

## *Pseudognaphalium aldunateoides* back in *Gnaphalium* (Compositae: Gnaphalieae)

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Editor: A. Susanna

Received 11 May 2017; accepted 10 December 2017; published online 12 July 2018

### Abstract

*PSEUDOGNAPHALIUM ALDUNATEOIDES* BACK IN *GNAPHALIUM* (COMPOSITAE: GNAPHALIEAE).— Generic classification of some members of the tribe Gnaphalieae (Compositae) and in particular the generic delimitation of the old genus *Gnaphalium* has been long problematic. The genus *Pseudognaphalium* was first split from *Gnaphalium* based on morphology and later supported by molecular phylogenies. However, the generic identity of some species remains doubtful. Here we provide a morphological study of *Pseudognaphalium aldunateoides*, which is compared with the type species of *Gnaphalium* (*Gnaphalium uliginosum*) and *Pseudognaphalium* (*Gnaphalium oxyphyllum*). We also include the three species in a nuclear ribosomal DNA (nrDNA) and a plastid (cpDNA) molecular phylogeny of the tribe Gnaphalieae. Our results show that *P. aldunateoides* has a dimorphic pappus, character not present in the genus *Pseudognaphalium* but characteristic of the genus *Gnaphalium*. It also shows a stereome with intermediate features between the undivided stereome typical of *Gnaphalium* and the fenestrated stereome typical of *Pseudognaphalium*. In the nrDNA and the cpDNA trees, *P. aldunateoides* is placed within the *Gnaphalium s. str.* clade, not closely related to *Pseudognaphalium*. With all these evidence, we conclude that *P. aldunateoides* is correctly placed in *Gnaphalium*.

Key words: Asteraceae; ETS; ITS; molecular phylogeny; micromorphology; pappus; *rpl32-trnL* intergenic spacer; stereome.

### Resumen

*PSEUDOGNAPHALIUM ALDUNATEOIDES* DE NUEVO BAJO *GNAPHALIUM* (COMPOSITAE: GNAPHALIEAE).— La clasificación genérica de varios miembros de la tribu Gnaphalieae (Compositae) y en particular la delimitación genérica del antiguo género *Gnaphalium* ha sido problemática durante mucho tiempo. El género *Pseudognaphalium* fue escindido de *Gnaphalium* por su morfología lo que después fue apoyado por filogenias moleculares. Sin embargo, la identidad genérica de algunas especies todavía es dudosa. Aquí aportamos un estudio morfológico de *Pseudognaphalium aldunateoides*, que es comparado con las especies tipo de los géneros *Gnaphalium* (*Gnaphalium uliginosum*) y *Pseudognaphalium* (*Gnaphalium oxyphyllum*). También hemos incluido estas tres especies en filogenias moleculares de la tribu Gnaphalieae basadas en ADN ribosómico nuclear y ADN cloroplástico. Nuestros resultados muestran que *P. aldunateoides* tiene el vilano dimórfico, carácter que no está presente en el género *Pseudognaphalium* pero que, sin embargo, es característico del género *Gnaphalium*. Además, su estereoma muestra características intermedias entre el estereoma no dividido típico del género *Gnaphalium* y el estereoma fenestrado típico del género *Pseudognaphalium*. En ambas filogenias, *P. aldunateoides* se sitúa dentro del clado *Gnaphalium s. str.*, no próximamente emparentado con *Pseudognaphalium*. Con todas estas evidencias concluimos que *P. aldunateoides* se clasifica correctamente dentro de *Gnaphalium*.

Palabras clave: Asteraceae; ETS; ITS; espaciador intergénico *rpl32-trnL*; estereoma; filogenia molecular; micromorfología; vilano.

**Cómo citar este artículo / Citation**

Acosta-Maindo, A. & Galbany-Casals, M. 2018. *Pseudognaphalium aldunateoides* back in *Gnaphalium* (Compositae: Gnaphalieae). *Collectanea Botanica* 37: e012. <https://doi.org/10.3989/collectbot.2018.v37.012>

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**INTRODUCTION**

It has long been known that generic classification of some genera of the tribe Gnaphalieae (Asteraceae) is problematic, specially involving the large and heterogeneous *Helichrysum* Mill. and *Gnaphalium* L., as well as some other related genera such as *Pseudognaphalium* Kirp. (Hilliard & Burt, 1981; Anderberg, 1991; Galbany-Casals *et al.*, 2014). Hilliard & Burt (1981) made important advances in establishing new generic delimitations based on a critical and detailed morphological study of most controversial genera in Gnaphalieae. In their work, they proved the value of two features, among others: the nature of the stereome of involucral bracts and of the pappus.

The stereome is the thickened lower part of the involucral bract, often straw-coloured or green, contrasting with the thin lamina and pellucid margins (Hilliard & Burt, 1981). The stereome may be undivided in some genera: that is, it appears to be uniformly thickened, though sometimes the median vascular strand is visible and there may occasionally be minute, thin streaks in the upper part of the stereome of some bracts. Alternatively, in other genera, the stereome may be fenestrated, i.e. some distinct vascular strands lie in a translucent area of unthickened cells sharply distinguishable from the thickened cells of the rest of the stereome (Hilliard & Burt, 1981).

The pappus can be monomorphic, that is that bristles of pistillate and hermaphroditic florets have the same morphology, or alternatively, it can be dimorphic, and in this case bristles of pistillate and hermaphroditic florets have a different morphology.

Hilliard & Burt (1981) proposed a new concept for the old genus *Gnaphalium*, which they built around the type species, *Gnaphalium uliginosum* L. In this sense, the genus comprises woolly annual herbs with heterogamous capitula arranged in terminal clusters; capitula with pistillate florets much more numerous than hermaphroditic ones; involucral bracts with the stereome undivided or with a few thin streaks;

pappus bristles monomorphic or slightly dimorphic, with the tips scabrid or, when dimorphic, those of the hermaphroditic florets barbellate with clavate cells.

*Pseudognaphalium* was one of the segregated genera from the old concept of *Gnaphalium*. This genus is based on the Mexican species *Gnaphalium oxyphyllum* DC. Hilliard & Burt (1981) proposed that *Pseudognaphalium*, which at that moment only comprised the type species, should additionally include a number of American, Asian and African species of *Gnaphalium*, which had a close morphological resemblance to each other, but had little affinity with *Gnaphalium s. str.* These authors considered *Pseudognaphalium* morphologically more similar to *Helichrysum*, and particularly to *Helichrysum foetidum* (L.) Moench and related species (Hilliard & Burt, 1981). Although both *Gnaphalium* and *Pseudognaphalium* have pistillate florets outnumbering the hermaphroditic ones, they differ in the habit and general appearance (Hilliard & Burt, 1981), as well as in details of the involucral bracts. *Pseudognaphalium* species—except *Pseudognaphalium oligandrum* (DC.) Hilliard & B. L. Burt—have a fenestrated stereome and a monomorphic the pappus (Hilliard & Burt, 1981), and these characters are shared with the genus *Helichrysum*.

Anderberg (1991), based on cladistical analyses of many morphological characters, also concluded that *Pseudognaphalium* had little affinity with *Gnaphalium*, and formally transferred many species from *Gnaphalium* to *Pseudognaphalium*, rising the latter to *ca.* 90 species.

Recent molecular phylogenies have confirmed that *Pseudognaphalium* is more closely related to *Helichrysum* than to *Gnaphalium* (Smitsen *et al.*, 2011; Nie *et al.*, 2013, 2016; Galbany-Casals *et al.*, 2014). Actually, *Helichrysum* has been recovered as paraphyletic and it includes *Pseudognaphalium* and other genera such as *Achyrocline* (Less.) DC., *Anaphalis* DC. and *Humeocline* Anderb. (Smitsen

*et al.*, 2011; Galbany-Casals *et al.*, 2014; Nie *et al.*, 2016). They all constitute the HAP clade, which is a major component of the tribe Gnaphalieae (Smitsen *et al.*, 2011; Galbany-Casals *et al.*, 2014). *Gnaphalium s. str.* is not closely related to the HAP clade, since *G. uliginosum*, together with other species from the genus, are recovered in a clearly independent clade, closely related to the South African genus *Vellereophyton* Hilliard & B. L. Burtt in plastid DNA (cpDNA) based trees (Smitsen *et al.*, 2011) or to *Plecostachys* Hilliard & B. L. Burtt and *Syncarpha* DC. in nuclear ribosomal DNA (nrDNA) based trees (Smitsen *et al.*, 2011; Nie *et al.*, 2016).

Although a notable progress has been made in the last decades regarding the delimitation of these two genera, some particular species remain controversial. One case is *Pseudognaphalium aldunateoides* (J. Rémy) C. Monti, N. Bayón & Freire (Fig. 1), a species native to Central and South Chile and to West Argentina, where it grows in mossy places

and river margins, from sea level to 3700 m (Freire *et al.*, 2014a). This species was kept in *Gnaphalium* by Anderberg (1991) as *Gnaphalium aldunateoides* J. Rémy, but it was recently transferred to *Pseudognaphalium* by Monti *et al.* (2013), who argued that it has a fenestrated stereome, which is the primary morphological character that differentiates both genera. Although Monti *et al.* (2013) highlighted that some characters, such as a slightly dimorphic pappus, did not match the typical features of *Pseudognaphalium*, this was not considered sufficient evidence to keep the species in *Gnaphalium*. This species has never been included in any molecular work, so its phylogenetic position, which would clarify its generic identity, is unknown.

The aims of this work are to provide an additional morphological study of *P. aldunateoides* and to infer its phylogenetic position in the tribe Gnaphalieae based on nrDNA and plastid DNA markers in order to clarify its generic identity.



**Figure 1.** *Pseudognaphalium aldunateoides* in its natural habitat in Chile, Región IV Coquimbo, Sotaquí, Quebrada Seca (photograph: M. Galbany).

## MATERIALS AND METHODS

### Taxon sampling for molecular phylogeny

Sequences used in this work include newly generated sequences and previously published sequences. We have included two specimens of *Pseudognaphalium aldunateoides*, two specimens of *Pseudognaphalium oxyphyllum*—the type species of *Pseudognaphalium*—and 32 additional *Pseudognaphalium* species. The data set also contained eight different *Gnaphalium* species, including two specimens of *G. uliginosum*, the type species of *Gnaphalium*. Finally, we included a selection of 236 species of other Gnaphalieae genera in an attempt to represent all main clades recovered in previous phylogenetic works for the tribe (Galbany-Casals *et al.*, 2010, 2014; Smissen *et al.*, 2011; Freire *et al.*, 2014b; Nie *et al.*, 2016). Voucher details for all samples are shown in Appendix 1.

### DNA extraction

Total genomic DNA was isolated following the CTAB method of Doyle & Dickson (1987) as modified by Cullings (1992) and Tel-Zur *et al.* (1999) from silica-gel-dried leaves collected in the field or from herbarium material (CONC).

### nrDNA amplification strategies

The ITS nrDNA region (ITS1, 5.8S ribosomal gene, ITS2) was amplified using the 17SE forward and the 26SE reverse primers (Sun *et al.*, 1994). The profile used for amplification was as described in Galbany-Casals *et al.* (2004). The conserved 3' portion of the ETS nrDNA region was amplified using the forward primer Ast-1 and the reverse primer 18S-ETS (Markos & Baldwin, 2001). The profile used for amplification was as described in Galbany-Casals *et al.* (2009). In total, we included in the analyses 277 ITS sequences, of which four are new, and 281 ETS sequences, of which four are new (Appendix 1).

### cpDNA amplification strategies

The *rpl32-trnL* intergenic spacer was amplified using the forward primer rpl32F and the reverse primer trnL<sup>(UAG)</sup> (Shaw *et al.*, 2007). The profile used for amplification was as described in Galbany-Casals

*et al.* (2010). In total, we included in the analyses 220 *rpl32-trnL* sequences, of which three are new (Appendix 1).

### Purification of PCR products and sequencing

PCR products were purified with Exo-SAP-IT (USB Corp., Cleveland, Ohio, USA). Direct sequencing was conducted at the DNA Sequencing Core, CGRC/ICBR of the University of Florida, on an ABI 3730xl DNA Analyser (Applied Biosystems) using a Big Dye Terminator v3.1 kit (Applied Biosystems, Foster City, CA, USA).

### Alignments

Nucleotide sequences of the two data sets, nrDNA and cpDNA, were edited using Chromas v2.5.1 (Technelysium, Tewantin, Australia), Bioedit v7.2.5 (Hall, 1999) and MEGA v7.0.14 (Kumar *et al.*, 2016), and aligned visually or with the program Clustal X v2.1 (Thompson *et al.*, 1997) with subsequent visual inspection and manual correction. In the cpDNA data set, a fraction of nucleotides (from 144 to 652 bp, both included) of high variability and ambiguously aligned was manually excluded. Additional ambiguously aligned regions of the two data sets were detected and excluded with the use of Gblocks v0.91 (Castresana, 2000; Talavera & Castresana, 2007). It was used with relaxed conditions in order to preserve as much information as possible: “Minimum number of sequences for a conserved position” and “Minimum number of sequences for a flank position” were half the number of sequences +1, “Maximum number of contiguous nonconserved positions” was 10, “Minimum length of a block” was 5, and “Allowed gap positions” was “With half”. Final aligned length analysed for each region is shown in Table 1, with indication of the percentage of the original data sets that it represents after the exclusion of ambiguously aligned regions.

### Analyses

The phylogenetic relationships were examined analysing cpDNA and nrDNA separately, given the existence of several well-supported incongruent patterns in previous phylogenies (Smissen *et al.*, 2011; Galbany-Casals *et al.*, 2014).

For each data set, the best-available model of molecular evolution required for estimations of phylogeny was selected using the Akaike information criterion (AIC; Akaike, 1973) as implemented in the software MEGA v7.0.14 (Kumar *et al.*, 2016). The best-fitting model was used in each case (see Table 1).

In both data sets, *Athrixia phyllicoides* DC., *Relhania pungens* L'Hérit. and *Leysera gnaphalodes* (L.) L. were coded as outgroup taxa, based on previous studies (Galbany-Casals *et al.*, 2014; Freire *et al.*, 2014b; Nie *et al.*, 2016). Bayesian analyses were conducted using BEAST v1.8.3 (Drummond *et al.*, 2012) with the same parameters for both data sets. Clock model was coded as an "Uncorrelated relaxed clock" with a "Lognormal" distribution. The data sets were not partitioned by locus and the GTR + I + G nucleotide substitution model (Gu *et al.*, 1995) was used with the following conditions: "Base frequencies" was "Empirical" and "Number of Gamma Categories" was "4". The tree Prior was set as "Speciation: Yule Process" (Yule, 1925; Gernhard, 2008) and default prior distributions were chosen for all other parameters. After operator adjustment, four independent MCMC runs were performed, each run of 50 million generations and sampling every 5.000 generations. We verified the convergence of chains with Tracer v1.6 (Rambaut *et al.*, 2014) by checking that effective sample size values were adequate. The four runs were combined with LogCombiner v1.8.3 (Drummond *et al.*, 2012) after discarding the initial 10% generations of each as burn-in. A maximum clade credibility tree was obtained using TreeAnnotator v1.8.3 (Drummond & Rambaut, 2007) with the following conditions: "Target tree type" was "Maximum clade credibility tree", "Node heights" was "Mean heights" and no burn-in was performed. The resulting maximum clade credibility tree was transformed into a cladogram using

FigTree 1.4.3 (Rambaut, 2016). Posterior probability supports were considered to be significant for nodes with  $PP \geq 0.95$ , and only those are shown.

### Morphological study

The sequenced specimens of *P. aldunateoides* (Appendix 1) were identified using several keys (Reiche, 1903; Freire *et al.*, 2014a), and compared to the type specimen of the name *Gnaphalium aldunateoides*: "CHILE: Santiago, Feb 1839, Gay s. n." (P 00704557 photo!) (Monti *et al.*, 2013; Freire *et al.*, 2014a). Also, for the types of the generic names *Pseudognaphalium* and *Gnaphalium*, the two sequenced specimens of *P. oxyphyllum* and the two of *G. uliginosum* (Appendix 1) were identified using several keys (Holub, 1976; McVaugh, 1984; Espinosa-García, 2005; Nesom, 2006; Chen & Bayer, 2011) and they were compared to the corresponding type specimens: "Herb. Linn. No. 989.84" (LINN photo!) for *G. uliginosum* (Hilliard & Burtt, 1981; Jarvis, 1992) and "Villalpando au Sud est de Guanajuato, Méndez s. n." (G-DC photo!) for *G. oxyphyllum* (McVaugh, 1984).

The stereome and pappus characters were studied for the sequenced specimens of *P. oxyphyllum* and *P. aldunateoides*, along with nine additional specimens of *P. aldunateoides* and a specimen of *G. uliginosum* (Appendix 2). Involucral bracts were cleared in a commercial solution of sodium hypochlorite during 3–4 hours (Stace, 1965) to visualize if the stereome was undivided or fenestrated. The stereome and pappus bristles of female and hermaphroditic florets were observed using a Zeiss Axioscop compound microscope and photographed with a Jenoptik ProGresC3 digital camera using the program ProGresCapture7.

**Table 1.** Characteristics of data matrices and substitution models applied in the analyses.

	nrDNA (ITS + ETS)	cpDNA ( <i>rpl32-trnL</i> )
Number of taxa	283	220
Number of characters included after removing ambiguously aligned regions	973 (87% of the complete aligned data set)	508 (39% of the complete aligned data set)
Number of MCMC generations	50 million	50 million
Substitution model	GTR + I + G (Gu <i>et al.</i> , 1995)	GTR + I + G (Gu <i>et al.</i> , 1995)

## RESULTS

### Phylogenetic position of *Pseudognaphalium aldunateoides*

The nrDNA (Fig. 2) and cpDNA (Fig. 3) phylogenetic trees placed the genus *Pseudognaphalium* within the HAP clade, being part of the clade mainly constituted by the paraphyletic genus *Helichrysum*, which is in conformity with previous studies (Smitsen *et al.*, 2011; Galbany-Casals *et al.*, 2014; Nie *et al.*, 2016). While the nrDNA phylogeny showed *Pseudognaphalium* to be constituted by two well-supported and independent clades (Fig. 2, clades A.1 and A.2), cpDNA showed it to be constituted by three independent lineages (Fig. 3, clades A.1, A.2 and A.3). In both the nrDNA and the cpDNA trees, *P. oxyphyllum*, the type of *Pseudognaphalium*, was included in a clade with other species of *Pseudognaphalium*.

Members of *Gnaphalium* were recovered in a clearly independent and well supported clade: in the nrDNA phylogeny, *Gnaphalium* was sister to some *Syncarpha* (Fig. 2, clade B), while the cpDNA phylogeny indicated it to be more closely related to *Vellereophyton* (Fig. 3, clade B), what in both cases agree with previous studies (Smitsen *et al.*, 2011; Galbany-Casals *et al.*, 2014; Nie *et al.*, 2016). In both phylogenies, the *Gnaphalium* clade included the type species *G. uliginosum*.

Both in the nrDNA tree (Fig. 2, clade B) and the cpDNA tree (Fig. 3, clade B), *P. aldunateoides* was not placed in the HAP clade with the other *Pseudognaphalium* species, but in the *Gnaphalium* clade.

### Morphological study

With regards to the habit and general appearance, the studied specimens of *P. aldunateoides* are dwarf, multistemmed, ascending to erect annual plants with concolorous leaves whitish-woolly on both faces, few capitula arranged in corymbs and subtended by linear leaves, and campanulate involucre composed of involucre bracts whitish at the apex (Fig. 1). They match the descriptions of the species (Reiche, 1903; Freire *et al.*, 2014a) and the type material.

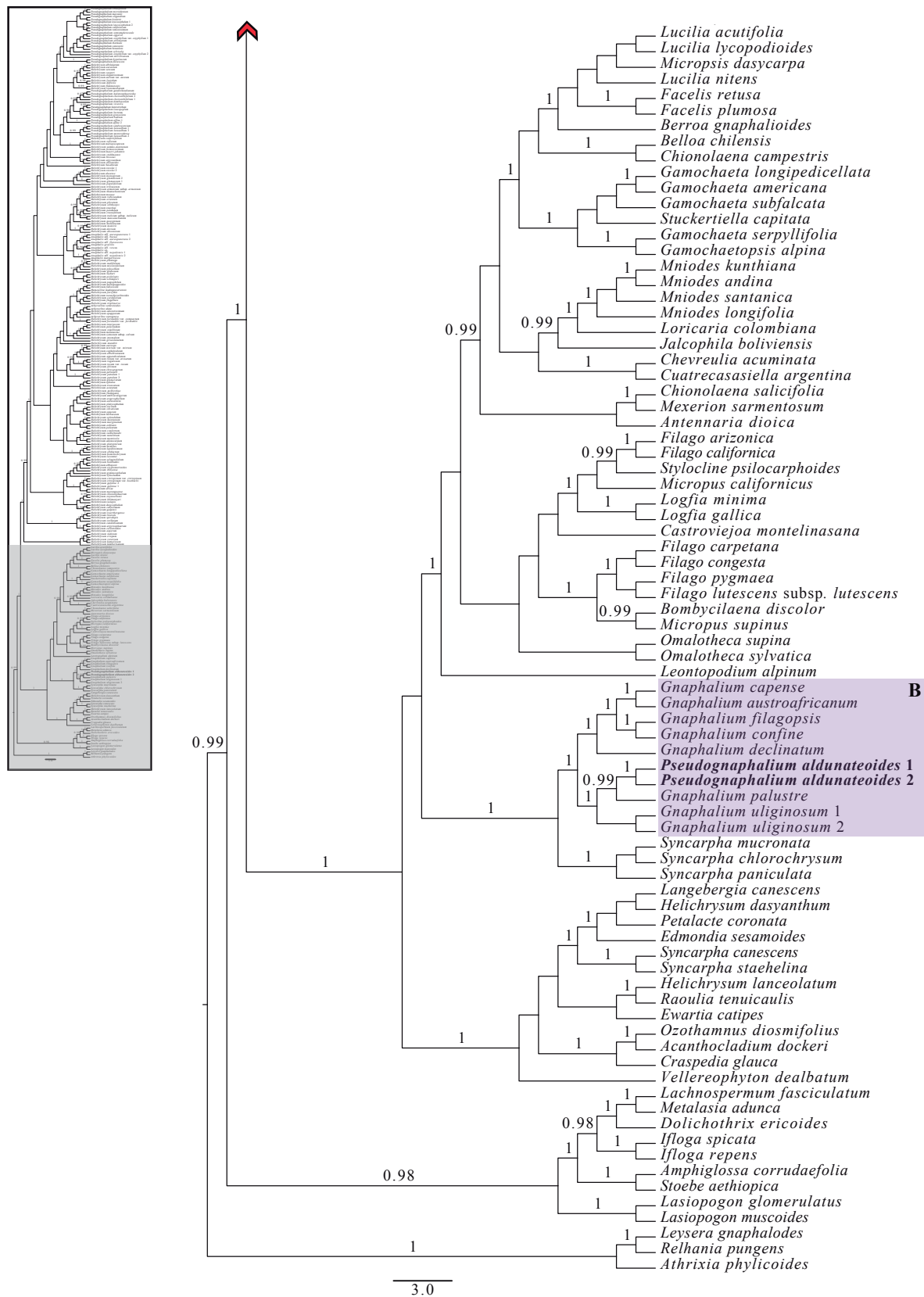
The pappus of *P. aldunateoides* is slightly to markedly dimorphic, i.e. the pappus bristles of hermaphroditic florets are subclavate, making the bris-

les noticeably wider (Fig. 4.1) than those of pistillate florets, which have obtuse cells at the tips instead (Fig. 4.2). The stereome is variable. In some specimens it fits the description of undivided stereome, i.e. it is uniformly thickened, except for some minute, thin translucent streaks in the upper part of the stereome. In others specimens the translucent area of unthickened cells of the stereome is rather big, and in this cases it resembles a fenestrated stereome (Fig. 5.1). However, in all cases the translucent area is limited to the upper part of the stereome.

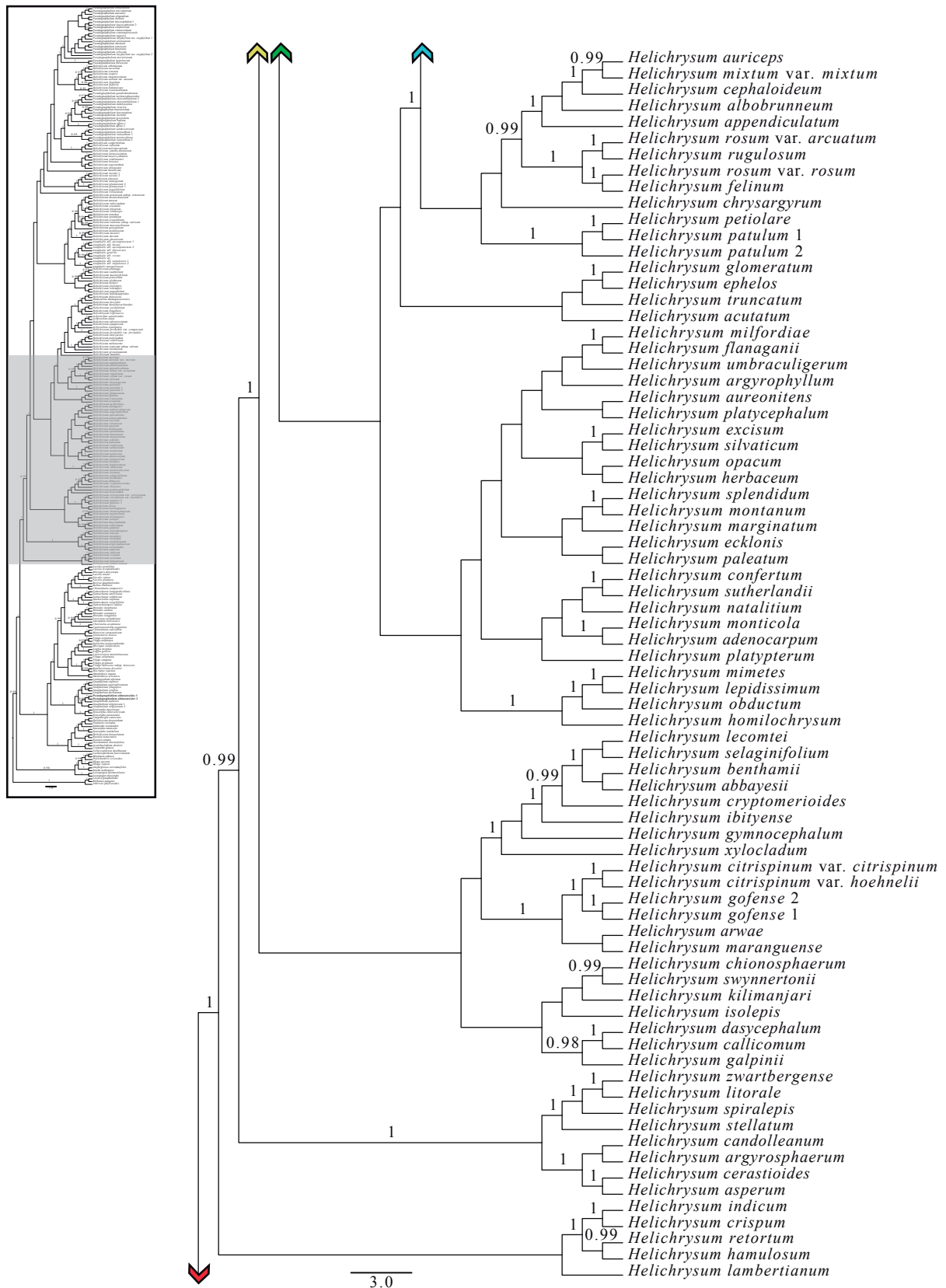
*Gnaphalium uliginosum* shows distinctly, though slightly, dimorphic pappus bristles (Fig. 4.3 and 4.4) as described by Hilliard & Burtt (1981) and an undivided stereome with few thin streaks (Fig. 5.2). *Pseudognaphalium oxyphyllum* displays a monomorphic pappus (Fig. 4.5 and 4.6) and a fenestrated stereome (Fig. 5.3). Hence either species agrees in its diagnostic morphological characters with the genus for which it provides the type of the name.

## DISCUSSION

The study of Hilliard & Burtt (1981) demonstrated the great value of the stereome characters in the generic delimitation of Gnaphalieae, as genera are usually uniform—with few exceptions—for stereome anatomy. Although fenestrated stereomes present no doubt, Hilliard & Burtt (1981) commented that undivided stereomes, even being mostly opaque, can sometimes present median vascular strands visible and there may occasionally be minute, thin streaks in the upper part of the stereome of some bracts. This is the case of *G. uliginosum* (Fig. 5.2) and some specimens of *P. aldunateoides*. However, in other specimens of *P. aldunateoides*, the translucent area can be larger and resemble a fenestrated stereome (Fig. 5.1). Due to the presence of this translucent area, the stereome of *P. aldunateoides* was interpreted as fenestrated by Monti *et al.* (2013), and this was the main reason to support the combination of this species under *Pseudognaphalium*. However, the translucent area in *P. aldunateoides*' bracts is smaller than in a typical fenestrated stereome (Fig. 5.3) and is limited to the upper part of the stereome. In conclusion, *P. aldunateoides*' stereomes present intermediate characteristics between undivided and fenestrated stereomes.

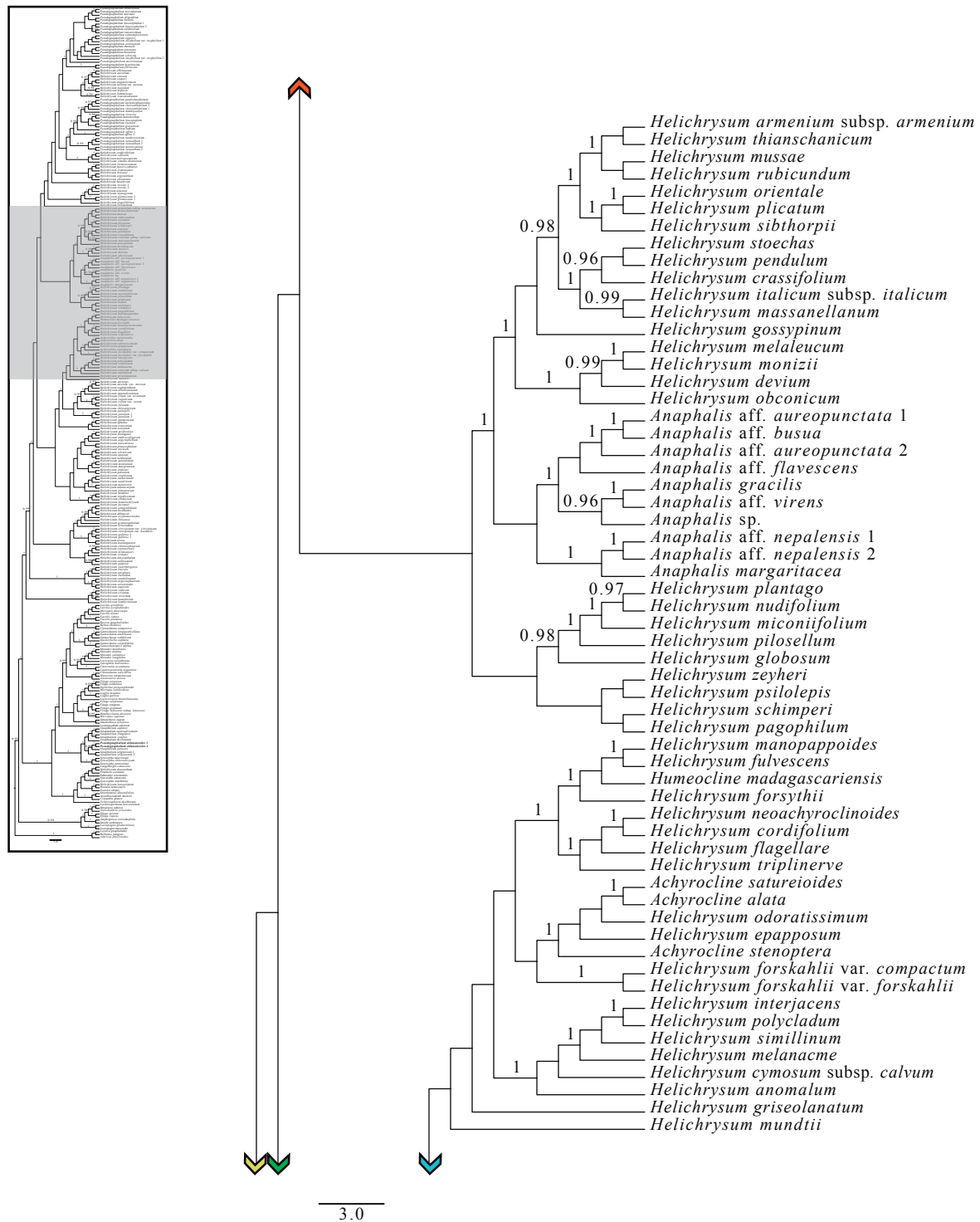


**Figure 2.** nrDNA (ITS and 3' ETS regions) maximum credibility tree obtained from the BEAST analyses of the Gnaphalieae. Only  $\geq 0.95$  Bayesian posterior probabilities values are shown. Species of the genera *Pseudognaphalium* and *Gnaphalium* are highlighted in coloured boxes. Clades discussed in the text are labeled with capital letters and numbers.



**Figure 2 (cont.).** nrDNA (ITS and 3' ETS regions) maximum credibility tree obtained from the BEAST analyses of the Gnaphalieae. Only  $\geq 0.95$  Bayesian posterior probabilities values are shown. Species of the genera *Pseudognaphalium* and *Gnaphalium* are highlighted in coloured boxes. Clades discussed in the text are labeled with capital letters and numbers.

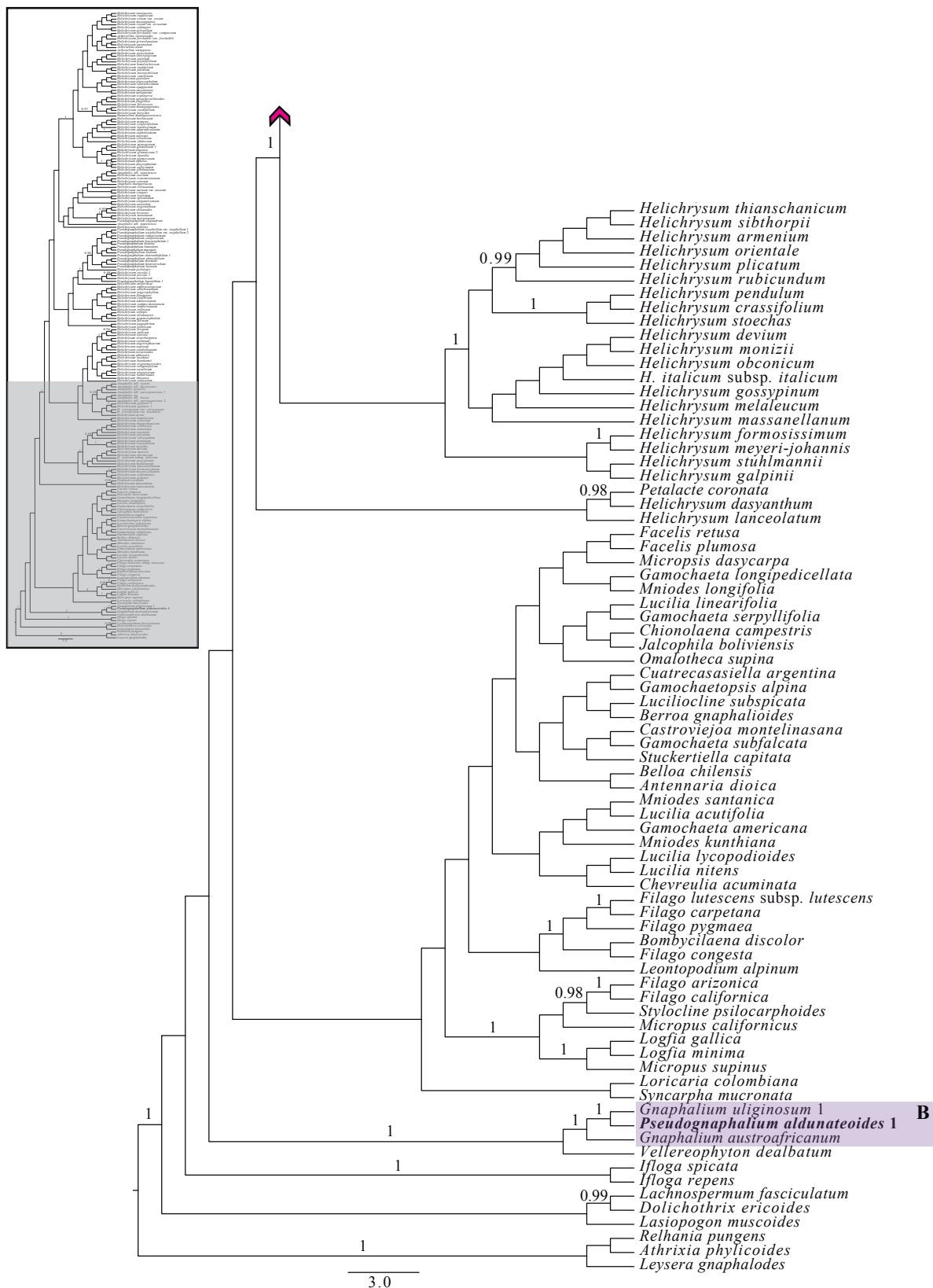




**Figure 2 (cont.).** nrDNA (ITS and 3' ETS regions) maximum credibility tree obtained from the BEAST analyses of the Gnaphalieae. Only  $\geq 0.95$  Bayesian posterior probabilities values are shown. Species of the genera *Pseudognaphalium* and *Gnaphalium* are highlighted in coloured boxes. Clades discussed in the text are labeled with capital letters and numbers.



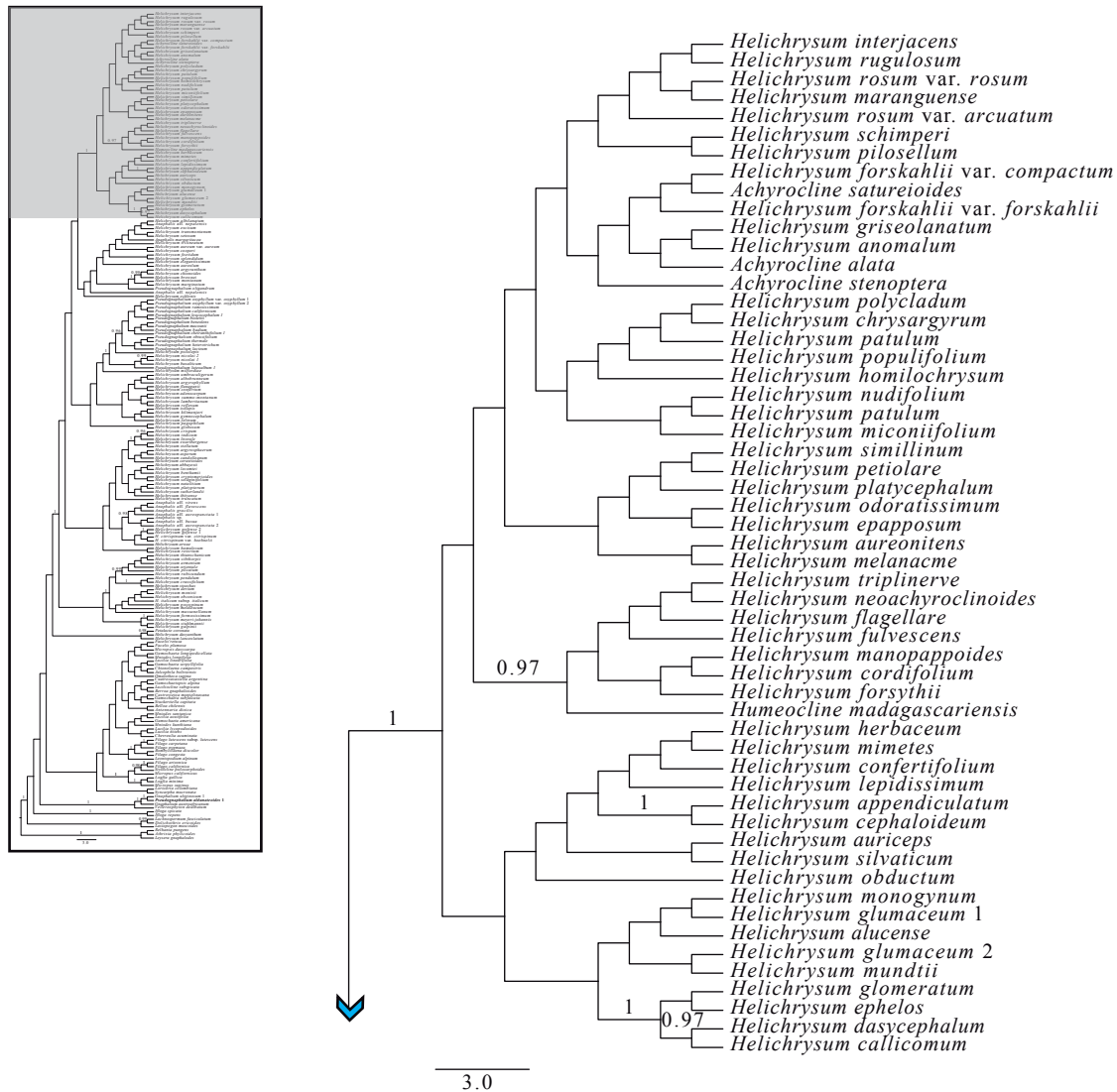
**Figure 2 (cont.).** nrDNA (ITS and 3' ETS regions) maximum credibility tree obtained from the BEAST analyses of the Gnaphalieae. Only  $\geq 0.95$  Bayesian posterior probabilities values are shown. Species of the genera *Pseudognaphalium* and *Gnaphalium* are highlighted in coloured boxes. Clades discussed in the text are labeled with capital letters and numbers.



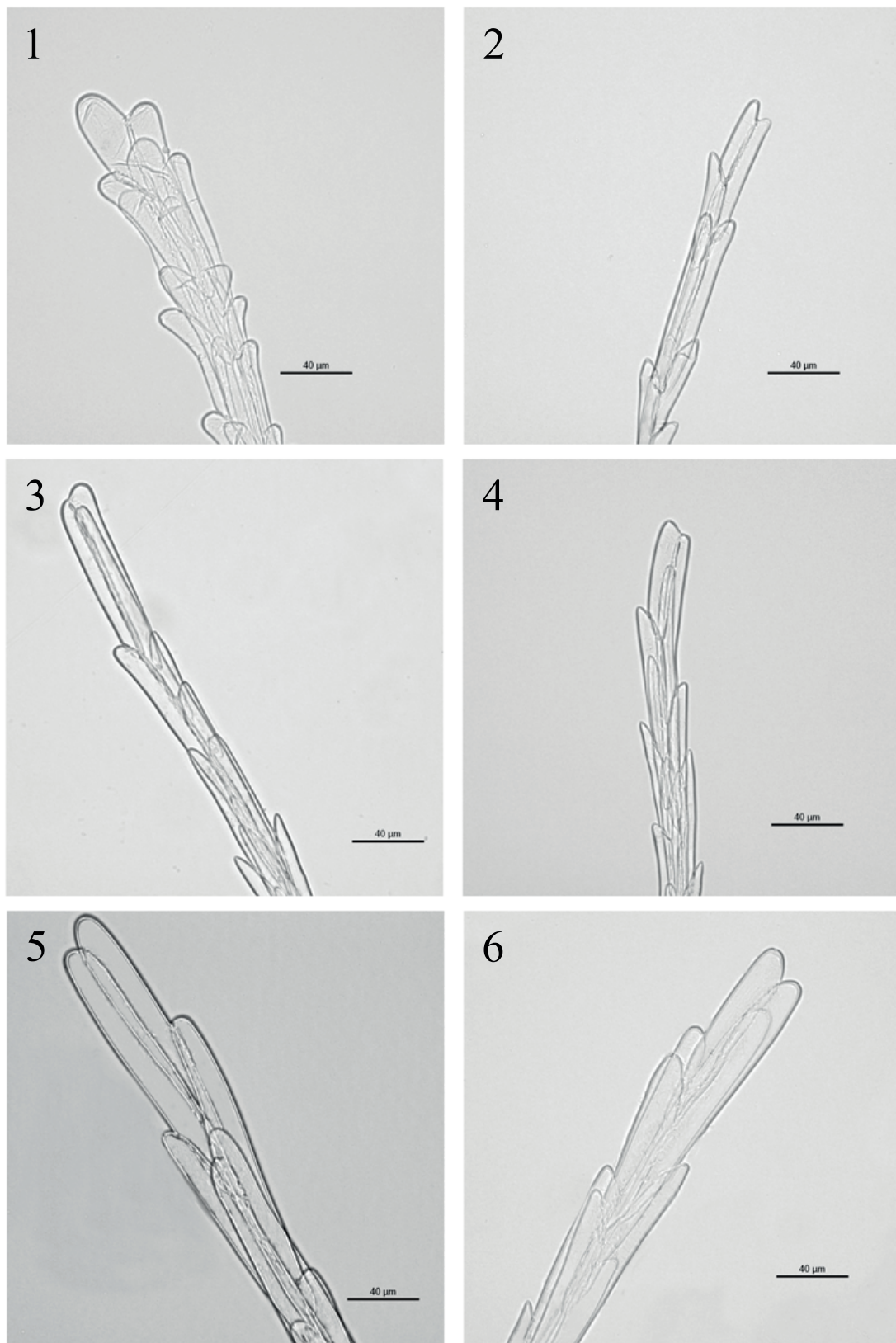
**Figure 3.** cpDNA (*rpl32-trnL* intergenic spacer) maximum credibility tree obtained from the BEAST analyses of the Gnaphalieae. Only  $\geq 0.95$  Bayesian posterior probabilities values are shown. Species of the genera *Pseudognaphalium* and *Gnaphalium* are highlighted in coloured boxes. Clades discussed in the text are labeled with capital letters and numbers.



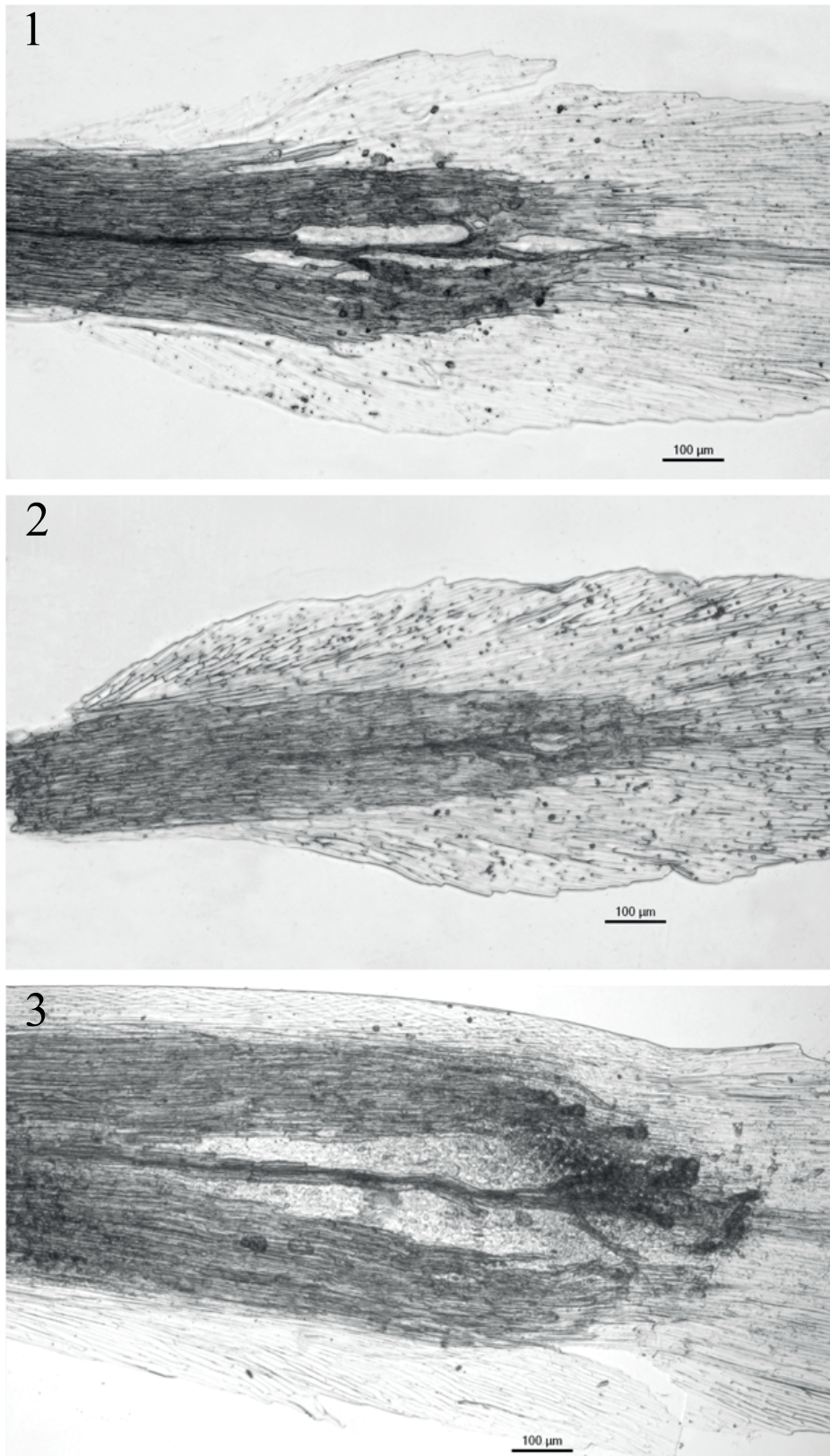
**Figure 3 (cont.).** cpDNA (*rpl32-trnL* intergenic spacer) maximum credibility tree obtained from the BEAST analyses of the Gnaphalieae. Only  $\geq 0.95$  Bayesian posterior probabilities values are shown. Species of the genera *Pseudognaphalium* and *Gnaphalium* are highlighted in coloured boxes. Clades discussed in the text are labeled with capital letters and numbers.



**Figure 3 (cont.).** cpDNA (*rpl32-trnL* intergenic spacer) maximum credibility tree obtained from the BEAST analyses of the Gnaphalieae. Only  $\geq 0.95$  Bayesian posterior probabilities values are shown. Species of the genera *Pseudognaphalium* and *Gnaphalium* are highlighted in coloured boxes. Clades discussed in the text are labeled with capital letters and numbers.



**Figure 4.** Pappus bristles showing tip cells. Left column: pappus bristle of hermaphroditic florets. Right column: pappus bristle of pistillate florets. (1) and (2) *Pseudognaphalium aldunateoides* (Galbany 2525 & Arrabal, BC); (3) and (4) *Gnaphalium uliginosum* (Galbany 2090 & Arrabal, BC); (5) and (6) *Pseudognaphalium oxyphyllum* (Galbany 2480 & Arrabal, BC). Scale bar 1–6 = 40 µm.



**Figure 5.** Involucral bracts showing the stereome: (1) *Pseudognaphalium aldunateoides* (Galbany 2525 & Arrabal, BC); (2) *Gnaphalium uliginosum* (Galbany 2090 & Arrabal, BC); (3) *Pseudognaphalium oxyphyllum* (Galbany 2480 & Arrabal, BC). Scale bar 1–3 = 100 µm.

Regarding pappus morphology, our morphological study shows that the pappus of *P. aldunateoides* is always dimorphic. While this character is variable in *Gnaphalium* (Hilliard & Burt, 1981), the pappus is always monomorphic in the genus *Pseudognaphalium* (Anderberg, 1991). Monti *et al.* (2013) already noticed the dimorphic pappus of *P. aldunateoides*, but they considered it to be an exception in *Pseudognaphalium*.

Considering the phylogenetic position of *P. aldunateoides* within the *Gnaphalium* clade, both in the nrDNA (Fig. 2, clade B) and the cpDNA (Fig. 3, clade B) phylogenetic trees, it is clear that this species should be classified as a member of *Gnaphalium*. In the nrDNA tree (Fig. 2), *Gnaphalium* is composed of two main clades, one constituted by all the African species included—from *Gnaphalium capense* Hilliard to *Gnaphalium declinatum* L. f.—and the other constituted by European and American species. Within the latter, *G. aldunateoides* is sister to *Gnaphalium palustre* Nutt., a North American species. Although there seems to be a geographical pattern in the phylogenetic relationships obtained, the sampling of the genus is too scarce to venture any conclusions.

Our results confirm the predictive value of morphological characters in the generic delimitation of Gnaphalieae, as Hilliard & Burt (1981) already highlighted with insight, taking into account that they did not count with molecular phylogenies at that time. Moreover, our results also agree with Anderberg's (1991) proposal based on morphological characters, in which more than 70 species were transferred from *Gnaphalium* to *Pseudognaphalium* but *P. aldunateoides* was left as *G. aldunateoides*. However, we show that the stereome can sometimes be variable within a species, and present intermediate characteristics that can make it difficult to be assigned to one of the two described states. In conclusion, this character should always be examined in several specimens, and should not be used alone for generic delimitation, but in combination with other morphological characters and with molecular data.

*Gnaphalium perpusillum* Phil. was described on the basis of single-stemmed dwarf plants 1.5 cm high [CHILE. Coquimbo: Sotaqui, Jan 1837, Gay 739 (holotype, SGO 64448!); Monti *et al.*, 2013; Freire *et al.*, 2014a]. Although one of our two studied specimens of *G. aldunateoides* was collected in the type locality of *G. perpusillum*, it does not match *G. perpusillum*'s description (Reiche, 1903) in that

it is multistemmed, branched from the base and 6 to 10 cm high. These two species were presented separately in the morphological study of Monti *et al.* (2013), in which they were both transferred to *Pseudognaphalium*. In that work, the studied specimens of *G. perpusillum* were reported to have a dimorphic pappus and a fenestrated stereome, but the figure showed it has intermediate characteristics, being similar to that of *G. aldunateoides*. Later on, Freire *et al.* (2014a) stated that the diagnostic characters of *G. perpusillum* are variable features throughout the range of *G. aldunateoides* and synonymised both taxa under the latter. With the evidence of morphological characters, *P. perpusillum* should be also placed under *Gnaphalium* as *G. perpusillum*, if considered as a separate species.

## ACKNOWLEDGMENTS

M. G.-C. greatly appreciates S. Arrabal's help, enthusiastic support, dedication and joy in all the shared field expeditions. O. Hinojosa, D. Juárez and S. Teillier provided very valuable help and advice for field trips and plant collections and they are gratefully acknowledged. We thank S. Magallón for organising the stay of M. G.-C. at the "Universidad Nacional Autónoma de México". We thank the staff of the herbaria BC (N. Nualart), CONC (A. Marticorena), MEXU (D. Gernandt and L. Villaseñor) and SGO (G. Rojas) for kindly receiving M. G.-C., providing specimens for this study and/or institutional support for plant collections. L. Guàrdia provided the microscope and camera and technical support necessary for using them. J. Requena provided technical support in the lab. P. Carnicero provided helpful advice for phylogenetic analyses. G. Acosta and M. Balaguer provided informatics support for running phylogenetic analyses. We thank S. Freire and C. Monti for critically reading the manuscript and providing interesting discussion. Two anonymous reviewers contributed to improve the paper. M. G.-C. benefitted from a "Systematics Research fund" from the Systematics Association and the Linnean Society of London and a "Beca Iberoamérica Jóvenes Profesores Investigadores" from "Banco Santander", which partly financed the stays and field work in Chile and Mexico, respectively. The Catalan government ("Ajuts a grups consolidats" 2014-SGR 514) partly financed this work.

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**Appendix 1.** Species included in molecular analyses with voucher information and INSDC (International Nucleotide Sequence Database Collaboration) accession numbers (ITS, ETS, *rpl32-trnL* intergenic spacer). Newly generated sequences are marked with an asterisk (\*), hyphens (-) indicate missing sequences. Acronyms of the herbaria follow *Index Herbariorum* (Thiers, 2017).

*Acanthocladium dockeri* F. Muell.: Australia, Bayer 99011 (SA); JQ95655, JQ956648, -. *Achyrocline alata* (Kunth) DC.: Brasil, Rio Grande do Sul, São Francisco de Paula, *Grazziotin 8941 et al.* (W 1995-4937); HG797714, HG797978, HG798135. *Achyrocline satureioides* (Lam.) DC.: Argentina, Entre Ríos, Departamento Colón, *D. G. Gutiérrez 658* (LP); HG797713, HG797976, HG798133. *Achyrocline stenoptera* (DC.) Hilliard & B. L. Burt: Tanzania, Olmoti, *Galbany & Arrabal s. n.* (BC 867819); FJ211449 and FJ211507, HG797977, HG798134. *Amphiglossa corrudaefolia* DC.: South Africa, Prince Albert, *Koekemoer 1291* (BOL); JF911388, FM173124, -. *Anaphalis* aff. *aureopunctata* Lingelsh. & Borza (1): China, Sichuan Province, *Boufford 35751 et al.* (HUH); HG797715, HG797979, HG798136. *Anaphalis* aff. *aureopunctata* Lingelsh. & Borza (2): China, Sichuan Province, *Boufford 32622 et al.* (HUH); HG797716, HG797980, HG798137. *Anaphalis* aff. *busua* DC.: China, Sichuan Province, *Boufford 37045 et al.* (HUH); HG797717, HG797981, HG798138. *Anaphalis* aff. *flavescens* Hand.-Mazz.: China, Xizang (Tibet) Province, *Boufford 31246 et al.* (HUH); HG797718, HG797982, HG798139. *Anaphalis* aff. *nepalensis* (Spreng.) Hand.-Mazz. (1): China, Sichuan Province, *Boufford 36783 et al.* (HUH); HG797720, HG797984, HG798141. *Anaphalis* aff. *nepalensis* (Spreng.) Hand.-Mazz. (2): China, Xizang (Tibet) Province, *Boufford 31830 et al.* (HUH); HG797721, HG797985, HG798142. *Anaphalis* aff. *virens* C. C. Chang: China, Xizang (Tibet) Province, *Boufford 31568 et al.* (HUH); HG797722, HG797986, HG798143. *Anaphalis gracilis* Hand.-Mazz.: China, Sichuan Province, *Boufford 34675 et al.* (HUH); HG797719, HG797983, HG798140. *Anaphalis margaritacea* (L.) Benth. & Hook. f.: Canada, *J. M. Blanco & E. Blanco s. n.* (BC); FN645827, FN645632, FN649352. *Anaphalis* sp.: China, Sichuan Province, *Boufford 32750 et al.* (HUH);

HG797723, HG797987, HG798144. *Antennaria dioica* (L.) Gaertn.: Spain, Huesca, *Santos-Vicente et al. MS 428* (SALA); FN645833, FN645610, FN649336. *Athrixia phyllicoides* DC.: South Africa, Eastern Cape Province, *Romo 14395 et al.* (BC); FN645816, FN645634, FN649330. *Belloa chilensis* (Hook. & Arn.) J. Rémy: Argentina, Rio Negro, Bariloche, PN Nahuel Huapi, Co. Tronador, *C. Ezcurra 2262* (BCRU); KM091388, KM091349, KM091343. *Berroa gnaphalioides* (Less.) Beauverd: Uruguay, San José de Mayo, Kiyú, 17-12-2008, *Urtubey et al. 391* (SI); KM091386, KM091355, KM091325. *Bombycilaena discolor* (Pers.) M. Lánz: Spain, Zamora, Cañizal, *Martínez-Ortega 1819 & Andrés-Sánchez* (SALA 134225), FN645843, FN645560, FN649364. *Castroviejoa montelinasana* (Schmid) Galbany, L. Sáez & Benedí: Italy, Sardinia, Monte Línas, *Galbany & Sáez s. n.* (BCN 4644); AY445229, FN645559, FN649341. *Chevreulia acuminata* Less.: Argentina, Jujuy, Palpalá, Villa de Las Seranías de Zapla, *Urtubey & Freire 425* (SI); KM091392, KM091361, KM091322. *Chionolaena campestris* Deble: Brasil, Minas Gerais, Parque Estadual de Ibitipoca, *R. Mello-Silva et al. 3257* (SPF); KM091407, KM091377, KM091338. *Chionolaena salicifolia* (Bertol.) G. L. Nesom: Mexico, Oaxaca, *Ernst 2764* (US); KT865467, KT865263, -. *Craspedia glauca* Spreng.: Australia, Tasmania, Eaglehawk Neck, *Ford & Purves 21/03* (CHR 565520); EF187655, EF187629, -. *Cuatrecasasiella argentina* (Cabrera) H. Rob.: Bolivia, La Paz, Tamayo, Ulla-Ulla, reserva de Apolobamba, Co. Puntani, *Urtubey et al. 497* (SI); KM091401, KM091366, KM091337. *Dolichoerix ericoides* (Lam.) Hilliard & B. L. Burt: South Africa, Western Cape Province, *Romo 14514 et al.* (BC); FN645828, FN645622, FN649332. *Edmondia sesamoides* (L.) Hilliard: South Africa, Jonaskop, *Bergh 1130* (NBG); JF893882, FM173129, -. *Ewartia catipes* Beauverd: Australia, Tasmania, Ben Lomond, *Ward 94098/9* (CANU 37226); U95290, FJ404694, -. *Facelis plumosa* (Wedd.) Sch. Bip.: Bolivia, La Paz, Murillo, Camino antiguo a Unduavi, subiendo el valle de Chuquiaguillo, *Urtubey et al. 470* (SI); KM091394, KM091372, KM091345. *Facelis retusa* (Lam.) Sch. Bip.: Argentina, Córdoba, Calamuchita, *Urtubey & Baztarrica 202* (SI); KM091385, KM091352, KM091321. *Filago arizonica* A. Gray: Mexico, Baja California, Valle Las Palmas, Cerro

Bola, *Boyd 10377 et al.* (RSA 657500); FN645839, FN645615, FN649343. ***Filago californica*** Nutt.: United States of America, Esmeralda Co., Tule Canyon, *Tiehm 14663* (RSA 713363); FN645840, FN645616, FN649344. ***Filago carpetana*** (Lange) Chrtek & Holub; Spain, Cáceres, Logrosán, Las Chamizas, *Santos-Vicente 566 et al.* (SALA 134319); FN645858, FN645568, FN649372. ***Filago congesta*** DC.: Spain, Granada, Baza, *Andrés-Sánchez 52 & Martínez-Ortega* (SALA 134203), FN645848, FN645577, FN649382. ***Filago lutescens*** Jord. subsp. *lutescens*: Spain, Ávila, Navaceda de Tormes, *Martínez-Ortega 1829* (SALA 134165); FN645882, FN645596, FN649396. ***Filago pygmaea*** L.: Spain, Badajoz, Monesterio, *Santos-Vicente 563 et al.* (SALA 134315); FN645868, FN645574, FN649379. ***Gamochaeta americana*** (Mill.) Wedd.: Argentina, Neuquén, Aluminé, camino de Moquehue a Norquínco, *Urtubey 410 et al.* (SI); Argentina, Buenos Aires, La Plata, *Urtubey 187* (LP); KM091411, KM091382, KM091348. ***Gamochaeta longipedicellata*** Cabrera: Bolivia, La Paz, Murillo, *Urtubey 473 et al.* (SI); KM091410, KM091381, KM091347. ***Gamochaeta serpyllifolia*** Wedd.: Chile, XIV Región de Los Ríos, Valdivia, comuna de Panguipulli, faldeos Volcán Chosueno, *M. Baeza 4357* (CONC); KM091409, KM091380, KM091346. ***Gamochaeta subfalcata*** (Cabrera) Cabrera: Spain, Girona, between Mollet de Perelada and St. Climent, *Galbany et al. s. n.* (BCN); FN645834, FN645557, FN649338. ***Gamochaetopsis alpina*** (Poepp.) Anderb. & Freire: Argentina, Río Negro, Bariloche, Co. Tronador, *N. Bayón 1339* (LPAG); KM091390, KM091356, KM091326. ***Gnaphalium austroafricanum*** Hilliard: South Africa, Kwazulu-Natal Province, *Romo 14365 et al.* (BC); FN645830, FN645630, FN649353. ***Gnaphalium capense*** Hilliard: South Africa, Western Cape, *Koekemoer 3117* (US); KT865479, KT865281, - . ***Gnaphalium confine*** Harv.: Sudwest Afrika, *Volk 667* (US); KT865480, KT865282, - . ***Gnaphalium declinatum*** L. f.: South Africa, Western Cape, *Elim, F, N. G. Bergh 1073*; - , FR821617, - . ***Gnaphalium filagopsis*** Hilliard & B. L. Burt: Namibia, *Seydel 2674* (US); - , KT865283, - . ***Gnaphalium palustre*** Nutt.: United States of America, Nevada, *Arnold 11941* (US); KT865481, KT865285, - . ***Gnaphalium uliginosum*** L. (1): Armenia, Shirak Province, *Vitek et al. s. n.* (BCN 39933); FN645823, FN645624, FN649359. ***Gnaphalium uliginosum*** L. (2): Austria, Zwettl, *Wallnofer 13757* (US); KT865482, KT865288, - . ***Helichrysum abbayesii*** Humbert: Madagascar, Fianarantsoa Province, Maharumona road, *Bayer MAD-04026 et al.* (CANB 660363); HG797724, HG797988, HG798145. ***Helichrysum acutatum*** DC.: South Africa, Mpumalanga Province, *Romo 14596 et al.* (BC 867799); FJ211457 and FJ211515, HG797989, - . ***Helichrysum adenocarpum*** DC.: South Africa, Mpumalanga Province, *Romo 14611 et al.* (BC 867814); HG797725, HG797990, HG798146. ***Helichrysum albilanatum*** Hilliard: South Africa, Mpumalanga Province, *Romo 14603 et al.* (BC 867806); HG797726, HG797991, HG798147. ***Helichrysum albobrunneum*** S. Moore: Lesotho, ex Roy. Bot. Gard. Kew (BCN 6097); AY445215, HG797992, HG798148. ***Helichrysum alucense*** García-Cas., S. Scholz & E. Hernández: Spain, Canary Islands, La Gomera, *García Casanova s. n.* (TFC 36682); AY445223, HG797993, HG798149. ***Helichrysum anomalum*** Less.: South Africa, Eastern Cape Province, *Romo 14463 et al.* (BC 867691); HG797727, HG797994, HG798150. ***Helichrysum appendiculatum*** (L. f.) Less.: South Africa, Kwazulu-Natal Province, *Romo 14362 et al.* (BC 867635); HG797728, HG797995, HG798151. ***Helichrysum argyranthum*** O. Hoffm.: Tanzania, Olmoti, *Galbany & Arrabal s. n.* (BC 867822); FJ211465 and FJ211523, HG797996, HG798152. ***Helichrysum argyrophyllum*** DC.: South Africa, Eastern Cape Province, *Romo 14472 et al.* (BC 867699); HG797729, HG797997, HG798153. ***Helichrysum argyrosphaerum*** DC.: South Africa, Free State Province, *Koekemoer 3532* (BC); HG797730, HG797998, HG798154. ***Helichrysum armenium*** DC. subsp. *armenium*: Turkey, Adiyaman, *Susanna 2346 et al.* (BCN 6127); AY445208, FJ211577, HG798155. ***Helichrysum arwae*** J. R. I. Wood: Yemen, ex Roy. Bot. Gard. Kew (BCN 6103); AY445219, HG797999, HG798156. ***Helichrysum asperum*** (Thunb.) Hilliard & B. L. Burt var. *albidulum* (DC.) Hilliard: South Africa, Western Cape Province, *Romo 14526 et al.* (BC 867744); FJ211470 and FJ211528, HG798000, HG798157. ***Helichrysum aureolum*** Hilliard: South Africa, Mpumalanga Province, *Koekemoer 3494* (BC); HG797731, HG798001, HG798158. ***Helichrysum aureonitens*** Sch. Bip.: South Africa, Mpumalanga Province, *Romo 14579 et al.* (BC 867786); HG797732, HG798002, HG798159. ***Helichrysum aureum*** (Houtt.) Merrill

- var. **aureum**: South Africa, Eastern Cape Province, *Romo 14414 et al.* (BC 867667); HG797733, HG798003, HG798160. **Helichrysum auriceps** Hilliard: South Africa, Kwazulu-Natal Province, *Romo 14371 et al.* (BC 867644); HG797734, HG798004, HG798161. **Helichrysum basalticum** Hilliard: Lesotho, ex Roy. Bot. Gard. Kew (BCN 6095); AY445211, HG798005, HG798162. **Helichrysum benthamii** R. Vig. & Humbert: Madagascar, Fianarantsoa Province, Massif de Itremo, *Bayer MAD-04031 et al.* (CANB 660368); HG797735, HG798006, HG798163. **Helichrysum brownei** S. Moore: Kenya, Mount Kenya, *Galbany & Arrabal s. n.* (BC 867843); FJ211464 and FJ211522, HG798007, HG798164. **Helichrysum callicomum** Harv.: South Africa, Free State Province, *Romo 14342 et al.* (BC 867623); FJ211473 and FJ211531, HG798008, HG798165. **Helichrysum candollea-num** Buek: Mozambique, Gaza Province, *Burrows 8560* (Buffelskloof herb.); HG797736, HG798009, HG798166. **Helichrysum cephaloideum** DC.: South Africa, Mpumalanga Province, *Romo 14578 et al.* (BC 867785); HG797737, HG798010, HG798167. **Helichrysum cerastioides** DC.: South Africa, Mpumalanga Province, *Burrows 8508* (Buffelskloof herb.); HG797738, HG798011, HG798168. **Helichrysum chionoides** Philipson: Kenya, Mount Kenya, *Galbany & Arrabal s. n.* (BC 867840); FJ211463 and FJ211521, HG798012, HG798169. **Helichrysum chionosphaerum** DC.: South Africa, Eastern Cape Province, *Romo 14450 et al.* (BC 867682); FJ211461 and FJ211519, HG798013, - . **Helichrysum chrysargyrum** Moeser: South Africa, Mpumalanga Province, *McMurtry 8871* (Buffelskloof herb.); HG797739, HG798014, HG798170. **Helichrysum citrispinum** Del. var. **citrispinum**: Ethiopia, Mount Choke, *Aldasoro 9952 & Alarcón* (BC); HG797740, HG798015, HG798171. **Helichrysum citrispinum** Del. var. **hoehnelii** (Schweinf.) Hedberg: Ethiopia, Bale Mountains plateau, *Aldasoro 10378 & Alarcón* (BC); HG797741, HG798016, HG798172. **Helichrysum confertifolium** Klatt: South Africa, Mpumalanga Province, *Romo 14599 et al.* (BC 867802); HG797742, HG798017, HG798173. **Helichrysum confertum** N. E. Br.: Ex Roy. Bot. Gard. Kew (BCN 6096); AY445214, HG798018, HG798174. **Helichrysum cooperi** Harv.: South Africa, Free State Province, *Romo 14345 et al.* (BC 867626); HG797743, HG798019, HG798175. **Helichrysum cordifolium** DC.: Madagascar, Antananarivo Province, *Bayer MAD-04003 et al.* (CANB 660340); HG797744, HG798020, HG798176. **Helichrysum crassifolium** (L.) D. Don: Spain, Balearic Islands, Majorca, *Galbany & Sáez s. n.* (BCN 6117); AY445190, FJ211540, HG798177. **Helichrysum crispum** (L.) D. Don: South Africa, Western Cape Province, *Romo 14532 et al.* (BC 867748); HG797746, HG798022, HG798179. **Helichrysum cryptomerioides** Baker: Madagascar, Fianarantsoa Province, Massif de Itremo, *Bayer MAD-04045 et al.* (CANB 660382); HG797745, HG798021, HG798178. **Helichrysum cymosum** (L.) D. Don subsp. **calvum** Hilliard: South Africa, Eastern Cape Province, *Romo 14410 et al.* (BC 867663); HG797748, HG798024, - . **Helichrysum dasyanthum** (Willd.) Sweet: Ex J. Bot. Mar i Murtra, Blanes (BCN 6107); AY445226, HM450869, HG798181. **Helichrysum dasycephalum** O. Hoffm.: South Africa, Eastern Cape Province, *Romo 14411 et al.* (BC 867664); HG797749, HG798025, HG798182. **Helichrysum devium** J. Y. Johnson: Portugal, Madeira Island, *Jardim s. n.* (MADJ); FJ211441 and FJ211499, FJ211579, HG798183. **Helichrysum difficile** Hilliard: South Africa, Mpumalanga Province, *Romo 14588B et al.* (BC 867793); HG797750, HG798026, - . **Helichrysum ecklonis** Sond.: South Africa, Eastern Cape Province, *Romo 14485 et al.* (BC 867712); HG797751, HG798027, HG798184. **Helichrysum elegantissimum** DC.: South Africa, Eastern Cape Province, *Romo 14435 et al.* (BC 867676); HG797752, HG798028, HG798185. **Helichrysum epapposum** H. Bol.: South Africa, Mpumalanga Province, *Romo 14581 et al.* (BC 867788); FJ211459 and FJ211517, HG798029, HG798186. **Helichrysum ephelos** Hilliard: South Africa, Mpumalanga Province, *Romo 14601 et al.* (BC 867804); HG797753, HG798030, HG798187. **Helichrysum excisum** (Thunb.) Less.: South Africa, Western Cape Province, *Koekemoer 3433* (BC); HG797754, HG798031, HG798188. **Helichrysum felinum** Less.: South Africa, Eastern Cape Province, *Romo 14469 et al.* (BC 867696); HG797755, HG798032, HG798189. **Helichrysum flagellare** Bak: Madagascar, Antananarivo Province, *Bayer MAD04004 et al.* (CANB 660341); HG797756, HG798033, HG798190. **Helichrysum flammeiceps** Brenan: Malawi, Nyika National Park, *Koekemoer 1854* (BC); HG797757, HG798034, - . **Helichrysum flanaganii** H. Bol.: South Africa, Eastern Cape Province, *Romo 14424*

*et al.* (BC 867673); HG797758, HG798035, HG798191. *Helichrysum foetidum* (L.) Moench: Ex Dresden Bot. Gard. (BCN 8219); AY445221, HG798036, HG798192. *Helichrysum formosissimum* (Sch. Bip.) A. Rich.: Kenya, Mount Kenya, Galbany & Arrabal *s. n.* (BC 867832); FJ211446 and FJ211504, HG798037, HG798193. *Helichrysum forskahlii* (J. F. Gmel.) Hilliard & B. L. Burtt var. *compactum* (Vatke) Mesfin: Kenya, Mount Kenya, Galbany & Arrabal *s. n.* (BC 867830); HG797759, HG798038, HG798194. *Helichrysum forskahlii* (J. F. Gmel.) Hilliard & B. L. Burtt var. *forskahlii*: Tanzania, Empaakai, Galbany & Arrabal *s. n.* (BC 867823); FJ211447 and FJ211505, HG798039, HG798195. *Helichrysum forsythii* Humbert: Madagascar, Fianarantsoa Province, 30 km from Ivato, Bayer MAD-04021 *et al.* (CANB 660358); HG797760, HG798040, HG798196. *Helichrysum fulvescens* DC.: Madagascar, Antananarivo Province, Bayer MAD04001 *et al.* (CANB 660338); HG797761, HG798041, HG798197. *Helichrysum galpinii* N. E. Br.: South Africa, Mpumalanga Province, Romo 14569 *et al.* (BC 867776); HG797762, HG798042, HG798198. *Helichrysum globosum* A. Rich.: Kenya, Mount Kenya, Galbany & Arrabal *s. n.* (BC 867838); FJ211454 and FJ211512, HG798043, HG798199. *Helichrysum glomeratum* Klatt: South Africa, Kwazulu-Natal Province, Romo 14390 *et al.* (BC 867657); FJ211474 and FJ211532, HG798044, HG798200. *Helichrysum glumaceum* DC. (1): Oman, Musadam, McLeish 3727 (E 121502); FJ211469 and FJ211527, HG798045, HG798201. *Helichrysum glumaceum* DC. (2): Ethiopia, SW of Negele, Aldasoro 10262 & Alarcón (BC); HG797763, HG798046, HG798202. *Helichrysum gofense* Cufod. (1): Ethiopia, Bale Mountains plateau, Aldasoro 10336 & Alarcón (BC); HG797764, HG798047, HG798203. *Helichrysum gofense* Cufod. (2): Ethiopia, Bale Mountains plateau, Aldasoro 10376 & Alarcón (BC); HG797765, HG798048, HG798204. *Helichrysum gossypinum* Sch. Bip.: Spain, Canary Islands, Lanzarote, Galbany & Arrabal *s. n.* (BCN 25226); FJ211440 and FJ211498, FJ211578, HG798205. *Helichrysum griseolanatum* Hilliard: South Africa, Eastern Cape Province, Romo 14413 *et al.* (BC 867666); FJ211476 and FJ211534, HG798049, HG798206. *Helichrysum gymnocephalum* (DC.) Humbert: Madagascar, Antananarivo Province, Mt. Ibity, Bayer MAD-04053 *et al.* (CANB 660390); HG797766, HG798050, HG798207. *Helichrysum hamulosum* DC.: South Africa, Western Cape Province, Romo 14540 *et al.* (BC 867751); HG797767, HG798051, HG798208. *Helichrysum herbaceum* (Andr.) Sweet: South Africa, Kwazulu-Natal Province, Romo 14369 *et al.* (BC 867642); HG797768, HG798052, HG798209. *Helichrysum homilochrysum* S. Moore: South Africa, Mpumalanga Province, Burrows 7748 (Buffelskloof herb.); HG797769, HG798053, HG798210. *Helichrysum ibityense* Humbert: Madagascar, Fianarantsoa Province, Ambatosira, Bayer MAD-04052 *et al.* (CANB 660389); HG797770, HG798054, HG798211. *Helichrysum indicum* (L.) Grierson: South Africa, Western Cape Province, Romo 14547 *et al.* (BC 867758); HG797771, HG798055, HG798212. *Helichrysum interjacens* Hilliard: South Africa, Mpumalanga Province, Romo 14570 *et al.* (BC 867777); HG797772, HG798056, HG798213. *Helichrysum isolepis* H. Bol.: South Africa, Eastern Cape Province, Romo 14477 *et al.* (BC 867704); HG797773, HG798057, HG798214. *Helichrysum italicum* (Roth) G. Don subsp. *italicum*: Bosnia-Herzegovina, Herzegovina, Redžić *et al. s. n.* (BCN 20756); FJ211422 and FJ211480, FJ211548, HG798215. *Helichrysum kilimanjari* Oliv.: Kenya, Mount Kenya, Galbany & Arrabal *s. n.* (BC 867836); FJ211453 and FJ211511, HG798058, HG798217. *Helichrysum lambertianum* DC.: South Africa, Western Cape Province, Romo 14556 *et al.* (BC 867767); FJ211472 and FJ211530, HG798059, HG798218. *Helichrysum lanceolatum* (Buchanan) Kirk: New Zealand, Nelson, Pelorus Valley, Glenny 8969 (CHR 574730); HM244720, HM450855, HG798219. *Helichrysum lecomtei* R. Vig. & Humbert: Madagascar, Fianarantsoa Province, Analamay, Bayer MAD-04016 *et al.* (CANB 660353); HG797774, HG798060, HG798220. *Helichrysum lepidissimum* S. Moore: South Africa, Mpumalanga Province, Burrows *s. n.* (Buffelskloof herb.); HG797775, HG798061, HG798221. *Helichrysum litorale* H. Bol.: South Africa, Eastern Cape Province, Romo 14500 *et al.* (BC 867722); HM244706, HG798062, HG798222. *Helichrysum manopapoides* Humbert: Madagascar, Bayer MAD-04023 *et al.* (CANB 660360); HG797776, HG798063, HG798223. *Helichrysum maranguense* O. Hoffm.: Tanzania, Empaakai, Galbany & Arrabal *s. n.* (BC 867825); FJ211452 and FJ211510, HG798064, HG798224. *Helichrysum marginatum* DC.: South

- Africa, Eastern Cape Province, *Romo 14434 et al.* (BC 867675); FJ211460 and FJ211518, HG798065, HG798225. ***Helichrysum mariepsopicum*** Hilliard: South Africa, Mpumalanga Province, *Romo 14592 et al.* (BC 867795); HG797777, HG798066, - . ***Helichrysum massanellanum*** Herrando, J. M. Blanco, L. Sáez & Galbany: Spain, Balearic Islands, Majorca, *Galbany & Sáez s. n.* (BCN 6115); AY445195, FJ211546, HG798216. ***Helichrysum melaleucum*** Rchb. ex Holl: Portugal, Madeira Island, *Jardim s. n.* (MADJ); FJ211443 and FJ211501, FJ211581, HG798226. ***Helichrysum melanacme*** DC.: South Africa, Free State Province, *Romo 14334 et al.* (BC 867616); HG797778, HG798067, HG798227. ***Helichrysum meyeri-johannis*** Engl.: Kenya, ex Roy. Bot. Gard. Kew (BCN 6104); AY445216, HG798068, HG798228. ***Helichrysum miconiifolium*** DC.: South Africa, Free State Province, *Romo 14348 et al.* (BC 867629); HG797779, HG798069, HG798229. ***Helichrysum milfordiae*** Killick: Lesotho, ex Roy. Bot. Gard. Kew (BCN 6101); AY445212, FJ211537, HG798230. ***Helichrysum mimetes*** S. Moore: South Africa, Mpumalanga Province, *Romo 14610 et al.* (BC 867813); FJ211462 and FJ211520, HG798070, HG798231. ***Helichrysum mixtum*** (O. Kuntze) Moeser var. *mixtum*: South Africa, Kwazulu-Natal Province, *Romo 14374 et al.* (BC 867647); HG797780, HG798071, - . ***Helichrysum monizii*** Lowe: Portugal, Madeira Island, *Jardim s. n.* (MADJ); FJ211444 and FJ211502, FJ211582, HG798232. ***Helichrysum monogynum*** B. L. Burtt & Sunding: Spain, Canary Islands, Lanzarote, *Galbany & Arrabal s. n.* (BCN 25227); FJ211468 and FJ211526, HG798072, HG798233. ***Helichrysum montanum*** DC.: South Africa, Kwazulu-Natal Province, *Romo 14392 et al.* (BC 867659); HG797781, HG798073, HG798234. ***Helichrysum monticola*** Hilliard: South Africa, Mpumalanga Province, *Romo 14591 et al.* (BC 867794); HG797782, HG798074, - . ***Helichrysum mundtii*** Harv.: South Africa, Kwazulu-Natal Province, *Romo 14368 et al.* (BC 867641); HG797783, HG798075, HG798235. ***Helichrysum mussae*** Nevski: Tadzhikistan, Zeravshchan Mts., *Filatov et al. 81* (LE); FJ211426 and FJ211484, FJ211555, - . ***Helichrysum natalitium*** DC.: South Africa, Kwazulu-Natal Province, *Burrows 8431* (Buffelskloof herb.); HG797784, HG798076, HG798236. ***Helichrysum neoachyroclinoides*** Humbert: Madagascar, Antananarivo Province, Mt. Ibity, *Bayer MAD-04067 et al.* (CANB 660404); HG797785, HG798077, HG798237. ***Helichrysum nicolai*** N. Kilian, Galbany & Oberpr. (1): Cape Verde, São Nicolau, Alto das Cabaças, *Galbany 2111-3 & Molero* (BC); FN691030, HG798078, HG798238. ***Helichrysum nicolai*** N. Kilian, Galbany & Oberpr. (2): Cape Verde, São Nicolau, Alto das Cabaças, *Galbany 2111-17 & Molero* (BC); FN691031, HG798079, HG798239. ***Helichrysum nudifolium*** (L.) Less.: Kenya, Mount Kenya, *Galbany & Arrabal s. n.* (BC 867834); FJ211456 and FJ211514, HG798080, HG798240. ***Helichrysum obconicum*** DC.: Portugal, Madeira Island, *Jardim s. n.* (MADJ); FJ211442 and FJ211500, FJ211580, HG798241. ***Helichrysum obductum*** H. Bol.: South Africa, Mpumalanga Province, *Romo 14573 et al.* (BC 867780); HG797786, HG798081, HG798242. ***Helichrysum odoratissimum*** (L.) Sweet: Tanzania, Olmoti, *Galbany & Arrabal s. n.* (BC 867820); FJ211448 and FJ211506; HG798082, HG798243. ***Helichrysum opacum*** Klatt: South Africa, Mpumalanga Province, *Romo 14593 et al.* (BC 867796); HG797787, HG798083, - . ***Helichrysum orientale*** (L.) Gaertn.: Greece, Crete, ex Roy. Bot. Gard. Kew (BCN 6098); AY445205, FJ211567, HG798244. ***Helichrysum pagophilum*** M. D. Hend.: Lesotho, ex Roy. Bot. Gard. Kew (BCN 6100); AY445217, HG798084, HG798245. ***Helichrysum paleatum*** Hilliard: South Africa, Kwazulu-Natal Province, *Romo 14385 et al.* (BC 867652); HG797788, HG798085, - . ***Helichrysum patulum*** (L.) D. Don (1): South Africa, Western Cape Province, *Romo 14507 et al.* (BC 867729); HG797789, HG798086, HG798246. ***Helichrysum patulum*** (L.) D. Don (2): South Africa, Western Cape Province, *Romo 14527 et al.* (BC 867745); HG797790, HG798087, HG798247. ***Helichrysum pendulum*** (C. Presl) C. Presl: Spain, Balearic Islands, Ibiza, *Sáez s. n.* (BCN 6118); AY445189, FJ211539, HG798248. ***Helichrysum petiolare*** Hilliard & B. L. Burtt: Ex J. Bot. Mar i Murtra, Blanes (BCN 6110); AY445213, HG798088, HG798249. ***Helichrysum pilosellum*** (L. f.) Less.: South Africa, Mpumalanga Province, *Romo 14597 et al.* (BC 867800); HG797791, HG798089, HG798250. ***Helichrysum plantago*** DC.: Madagascar, Antananarivo Province, Mt. Ibity, *Bayer MAD-04062 et al.* (CANB 660399); HG797792, HG798090, - . ***Helichrysum platycephalum*** Baker: Madagascar, Fianarantsoa

- Province, *Bayer MAD-04022 et al.* (CANB 660359); HG797793, HG798091, HG798251. ***Helichrysum platypterum*** DC.: South Africa, Kwazulu-Natal Province, *Romo 14360 et al.* (BC 867634); FJ211458 and FJ211516, HG798092, HG798252. ***Helichrysum plicatum*** DC.: Turkey, Sivas, *Susanna 2419 et al.* (BCN 6129); AY445201, FJ211556, HG798253. ***Helichrysum polycladum*** Klatt: South Africa, Mpumalanga Province, *Romo 14598 et al.* (BC 867801); HG797794, HG798093, HG798254. ***Helichrysum populifolium*** DC.: South Africa, ex Silverhill Seeds (BCN 8218); AY445210, FJ211538, HG798255. ***Helichrysum psilolepis*** Harv.: South Africa, Eastern Cape Province, *Romo 14461 et al.* (BC 867689); HG797795, HG798094, HG798256. ***Helichrysum reflexum*** N. E. Br.: South Africa, Mpumalanga Province, *Romo 14571 et al.* (BC 867778); FJ211445 and FJ211503, HG798095, HG798257. ***Helichrysum retortum*** (L.) Willd.: South Africa, ex Silverhill Seeds (BCN 6112); AY445222, HG798096, HG798258. ***Helichrysum rosum*** (Berg.) Less. var. *arcuatum* Hilliard: South Africa, Eastern Cape Province, *Romo 14494 et al.* (BC 867718); HG797797, HG798098, HG798260. ***Helichrysum rosum*** (Berg.) Less. var. *rosum*: South Africa, Eastern Cape Province, *Romo 14462 et al.* (BC 867690); HG797796, HG798097, HG798259. ***Helichrysum rubicundum*** (K. Koch) Bornm.: Iran, Azarbaijan, *Termeh et al. s. n.* (IRAN 35924,4); FJ211437 and FJ211495, FJ211573, HG798261. ***Helichrysum rugulosum*** Less.: South Africa, Free State Province, *Romo 14331 et al.* (BC 867613); FJ211471 and FJ211529, HG798099, HG798262. ***Helichrysum schimperi*** (A. Rich.) Moeser: Tanzania, Olmoti, *Galbany & Arrabal s. n.* (BC 867821); FJ211451 and FJ211509, HG798100, HG798263. ***Helichrysum selaginifolium*** R. Vig. & Humbert: Madagascar, Antananarivo Province, Mt. Ibity, *Bayer MAD-04074 et al.* (CANB 660411); HG797798, HG798101, HG798264. ***Helichrysum setosum*** Harv.: Tanzania, Empaakai, *Galbany & Arrabal s. n.* (BC 867824); FJ211467 and FJ211525, HG798102, HG798265. ***Helichrysum sibthorpii*** Rouy: Greece, ex Roy. Bot. Gard. Kew (BCN 6099); AY445203, FJ211561, HG798266. ***Helichrysum silvaticum*** Hilliard: Mozambique, Licuati Sand Forest, *McMurtry 11424* (Buffelskloof herb.); HG797799, HG798103, HG798267. ***Helichrysum simillinum*** DC.: South Africa, Kwazulu-Natal Province, *Romo 14364 et al.* (BC 867637); HG797800, HG798104, HG798268. ***Helichrysum spiralepis*** Hilliard & B. L. Burtt: South Africa, Kwazulu-Natal Province, *Romo 14372 et al.* (BC 867645); FJ211477 and FJ211535, HG798105, - . ***Helichrysum splendidum*** (Thunb.) Less.: Ex Roy. Bot. Gard. Kew (BCN 6102); AY445218, HG798106, HG798269. ***Helichrysum stellatum*** (L.) Less.: South Africa, Northern Cape Province, *Koekemoer 3513* (BC); HG797801, HG798107, HG798270. ***Helichrysum stoechas*** (L.) Moench: Spain, Lleida, *Galbany s. n.* (BCN 6114); AY445193, FJ211543, FN649351. ***Helichrysum stuhlmannii*** O. Hoffm.: Uganda, Rwenzori Mts., *Roquet s. n.* (BC 867841); FJ211466 and FJ211524, HG798108, HG798271. ***Helichrysum summo-montanum*** Verdoorn: South Africa, Mpumalanga Province, *Burrows 7370* (Buffelskloof herb.); HG797802, HG798109, HG798272. ***Helichrysum sutherlandii*** Harv.: South Africa, Kwazulu-Natal Province, *Romo 14370 et al.* (BC 867643); HG797803, HG798110, HG798273. ***Helichrysum swynnertonii*** S. Moore: South Africa, Mpumalanga Province, *Camacho s. n.* (Buffelskloof herb.); HG797804, HG798111, - . ***Helichrysum thianschanicum*** Regel: Ex Hortus Botanicus Táhor (BCN 10337); AY445200, FJ211554, HG798274. ***Helichrysum transmontanum*** Hilliard: South Africa, Mpumalanga Province, *Burrows 7543* (Buffelskloof herb.); HG797805, HG798112, HG798275. ***Helichrysum trilineatum*** DC.: South Africa, Eastern Cape Province, *Romo 14416 et al.* (BC 867669); HG797806, HG798113, HG798276. ***Helichrysum triplinerve*** DC.: Madagascar, Fianarantsoa Province, *Bayer MAD-04057 et al.* (CANB 660394); HG797807, HG798114, HG798277. ***Helichrysum truncatum*** Burtt Davy: South Africa, Mpumalanga Province, *Romo 14574 et al.* (BC 867781); HG797808, HG798115, HG798278. ***Helichrysum umbraculigerum*** Less.: South Africa, Kwazulu-Natal Province, *Romo 14366 et al.* (BC 867639); FJ211450 and FJ211508, HG798116, HG798279. ***Helichrysum xylocladum*** Humbert: Madagascar, Antananarivo Province, Mt. Ibity, *Bayer MAD-04073 et al.* (CANB 660410); HG797809, HG798117, - . ***Helichrysum zeyheri*** Less.: South Africa, Western Cape Province, *Romo 14542 et al.* (BC 867754); FJ211478 and FJ211536, HG798118, - . ***Helichrysum zwartbergense*** H. Bol.: South Africa, Western Cape Province, *Romo 14520 et al.* (BC 867739); HM244707, HG798119, HG798280. ***Humeocline***



- madagascariensis* (Humb.) Anderb.: Madagascar, Antananarivo Province, Mt. Ibity, *Bayer MAD-04061 et al.* (CANB 660398); HG797810, HG798120, HG798281. *Ifloga repens* (L.) Hilliard: Republic of South Africa, Northern Cape, Namakwa N. P., *Koekemoer 3277* (BC); FN645826, FN645628, FN649357. *Ifloga spicata* (Forssk.) Sch. Bip.: Spain, Almería, Cuevas de Almanzora, *Santos-Vicente 534 et al.* (SALA 134240); FN645825, FN645627, FN649356. *Jalcephala boliviana* Anderb. & Freire: Bolivia, La Paz, Tamayo, Ulla-Ulla, reserva de Apolobamba, Co. Puntani, *Urtubey 488 et al.* (SI); KM091402, KM091370, KM091342. *Lachnospermum fasciculatum* (Thunb.) Baill.: Republic of South Africa, Western Cape Province, between Op-die-berg and Citrusdal, *Romo 14559 et al.* (BC), FN645829, FN645623, FN649333. *Langebergia canescens* (DC.) Anderb.: South Africa, Western Cape Province, *Bayer & Puttock s. n.* (CANB 499988); HG797811, HG798121, - . *Lasiopogon glomerulatus* (Harv.) Hilliard: South Africa, *SAF-96180* (F); KT865529, KT865345, - . *Lasiopogon muscoides* (Desf.) DC.: Spain, Almería, Cuevas de Almanzora, *Santos-Vicente 499 et al.* (SALA), FN645831, FN645629, FN649334. *Leontopodium alpinum* Cass.: Spain, Huesca, Posets, *Roquet s. n.* (BC); FN645824, FN645625, FN649348. *Leysera gnaphalodes* (L.) L.: South Africa, Western Cape Province, *Romo 14546 et al.* (BC 867757); FN645815, FN645636, FN649329. *Logfia gallica* (L.) Coss. & Germ.: Spain, Almería, Sorbas, *Martínez-Ortega 1796 et al.* (SALA 134224), FN645838, FN645556, FN649339. *Logfia minima* (Sm.) Dumort.: Spain, Salamanca, San Miguel de Valero, *Martínez-Ortega 1805* (SALA 134219); FN645817, FN645613, FN649347. *Loricaria colombiana* Cuatrec.: Colombia, Tolima, *J. C. Ospina 6400* (SI). Colombia, Caldas, *D. Sanin E 89* (SI); KM091404, KM091371, KM091330. *Lucilia acutifolia* (Poir.) Cass.: Argentina, Buenos Aires, Tandil, *Urtubey 512* (SI); KM091396, KM091374, KM091332. *Lucilia linearifolia* Baker: Argentina, Jujuy, Villa de la Sierras de Zapla, Co. de La Cruz, *Urtubey & Freire 427* (SI); - , - , KM091324. *Lucilia lycopodioides* (Less.) Freire: Argentina, Jujuy, Villa de la Sierras de Zapla, Co. de La Cruz, *Urtubey & Freire 426* (SI); KM091384, KM091357, KM091323. *Lucilia nitens* Less.: Uruguay, Montevideo, Carrasco, *Urtubey 394* (SI); KM091399, KM091353, KM091331. *Luciliocline subspicata* (Wedd.) Anderb. & Freire: Bolivia, Oruro, Sajama, colina Pacollo, *S. Beck 30693* (LPB); - , - , KM091344. *Metalasia adunca* Less.: South Africa, *Karis & Arnerup 996* (S); JF893847, JF893752, - . *Mexerion sarmentosum* (Klatt) G. L. Nesom: Mexico, Mexico state, *Beaman 1932* (US); KT865561, KT865380, - . *Micropsis dasycarpa* (Griseb.) Beauverd: Argentina, Buenos Aires, Tandil, La Cascada, *Urtubey & Freire 543* (SI); KM091408, KM091378, KM091339. *Micropus californicus* Fischer & C. A. Meyer: United States, Butte Co., N side of Bardees Bar Road, *Ahart 12624* (RSA 712992); FN645821, FN645621, FN649350. *Micropus supinus* L.: Spain, Salamanca, Martín de Yeltes, *Rico 7883* (SALA); FN645818, FN645609, FN649335. *Mniodes andina* (A. Gray) Cuatrec.: Bolivia, Oruro, *X. Menhofer 1514* (LPB); - , - , KM091367, - . *Mniodes kunthiana* (DC.) Freire, Chemisquy, Anderb. & Urtubey: Bolivia, La Paz, Murillo, *Urtubey 475 et al.* (SI); KM091393, KM091365, KM091329. *Mniodes longifolia* (Cuatrec. & Aristeg.) Freire, Chemisquy, Anderb. & Urtubey: Bolivia, La Paz, Nor-Yungas, camino a Coroico, *Urtubey 507 et al.* (SI); KM091400, KM091364, KM091335. *Mniodes santanica* (Cabrera) Freire, Chemisquy, Anderb. & Urtubey: Argentina, Catamarca, Abato, Co. Manchado, *N. Bayón & J. Vera Bahima 1519* (LPAG); KM091397, KM091359, KM091336. *Omalotheca supina* (L.) DC.: Andorra, Port Creussans, *Galbany & Lluent s. n.* (BCN 6121); AY445230, FN645558, FN649354. *Omalotheca sylvatica* (L.) Sch. Bip. & F. W. Schultz: Switzerland, *Charpin & Hainard s. n.* (US); KT865568, KT865387, - . *Ozothamnus diosmifolius* (Vent.) DC.: Australia, New South Wales, *Bayer NSW 94-006* (NSW, ALTA); HM244716, HM450851, - . *Petalacte coronata* (L.) D. Don: South Africa, Western Cape Province, *Bayer & Chandler SAF-01095* (CANB 634589); HG797812, HG798122, HG798282. *Pseudognaphalium affine* (D. Don) Anderb. (1): Korea, Mt. Baika-san, *Cho YH et al. 090506-135* (KUN); KT865569, KT865390, - . *Pseudognaphalium affine* (D. Don) Anderb. (2): China, Hubei, *Nie 714* (KUN); JQ895515, JQ895378, - . *Pseudognaphalium aldunateoides* (J. Rémy) C. Monti, N. Bayón & Freire [*Gnaphalium aldunateoides* J. Rémy] (1): Chile, Región IV Coquimbo, Ilegando a Sotaquí desde Monte Patria o Combarbalá,

- Quebrada Seca, 30° 39' 29,1" S, 71° 05' 15,8" W, 98 m, *Galbany 2525 & Arrabal* (BC); \*MG649409, \*MG649413, \*MG649416. *Pseudognaphalium aldunateoides* (J. Rémy) C. Monti, N. Bayón & Freire [*Gnaphalium aldunateoides* J. Rémy] (2): Chile, Región Metropolitana, Prov. Chacabuco, Altos de Chicauma, sector tranque, 33° 10' S 70° 58' W, 2050 m, *N. García & L. Faúndez 177476* (CONC); \*MG649408, \*MG649412, - . *Pseudognaphalium attenuatum* (DC.) Anderb.: Mexico, Veracruz, *Robert Merrill King 4131* (US); KT865570, KT865391, - . *Pseudognaphalium badium* (Wedd.) Anderb.: Bolivia, La Paz, Murillo, *Urtubey 485 et al.* (SI); KM091405, KM091375, KM091333. *Pseudognaphalium beneolens* (Davidson) Anderb.: United States of America, California, San Diego Co., *Rebman 10825* (RSA 705579); HG797813, HG798123, HG798283. *Pseudognaphalium biolettii* Anderb.: United States of America, California, Los Angeles Co., *Sanders 25759* (RSA 712717); HG797814, HG798124, HG798284. *Pseudognaphalium californicum* (DC.) Anderb.: United States of America, California, Riverside Co., *Boyd 10845* (RSA 701560); HM244709; HG798125, HG798285. *Pseudognaphalium canescens* (DC.) Anderb.: Mexico, Sonora, *Spooner 2423* (US); JQ895522, JQ895385, - . *Pseudognaphalium cheiranthifolium* (Lam.) Hilliard & B. L. Burt (1): Chile, region VI, Pichilemu, *Carnicero-Campmany s. n.* (SI); HG797816, HG798127, HG798287. *Pseudognaphalium cheiranthifolium* (Lam.) Hilliard & B. L. Burt (2): Brazil, Curitiba, Cordeiro and *Barbosa 2173* (US); KT865571, KT865392, - . *Pseudognaphalium dombeyanum* (DC.) Anderb.: Peru, Pampa, *Carlos 16094* (US); KT865572, - , - . *Pseudognaphalium eggertii* (Urb.) Anderb.: Dominica, Baoruco, *Acevedo-Rdz 13172* (US); KT865573, KT865393, - . *Pseudognaphalium flavescens* (Kitam.) Anderb.: China, Xizang, *Xia 2730* (KUN); KT865574, KT865394, - . *Pseudognaphalium gaudichaudianum* (DC.) Anderb.: Bolivia, Murillo, *Solomon 16478* (US); KT865576, KT865396, - . *Pseudognaphalium graveolens* (Kunth) Anderb.: Peru, Cajamarca, *Becher & Terrones 2097* (US); KT865575, KT865395, - . *Pseudognaphalium heterotrichum* (Phil.) Anderb.: Chile, region III, Coquimbo, *Carnicero-Campmany s. n.* (SI); HG797815, HG798126, HG798286. *Pseudognaphalium hypoleucum* (DC.) Hilliard & B. L. Burt: China, Sichuan, *Nie 1191* (KUN); JQ895519, JQ895382, - . *Pseudognaphalium lacteum* (Meyen & Walp.) Anderb.: Argentina, Jujuy, Tumbaya, RP52, entre Purmamarca y Susques, pasando Ayo. Potrerillos, *Urtubey & Freire 436* (SI); KM091387, KM091362, KM091340. *Pseudognaphalium leucocephalum* (A. Gray) Anderb. (1): United States of America, California, Orange Co., *Roberts 6088* (RSA 703730); HG797817, HG798128, HG798288. *Pseudognaphalium leucocephalum* (A. Gray) Anderb. (2): Mexico, Sinaloa, *Kimnqch et al. 1992* (US); KT865578, KT865398, - . *Pseudognaphalium leucocephalum* (Cabrera) Anderb.: Bolivia, Franz, Tamayo, *Beck 32545* (US); KT865579, KT865399, - . *Pseudognaphalium luteoalbum* (L.) Hilliard & B. L. Burt (1): Portugal, Marinha Grande, *Susanna 2435 & Garcia-Jacas* (BCN 6125); AY445227, FN645633, FN649358. *Pseudognaphalium luteoalbum* (L.) Hilliard & B. L. Burt (2): Australia, Victoria, *Robert Merrill King 9742* (US); KT865581, KT865401, - . *Pseudognaphalium luteoalbum* (L.) Hilliard & B. L. Burt (3): Kenya, *Robert Merrill King 9800* (US); KT865580, KT865400, - . *Pseudognaphalium macounii* (Greene) Kartesz: United States of America, Utah, Daggett Co., *Goodrich 22823* (RSA 490532); HG797821, HG798132, HG798293. *Pseudognaphalium melanosphaeroides* (Sch. Bip. ex Wedd.) Anderb.: Bolivia, Cochabamba, *Gonzalo 58* (US); KT865582, KT865402, - . *Pseudognaphalium micradenium* (Weath.) G. L. Nesom: United States of America, Tennessee, Roane Co., *Patrick 3813*; JX524594, - , - . *Pseudognaphalium montevidense* (Spreng.) Anderb.: Argentina, Rio Negro, *Simon Pablo 860* (US); - , KT865403, - . *Pseudognaphalium moritzianum* (Klatt) V. M. Baddillo: Venezuela, Merida, *Robert Merrill King 10417* (US); - , KT865404, - . *Pseudognaphalium obtusifolium* (L.) Hilliard & B. L. Burt: United States of America, Iowa, Lucas Co., *Neese 11074* (RSA 299987); HG797818, HG798129, HG798290. *Pseudognaphalium oligandrum* (DC.) Hilliard & B. L. Burt: South Africa, Free State Province, *Romo 14336 et al.* (BC 867618); HM244708, HM450843, HG798289. *Pseudognaphalium oxyphyllum* (DC.) Kirp. var. *oxyphyllum* (1): Mexico, Estado de México, Alrededores de Xalatlaco, 19° 11' 31,5" N 99° 24' 38,2" W, 2831 m, *Galbany 2431 & Arrabal* (BC); \*MG649410, \*MG649414,

\*MG649417. \**Pseudognaphalium oxyphyllum* (DC.) Kirp. var. *oxyphyllum* (2): Mexico, Distrito Federal, Ciudad de México, Ciudad Universitaria, cerca de la estación de metrobus “Ciudad Universitaria”, entre la estación y la parada del Pumabus, 19° 19' 25,6" N 99° 11' 19,8" W, 2304 m, *Galbany 2480 & Arrabal* (BC); \*MG649411, \*MG649415, \*MG649418. *Pseudognaphalium ramosissimum* (Nutt.) Anderb.: United States of America, California, San Diego Co., *Sanders 31665* (RSA 713933); HG797819, HG798130, HG798291. *Pseudognaphalium sandwicense* (Gaudich.) Anderb.: United States of America, Hawaii, *Funk 12765* (US); KT865585, KT865409, - . *Pseudognaphalium semiamplexicaule* (DC.) Anderb.: Guatemala, Alta Verapaz, *Fother 11090* (US); KT865586, KT865410, - . *Pseudognaphalium sylvicola* (McVaugh) G. L. Nesom: Mexico, Chapingo, *Koch 82168* (US); KT865587, KT865411, - . *Pseudognaphalium thermale* (E. E. Nelson) G. L. Nesom: United States of America, California, T26N, R11E, *Ahart 12405* (RSA 716686); HG797820, HG798131, HG798292. *Pseudognaphalium viravira* (Molina) Anderb.: Chile, *Mahu 10213* (US); KT865589, KT865413, - . *Raoulia tenuicaulis* Hook. f.: New Zealand, Gisborne, mouth of Motu River, *Smisson s. n.* (CHR 607934); HM244728, HM450865, - . *Relhania pungens* L'Hérit.: South Africa, Western Cape Province, *Koekemoer 3427* (BC); FN645814; FN645635; FN649331. *Stoebe aethiopica* L.: South Africa, Cederberg, *Karis & Swenson 919* (S); JF893878, FM173147, - . *Stuckertiella capitata* (Wedd.) Beauverd: Bolivia, La Paz, Murillo, Camino antiguo a Unduavi, subiendo el valle de Chuquiaguillo, *Urtubey 469 et al.* (SI); KM091398, KM091369, KM091341. *Stylocline psilocarphoides* M. Peck: United States, Lyon co., Pine Nut Mts., *Tiehm 14828* (RSA 712497); FN645819, FN645619, FN649346. *Syncarpha canescens* (L.) B. Nord.: South Africa, Cape Town, *Bergh 1222* (NBG); JF893884, FM173153, - . *Syncarpha chlorochrysum* (DC.) B. Nord.: South Africa, Western Cape, *Koekemoer 3424* (US); KT865598, KT865426, - . *Syncarpha mucronata* (P. J. Bergius) B. Nord.: South Africa, Western Cape Province, *Romo 14511 et al.* (BC 867732); FJ211421 and FJ211479, FN645626, FN649360. *Syncarpha paniculata* (L.) B. Nord.: South Africa, Western Cape, *Koekemoer 3428* (US); KT865599, KT865427, - . *Syncarpha staehelina* (L.) B. Nord.:

South Africa, Western Cape, *Koekemoer 3481* (US); KT865600, KT865428, - . *Vellereophyton dealbatum* (Thunb.) Hilliard & B. L. Burt: South Africa, Western Cape Province, *Romo 14549 et al.* (BC); FN645832, FN645631, FN649355.

## Appendix 2. Material examined for morphological studies.

*Gnaphalium uliginosum* L.: France: Gruy-les-Surance, vores de camps i camins, *Arrabal & Galbany 2090* (BC). *Pseudognaphalium aldunateoides* (J. Rémy) C. Monti, N. Bayón & Freire: Chile: Prov. de Bío-Bío, Negrete, a orillas del Biobío, en la ribera Norte del río, *A. Pfister s. n.* (CONC 10502); Prov. Aconcagua, Putaendo, Laguna del Copin, 2620 m, crece en las planicias húmedas de las cordilleras de Aconcagua, *Parra 37* (CONC 116325); Prov. Cautin, Temuco, Río Cautin, 120 m, *Montero 5728* (CONC 75310); Prov. Valparaíso, Dpto. Valparaíso, Lago Peñuelas, *Ricardi 5445* (CONC 89745); VII Región, Prov. Linares, Quella Sur, 36° 05' S 72° 08' W, 120 m, en cultivo de arroz, a orillas del pretil, escasa, *Matthei & Quezada 1420* (CONC 110827); Cauquenes, approximately 2 km south of Chanco, on west side of road, 35° 45' S 72° 32' W, 50 m, *Bliss 2272* (CONC 145334); Reg. Metropolitana, San José de Maipo, Cajón del Morales, 33° 46' S 70° 04' W, 2450 m, entre la laguna y el glaciar, *Teillier & Márquez 5316* (CONC 156533); Reg. Metropolitana, Prov. Chacabuco, Altos de Chicauma, sector tranque, 33° 10' S 70° 58' W, 2050 m, *García & Faúndez 3613* (CONC 177476); VIII Región, Prov. Ñuble, Ninhue, Río Ninhue, km 32 desde San Gregorio a Pocillas, 36° 08' S 72° 05' W, 190 m, *Mihoc, Marticorena, Gómez & Negritto 6227* (CONC 161086); Región IV Coquimbo, llegando a Sotaquí desde Monte Patria o Combarbalá, Quebrada Seca, 30° 39' 29,1" S, 71° 05' 15,8" W, 98 m, *Galbany 2525 & Arrabal* (BC). *Pseudognaphalium oxyphyllum* (DC.) Kirp. var. *oxyphyllum*: Mexico: Estado de México, Alrededores de Xatlaco, 19° 11' 31,5" N 99° 24' 38,2" W, 2831 m, *Galbany 2431 & Arrabal* (BC); Distrito Federal, Ciudad de México, Ciudad Universitaria, cerca de la estación de metrobus “Ciudad Universitaria”, entre la estación y la parada del Pumabus, 19° 19' 25,6" N 99° 11' 19,8" W, 2304 m, *Galbany 2480 & Arrabal* (BC).