTINA. Jujuy: Dept. Yavi, Yavi,

TABLE 1. Summary of the species richness, distribution, and important morphological characters for the genera included in this study. Elevation refers to the elevation range the species grow at and is given in meters/feet above sea level.

Genus	No. species	Distribution	Elevation	Leaf margin	Corolla color	Corolla lip	Ploidy level
<i>Bartsia</i>	1	Europe (Alps and Scandinavia), Greenland, Hudson Bay	0–2500/0–8200	Serrate	Purple	Deflexed	Diploid
<i>Bellardia</i>	2	Mediterranean Region, coastal regions of Australia, Chile, and southwestern United States	0–500/0–1600	Dentate	White or yellow	Deflexed	Diploid or tetraploid
<i>Neobartsia</i>	47	High elevation Andes in South America	2800–4850/9180–15800	Serrate to crenate	Purple, yellow, white, light green	Deflexed or straight	Diploid or tetraploid
<i>Parentucellia</i>	1	Mediterranean Region, coastal regions of Australia, Chile, and southwestern United States	0–500/0–1600	Dentate	Red to purple	Deflexed	Tetraploid

3400 m, 1 Jan 1902, *Fries 1713a* (Holotype: S; Isotypes: CORD, LD).

Neobartsia bartsioides (Hook.) Uribe-Convers & Tank, comb. nov. Basionym: *Lamourouxia bartsioides* Hook., Bot. misc. 2: 234. 1831. *Bartsia bartsioides* Edwin, Field Mus. Nat. Hist., Bot. Ser. 13: 492. 1971. *Bartsia densiflora* Benth., nom. superfl., in Candolle, Prodr. 10: 548. 1846. TYPE: PERU. Lima: Prov. Canta, valley of Canta, *Cruckshanks s.n.* (Holotype: K).

Bartsia calycina Diels, Bot. Jahrb. Syst. 37: 432. 1906. TYPE: PERU. Ancash: Prov. Huaylas, below Hda. Cajabamba, W slopes of the Cordillera Negra, SW of Caraz, 3000–3500 m, May 1903, *Weberbauer 3166* (Holotype: B destroyed; Lectotype: G [designated by Molau in Opera Bot. 102: 76. 1990]).

Euphrasia subulata Ruiz & Pavón ex A. López, An. Inst. bot. Cavanilles 17: 455. 1959 (not validly published, nomenclatural type not designated).

Neobartsia camporum (Diels) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia camporum* Diels, Bot. Jahrb. Syst. 37: 433. 1906. TYPE: PERU. Cuzco: Prov. Cuzco, ruins of Sacsayhuaman just above Cuzco, 3500–3600 m, May 1905, *Weberbauer 4864* (Holotype: B destroyed; Lectotype: G [designated by Molau in Opera Bot. 102: 76. 1990]).

Neobartsia canescens (Wedd.) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia canescens* Wedd., Chlor. Andina 2: 123. 1860. TYPE: PERU. Lima, Sine loco (probably Baños de Churín, prov. Cajatambo), *Dombey s.n.* (Isotype: PH, Lectotype: P, designated by Molau in Opera Bot. 102: 76. 1990).

Bellardia canescens (Wedd.) A. Fleischm. & Heubl, Taxon 61(6): 1282. 2012.

Bartsia cinerea Diels, Bot. Jahrb. Syst. 31: 432. 1906. TYPE: PERU. Ancash: Prov. Bolognesi, between Chiquián and Tallenga (N of Aquia), 3300–3600 m, Apr 1903, *Weberbauer 2858* (Holotype: B destroyed, not represented in photograph, Isotypes: not found).

Neobartsia chilensis (Benth.) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia chilensis* Benth. in Candolle, Prodr. 10: 548. 1846. TYPE: CHILE. Valparaíso: Dept. Quillota, La Palma, Quillota, Oct 1829, *Bertero 1072* (Lectotype: G [designated by Molau in Opera Bot. 102: 76. 1990]; Isolectotypes: F, G, GH, P).

Neobartsia crenata (Molau) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia crenata* Molau, Opera Bot. 102: 76. 1990. TYPE: BOLIVIA. Cochabamba: Prov. Quillacollo, SE slopes of Cerro Tunari, between Quillacollo and Morochata. 40–45 km by road from Cochabamba, ca 3950 m, 10 Mar 1983, *Molau 690* (Holotype: S; Isotypes: GB, LPB).

Neobartsia crenoloba (Wedd.) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia crenoloba* Wedd., Chlor. And. 2: 124. 1860. TYPE: BOLIVIA. Potosí: Prov. Modesto Omiste, Quebrada Honda, *d'Orbigny 1315* (Holotype: P; Fragment: F).

Neobartsia crisafullii (N. Holmgren) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia crisafullii* N. Holmgren in Harling & Sparre (eds.), Flora of Ecuador 21: 165. 1984. TYPE: ECUADOR. Azuay: Páramo de Tinajillas, ca 42 km S of Cuenca on road to Loja, 1.6 km N of summit, 3560 m,

27 Jul 1982, *Holmgren, Crisafulli, Boeke & Clemants 10164* (Holotype: NY; Isotypes: AAU, GB, QCA, S).

Neobartsia crisafullii (N. Holmgren) Uribe-Convers & Tank subsp. **acutiloba** (Molau) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia crisafullii* N. Holmgren subsp. *acutiloba* Molau, Opera Bot. 102: 76. 1990. TYPE: PERU. Huánuco: Prov. Huánuco, Mito, ca 25 km (air dist.) W of Huánuco, ca 2750 m, 8–22 Jul 1922, *Macbride & Featherstone 1495* (Holotype: F; Isotype: PH).

Neobartsia diffusa (Benth.) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia diffusa* Benth. in Candolle, Prodr. 10: 548. 1846. TYPE: PERU. Dept. Lima/Junín: Casapi, *Mathews s.n.* (Holotype: K). *Bartsia frigida* Diels, Bot. Jahrb. Syst. 37: 431. 1906. TYPE: PERU. Junín: Prov. Yauli, near Arapa, above Yauli along the Lima-Oroya railroad, 4400 m, Jan 1902, *Weberbauer 271* (Holotype: B, destroyed).

Neobartsia elachophylla (Diels) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia elachophylla* Diels, Bot. Jahrb. Syst. 37: 431. 1906. TYPE: PERU. Junín: Prov. Tarma, mountains W of Huacapistana, 3000–3100 m, Jan 1903, *Weberbauer 2087* (Holotype: B destroyed; Lectotype G [designated by Molau in Opera Bot. 102: 76. 1990]; Isotype: MOL).

Euphrasia incana Ruiz & Pavón ex A. López, Anal. Inst. bot. Cavanilles 17: 456. 1959 (not validly published, nomenclatural type not designated). *Euphrasia sagittata* Ruiz & Pavón ex A. López, Anal. Inst. bot. Cavanilles 17: 454. 1959 (not validly published, nomenclatural type not designated).

Bartsia glabra Edwin, Phytologia 19: 365. 1970. TYPE: PERU. Amazonas: Prov. Chachapoyas, Cerro de Fraijaco (Huau-huni), NE of Tambo de Ventilla, 3500 m, 7 Jul 1948, *Pennell 15878* (Holotype: PH; Isotypes: BM, GH, NY, US, USM).

Neobartsia elongata (Wedd.) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia elongata* Wedd., Chlor. And. 2: 121. 1860. TYPE: PERU. Cuzco: “Cordillères de Cuzco”, *Gay 348* (Holotype: P). *Bartsia simulans* Edwin, Phytologia 19: 367. 1970. TYPE: PERU. Puno: Prov. Puno, San Antonio de Esquilache, ca 4700 m, 16 May 1937, *Stafford 743* (Holotype: BM; Isotype: K).

Neobartsia fiebrigii (Diels) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia fiebrigii* Diels, Bot. Jahrb. Syst. 31: 430. 1906. TYPE: ARGENTINA. Salta: Dept. Santa Victoria, Toldos, S of Río Bermejo, 2200 m, 11 Dec 1903, *Fiebrig 2390* (Holotype: B destroyed; Lectotype: K [designated by Molau in Opera Bot. 102: 76. 1990]; Isotypes: BM, G, L).

Bartsia curtiflora Edwin, Phytologia 19: 363. 1970. TYPE: PERU. Cuzco: Prov. Urubamba, Ollantaytambo, 3000–3100 m, 26 Apr 1925, *Pennell 13643* (Holotype: K; Isotypes: BM, G, GH, NY, PH, S, US).

Neobartsia filiformis (Wedd.) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia filiformis* Wedd., Chl. And. 2: 126. 1860. TYPE: BOLIVIA. La Paz: Prov. Larecaja, between Tipuani and Apolobamba, 2500 m, May 1847, *Weddell 4596* (Lectotype P [designated by Molau in Opera Bot. 102: 76. 1990]; Isolectotypes: F, PH).

Bartsia viridis Edwin, Phytologia 19: 367. 1970. TYPE: PERU. Cuzco: Prov. Paucartambo, Paso de Tres Cruces, Cerro de

Cusilluyoc, 3700–3900 m, 3 May 1925, *Pennell 13826* (Holotype: F; Isotypes: BM, G, GH, K, M, NY, PH, S, US).

Neobartsia flava (Molau) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia flava* Molau, Opera Bot. 102: 76. 1990. TYPE: PERU. Cajamarca: Prov. Celendín, Rio Sendamal Valley, NE of Cruz Conga, 68–72 km from Cajamarca on road to Celendín, 3250–3300 m, 27 Mar 1985, *Molau, Sánchez Vega & Öhman 1760* (Holotype: GB; Isotypes: CPUN, GB, HUT).

Neobartsia flava (Molau) Uribe-Convers & Tank **subsp. minor** (Molau) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia flava* Molau subsp. *minor* Molau, Opera Bot. 102: 76. 1990. TYPE: PERU. Cajamarca: Prov. Cajamarca, Cerro Negro, 1–3 km SE, of (above) Abra Gavilán, ca 13 km (air dist.) SSE of Cajamarca, rocky jalca, 3400–3560 m, 18 Mar 1988, *Molau & Eriksen 3337* (Holotype: GB; Isotypes: AAU, CPUN).

Neobartsia glandulifera (Molau) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia glandulifera* Molau, Opera Bot. 102: 76. 1990. TYPE: COLOMBIA. Santander: Edge of Páramo de Las Vetas, 3300–3700 m, 20–21 Dec 1926, *Killip & Smith 15605* (Holotype: NY; Isotypes: BR, G, GH, K, P, PH, S, UC, US).

Neobartsia inaequalis (Benth.) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia inaequalis* Benth. in Candolle, Prodr. 10: 548. 1846. TYPE: COLOMBIA. Cundinamarca: Bogotá, *Goudot s.n.* (Lectotype: K [designated by Molau in Opera Bot. 102: 76. 1990]; Isotypes: G, OXF, P, US).

Bartsia laxiflora Benth. in Candolle, Prodr. 10: 548. 1846. TYPE: ECUADOR. Pichincha: Cerro Pichincha, *Jameson s.n.* (Holotype: K).

Neobartsia inaequalis (Benth.) Uribe-Convers & Tank **subsp. brachyantha** (Diels) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia brachyantha* Diels, Bot. Jahrb. Syst. 37: 431. 1906. TYPE: PERU. Puno: Prov. Sandia, above Cuyocuyo, 3600–3800 m, May 1902, *Weberbauer 919* (Holotype: B, destroyed, no isotypes found). NEOTYPE: PERU. Puno: Prov. Sandia, Sandia, 13 Mar 1902, *Weberbauer 510* (Neotype: PH [designated by Molau in Opera Bot. 102: 76. 1990]). *Bartsia inaequalis* Benth. subsp. *brachyantha* Molau, Opera Bot. 102: 76. 1990.

Bartsia altissima Rusby, Phytologia 1: 75. 1934. TYPE: BOLIVIA. La Paz: Prov. Nor Yungas, Pongo, Unduavi Valley, 3650 m, Feb 1926, *Tare 222* (Holotype: NY; Isotype: NY).

Neobartsia inaequalis (Beth.) Uribe-Convers & Tank **subsp. duripilis** (Edwin) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia duripilis* Edwin, Phytologia 19: 364. 1970. TYPE: PERU. Ayacucho: Prov. Huanta, Putis, upper Río Chuimacota Valley, 3200–3300 m, 27 Feb–12 Mar 1926, *Weberbauer 7533* (Holotype: F; Isotypes: NY, PH, U, WIS). *Bartsia inaequalis* Benth. subsp. *duripilis* Molau, Opera Bot. 102: 76. 1990.

Euphrasia rubescens Ruiz & Pavón ex A. López, An. Inst. bot. Cavanilles 17: 457. 1959 (not validly published, nomenclatural type not designated).

Neobartsia integrifolia (Wedd.) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia integrifolia* Wedd., Chlor. And. 2: 131. 1860. TYPE: PERU. Dept. unknown (dept. Lima

according to the protologue, uncertain): Sine loco, Jun 1847, *Castelnau s.n.* (Lectotype: P [designated by Molau in Opera Bot. 102: 76. 1990]; Isolectotype: PH).

Neobartsia jujuyensis (Cabrera & Botta) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia jujuyensis* Cabrera & Botta, Hickenia 2(9): 46. 1992. TYPE: ARGENTINA, Provincia de Jujuy, Departamento Valle Grande, camino a Alto Calilegua, Tolditos, 30-Dec-1977. *R. Kiesling, E. Ullbarri y A. López 1553* (Holotype: SI).

Neobartsia laniflora (Benth.) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia laniflora* Benth. in Candolle, Prodr. 10: 548. 1846. TYPE: COLOMBIA. Magdalena: Sierra Nevada de Santa Marta, July 1844, *Purdie s.n.* (Holotype: K).

Bartsia spissifolia Pennell in Steyermark, Fieldiana Bot. 28 (3): 516. 1953. TYPE: VENEZUELA. Mérida: Páramo de Pozo Negro, between San José and Beguilla, 2590–3220 m, 3 May 1944, *Steyermark 56286* (Holotype: F).

Bartsia tachirensis Pennell in Steyermark, Fieldiana Bot. 28 (3): 516. 1953. TYPE: VENEZUELA. Táchira: limestone outcrops of Páramo de Tamá. 3045–3475 m, 15 Jul 1944. *Steyermark 57409* (Holotype: PH; Isotypes: F, NY, US).

Neobartsia laticrenata (Benth.) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia laticrenata* Benth. in Candolle, Prodr. 10: 548. 1846. TYPE: ECUADOR. Napo: On the boggy outlet of the Laguna Mica near Antisana, ca 4000 m, 1843, *Hartweg 1289* (Lectotype: K [designated by Molau in Opera Bot. 102: 76. 1990]; Isotypes: BM, BREM, CCE, E, G, LD, OXF, P, W).

Neobartsia lydiae (Sylvester) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia lydiae* Sylvester, Phytotaxa 164(1): 41. 2014. TYPE: PERU. Cusco, Prov. Urubamba: Distr. Urubamba, Área de Conservación Privada (ACP) Mantamay, 10 km up the valley from Yanahuara in the small valley 3 km E of laguna Ipsaycocha, forest on the SW side of laguna Manalloqsa, 4614m, S13°11'59.2" W72°08'39.9", 23 June 2012, *S.P. Sylvester 1754* (Holotype USM!, Isotypes CUZ!, GB!, ID!, MO!, ZI).

Neobartsia melampyroides (Kunth) Uribe-Convers & Tank, comb. nov. Basionym: *Euphrasia melampyroides* Kunth in Humboldt, Bonpland and Kunth, Nov. gen. sp. 2: 334. 1818. TYPE: ECUADOR. Pichincha: Cachabamba plain and near Pintag, foothills of Antisana, 3300–3900 m, May 1802, *Bonpland 1406* (Lectotype: B-WILLD [designated by Molau in Opera Bot. 102: 76. 1990]; Isotype: H). *Bartsia melampyroides* Benth. in Candolle, Prodr. 10: 548. 1846. *Bartsia gracilis* Benth. in Candolle, Prodr. 10: 548. 1846. TYPE: ECUADOR. Chimborazo: Hda. Chuquipucyu ("Hda. Chuquipoyo"), ca 6 km SW of summit of the Ambato-Riobamba road, ca 3300 m, *Hartweg 1291* (Lectotype: K [designated by Molau in Opera Bot. 102: 76. 1990]; Isotypes: BM, BR, BREM, CGE, E, F, G, LD, LE, OXF, P, W). *Bartsia euphrasioides* Wedd., Chlor. And. 2: 130. 1860. TYPE: ECUADOR. Pichincha(∼): Andes of Quito, ca. 3950 m, *Jameson 477* (Holotype: P; Isotypes: E, G, K).

Bartsia elongata Wedd. β *Pusilla* Wedd., Chlor. And. 2: 127. 1860. TYPE: PERU. Puno: Prov. Carabaya, Jun – Jul 1847, *Weddell 4658* (Holotype: P).

- Neobartsia mutica** (Kunth) Uribe-Convers & Tank, comb. nov. Basionym: *Euphrasia mutica* Kunth in Humboldt, Bonpland and Kunth, Nov. gen. sp. 2: 334. 1818. TYPE: PERU. Piura: Prov. Ayabaca, between Lucarque and Ayabaca, ca 2400 m, Aug 1802, *Bonpland 3466* (Lectotype: P, designated by Molau in Opera Bot. 102: 58. 1990, Isotype: H, F fragment).
- Bellardia mutica* (Kunth) A. Fleischm. & Heubl, Taxon 61(6): 1282. 2012.
- Bartsia hispida* Benth. in Humboldt, Bonpland and Kunth, Nov. gen. sp. 2: 547. 1818. TYPE: PERU. Amazonas: Province of Chachapoyas, *Mathews 788* (Holotype: K, Isotypes: G, OXF).
- Bartsia campii* N. Holmgren in Harling & Sparre (eds.), Flora of Ecuador 21: 159. 1984. TYPE: ECUADOR. Chimborazo: Canyon of the Río Chanchán, above Huigra. 1500–2150 m, 29–37 May 1945, *Camp E-3501* (Holotype: NY; Isotype PH). *Bartsia patriciae* N. Holmgren, in Harling & Sparre (eds.), Flora of Ecuador 21: 158. 1984. TYPE: ECUADOR. Pichincha: 23 km E of (above) Tandapi on road from Santo Domingo to Alóag, 2510 m, 8 Jul 1982, *Holmgren & Holmgren 10072* (Holotype: NY; Isotypes: AAU, cB, QCA, S).
- Neobartsia orthocarpiflora** (Benth.) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia orthocarpiflora* Benth. in Candolle, Prodr. 10: 548. 1846. TYPE: ECUADOR. Pichincha: Andes of Quito, *Jameson s.n.* (Holotype: K). *Bartsia breviflora* Benth., in Candolle, Prodr. 10: 548. 1846. TYPE: ECUADOR. Pichincha: Cerro Pichincha, *Hall 49* (Lectotype: K [designated by Molau in Opera Bot. 102: 76. 1990]).
- Bartsia heterophylla* Wedd., Chl. And. 2: 129. 1860. TYPE: COLOMBIA. Nariño: Province of Tuquerres, 3000–3500 m, *Triana s.n.* (Lectotype: P [designated by Molau in Opera Bot. 102: 76. 1990]; Isotypes: BM, G, W; Fragments: F, PH).
- Bartsia laxissima* Danguy & Chermezon, Bull. Mus. Hist. Nat. (Paris) 28: 436. 1922. TYPE: ECUADOR, Prov. unknown: Naes, Feb 1903, *Rivet 354* (Holotype: P).
- Neobartsia orthocarpiflora** (Benth.) Uribe-Convers & Tank **subsp. villosa** (Molau) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia orthocarpiflora* Benth. subsp. *villosa* Molau, Opera Bot. 102: 76. 1990. TYPE: COLOMBIA. Risaralda: Cerro Tatamá, Cordillera Occidental, moist grassy páramo, 3400–3700 m, 8–10 Sep 1922, *Pennell 10577* (Holotype: GH; Isotypes: F, NY, PH, US).
- Neobartsia patens** (Benth.) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia patens* Benth. in Candolle, Prodr. 10: 548. 1846. TYPE: PERU. Sine loco, *Mathews 898* (Lectotype: CGE [herb. Lindley] [designated by Molau in Opera Bot. 102: 76. 1990; Isotype: CGE [herb. Lemann]).
- Neobartsia pauciflora** (Molau) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia pauciflora* Molau, Opera Bot. 102: 76. 1990. TYPE: BOLIVIA. La Paz: Prov. Murillo, La Rinconada, NE of La Paz, just below summit of road to Unduavi, ca 4200 m, 10 Feb 1921, *Asplund 2392* (Holotype: UPS; Isotypes: S, US).
- Neobartsia pedicularoides** (Benth.) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia pedicularoides* Benth. in Candolle, Prodr. 10: 548. 1846. TYPE: ECUADOR. Napo: On the boggy outlet of Laguna Micacocha (Mica), plains SW of Nevado de Antisana, ca 4100 m, *Hartweg 1290* (Holotype: K; Isotypes: BM, CGE, E; G, LD, OXF, P, W).
- Bartsia parvifolia* Benth., in Candolle, Prodr. 10: 545. 1846. TYPE: VENEZUELA. Mérida: Sierra Nevada de Mérida, ca 3300 m, Aug 1842, *Linden 423* (Holotype: K; Isotypes: BM, G, OXF, P, W; Fragment: F).
- Bartsia biloba* Wedd., Chl. And. 2: 123. 1860. TYPE: PERU. Cuzco: Sine loco, 1839–40, *Gay 909* (Lectotype: P [designated by Molau in Opera Bot. 102: 76. 1990]).
- Neobartsia peruviana** (Walp.) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia peruviana* Walp., Nov. Act. Acad. Caes. Leopold. Carol. 19 Suppl. 1: 400. 1843. TYPE: PERU. Puno: Prov. Chuquito, Pizacoma, ca 4600 m, 31 Apr 1831, *Meyen s.n.* (Lectotype: K [designated by Molau in Opera Bot. 102: 76. 1990]; Isotype: BR).
- Bartsia meyeniana* Benth. in Candolle, Prodr. 10: 545. 1846. TYPE: CHILE. Parinacota: Tacora, close to the Peruvian border, ca 70 km (air dist.) NE of Tacna, ca 4600 m, 1831, *Meyen s.n.* (Holotype: K).
- Bartsia subinclusa* Benth. in Candolle, Prodr. 10: 545. 1846. TYPE: PERU. Puno: Prov. Chuquito, Pizacoma, ca 4600 m, Apr 1831, *Meyen s.n.* (Holotype: K).
- Neobartsia pumila** (Benth.) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia pumila* Benth. in Candolle, Prodr. 10: 548. 1846. TYPE: ECUADOR. Pichincha/Napo: Andes of Quito, 1845, *Jameson s.n.* (Holotype: K).
- Neobartsia pyricarpa** (Molau) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia pyricarpa* Molau, Opera Bot. 102: 76. 1990. TYPE: PERU. Cajamarca: Prov. Cajamarca, Cumbemayo ca. 11 km (air dist.) WSW of Cajamarca, 3400–3450 m, 24 Mar 1985, *Molau, Sánchez Vegas & Öhman 1681* (Holotype: GB; Isotypes: HUT, CPUN).
- Neobartsia ramosa** (Molau) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia ramosa* Molau, Opera Bot. 102: 76. 1990. TYPE: ECUADOR. Napo: Páramo de Guamaní, 1.5–2 km N of the summit of the Quito-Baeza road, 4200–4300 m, 21 Dec 1987, *Molau & Eriksen 2114* (Holotype: GB; Isotypes: AAU, QCA, QCNE).
- Neobartsia remota** (Molau) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia remota* Molau, Opera Bot. 102: 76. 1990. TYPE: PERU. Lima: Prov. Canta, along Río Chillón, near Obrajillo (ca 2 km NE of Canta), 2200–2500 m, 10–15 Jun 1925, *Pennell 14326* (Holotype: PH; Isotypes: BM, F, GH, NY, US).
- Neobartsia rigida** (Molau) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia rigida* Molau, Opera Bot. 102: 76. 1990. TYPE: PERU. Lima: Prov. Huarochirí, Río Blanco, upper Rímac Valley, ca 3650 m, 8–19 May 1922, *Macbride & Featherstone 735* (Holotype: F; Isotype: PH).
- Neobartsia santolinifolia** (Kunth) Uribe-Convers & Tank, comb. nov. Basionym: *Euphrasia santolinaefolia* Kunth in Humboldt, Bonpland & Kunth, Nov. gen. sp. 2: 333. 1818. TYPE: COLOMBIA. Cundinamarca: Between Soacha and Santa Fé de Bogotá, just SW of Bogotá, ca 2500 m, Jul 1802, *Bonpland s.n.* (Lectotype: P [designated by Molau in Opera Bot. 102: 76. 1990]; Isotypes: H, P).

- Bartsia santolinifolia* (Kunth) Benth in Candolle, Prodr. 10: 548. 1846.
- Neobartsia sericea** (Molau) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia sericea* Molau, Opera Bot. 102: 76. 1990. TYPE: PERU. Cajamarca: Cumbemayo, ca 11 km (air dist.) WSW of Cajamarca, 3400–3500 m, 24 Mar 1985, Molau, Öhman & Sánchez Vega 1682 (Holotype: GB; Isotypes: CPUN, HUT).
- Neobartsia serrata** (Molau) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia serrata* Molau, Opera Bot. 102: 76. 1990. TYPE: PERU. Arequipa: Prov. Arequipa, canyon above Arequipa, 3100–3300 m, 26–28 May 1925, Pennell 14276 (Holotype: NY; Isotypes: B, BM, F, G, GH, K, M, PH, S, US, WIS).
- Neobartsia stricta** (Kunth) Uribe-Convers & Tank, comb. nov. Basionym: *Euphrasia stricta* Kunth in Humboldt, Bonpland & Kunth, Nov. gen. sp. 2: 333. 1818. TYPE: ECUADOR. Prov. Pichincha/Napo: Above the village of Chillo and on the slopes of Volcán Antisana, 2500–3100 m, May 1802, Bonpland s.n. (Lectotype: B-WILLD no. 11166 [designated by Molau in Opera Bot. 102: 76. 1990]). *Bartsia stricta* (Kunth) Benth. in Candolle, Prodr. 10: 548. 1846.
- Neobartsia strigosa** (Molau) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia strigosa* Molau, Opera Bot. 102: 76. 1990. TYPE: PERU. Lima: Prov. Huarochirí, Río Blanco, upper Rímac Valley, 3000–3500 m, 15–17 Apr 1929, Killip & Smith 21608 (Holotype: US; Isotypes: F, NY, PH).
- Neobartsia tenuis** (Molau) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia tenuis* Molau, Opera Bot. 102: 76. 1990. TYPE: PERU. Cajamarca: Prov. Cajamarca, Abra El Gavilán, S of Cajamarca, summit area along road to Chilete, 3100–3150 m, 23 Mar 1985, Molau, Öhman & Sánchez Vega 1658 (Holotype: GB; Isotypes: CPUN, HUT).
- Neobartsia thiantha** (Diels) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia thiantha* Diels, Bot. Jahrb. Syst. 37: 432. 1906. TYPE: PERU. Cuzco: Prov. Cuzco, ruins of Sacsayhuaman, 3500 m, 17 Mar 1985, Molau & Öhman 1606 (Neotype: GB [designated by Molau in Opera Bot. 102: 76. 1990]; Isoneotypes: CPUN, HUT); both syntypes cited in the protologue (i.e. *Weberbauer* 3834 and 4858) were destroyed at B and no duplicates have been found. *Bartsia anomala* Edwin, Phytologia 19: 362. 1970. TYPE: PERU. Cuzco: Prov. Paucartambo, on trail from Paucartambo to Vilcanota, Cerro de Colquepata, 3400–3700 m, 7 May 1925, Pennell 14176 (Holotype: BM; Isotypes: GH, NY, PH, US). *Bartsia aurea* Edwin, Phytologia 19: 363. 1970, no holotype was given in the protologue, not validly published.
- Neobartsia tomentosa** (Molau) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia tomentosa* Molau, Opera Bot. 102: 76. 1990. TYPE: PERU. Cajamarca: Prov. Cajamarca, Cumbemayo, ca 11 km (air dist.) WSW of Cajamarca, 3450–3500 m, 29 Mar 1985, Molau, Sánchez Vega & Öhman 1680 (Holotype: GB; Isotypes: CPUN, HUT).
- Neobartsia trichophylla** (Wedd.) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia trichophylla* Wedd., Chl. And. 2: 122. 1860. TYPE: PERU. Puno: between Puno and Arequipa, 4000 m, 1847, Weddell s.n. (Holotype: P).
- Bartsia ciliolata* Wedd., Chl. And. 2: 123. 1860. TYPE: BOLIVIA. La Paz: Prov. Larecaja, Cordillera de Sorata, 1850, Mandon 114 (Holotype: P). *Bartsia sanguinea* Diels, Bot. Jahrb. Syst. 37: 433. 1906. TYPE: BOLIVIA. La Paz: Prov. Larecaja, above Sorata, ca. 4000 m (13,000 ft, says incorrectly 8000 ft on some labels to the collection), Feb 1886, Rusby 1092 (Lectotype: NY [designated by Molau in Opera Bot. 102: 76. 1990]; Isotypes: BM, E, F, G, GH, K, MICH, MO, NY, P, PH, US). *Bartsia guggenheimiana* Rusby, Phytologia 1: 76. 1934. TYPE: BOLIVIA. La Paz: Prov. Nor Yungas, Alaska Mine, above El Pongo, ca. 4200 m, 1–4 Mar 1926, Tate 64 (Holotype: NY; Isotype: PH).
- Bartsia pedicellata* Edwin, Phytologia 19: 366. 1970. TYPE: PERU. Cuzco: Prov. Paucartambo, between Paucartambo and Tres Cruces, Cerro de Cusilluyoc, 3500–3800 m, 2–6 May 1925, Pennell 13815 (Holotype: F; Isotypes: BM, G, K, M, NY, PH, S, US, USM, WIS).
- Neobartsia tricolor** (Molau) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia tricolor* Molau, Opera Bot. 102: 76. 1990. TYPE: PERU. Ancash: Prov. Huaraz, upper W slopes of the Cordillera Negra, 35–37 km from Huaraz on road to Casma, 2–3 km W of the pass (Punta Callán), ca. 4000 m, 29 Jan 1983, Molau, Dillon & Matekaitis 538 (Holotype: GB; Isotypes: S, USM).
- Neobartsia weberbaueri** (Diels) Uribe-Convers & Tank, comb. nov. Basionym: *Bartsia weberbaueri* Diels, Bot. Jahrb. Syst. 37: 431. 1906. TYPE: PERU. Ancash: Prov. Bolognesi, above Ocros, 3500–3700 m, 28 Mar 1893, *Weberbauer* 2692 (Holotype: B destroyed; Lectotype: G [designated by Molau in Opera Bot. 102: 76. 1990]; Isotype: PH).

Mediterranean Species—In order to reflect the monophyly and distinctiveness of the South American species in the classification proposed here, the taxon *Bellardia latifolia* needs to revert to its previous taxonomic classification, i.e. *Parentucellia latifolia*. Scheunert et al. (2012) expanded the genus *Bellardia* to include both species of the previous genus *Parentucellia* because these taxa did not form a clade in their analyses. However, given that our results show that *Parentucellia latifolia* is sister to the *Neobartsia* clade and that *Bellardia viscosa* forms a clade with *Bellardia trixago*, the name *Parentucellia latifolia* becomes useful again.

Interestingly, Scheunert et al. (2012) rearranged the two previous species of *Parentucellia* but disregarded the generic type *P. floribunda* Viv. and the implications concerning this third species. Although we were not able to include *P. floribunda* in our study, we have investigated the history of this species and how the genus was described. In the original publication, Domenico Viviani (1824) described the genus providing a description and a drawing of *P. floribunda*, but he did not specify a type specimen. We have examined a high-resolution photo of the single specimen of *P. floribunda* that we have been able to find in any major herbaria (Voucher No. P03934257, Muséum National d'Histoire Naturelle [P], Paris, France), and based on the photo and the original description for this species (Viviani 1824), as well as the original description of *P. latifolia* and *B. viscosa* (Caruel 1885), it is clear that *P. floribunda* is the same taxon as *P. latifolia*. This means that *P. floribunda* has been collected and misidentified for a long time. Moreover, the Plant List (<http://www.theplantlist.org>, last accessed on March 22nd 2016) lists *P. floribunda* as an unresolved name and suggests it is a synonym of *Bartsia*

latifolia (L.) Sm., a synonym itself of *P. latifolia*. Flora Europaea (Tutin 1973), the Families and Genera of Vascular Plants (Fischer 2004), and Mabberley's Plant-Book (Mabberley 2008) all recognize the genus *Parentucellia* to have only two species (*P. latifolia* and *B. viscosa*), supporting that the name *P. floribunda* has been neglected and that all the collections have been made under *P. latifolia*. *P. floribunda* and *P. latifolia* share diagnostic characters that separate them from *Bellardia viscosa*, mainly i) the smaller size: 5–30 cm (10–70 cm for *B. viscosa*), ii) the purple corolla (white in *B. viscosa*), iii) the short corolla tube, almost as long as the calyx (long tube in *B. viscosa*), iv) the persistent corolla (caducous in *B. viscosa*), and v) the glabrous capsule (pubescent in *B. viscosa*). Based on these characteristics it is evident that the names *P. latifolia* and *P. floribunda* are synonyms and that they should be consolidated into one. Although the first assumption would be to synonymize *P. latifolia* under the generic type *P. floribunda*, after careful review of their taxonomic history and alternative synonymous names, one can discover that the name *P. latifolia* should be used instead, because it was described by Linnaeus in 1753 as *Euphrasia latifolia* L., and thus, has priority over *P. floribunda* (published in 1824).

Parentucellia latifolia (L.) Caruel. Basionym: *Euphrasia latifolia* L., Sp. Pl. 2: 604. 1753. LECTOTYPE (designated by Sutton in Jarvis, Order Out Of Chaos: 514. 2007): [icon.] *Euphrasia pratensis Italica latifolia* Morison, Pl. Hist. Univ. 3: 431, s. 11, t. 24, f. 8. 1699.

Bartsia latifolia (L.) Sm., Flora Graeca 6: 69. 1827.

Bellardia latifolia (L.) Cuatrec., Trab. Mus. Ci. Nat. Barcelona 12: 428. 1929.

Finally, to facilitate communication within the Rhinanthaeae clade, we also propose a clade name for *Neobartsia* and its close Mediterranean relatives.

Molaua Uribe-Convers & Tank, new clade name. Definition (node-based): most inclusive clade that includes *Bellardia trixago* (L.) All. 1785, *Parentucellia latifolia* (L.) Caruel 1885, and *Neobartsia santolinifolia* (Kunth) Uribe-Convers & Tank 2016. There is no preexisting scientific name for this clade. The name *Molaua* is chosen to honor Prof. Ulf Molau, University of Gothenburg, for his dedication and excellent work on the former *Bartsia* species.

KEY TO THE GENERA IN THE CLADE *MOLAU*

1. Annual or perennial plants; lower corolla lip erect or deflected, dorsal gibbae rare. If lower corolla lip is deflected, lateral lobes as wide as the central one. High elevation Andean (Páramo ecosystem) distribution *Neobartsia*
1. Annual plants; lower corolla lip deflected with conspicuous dorsal gibbae (humps), the lateral lobes wider than the central one. Mediterranean distribution or subtropical dry climate (Mediterranean-like climate in western USA, Australia, lowland Chile) 2
 2. Corolla red to purple, plants 5–30 cm *Parentucellia latifolia*
 2. Corolla white to pale yellow, plants 10–70 cm 3
 3. Corolla white, the galea dorsally suffused with purple, diploid plants *Bellardia trixago*
 3. Corolla yellow, the galea yellow, tetraploid plants *Bellardia viscosa*

KEY TO THE MORPHOLOGICAL SECTIONS OF *NEOBARTSIA*

1. Corolla lip deflexed, forming an angle with the tube *Diffusae*
1. Corolla lip erect/straight 2
 2. Calyx campanulate, the lobes—or at least their tips—reflexed from mid-anthesis; stigma more or less exerted *Laxae*
 2. Calyx tubular or urceolate, the lobes straight; stigma included 3
 3. Galea longer than the lip (1.3–3×); calyx lobes ovate or triangular *Orthocarpiflorae*
 3. Galea as long as the lip; calyx unequally cleft, the abaxial (dorsal) cleft the deepest *Strictae*

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