

# The *Lucilia* group (Asteraceae, Gnaphalieae): phylogenetic and taxonomic considerations based on molecular and morphological evidence

Susana E. Freire · M. Amelia Chemisquy ·  
Arne A. Anderberg · Stephan G. Beck ·  
Rosa I. Meneses · Benoît Loeuille · Estrella Urtubey

Received: 19 March 2014 / Accepted: 28 July 2014 / Published online: 14 August 2014  
© Springer-Verlag Wien 2014

**Abstract** The *Lucilia* group sensu Anderberg and Freire comprises nine South American genera: *Belloa*, *Berroa*, *Chevreulia*, *Cuatrecasasiella*, *Facelis*, *Gamochaetopsis*, *Jalcophila*, *Lucilia* and *Luciliocline*. The aims of this contribution were, using DNA sequences from plastid (*rpl32-trnL*, *trnL-F*) and nuclear (ITS and ETS) markers, together with morphological characters, to test the monophyly of the *Lucilia* group and provide new insight into generic circumscriptions. Our studies, including a broad taxon sampling of Gnaphalieae species, suggest that the *Lucilia* group is paraphyletic, since *Antennaria*, *Chionolaena*, *Gamochaeta*, *Loricaria*, *Micropsis*, *Mniodes* and

*Stuckertiella* are all nested within the *Lucilia* group. Morphology and molecular analyses combined showed that the traditional generic circumscription of most of the genera (e.g., *Berroa*, *Chevreulia*, *Chionolaena*, *Cuatrecasasiella*, *Facelis*, *Jalcophila* and *Micropsis*) correlates with the inferred phylogenetic relationships. Conversely, *Lucilia* and *Luciliocline* are non-monophyletic. *Lucilia* is nested in a clade with *Berroa*, *Facelis* and *Micropsis*. *Luciliocline* is strongly embedded within the clade *Belloa* pp + *Mniodes*. Our results are consistent with Dillon's study that considered *Belloa* as a monotypic genus (*B. chilensis*). *Luciliocline* and the remaining species of *Belloa* are accommodated in the genus *Mniodes*, and the necessary combinations are proposed for the expanded *Mniodes*. All the analyses showed that the monotypic genera *Stuckertiella* and *Gamochaetopsis* are in a well-supported clade nested within *Gamochaeta*, which implies that taxonomic changes are required also for these genera. Internal relationships in the group and the key morphological characters used in the taxonomy of the group, as well as incongruences found between morphological and molecular analyses, are discussed.

**Electronic supplementary material** The online version of this article (doi:10.1007/s00606-014-1147-0) contains supplementary material, which is available to authorized users.

S. E. Freire (✉) · E. Urtubey  
Instituto de Botánica Darwinion-CONICET, Labardén 200,  
CC 22, B1642 HYD San Isidro, Argentina  
e-mail: sfreire@darwin.edu.ar

M. A. Chemisquy  
Museo Argentino de Ciencias Naturales “Bernardino  
Rivadavia”-CONICET, Av. Angel Gallardo 470,  
C1405DJR Ciudad Autónoma de Buenos Aires, Argentina

A. A. Anderberg  
Swedish Museum of Natural History, P. O. Box 50007,  
104 05 Stockholm, Sweden

S. G. Beck · R. I. Meneses  
Herbario Nacional de Bolivia, Museo Nacional de Historia  
Natural, Universidad Mayor de San Andrés,  
CC 10077 La Paz, Bolivia

B. Loeuille  
Departamento de Botânica, Laboratório de Sistemática Vegetal,  
Rua Do Matão, Travessa 14 no 321, Cidade Universitária,  
São Paulo 05508-090, Brazil

**Keywords** *Belloa* · ETS · ITS · *Mniodes* · *rpl32-trnL* · *trnL-F*

## Introduction

The *Lucilia* group was first recognized by Merxmüller et al. (1977) as a subgroup of the tribe Inuleae, subtribe Gnaphaliinae. It was defined by its dorsally pubescent style branches and consisted of 12 genera, *Belloa*, *Berroa*, *Chevreulia*, *Facelis*, *Leucopholis*, *Lucilia*, probably *Gnaphaliothammus* and *Raouliopsis*, and the dioecious or

subdioecious genera *Chionolaena*, *Luciliopsis*, *Mniodes* and *Oligandra* (Table 1). A few years later, Robinson (1985) considered *Luciliopsis* to be a synonym of *Facelis*, placing two of its three species in the new genus *Cuatrecasasiella*. Anderberg and Freire (1990a) later showed that the type of the genus *Luciliopsis* belongs in *Chaetanthera* of the Mutisieae. Two genera were added to this group, *Jalcophila* (Dillon and Sagastegui-Alva 1986) and *Novenia* (Freire 1986a). *Oligandra* was stated later by Freire (1989) to be a synonym of *Lucilia*, whereas *Leucopholis* was a synonym of *Chionolaena* (Anderberg 1991; Freire 1993). Based on a morphological cladistic analysis, Anderberg (1991) established five subtribes for the tribe Gnaphalieae: Angianthinae Benth., Relhaniinae Less., Cassiniinae Anderb., Gnaphaliinae, and Loricariinae Anderb. That study indicated that the *Lucilia* group, as earlier understood, was a highly polyphyletic assemblage and also excluded *Novenia* from the Gnaphalieae. The remaining genera were placed in three clades, one composed of *Gnaphaliothamnus* and *Chionolaena* (subtribe Cassiniinae), the second including *Loricaria*, *Mniodes* and *Raouliopsis* (subtribe Loricariinae) and the third one, *Lucilia* group s. str. (subtribe Gnaphaliinae), was composed of *Belloa*, *Berroa*, *Chevreulia*, *Cuatrecasasiella*, *Facelis*, *Lucilia* and *Jalcophila*. Subsequently, Anderberg and Freire (1991) added two further taxa to the *Lucilia* group s. str., viz. *Gamochoetopsis* and *Lucilicline*. Both were segregated from *Lucilia* which was shown to be non-monophyletic. Anderberg and Freire (1991) recognized a *Lucilia* group s. str., comprising nine genera (Table 1) with the following traits: very slender pappus bristles basally connate, dorsally pubescent style branches, purple tipped florets and polychromous phyllaries. Later, Dillon (2003), based on a previous cladistic analysis of morphological characters (Dillon 2000) revealed the need for a new circumscription for the group, suggesting a close potential relationship between *Chionolaena*, *Gamochoeta*, *Micropsis*, *Stuckertiella* and the other members of the *Lucilia* group (Table 1).

Most of the genera included in the *Lucilia* group have been monographed since they were described, i.e., *Berroa*, *Facelis*, *Micropsis* and *Stuckertiella* (Beauverd 1913a, b, c, d); *Loricaria* and *Mniodes* (Cuatrecasas 1954a, b); *Belloa* (Cabrera 1958); *Lucilia* (Freire 1986b); *Jalcophila* (Dillon and Sagastegui-Alva 1986); *Chionolaena* (Freire 1993; Nesom 2001; Loeuille et al. 2011); *Lucilicline* (Anderberg and Freire 1991); *Gamochoeta* (Nesom 1990a; Freire and Iharlegui 1997), but most of their species have been placed in two or more different genera (Table 1). The delimitation of the genus *Lucilia* is probably the most controversial, and the limits between *Lucilia*, *Belloa* and *Lucilicline* have been discussed in recent years. As an example, Rémy (1847) created *Belloa* on the basis of *Lucilia chilensis*. Cabrera (1958) expanded the monotypic genus *Belloa* to 11

species. Dillon and Sagastegui-Alva (1985) described three new species of *Belloa* and transferred another four to this genus (one from *Mniodes* and three from *Lucilia*), raising the number of *Belloa* species to 18 (Dillon and Sagastegui-Alva 1991) or 16 (Dillon and Sagastegui-Alva 1992). Freire (1986b, 1987) merged *Belloa* with *Lucilia*. Anderberg and Freire (1991) maintained *Belloa* as an independent genus for the species with prostrate stems and proposed the genus *Lucilicline* for the species with erect or ascending stems. Finally, Dillon (2003) recognized *Belloa* as a monotypic genus and transferred the remaining species of *Belloa* to *Lucilicline*. The evident instability in the classification of the *Lucilia* group reflects the general scarcity of morphological characters traditionally considered relevant for the classification of the group and their high level of homoplasy. This affects mainly not only the generic boundaries, but also the circumscription of the *Lucilia* group, and this urged for an investigation based on molecular data to shed light on the classification.

In this context, a phylogenetic analysis including molecular and morphological information could be useful to elucidate the taxonomic arrangement of the taxa mentioned above. Both chloroplast and nuclear DNA markers have been used previously to address the phylogenetic relationships in the tribe Gnaphalieae, mainly focused on African and Australian taxa (Bergh and Linder 2009; Bayer et al. 2000, 2002; Galbany-Casals et al. 2010; Smissen et al. 2011), but molecular information on South American groups remains unknown or poorly studied (Ward et al. 2009).

The aims of this work were, using two plastid (*rpl32-trnL* and *trnL-F*) and two nuclear DNA regions (ITS and ETS), to test the various hypotheses of relationships within the *Lucilia* group, using a broad sampling of the Gnaphalieae.

## Materials and methods

### Taxon sampling

A special effort was made to cover the morphological and geographical variation of *Lucilia* group and allied genera in South America. The sampling for plastid and nuclear sequencing includes material from Argentina, Bolivia, Brazil, Chile, Colombia and Ecuador. The analyses comprised a total of 56 species, 21 belonging to the *Lucilia* group sensu Anderberg and Freire (1991), representing 51 % of the group. At least one species each of the 9 genera included in this group were used in the analyses (Appendix 1 in ESM). In order to assess the placement of the *Lucilia* group members within the tribe, 35 species belonging to closely related genera were used as outgroups

**Table 1** Comparison of the genera composition of *Lucilia* group and its genera (in bold face taxa with different placement) through the treatments

References	Genera	Nr of species and distribution	Species	
Merxmüller et al. (1977), 12 genera	<i>Belloa</i>	11, S. America	None mentioned	
<i>Lucilia</i> group	<i>Berroa</i>	1, S. America	None mentioned	
	<i>Chevreulia</i>	6, S. America	None mentioned	
	<b><i>Chionolaena</i></b>	c. 8, Mexico, Colombia, Brazil	None mentioned	
	<i>Facelis</i>	4, S. America	None mentioned	
	<b><i>Gnaphaliothamnus</i></b>	1, Mexico, Guatemala	None mentioned	
	<b><i>Leucopholis</i></b>	4, Brazil	None mentioned	
	<i>Lucilia</i>	c. 20, S. America	None mentioned	
	<i>Lucilitopsis</i>	4, S. America	None mentioned	
	<b><i>Mniodes</i></b>	5, Andean Peru	None mentioned	
	<i>Oligandra</i>	3, S. America	None mentioned	
	<b><i>Raoultopsis</i></b>	2, Andean Colombia	None mentioned	
	Anderberg (1991), 7 genera	<i>Belloa</i>	12, S. America	<i>B. burkartii</i> (=Lucilia burkartii), <i>B. catamarzensis</i> (=Lucilia catamarzensis), <i>B. chilensis</i> (=Lucilia nivea), <i>B. longifolia</i> (=Lucilia longifolia), <i>B. lopezmirandae</i> (=B. turneri), <i>Lucilia lopezmirandae</i> , <i>B. pickeringii</i> (=Lucilia pickeringii), <i>B. piptolepis</i> (=Lucilia piptolepis), <i>B. plicatifolia</i> (=Lucilia plicatifolia), <i>B. radians</i> (=Lucilia radians), <i>B. santanica</i> (=Lucilia santanica), <i>Belloa spathulifolia</i> , <i>B. schultzei</i> (=B. cerrateae, <i>Lucilia schultzei</i> , <i>Mniodes cerrateae</i> ), <i>Belloa subspicata</i> (=Lucilia subspicata)
	South American <i>Lucilia</i> group	<i>Berroa</i>	1, S. America	<i>B. gnaphalioides</i>
<i>Chevreulia</i>		5, S. America	<i>C. acuminata</i> , <i>C. diemii</i> , <i>C. lycopodioides</i> , <i>C. pusilla</i> , <i>C. sarmentosa</i>	
<i>Cuatrecasasiella</i> (=Lucilitopsis pp.)		2, S. America	<i>C. isernii</i> (=Lucilitopsis isernii), <i>C. argentina</i> (=Lucilitopsis argentina)	
<i>Facelis</i>		3, S. America	<i>F. lastiocarpa</i> , <i>F. plumosa</i> , <i>F. retusa</i>	
<i>Lucilia</i> (including <i>Oligandra</i> )		11, S. America	<i>L. acutifolia</i> , <i>L. alpina</i> , <i>L. eriophora</i> , <i>L. ferruginea</i> , <i>L. kunthiana</i> , <i>L. lehmannii</i> , <i>L. linearifolia</i> , <i>L. lycopodioides</i> (=Oligandra lycopodioides), <i>L. nitens</i> , <i>L. recurva</i> , <i>L. tomentosa</i>	
<i>Jalcophila</i>		3, S. America	<i>J. bolivianensis</i> , <i>J. ecuadoriensis</i> , <i>J. peruviana</i>	
<i>Belloa</i>		9, Andean Venezuela to Chile	<i>B. chilensis</i> (=Lucilia araucana, <i>L. nivea</i> , Freire 1986b), <i>B. kunthiana</i> (=Lucilia conoidea, Freire 1986b), <i>B. lehmannii</i> , <i>B. longifolia</i> , <i>B. pickeringii</i> , <i>B. piptolepis</i> , <i>B. plicatifolia</i> , <i>B. radians</i> , <i>B. schultzei</i>	

Table 1 continued

References	Genera	Nr of species and distribution	Species	
South American <i>Lucilia</i> group	<i>Berroa</i>	1, Brazil, Uruguay, Argentina	<i>B. gnaphalioides</i>	
	<i>Chevreulia</i>	5, Brazil, Bolivia, Paraguay, Uruguay, Chile, Argentina and Falkland Islands	<i>C. acuminata</i> , <i>C. dtiemii</i> , <i>C. lycopodioides</i> , <i>C. pusilla</i> , <i>C. sarmentosa</i>	
	<i>Cuatrecasasiella</i>	2, Andean Ecuador to Argentina	<i>C. isernii</i> , <i>C. argentina</i>	
	<i>Facelis</i>	3, Brazil, Peru, Bolivia, Paraguay, Chile, Uruguay, Argentina	<i>F. lasiocarpa</i> , <i>F. plumosa</i> , <i>F. retusa</i>	
	<i>Gamochaetopsis</i>	1, Andean Chile, Argentina	<i>G. alpina</i> (= <i>Lucilia alpina</i> )	
	<i>Jalcophila</i>	3, Andean Ecuador, Peru, Bolivia	<i>J. boliviensis</i> , <i>J. ecuadoriensis</i> , <i>J. peruviana</i>	
	<i>Lucilia</i>	8, Brazil, Paraguay, Uruguay, Argentina, Andean Bolivia, Argentina, Chile	<i>L. acutifolia</i> , <i>L. eriophora</i> , <i>L. ferruginea</i> , <i>L. linearifolia</i> , <i>L. lycopodioides</i> , <i>L. nitens</i> , <i>L. recurva</i> , <i>L. tomentosa</i>	
	<i>Luciliocline</i>	5, Andean Peru, Bolivia, Argentina	<i>L. burkartii</i> , <i>L. catamarcensis</i> , <i>L. lopezmirandae</i> (= <i>L. turneri</i> ), <i>L. santanica</i> (= <i>L. spathulifolia</i> ), <i>L. subspicata</i>	
	Dillon (2003), 13 genera	1, Austral Chile and Argentina	<i>B. chilensis</i>	
	<i>Lucilia</i> group	<i>Berroa</i>	1, S. America	<i>B. gnaphalioides</i>
		<i>Chevreulia</i>	6, Austral S. America	None mentioned
		<b><i>Chionolaena</i></b> (including <i>Leucopholis</i> )	Not stated	None mentioned
		<i>Cuatrecasasiella</i>	2, Northern and Southern Andes	None mentioned
<i>Facelis</i>		Not stated	None mentioned	
<b><i>Gamochaeta</i></b>		c. 80, New World	<i>G. boliviensis</i> (= <i>Jalcophila boliviensis</i> ), None mentioned	
<i>Gamochaetopsis</i>		1, Andean Chile and Argentina	<i>G. alpina</i> (= <i>Lucilia alpina</i> )	
<i>Jalcophila</i>		3, Northern Andes	<i>J. colombiana</i> , <i>J. ecuadoriensis</i> , <i>J. peruviana</i>	
<i>Lucilia</i>		12, Brazil, Paraguay, Uruguay, Argentina, Andean Venezuela to Chile	<i>L. acutifolia</i> , <i>L. araucana</i> , <i>L. conoidea</i> , <i>L. eriophora</i> , <i>L. ferruginea</i> , <i>L. kunthiana</i> , <i>L. linearifolia</i> , <i>L. lycopodioides</i> , <i>L. nitens</i> , <i>L. nivea</i> , <i>L. recurva</i> , <i>L. tomentosa</i>	
<i>Luciliocline</i>		13 Andean Venezuela to Chile and Argentina	<i>L. burkartii</i> , <i>L. catamarcensis</i> , <i>L. longifolia</i> , <i>L. lopezmirandae</i> , <i>L. pickeringii</i> , <i>L. pipitolepis</i> , <i>L. plicatifolia</i> , <i>L. radians</i> , <i>L. santanica</i> , <i>L. schultzei</i> , <i>L. spathulifolia</i> , <i>L. subspicata</i> , <i>L. turneri</i>	
<b><i>Micropsis</i></b>		Not stated, S. America	None mentioned	
<b><i>Stuckertiella</i></b>		Not stated, S. America	None mentioned	

(Appendix 1 in ESM). Trees were rooted with *Relhania* as outgroup.

Using DNA obtained from plants collected in wild populations and dried in silica gel, or from herbarium material, a total of 117 sequences (representing 36 species) were generated for this study, while 64 sequences (for 20 species from the outgroups) were obtained from GenBank (see Appendix 1 in ESM). A complete list of the specimens used in this study, the locality where each specimen was collected, the herbarium voucher information and GenBank accession numbers are shown in the Appendix 1 in ESM.

#### Morphological characters

For the morphological matrix, 21 ingroup taxa and 12 outgroup taxa (*Achyrocline ramosissima*, *A. tomentosa*, *Antennaria dioica*, *Chionolaena arbuscula*, *C. campestris*, *Gamochaeta serpyllifolia*, *Loricaria colombiana*, *Microp-sis dasycarpa*, *Mniodes andina*, *Pseudognaphalium badi-um*, *P. lacteum*, *Stuckertiella capitata*), were analyzed using 35 morphological characters taken from a previous work (Anderberg and Freire 1991) and adding the following character, i.e., leaves not densely imbricate (0)/densely imbricate (1) (Appendix 2 in ESM). Characters were taken from direct examination of herbarium specimens (Appendix 1 in ESM), and information was completed from literature (Anderberg and Freire 1991).

#### Molecular methods

Total genomic DNA from silica-dried material was extracted using a modified CTAB protocol from Doyle and Dickson (1987), while exactions from herbarium material were performed using the DNeasy Plant Mini Kit (QIAGEN Inc., Hilden, Germany). Genomic DNA was used as a template to amplify four regions: the chloroplast fragment containing the *trnL* (UAA) intron and the intergenic spacer between the *trnL* (UAA) 3' exon and the *trnF* (GAA) gene (*trnL*-F region) using primers C and F from Taberlet et al. (1991); the *rpl32-trnL* intergenic spacer (chloroplast) using primers *rpl32F* and *trnL*(UAG) from Shaw et al. (2007); the nuclear region ETS using the reverse primer 18S-ETS (Baldwin and Markos 1998) and one of the following forward primers: AST1, ETS1 or ETS2 (Bayer et al. 2002); and the nuclear marker ITS using the primers ITS4 and ITS5 from White et al. (1990).

Polymerase chain reactions (PCR) were carried out on 25  $\mu$ l volumes, each reaction containing between 50 and 100 ng of DNA, 1.5 U of Taq polymerase (Invitrogen Life Technologies, São Paulo, Brazil), 1  $\times$  PCR buffer, 5 mM MgCl<sub>2</sub>, 0.2 mM of each primer and 0.025 mM dNTP each. In species for which these protocols were unsuccessful, 0.4 % bovine serum albumin was included as additive to

increase the yield of PCR reactions. The annealing temperatures ranged between 48 and 52 °C for the chloroplast markers and 56–60 °C for the nuclear markers. PCR products were electrophoresed on a 1 % TBE agarose gel stained with SYBR safe DNA gel stain (Invitrogen, Brazil). Macrogen Inc. (Korea) performed the cleaning of the PCR products using the Montage PCR purification kit from Millipore following the manufacturer's protocol. Sequencing reactions were also performed by Macrogen Inc.

#### Sequence analyses

Sequence data were edited and contigs assembled using the program Chromas Pro ver. 1.34 (Technelysium Pty, Ltd, Tewantin, Australia), and the matrix was edited using the software BioEdit (Hall 1999). Sequences were aligned using the program MAFFT (<http://mafft.cbrc.jp/alignment/server/>; Katoh et al. 2002), using the default parameters and an automatic alignment strategy, with subsequent visual inspection and manual revision. Data matrices are deposited on TreeBase (accession number 16182).

#### Phylogenetic analyses

Three maximum parsimony analyses were conducted, the first including only the nuclear markers, the second including the complete molecular data set and the third combining the molecular information with the morphological data in a combined analysis (Nixon and Carpenter 1996). Searches were carried out using the software TNT (Goloboff et al. 2008), with the characters equally weighted and considering gaps as missing data. The heuristic searches were performed as follows: 1,000 series of random addition sequences (RAS), swapping the trees with tree bisection-reconnection (TBR), plus an additional rearrangement of all the most parsimonious trees found. Branch support was evaluated using Jackknifing (JK; Farris et al. 1996), which was calculated by performing 5,000 pseudoreplicates, each consisting of 10 RAS.

Bayesian inference of phylogeny with posterior probabilities (PP) was conducted with MrBayes ver. 3.2.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003) for the three combined analyses mentioned above. The models of molecular evolution were selected using the Akaike Information Criterion (AIC) as implemented in jModelTest ver. 2.1.4 (Table 2; Guindon and Gascuel 2003; Darriba et al. 2012). The chosen models were GTR + G for *rpl32-trnL*, *trnL*-F, ETS and GTR + I + G for ITS. The standard discrete model was used for the morphological data (Lewis 2001). Searches used default settings for all parameters. Four simultaneous independent runs initiated from random start trees were run

**Table 2** Main characteristics and results for the different regions and datasets analyzed

	ITS	ETS	<i>rp132-trnL</i>	<i>trnL-F</i>	ITS + ETS	Molecular data set	Simultaneous analysis
Number of taxa	45	54	39	43	55	56	56
Sequence length (bp)	605 ( <i>S. muelleri</i> ) to 626 ( <i>P. serpyllifolia</i> )	465 ( <i>G. uliginosum</i> ) to 485 ( <i>R. pungens</i> )	436 ( <i>Leontopodium</i> ) to 692 ( <i>R. pungens</i> )	814 ( <i>L. nitens</i> and <i>L. acutifolia</i> ) to 852 ( <i>Pseudognaphalium</i> )	—	—	—
Aligned length (bp)	636	507	830	944	1,143	2,917	2,953
Parsimony informative characters	153	149	87	60	302	617	651
Number of most parsimonious trees	—	—	—	—	8	24	10
Number of steps	—	—	—	—	912	1,672	1,857
Consistency index	—	—	—	—	0.52	0.67	0.47
Retention index	—	—	—	—	0.69	0.69	0.36
Model of molecular evolution	GTR + I + G	GTR + G	GTR + G	GTR + G	Each region its model	Each region its model	Each region its model + standard discrete model

Indices and number of steps were calculated excluding uninformative characters

for 10 million generations, sampling from the posterior distribution of trees every 1,000 generations (for a total of 10,000 samples). Several strategies were employed to confirm that chains had achieved stationarity and the appropriate burn-in for each analysis was determined: (1) we plotted overall—lnL, (2) we examined the standard deviation of split frequencies, (3) we examined the potential scale reduction factor (PSRF) and (4) we checked graphically the convergence of the MCMC by monitoring the cumulative posterior split probabilities and among-run variability of split frequencies using the online tool AWTY (Wilgenbusch et al. 2004). A total of 25 % of the samples were discarded as burn-in.

Bayesian posterior probabilities (PP) values were described as high (0.95–1.00), moderate (0.90–0.94) and low (0.50–0.89), while parsimony jackknife (JK) values were described as high, (90–100 %), moderate (70–89 %) and low ( $\leq 69$  %). Jackknife values of less than 50 %, though extremely low, were also considered since in some cases they can be showing just lack of information instead of inconsistencies in the phylogenetic signal (Goloboff et al. 2003). Nodes with Bayesian posterior probabilities of less than 0.5 were considered as unsupported and the values are not reported.

## Results

In total we included in the analyses 54 ETS sequences, of which 35 are new; 45 ITS sequences, of which 28 are new; 39 *rp132-trnL*, intergenic spacer sequences, of which 28 are new; and 43 *trnL* intron intergeneric spacer sequences, from which 26 are new (Appendix 1 in ESM). The main characteristics of the datasets, along with the corresponding tree statistics are summarized in Table 2.

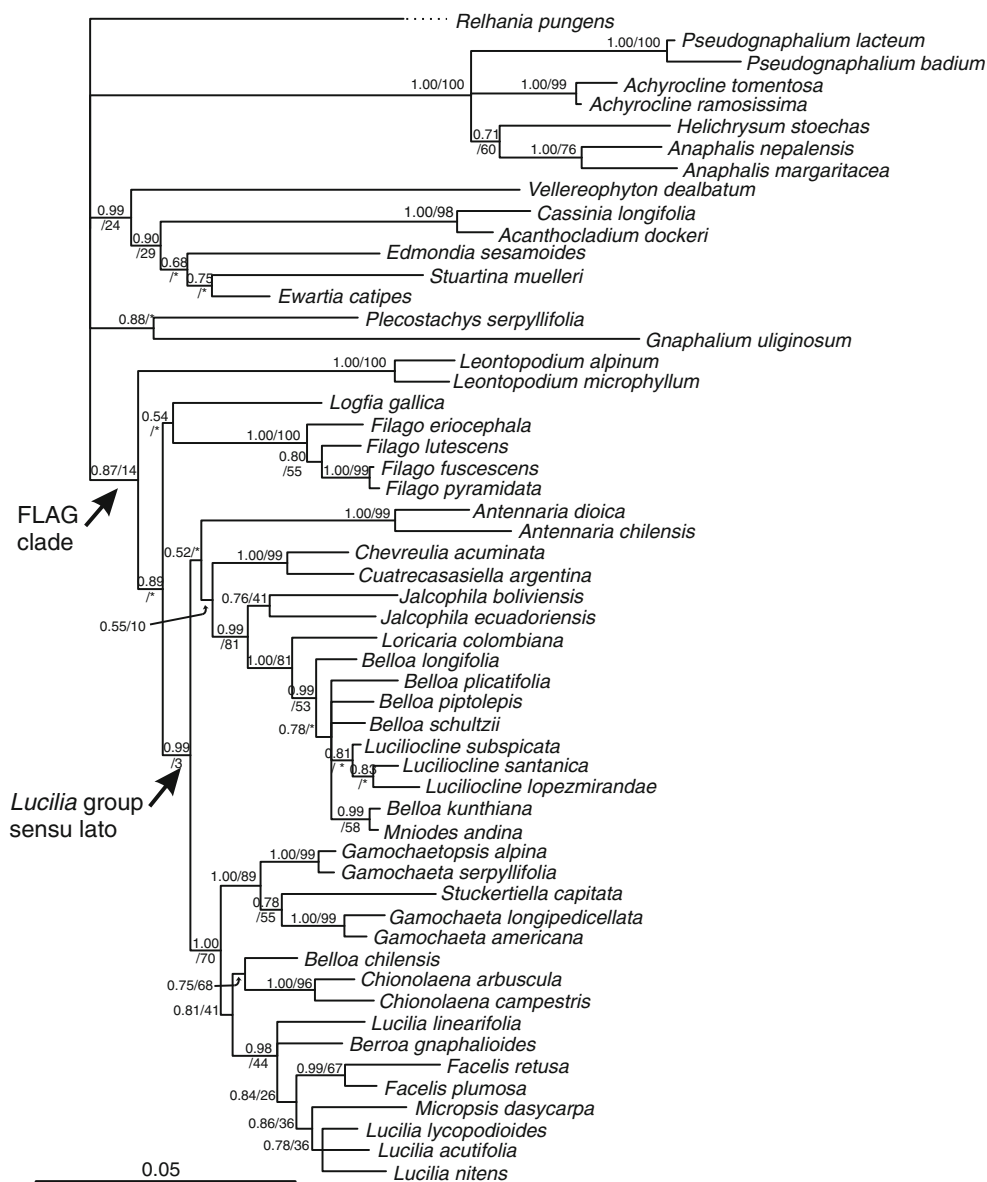
Both Parsimony and Bayesian inference analyses showed highly congruent topologies for molecular data or combination of molecular data and morphological characters. All the analyses showed short branches for the *Lucilia* group, mainly in the nodes (Figs. 1, 2, 3).

The analysis of the plastid markers resulted in a highly polytomized tree, with almost no support and no resolution below the node that groups the FLAG clade (tree not shown), so they are not described here.

### Nuclear markers (ITS+ETS)

The nuclear markers combined showed that the *Lucilia* group as previously circumscribed is not monophyletic, due to the inclusion of *Antennaria*, *Gamochoaeta*, *Stuckertiella*, *Micropsis*, *Loricaria*, *Chionolaena* and *Mniodes* (Fig. 1) in a high supported clade for the Bayesian analysis (0.99 PP, 3 % JK). Most of the basal nodes (from the

**Fig. 1** Consensus phylogram obtained from the Bayesian analysis of ITS + ETS sequences (nuclear markers). Bayesian posterior probabilities (PP) and Jackknife values from the parsimony analyses are shown associated with the branches. An asterisk indicates a branch missing from the parsimony analysis. Dotted branches were shortened to have a clearer topology

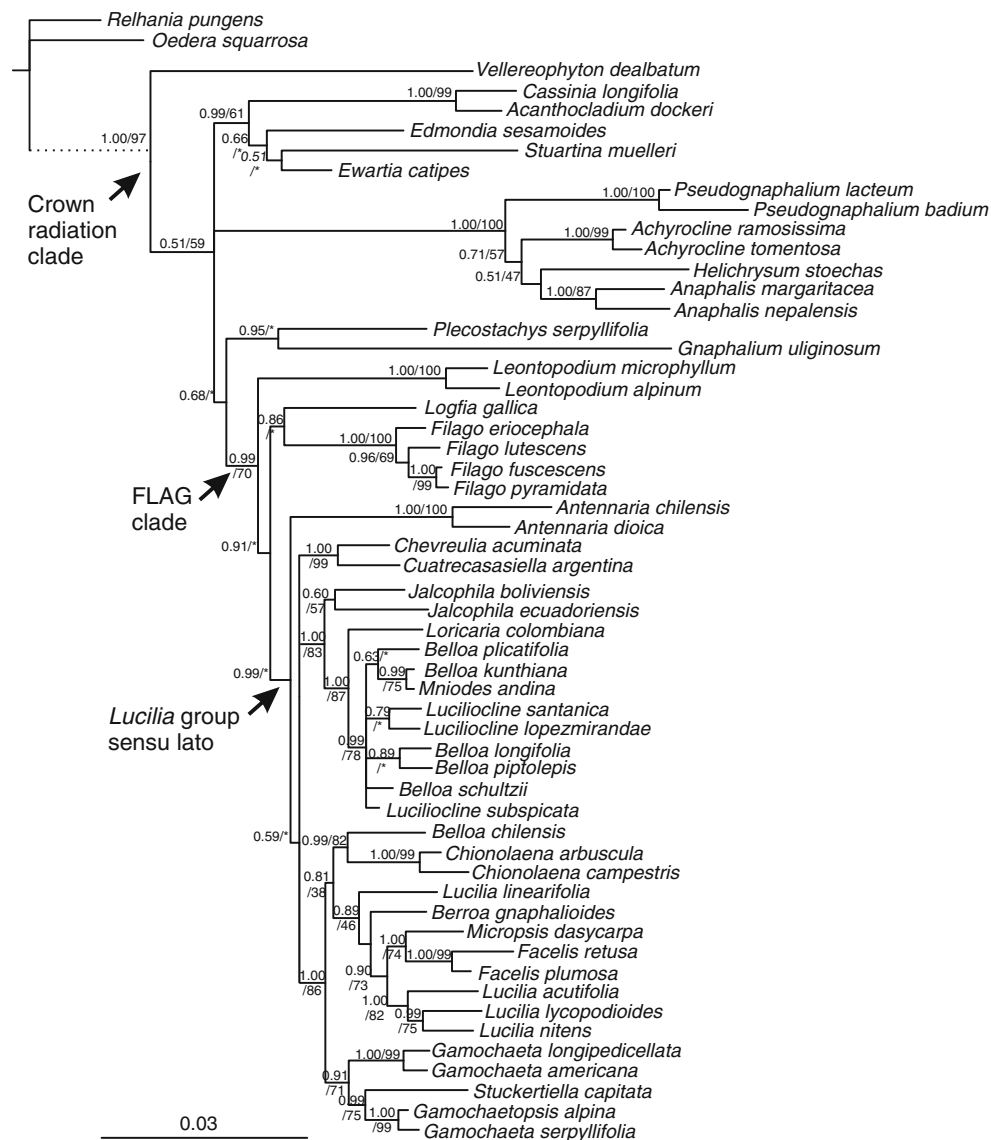


outgroups) were lost in the parsimony analysis, having a tree with more polytomies as a result of that analysis (Fig. 1). However, inside the *Lucilia* group s.l. both analyses showed almost the same topology (with the exception of the placement of the *Antennaria* clade, and the inner structure of the *Belloa* + *Luciliochline* + *Mniodes* clade) (Fig. 1). Since the clades of the *Lucilia* group s.l. are also present in the other analyses, they will be discussed in detail below, in the combined analysis.

Complete molecular data set (*trnL-F* + *rpl32-trnL* + ITS + ETS)

The analysis of the four molecular markers (Fig. 2) recovered the same topology provided by the nuclear

analysis, with two exceptions: *Micropsis* is grouped together with two species of *Facelis* (vs. with three species of *Lucilia* in the nuclear analysis; Fig. 1) and *Luciliocline subspicata* is placed in a basal polytomy of the *Belloa* pp + the remaining two species of *Luciliochline* + *Mniodes* clade (Fig. 2) (vs. grouped with the remaining two species of *Luciliochline* in nuclear DNA analysis; Fig. 1). The major difference between the parsimony and the Bayesian analyses is that the first fails to recover the *Lucilia* group s.l. as monophyletic (Fig. 2), but instead places the major clades that conform it as a polytomy (not shown). Since the polytomy does not contradict the topology obtained in the Bayesian analysis, we consider the results of this analysis as valid.



**Fig. 2** Consensus phylogram obtained from the Bayesian analysis of the complete molecular dataset (ITS + ETS + *rpl32-trnL* intergenic spacer + *trnL* intron + *trnL-F* intergenic spacer sequences). Bayesian posterior probabilities (PP) and Jackknife values from the

parsimony analyses are shown associated with the branches. An asterisk indicates maximum support for both analyses (i.e., >0.99 and 98 %). Dotted branches were shortened to have a clearer topology

Combined analysis (molecular data + morphological characters)

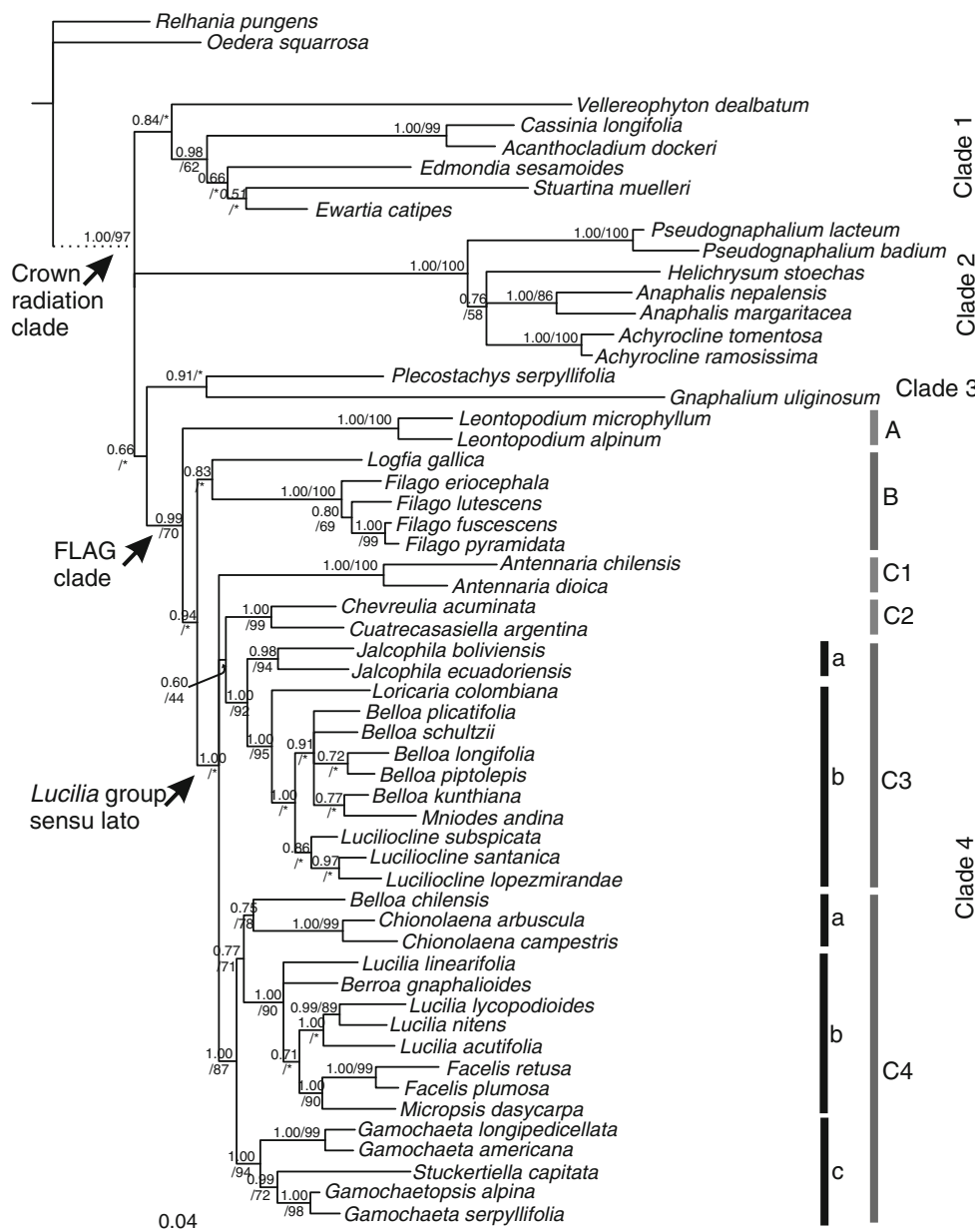
Considering both the Parsimony and the Bayesian combined analyses, the Bayesian inference gave the highest resolution. Therefore, we adopt the hypothesis obtained from Bayesian analysis for description and discussion of the results. This topology is shown with the addition of PP/JK values (Fig. 3).

From the topology inferred by Bayesian analysis, and following the *Relhania* and *Oedera* clades, four clades were recovered. One, clade was constituted by six genera, *Vellereophyton*, *Cassinia*, *Acanthocladium*, *Edmondia*,

*Stuartina*, and *Ewartia* (clade 1, 0.84 PP); a second one (clade 2, 1.00 PP, 100 % JK), was constituted by the genera *Pseudognaphalium* (*P. badium*, *P. lacteum*), *Helichrysum* (*H. stoechas*), *Anaphalis* (*A. nepalensis*, *A. margaritacea*), and *Achyrocline* (*A. tomentosa*, *A. ramosissima*); the third one (clade 3, 0.91 PP) was constituted by *Plecostachys serpyllifolia* and *Gnaphalium uliginosum*, and the fourth clade (clade 4, 0.96 PP, 70/JK) comprised the rest of the genera included in the analyses.

One major clade can be identified within clade 4, which is missing in the parsimony analysis (Fig. 3): clade C (1.00 PP) subdivided into clade C.1 (1.00 PP, 100 % JK) including *Antennaria chilensis* and *A. dioica*; clade C.2





**Fig. 3** Consensus phylogram obtained from the bayesian combined analysis (molecular data set + morphology). Bayesian posterior probabilities (PP) and Jackknife values from the parsimony analyses are shown associated with the branches. An asterisk indicates a

branch missing from the parsimony analysis. Resolution of clade C1 in the parsimony analysis. Dotted branches were shortened to have a clearer topology

(1.00 PP, 99 % JK) including *Chevreulia acuminata* and *Cuatrecasasiella argentina*; clade C.3 (1.00 PP, 92 % JK) with two subclades, C.3a (0.98 PP; 94 % JK) including *Jalcophila boliviensis* and *J. ecuadoriensis*; and subclade C.3b (1.00 PP, 95 % JK) including *Loricaria colombiana*, *Belloa plicatifolia*, *B. schultzei*, *B. longifolia*, *B. piptolepis*, *B. kunthiana*, *Mniodes andina*, *Luciliocline subspicata*, *L. santanica*, and *L. lopezmirandae*. Finally, clade C.4 (1.00 PP, 87 % JK) which could be subdivided into subclades, subclade C.4a (0.75 PP, 78 % JK) including *Belloa chilensis*,

*Chionolaena arbuscula*, *C. campestris*; subclade C.4b (1.00 PP, 90 % JK) including *Lucilia linearifolia*, *Berroa gnaphalioides*, *Lucilia lycopodioides*, *L. nitens*, *L. acutifolia*, *Facelis retusa*, *F. plumosa*, and *Micropsis dasycarpa*; and subclade C.4c (1.00 PP, 94 % JK) including *Gamochaeta longipedicellata*, *G. americana*, *Stuckertiella capitata*, *Gamochaetopsis alpina*, and *Gamochaeta serpyllifolia*.

Two minor clades can be also identified within clade 4 (Fig. 3): clade A (1.00 PP, 100 % JK) and clade B (0.83 PP) composed of the genera *Leontopodium*, and

*Logfia* + *Filago*, respectively. These two clades were recovered as sister clades of clade C.

## Discussion

The present analyses of Gnaphalieae are consistent with previous phylogenies (Bergh and Linder 2009; Ward et al. 2009; Galbany-Casals et al. 2010; Smitsen et al. 2011) showing a relatively small southern African clade, i.e., ‘*Relhania* and *Oedera* clades’ at the base and then a ‘crown radiation’ including African and non-African taxa. Within the ‘crown radiation’ two of the four clades recovered are also equivalent to those found in previous phylogenies (Bergh and Linder 2009; Ward et al. 2009; Galbany-Casals et al. 2010; Smitsen et al. 2011), i.e., clade 2 formed by *Helichrysum*, *Anaphalis* and *Pseudognaphalium*, called HAP clade (for the first letters of the genera, according to Smitsen et al. 2011) which showed the maximum statistical support (Figs. 2, 3) and the highly supported clade 4, formed by *Filago*, *Logfia*, *Leontopodium*, *Antennaria*, *Gamochaeta*, called FLAG clade (for the first letters of the large genera, according to Galbany-Casals et al. 2010) (Figs. 2, 3), principally distributed in Eurasia and America.

Clade 3 comprises *Gnaphalium uliginosum* and *Plecostachys serpyllifolia* (with moderate support in the combined analyses; Fig. 3), both belonging to subtribe Gnaphaliinae (Anderberg 1991). Unlike Bergh and Linder’s (2009) phylogeny, *Plecostachys serpyllifolia*, from South Africa, was not grouped within the FLAG clade.

Clade 1 comprises six taxa (with low support in the combined analyses; Fig. 3): *Vellereophyton dealbatum* (subtribe Gnaphaliinae-*Gnaphalium* group; Anderberg 1991), from South Africa, as sister species to two subclades: the first one was composed of *Edmondia sesamoides* (subtribe Gnaphaliinae-*Syncarpha* group; Anderberg 1991) from South Africa, and two Australian species, *Ewartia catipes* (subtribe Cassiniinae-*Anaphalis* group; Anderberg 1991), and *Stuartina muelleri* (subtribe Gnaphaliinae-*Gnaphalium* group; Anderberg 1991); and a second subclade was composed of two other Australian species, *Acanthocladium dockeri* (subtribe Cassiniinae; Anderberg 1991) and *Cassinia longifolia* (subtribe Cassiniinae-*Cassinia* group; Anderberg 1991).

From these four clades, only clade 2 (HAP clade) is recovered in the phylogeny of Gnaphaliinae by Anderberg (1991). The remaining three clades show, as was previously noted (Bayer et al. 2000, 2002; Ward et al. 2009; Galbany-Casals 2010; Smitsen et al. 2011), with the necessary caution due to the limited sampling of our study, that DNA data do not support some of the relationships among groups of genera and subtribes identified by Anderberg (1991), for example in clade 4 (FLAG clade), *Leontopodium* and

*Logfia* + *Filago* are related to *Antennaria* (instead of *Leontopodium* and *Filago* placed in the subtribe Gnaphaliinae, and *Antennaria* placed in the subtribe Cassiniinae), or in clade 1, *Acanthocladium* and *Cassinia* are related to *Edmondia* and *Stuartina* (instead of *Acanthocladium* and *Cassinia* placed in subtribe Cassiniinae, and *Edmondia* together with *Stuartina* in subtribe Gnaphaliinae, but in different groups, i.e., *Syncarpha* group and *Gnaphalium* group, respectively).

In general, South American taxa of Gnaphalieae have not been sampled in previous molecular phylogenetic analyses. Only Ward et al. (2009) included *Jalcophila* and *Mniodes* in their phylogeny of Gnaphalieae, in which *Jalcophila* (*J. peruviana*), *Mniodes* (*M. andina*) and *Gamochaeta* (*G. pensylvanica*) are all part of the ‘crown radiation’.

Generic composition of the *Lucilia* group s. lat.

The analysis of the complete molecular data set, and molecular data combined with morphological characters showed that the *Lucilia* group, as previously circumscribed, is not monophyletic. The combined analysis showed that the genera of the *Lucilia* group sensu Anderberg and Freire are grouped with seven other genera (clade C, Fig. 3): *Gamochaeta* is distributed in America with some species known as cosmopolitan weeds, *Stuckertiella*, *Micropsis*, *Loricaria* and *Mniodes* from South America, *Chionolaena* found in Central and South America, and *Antennaria* mainly distributed in Northern Hemisphere with only three species known from South America. Four of these genera were previously placed by Anderberg (1991) in subtribe Loricariinae (*Loricaria* and *Mniodes*) and subtribe Cassiniinae (*Antennaria* and *Chionolaena*). The relationship between these last two taxa of the tribe Cassiniinae and other members of the *Lucilia* group was previously suggested by Dillon (2003).

Anderberg and Freire (1991) diagnosed the South American *Lucilia* group by its very slender pappus bristles which are often connate in groups, dorsally pubescent style branches and polychromous involucre bracts. Only one morphological synapomorphy, i.e., slender pappus bristles basally connate or coherent at the base by patent cilia, was found for the ancestral node that defines the present arrangement of *Lucilia* group s. lat. Although, only two of c. 50 species of *Antennaria* were sampled in this study, and it possesses pappus bristles basally with patent cilia (vs. connate in the remaining taxa of *Lucilia* group), this genus was tentatively included here in this group.

Within these mainly American members, called *Lucilia* group s. lat., two main groups were recovered with our sampling. The first one (clade C2 + C3, Fig. 3), comprises *Chevreulia*, *Cuatrecasasiella*, *Jalcophila*, *Loricaria*,

*Belloa* pro parte, *Mniodes* and *Luciliocline*, principally characterized by having caespitose, subcaespitose or cushion forming habit (rarely shrubs), with leaves arranged in rosettes or densely imbricate, and achenial trichomes globose or clavate (rarely elongated) (Table 3; Figs. 4, 6g). The second one (clade C4, Fig. 3) comprised *Belloa chilensis*, *Chionolaena*, *Lucilia*, *Berroa*, *Facelis*, *Micropsis*, *Gamochaeta*, *Stuckertiella* and *Gamochaetopsis*, principally characterized by having ascending or erect stems (rarely prostrate), with leaves commonly scattered, and achenial trichomes elongated (Table 3; Figs. 5, 6i). They also conform, each one, two geographical well-defined groups. In fact, the genera of clade C4 occur mainly at low altitude areas in southern Brazil, Uruguay, eastern Paraguay and northern Argentina, but except *Berroa* and *Micropsis*, they also include species from some part of the Andes. Conversely, most genera of the clade C2+C3 are endemic to the Andes; only *Chevreulia* includes species from low altitudes. A minor third group (clade C1, Fig. 3) was also recovered with our sampling which comprises the genus *Antennaria*, from arctic to temperate regions of the Northern hemisphere with only three species in the Andes of South America, and principally characterized by having dioecious and often apomictic habit, with ascending or erect stems, leaves alternate, often rosulate and achenial trichomes usually clavate. The genus *Mniodes* was also considered by Merxmüller et al. (1977) to be a member of the *Lucilia* group. However, Anderberg (1991) placed *Mniodes* with *Loricaria* (Fig. 4b) in the subtribe Loricariinae because of its dioecy habit. Our results show that both genera are nested within clade C of the *Lucilia* group (Figs. 1, 2, 3).

The close relationship between *Facelis* and *Micropsis* (Fig. 5c, d) had been previously recognized by Dillon (2003). *Micropsis*, which is a genus of five species restricted to South America, was defined by paleaceous receptacles where paleae enclose the florets, and consequently associated with the genera of the *Filago* group by Anderberg (1991). As such, the strong support in the combined analysis (Fig. 3) for the clade of *Micropsis* + *Facelis* confirms the inclusion of *Micropsis* in the *Lucilia* group.

The genus *Chionolaena* (Fig. 5f) was considered by Merxmüller et al. (1977) to be a member of the *Lucilia* group. Later, Anderberg (1991) placed *Chionolaena* (including *Leucopholis*), in the *Anaphalis* group (subtribe Cassiniinae), principally diagnosed by having disc florets functionally male. Subsequently, Dillon (2003) suggested a close potential relationship between *Chionolaena* and the other members of the *Lucilia* group. Our results are consistent with those of Merxmüller et al. and Dillon's placement of genus *Chionolaena* within the *Lucilia* group (Fig. 3).

Anderberg and Freire (1991) considered *Gamochaeta* to be the sister taxon of the *Lucilia* group. *Gamochaeta*

(Fig. 5h) was not considered by these authors as belonging to the *Lucilia* group, since it possesses truncate style branches apically pilose (vs. style branches dorsally pilose, Fig. 6a–e). Dillon (2003) suggested a relationship between *Gamochaeta* and other members of the *Lucilia* group, which was confirmed by our results, which show that *Gamochaeta* and its sister genus *Stuckertiella* (Fig. 5i) are nested with *Gamochaetopsis* (Fig. 5g) within clade C (Fig. 3).

In our analyses including molecular markers and a combination of molecular and morphological data, some main clades correspond to those recognized in previous morphological phylogenies. As such, for discussion of systematic relationships of *Facelis*, *Chevreulia*, *Cuatrecasasiella* and *Jalcophila* we refer to Anderberg and Freire (1991) with which our phylogenetic inferences are congruent. *Gnaphaliothamnus*, which was considered as a synonym of *Chionolaena* (Nesom 2001; Loeuille et al. 2011) or as a distinct genus (Nesom 1990b, c; Anderberg 1991; Freire 1993), and *Raouliopsis*, have not been included in our analyses, so their phylogenetic positions remain untested.

#### Placement of the *Lucilia* group s. lat.

The position of *Lucilia* group s. lat., as defined in the present study, is the same in all trees, with *Leontopodium*, and *Filago* within the clade 4, i.e., the FLAG clade (Figs. 1, 2, 3). Smissen et al. (2011) hypothesized  $2n = 14$  as the base number for the tribe Gnaphalieae and a  $2n = 28$  ancestor for the FLAG clade (derived from  $2n = 14$  by polyploidy), showing multiple shifts from  $2n = 14$  to  $2n = 28$  in the tribe. In this sense, the counts of  $2n = 28$ , 56, 62, 63, 70, 80, 84, 85, 100 in *Antennaria*, Chouksanova et al. 1968; Juel 1900; Jörgensen et al. 1958; Löve and Löve 1982a, b; Packer and McPherson 1974; Urbanska-Worytkiewicz 1967;  $n = 14$  in *Chionolaena lavandulifolia* (= *Gnaphalium lavandulifolium*), De Jong and Longpre 1963;  $n = 14$  in *Gamochaeta spiciformis*, Moore 1981;  $n = ca. 14$  in *Loricaria thuyoides* Turner et al. 1967;  $2n = 28$  in *Lucilia acutifolia* and *L. nitens*, Freire 1986c;  $n = 12$  in *Luciliocline subspicata* (= *Belloa punae*), Fernández Casas and Fernández Piqueras 1981; and  $n = 11–12$  in *Stuckertiella capitata*, Spooner et al. 1995, are consistent with Smissen et al. hypothesis and provide good evidence that the *Lucilia* group is part of the FLAG clade.

#### Taxonomic implications

##### *Monophyly of Belloa and its relationships with Luciliocline and Mniodes*

Our results suggest that *Belloa* sensu Cabrera (1958) and sensu Anderberg and Freire (1991) is not monophyletic. Instead, these results are consistent with Dillon's study

**Table 3** Morphological characters of the genera of *Lucilia* group s. lat. (key characters in bold face)

Genus	Habit	Monoeious/dioecious	Leaf disposition	Capitula pedunculate at maturity	Disc florets	Sweeping-hairs of style branches	Florets enclosed by receptacular palaeae	Achenes	Achenial hairs	Pappus	Involucral bracts
<i>Antennaria</i>	Erect or ascending herbs	Dioecious (capitula homogamous)	Alternate	–	All functionally male	Dorsally	–	Not rostrate	Clavate	<b>Dimorphic coherent at base</b>	Monochromous
<i>Beloa</i>	<b>Caespitose, prostrate herbs</b>	Monoeious	Alternate	–	Perfect	Dorsally	–	Not rostrate	<b>Clavate to elongated</b>	Scabrid-basally connate	Polychromous-sterome entire
<i>Berroa</i>	Ascending herbs	Monoeious	Alternate	–	Perfect	Dorsally	–	Not rostrate	Elongated, <b>8–12 twisted apically</b>	<b>Plumose (scabrid above)</b> -basally connate	Polychromous-sterome entire
<i>Chevrelia</i>	Subcaespitose	Monoeious	<b>Opposite or rosulate</b>	+	Perfect	Dorsally	–	<b>Rostrate</b>	Clavate	Scabrid-basally connate	Polychromous-sterome entire
<i>Chionolaena</i>	<b>Shrubs</b>	Subdioecious (capitula heterogamous)	Alternate	–	<b>Functionally male</b>	Dorsally	–	Not rostrate	Elongated	<b>Barbellate</b> -basally connate	Monochromous-sterome entire
<i>Cuatrecasasiella</i>	Subcaespitose	Dioecious (capitula homogamous)	<b>Opposite</b>	–	All functionally male	Dorsally	–	Not rostrate	Absent	Scabrid-basally connate	Monochromous-sterome entire
<i>Facelis</i>	Erect or ascending herbs	Monoeious	Alternate	–	Perfect	Dorsally	–	Not rostrate	Elongated	<b>Plumose (scabrid above)</b> —basally connate	Polychromous-sterome divided
<i>Gamochoaeta</i>	Erect or ascending herbs	Monoeious	Alternate	–	Perfect	<b>Apically</b>	–	Not rostrate	<b>Globose</b>	Scabrid-basally connate	Polychromous-sterome entire
<i>Gamochoetopsis</i>	Prostrate to ascending herbs	Monoeious	Alternate	–	Perfect	<b>Apically</b>	–	Not rostrate	<b>Clavate</b>	Scabrid-basally connate	Polychromous-sterome entire (divided)
<i>Jalcofila</i>	Caespitose herbs	Monoeious	<b>Rosulate</b>	+	Perfect	Dorsally	–	Not rostrate	<b>Clavate</b>	Scabrid-basally connate	Monochromous-sterome entire
<i>Loricaria</i>	<b>Shrubs or subshrubs</b>	Dioecious (capitula homogamous)	<b>Densely imbricate-laterally compressed</b>	–	All functionally male	Dorsally	– (+)	Not rostrate	Absent	<b>Dimorphic</b> -scabrid-basally connate	Monochromous-sterome entire
<i>Lucilia</i>	<b>Erect or ascending herbs</b>	Monoeious or subdioecious (capitula heterogamous, rarely homogamous)	Alternate	–	Perfect or functionally male	Dorsally	–	Not rostrate	<b>Elongated</b>	Scabrid (rarely barbellate above)—basally connate	Polychromous-sterome entire or divided
<i>Mniodes</i>	<b>Ascending to caespitose herbs</b>	Monoeious or dioecious (capitula hetero- or homogamous)	<b>Alternate, rosulate or densely imbricate</b>	–	Perfect or all functionally male	Dorsally	–	Not rostrate	<b>Globose</b> (rarely elongated or absent)	Mono or dimorphic scabrid-basally connate	Polychromous-sterome entire (divided)

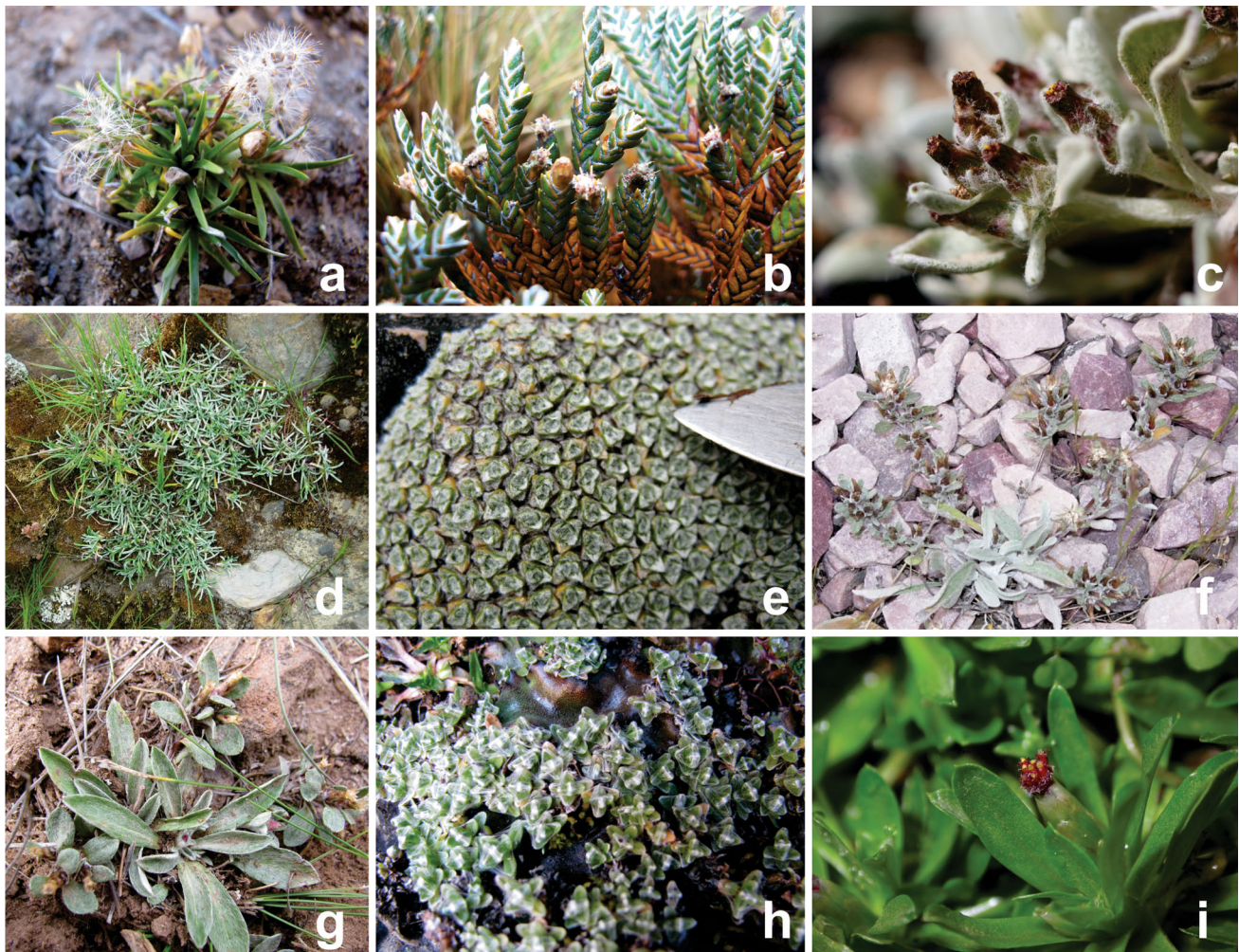
Table 3 continued

Genus	Habit	Monoeious/dioecious	Leaf disposition	Capitula pedunculate at maturity	Disc florets	Sweeping-hairs of style branches	Florets enclosed by receptacular paleae	Achenes	Achenial hairs	Pappus	Involucral bracts
<i>Micropsis</i>	Caespitose herbs	Monoeious	Alternate	-	Perfect	Dorsally	+	Not rostrate	Absent or elongated	Absent or composed of a short crown—basally connate	Monochromous-sterome entire
<i>Stackertiella</i>	Prostrate to ascending herbs	Subdioecious (capitula heterogamous)	Alternate	-	Functionally male	Apically	-	Not rostrate	Globose	Scarbrid—basally connate	Monochromous-sterome entire

(2003) that considered *Belloa* as a monotypic genus (*B. chilensis*). In fact, all the analyses show that the type species of *Belloa* (*B. chilensis*) of the Andes in the southern part of the continent is nested in the strongly supported clade C4 (Figs. 1, 2, 3), whereas the remaining sampled species of *Belloa* (excluding type) distributed in the Andes from Venezuela to north western Argentina were grouped with *Jalcophila*, *Loricaria*, *Mniodes* and *Luciliocline* in an also strongly supported clade C3 (Figs. 2, 3). The monotypic genus *Belloa* is here diagnosed by having prostrate stems, caespitose, closely leafy, solitary capitula surrounded by the terminal leaves, tubular corollas and clavate to elongate achenial trichomes (Figs. 5e, 6f, h, i).

Dillon (2003) transferred the remaining species of *Belloa* (except *B. kunthiana*) sensu Anderberg and Freire (1991) to *Luciliocline* and diagnosed this genus by its globose achenial trichomes (Fig. 6g). In this sense, *Belloa kunthiana* because of its elongated achenial trichomes was considered by this author as a member of the genus *Lucilia* [*Lucilia kunthiana* (DC.) Zardini]. However, in contrast to Dillon (2000, 2003), our results here showed *Belloa kunthiana* placed in the clade together with *Belloa* pro parte (excluding type) (Figs. 1, 2, 3), and morphologically *B. kunthiana* is more closely related to the other species of *Belloa* than to *Lucilia* because of its prostrate stems with rosulate leaves and leaf hairs with apical, flagellate cell slightly swollen at the base (vs. ascending or erect stems distantly leafy and leaf hairs with apical, flagellate cell bulbous at the base in *Lucilia*). This suggests that the resemblance of *Belloa kunthiana* to species of *Lucilia* regarding its elongated achenial trichomes is due to parallel evolution, which has led to non-monophyletic groups.

All the analyses showed the species of *Luciliocline* sensu Dillon (but including *Belloa kunthiana*) as a strong supported clade with *Mniodes* nested within it and *Loricaria* as its sister clade (Figs. 1, 2, 3). *Mniodes* and *Loricaria* (Fig. 4b–g) have little morphological similarity (i.e., leaves densely imbricate), but both were placed in the subtribe Loricariinae by Anderberg (1991) because of their dioecious habit. Instead, *Mniodes* is vegetatively similar to the highly reduced *Belloa* species (Fig. 4d, e), and strong support was recovered for the clade *Mniodes andina* + *Belloa kunthiana* in the analysis of the four molecular data sets (Fig. 2) and low support in the Bayesian combined analyses (Fig. 3). The phylogeny of the *Lucilia* group suggests at least three independent acquisitions of dioecy in *Jalcophila* clade, i.e., *Loricaria*, *Mniodes*, *Cutatrecasiella* and other three independent acquisitions of subdioecy (disc-florets functionally male) in the *Belloa* clade, i.e., *Chionolaena*, *Lucilia* (Freire 1989) and *Stackertiella* (Table 3). Since sex separation appears as an evolutionary convergence and may be the consequence of selective pressures particular to Andean environments, the



**Fig. 4** Morphological diversity in the *Lucilia* group s. lat.-clade C2 and C3: **a** *Jalcophila boliviensis* (photo S. Beck), **b** *Loricaria colombiana* (photo J.C. Ospina), **c** *Mniodes piptolepis* (photo F. O. Zuloaga), **d** *Mniodes kunthiana* (photo E. Urtubey), **e** *Mniodes*

*schultzei* (photo R.I. Meneses), **f** *Mniodes subspicata* (photo E. Urtubey), **g** *Mniodes santanica* (photo S. Beck), **h** *Cuatrecasasiella argentina* (photo S. Beck) and **i** *Chevreulia sarmentosa* (photo M. Bonifacino)

homogamous capitula cannot be a character diagnosing *Mniodes*.

Although in our combined Bayesian analysis the species of *Luciliocline* sensu Dillon appears as two subclades, i.e., the subclade *Belloa* pro parte with the genus *Mniodes* closely related to *Belloa kunthiana*, and the subclade *Luciliocline*, they are moderately and weakly supported, respectively (Fig. 3). In addition, as more specimens were examined, traditional morphological features that characterized each subclade including prostrate stems forming mats, being closely leafy, and solitary capitula (subclade *Belloa* pro parte + *Mniodes*), and ascending stems, distantly leafy with capitula arranged in glomerules (subclade *Luciliocline*) showed overlapping, i.e., ascending stems with capitula in glomerules are present in *Belloa piptolepis*.

*Mniodes* is the oldest generic epithet attached to this clade; consequently, here we delimit subclade *Belloa* pro

parte + *Mniodes* + subclade *Luciliocline* as *Mniodes* (A. Gray) Benth. (Figs. 3, 4c–g). Although there is no unequivocal synapomorphy for *Mniodes*, based on our own observations and literature, the species of this genus are relatively small plants ranging from pulvinate-caespitose with stems tightly compacted and densely leafy to subcaespitose with ascending stems densely leafy at the base, with capitula sessile, globose achenial trichomes only elongated in *B. kunthiana* and cytologically with a basic haploid number of  $n = 12$ .

#### *Placement of Jalcophila boliviensis*

*Jalcophila* includes four species; two of them (*J. boliviensis* and *J. ecuadoriensis*) were sampled in this study. The first one, *J. boliviensis* (Fig. 4a), was recognized as a member of *Jalcophila* (Anderberg 1991; Anderberg and

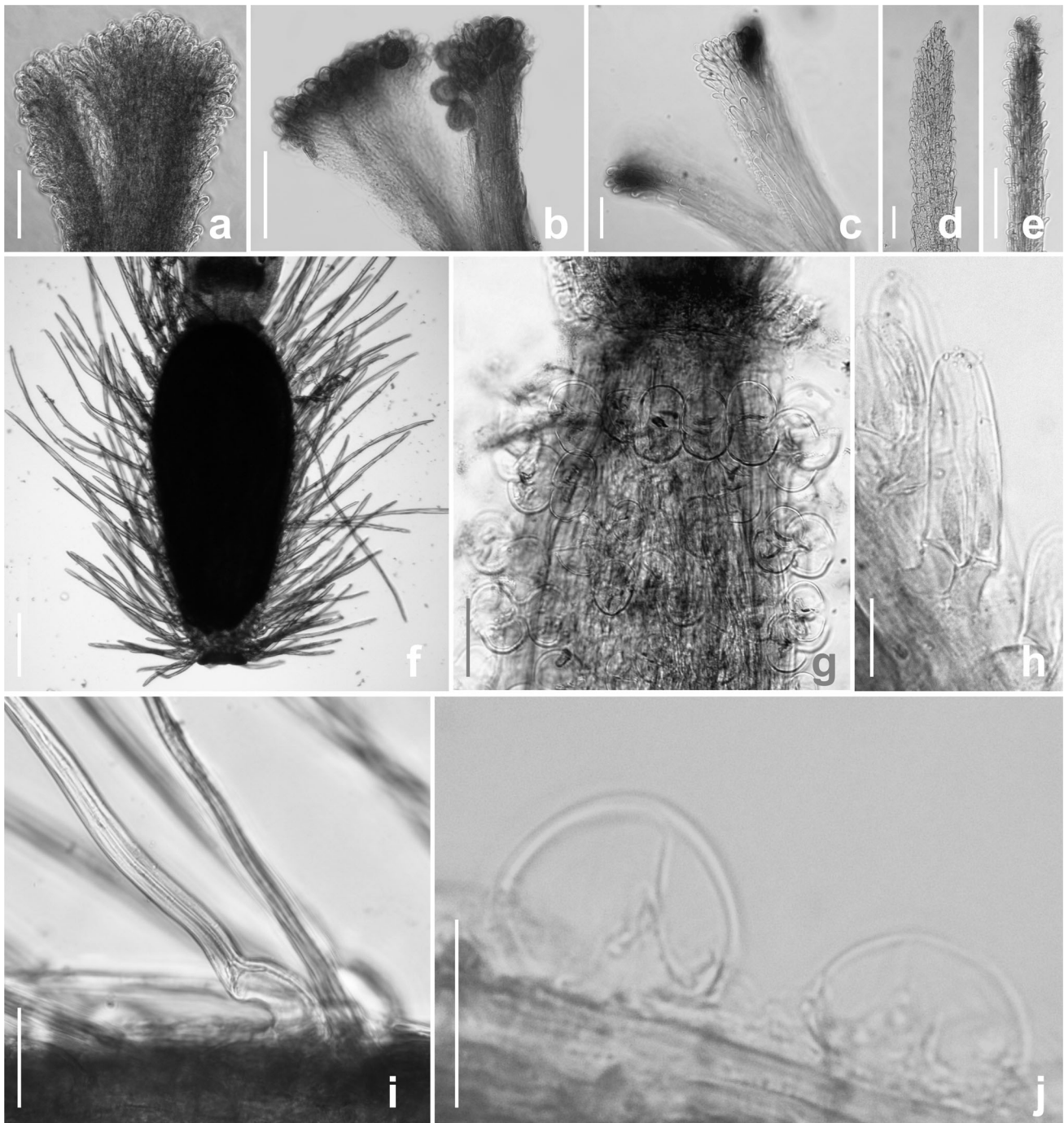


**Fig. 5** Morphological diversity in the *Lucilia* group s. lat.-clade C4: **a** *Berroa gnaphalioides* (photo M. Bonifacino), **b** *Lucilia acutifolia* (photo M. Bonifacino), **c** *Facelis retusa* (photo M. Bonifacino), **d** *Micropsis dasycarpa* (photo E. Urtubey), **e** *Belloa chilensis* (photo

M. Baeza), **f** *Chionolaena costaricensis* (photo M. Bonifacino), **g** *Gamochaetopsis alpina* (photo N. Bayón), **h** *Gamochaeta longipedicellata* (photo S. Beck) and **i** *Stuckertiella capitata* (photo S. Beck)

Freire 1991) but transferred to *Gamochaeta* by Dillon (2003). *Gamochaeta* and *Jalcophila boliviensis* are distantly related to each other in our results (Figs. 1, 2, 3). This treatment is congruent with the observations of the morphological features and previous treatments (Anderberg and Freire 1990b, 1991). Style branches of *Jalcophila boliviensis*

are dorsally papillose unlike those apically pilose in *Gamochaeta*. Involucral bracts of *Jalcophila boliviensis* are subequal, whereas in *Gamochaeta* the outermost bracts are shorter than the inner bracts. The capitula of *Jalcophila boliviensis* are pedunculate at maturity unlike those usually sessile in *Gamochaeta*. *Jalcophila boliviensis* shares these



**Fig. 6** Micrographs of some members of the *Lucilia* group s. lat.: **a–e** style branches of disc florets, **a** *Cuatrecasasiella argentina* (Urtubey et al. 474-SI), **b** *Gamochaeta neuquensis*, (Ezcurra 120-SI), **c** *Gamochaetopsis alpina* (Cabrera 5902-LP), **d** *Lucilia nitens*, (Urtubey 390-SI), **e** *Mniodes lopezmirandae* (Urtubey and Freire 433-SI); **f** achene with elongated hairs (*Belloa chilensis*, Ezcurra

2262-BCRU), **g** achene with globose hairs (*Mniodes lopezmirandae*, Urtubey and Freire 433-SI), **h** clavate achenial hairs (*Gamochaetopsis alpina*, Cabrera 5902-LP), **i** elongated achenial hairs (*Belloa chilensis*, Ezcurra 2262-BCRU) and **j** globose achenial hairs (*Gamochaeta grazielae*, Deble and Deble 4501-SI). Scale bars **a–d**, **g**, **i** 50  $\mu$ m, **e** 100  $\mu$ m, **f** 200  $\mu$ m, **h**, **j** 20  $\mu$ m

characters, i.e., dorsally papillose style branches, subequal involucre bracts and pedunculate capitula, with *J. ecuadoriensis*, and both species also have 4-lobed perfect florets. In addition, *Jalcophila boliviensis* and *J. ecuadoriensis* were

sister taxa in all the analyses, implying that the genus might be monophyletic. The type of *Jalcophila* was not included in our present analyses so the relationship between *J. boliviensis* and the generic type remains to be tested.



*Monophyly of Lucilia and its relationships with Berroa, Facelis and Micropsis*

*Lucilia*, *Berroa*, *Facelis* and *Micropsis* formed a well-supported clade within the clade C4 (Fig. 3). *Facelis* characterized by its plumose bristles pappus, scabrid above, and *Micropsis* characterized by its pappus absent or composed of a short crown, also formed a well-supported clade, and the first was monophyletic. The monotypic genus *Berroa*, diagnosed by its achenes with elongated 8–12 twisted apically hairs, was placed in a basal polytomy inside clade C4. Conversely, all the analyses showed the species of *Lucilia* sensu Anderberg and Freire, traditionally diagnosed by their elongated achenial trichomes, scabrid pappus and leaf hairs with apical, flagellate cell bulbous at the base, as non-monophyletic. In fact, although four of its eight species sampled in this study have been recognized as distinct and belonging to *Lucilia* in previous treatments (Freire 1986b; Anderberg 1991, Anderberg and Freire 1991; Dillon 2000, 2003), our data show *Lucilia linearifolia* in a basal polytomy and the remaining three species of *Lucilia* (*L. lycopodioides*, *L. nitens*, *L. acutifolia*) in a well-supported clade sister of *Facelis* + *Micropsis*. *Lucilia linearifolia* occurs in southern Brazil and northwestern Argentina and presents discolorous leaves. The remaining sampled species exhibit similar distribution (except *L. nitens* that is found in southern Brazil, Uruguay and north-eastern Argentina) and present concolorous leaves. Future studies employing more variable DNA regions, with more extensive sampling, will be valuable before a recircumscription of *Lucilia* can be proposed.

*Monophyly of Gamochaeta and its relationships with Stuckertiella and Gamochaetopsis*

Our results suggest that *Gamochaeta*, as currently defined, is not monophyletic. All the analyses showed the clade *Gamochaeta* + *Stuckertiella* + *Gamochaetopsis* as highly supported, as well as the clade *Gamochaeta serpyllifolia* + *Gamochaetopsis* (Figs. 1, 2, 3). *Stuckertiella* is a genus of two species confined to South America (Peru, Bolivia, Argentina), and it was characterized by having 4-merous florets. *Gamochaetopsis* is a monotypic genus restricted to austral Chile and adjacent Argentina, differentiated by its achenes with short clavate hairs. *Gamochaeta* includes c. 60 species (three were sampled in this study) in the New World with some species adventives in the Old World (Nesom 1990a). The close relationship between *Gamochaeta* and *Stuckertiella* had been previously inferred in a morphological phylogenetic analysis (Dillon 2000) and diagnosed by truncate apically pilose style branches and achenes with globose myxogenic twin hairs. *Gamochaetopsis* was recognized as an isolated

distinct genus (Anderberg and Freire 1991; Dillon 2000, 2003). The phylogeny of *Gamochaeta* is one of our ongoing projects, so before synonymizing *Gamochaetopsis* and *Stuckertiella* with *Gamochaeta*, we await the outcome of that work.

Taxonomic treatment of the *Lucilia* group s. lat.

Morphological characters for each genus are shown in Table 3. This treatment does not include the genera *Gamochaeta*, *Gamochaetopsis* and *Stuckertiella* which will be treated in a forthcoming paper.

**Belloa** J. Rémy in Gay, Fl. Chil. 3(3): 336. 1847. Type: *B. chilensis* (Hook. and Arn.) J. Rémy

=*Lucilia* Cass. sect. *Lucilioides* DC., Prodr. 7: 46. 1838.

One species, S. America (southern Andes): *Belloa chilensis* (Hook. and Arn.) J. Rémy, in Gay, Fl. Chil. 3(3): 336, t. 38. 1847 [= *Lucilia chilensis* Hook. and Arn., *Chevreulia nivea* Phil., *Gnaphalium andicola* Kuntze, *Lucilia araucana* Phil., *L. chilensis* Poepp. and Endl., *L. frigida* Reiche, *L. nivea* (Phil.) Cabrera]

**Berroa** Beauverd, Bull. Soc. Bot. Genève 5: 210. 1913. Type: *B. gnaphalioides* (Less.) Beauverd

One species, S. America (S Brazil, Uruguay, C and NE Argentina): *Berroa gnaphalioides* (Less.) Beauverd, Bull. Soc. Bot. Genève 5: 211. 1913 (= *Lucilia argentea* Hook. and Arn., *L. gnaphalioides* Less.)

**Chevreulia** Cassini, Bull. Soc. Philom. Paris, 1817: 69. 1817. Type: *C. sarmentosa* (Pers.) S.F. Blake

Six species, S. America (S Brazil, Bolivia, Paraguay, Uruguay, Chile, N and C Argentina, Falkland Islands): *Chevreulia acuminata* Less., Linnaea 5: 261. 1830 (= *C. elegans* Rusby; *C. diemi* Cabrera, Notas Mus. La Plata, Bot. 7: 114. 1942; *C. filiformis* Hook. and Arn., *C. longipes* Wedd.); *C. lycopodioides* (d'Urv.) DC., Prodr. 7: 45. 1838 (= *Gnaphalium lycopodioides* d'Urv.); *C. pusilla* DC., Prodr. 7: 45. 1838 (= *C. lanceolata* J. Rémy); *C. revoluta* A. A. Schneid. and R. Trevis., Syst. Bot. 36 (3): 782. 2011; *C. sarmentosa* (Pers.) S.F. Blake, Proc. Biol. Soc. Washington 38: 85. 1925 [= *Tussilago sarmentosa* Pers., *Chevreulia stolonifera* Cass., nom. illeg., *Chevreulia thouarsii* J. Rémy, nom. illeg., *Gnaphalium calycinum* Poir., *Xeranthemum caespitosum* (caespitosum) Thouars].

**Chionolaena** DC., Prodr. 5: 397. 1836. Type: *C. arbuscula* DC.

= *Leucopholis* Gardner, London J. Bot. 2: 10. 1843. Type: *L. phylicoides* Gardner

= *Parachionolaena* M.O. Dillon and Sagást. Arnela 1(2): 42. 1992. Type: *P. columbiana* (S.F. Blake) Dillon and Sagást.

= *Pseudoligandra* M.O. Dillon, Taxon 39(1): 127. 1990. Type: *P. chrysocoma* (Wedd.) Dillon and Sagást.

Twenty-seven species, C. and S. America (C Mexico, Costa Rica, Guatemala, N Colombia, S Brazil):

- Chionolaena adpressifolia* Loeuille, Kew Bull. 66: 263. 2011; *C. aecidiocephala* (Grierson) Anderb. and S.E. Freire, Notes Roy. Bot. Gard. Edinburgh 46: 40. 1989 [= *Anaphalis aecidiocephala* Grierson, *Gnaphalium aecidiocephalum* (Grierson) L.O. Williams]; *C. arbuscula* DC., Prodr. 5: 397. 1836; *C. campestris* Deble, Kew Bull. 66: 264. 2011; *C. canastrensis* J.N. Nakaj., Kew Bull. 66: 266. 2011; *C. capitata* (Baker) S.E. Freire [= *Achyrocline capitata* Baker, *Leucopholis capitata* (Baker) Cufod.]; *C. chrysocoma* (Wedd.) S.E. Freire, Ann. Missouri Bot. Gard. 80: 415. 1993 [= *Oligandra chrysocoma* Wedd., *Pseudoligandra chrysocoma* (Wedd.) M.O. Dillon and Sagást.]; *C. columbiana* S.F. Blake, J. Wash. Acad. Sci. 25: 312. 1935 [= *Parachionolaena columbiana* (S.F. Blake) M.O. Dillon and Sagást.]; *C. concinna* (A.Gray) Anderb. and S.E. Freire, Notes Roy. Bot. Gard. Edinburgh 46: 40. 1989 [= *Gnaphalium concinnum* A. Gray, *Anaphalis concinna* (A.Gray) Grierson]; *C. costaricensis* (G.L. Nesom) G.L. Nesom, Sida 19: 850. 2001 [= *Gnaphaliothamnus costaricensis* G.L. Nesom]; *C. cryptocephala* (G.L. Nesom) G.L. Nesom (= *Gnaphaliothamnus cryptocephalus* G.L. Nesom); *C. durangensis* (G.L. Nesom) G.L. Nesom, Sida 19: 850 (2001); *C. eleagnoides* Klatt, Leopoldina 23: 88. 1887 (= *Gnaphalium eleagnoides* (Klatt) S.F. Blake); *C. isabellae* Baker, in Martius, Fl. Bras. 6(3): 130. 1882 (= *C. glaziovii* Baker, *C. innovans* Wawra); *C. jeffreyi* H. Rob., Phytologia 55: 121. 1984; *C. juniperina* Loeuille, Kew Bull. 66(2): 268. 2011; *C. latifolia* (Benth.) Baker, in Martius, Fl. Bras. 6(3): 132. 1882 [= *Leucopholis latifolia* Benth., *Chionolaena breweri* Steyerm. and Maguirre, *C. glomerata* Baker, *Lucilia breweri* (Steyerm. and Maguire) V.M. Badillo]; *C. lavandulifolia* (Kunth) Benth. and Hook.f. ex B.D. Jacks., Index Kew. 1: 516. 1893 [= *Elichrysum lavandulifolium* Kunth, *Chionolaena lavandulaceum* (DC.) Hemsley, *Elichrysum lavandulifolium* (Wild.) D. Don, *Gnaphalium lavandulaceum* DC., *G. lavandulifolium* Willd., *G. lavandulifolium* (Kunth) S.F. Blake]; *C. lychnophorioides* Sch. Bip., Jahresber. Pollichia 20-21: 391. 1863; *C. macdonaldii* (G.L. Nesom) G.L. Nesom, Sida 19(4): 850. 2001 (= *Gnaphaliothamnus macdonaldii* G.L. Nesom); *C. mexicana* S.E. Freire, Ann. Missouri Bot. Gard. 80: 427. 1993; *C. phylicoides* (Gardner) Baker, in Martius, Fl. Bras. 6(3): 131. 1882 (= *Leucopholis phylicoides* Gardner); *C. salicifolia* (Bertol.) G.L. Nesom, Sida 19(4): 850. 2001 (= *Helichrysum salicifolium* Bertol., *Gnaphaliothamnus salicifolius* (Bertol.) G.L. Nesom); *C. sartorii* Klatt, Leopoldina Heft 23: 89. 1887 [= *Gnaphalium sartorii* (Klatt) F.J. Espinosa-García]; *C. seemannii* (Sch.Bip.) S.E. Freire, Ann. Missouri Bot. Gard. 80: 432. 1993 (= *Gnaphalium seemannii* Sch.Bip.); *C. stolonata* (S.F. Blake) Pruski, Phytoneuron 2012-1: 4 (= *Gnaphalium stolonatum* S.F. Blake); *C. wittigiana* Baker, in Martius, Fl. Bras. 6(3): 129. 1882.
- Cuatrecasasiella* H. Rob., Fl. Neotrop. Monogr. 2(Suppl.): 14. 1985. Type: *C. isernii* (Cuatrec.) H. Rob.
- Two species, S. America (Andes from Ecuador to N Argentina): *Cuatrecasasiella argentina* (Cabrera) H. Rob., Fl. Neotrop. Monogr. 2(Suppl.): 15. 1985 (= *Luciliopsis argentina* Cabrera); *C. isernii* (Cuatrec.) H. Rob., Fl. Neotrop. Monogr. 2(Suppl.): 15. 1985 (= *Luciliopsis isernii* Cuatrec.).
- Facelis* Cass., Bull. Sci. Soc. Philom. Paris (1819): 94. 1819. Type: *Facelis retusa* (Lam.) Sch. Bip.
- Three species, S. America (S Brazil, Peru, Bolivia, Paraguay, Chile, Uruguay, Argentina): *Facelis lasiocarpa* (Griseb.) Cabrera, Physis (Buenos Aires) 10: 280. 1931 (= *Filago lasiocarpa* Griseb., *Facelis capillaris* Rusby, *F. schultzi* Beauverd, *Lucilia erecta* Benoist); *F. plumosa* (Wedd.) Sch. Bip., Linnaea 34: 532. 1866 (= *Lucilia plumosa* Wedd., *Facelis weddelliana* Beauverd, nom. nov. pro *Lucilia plumosa* Wedd.); *F. retusa* (Lam.) Sch. Bip., Linnaea 34(5): 532. 1865 [= *Gnaphalium retusum* Lam., *Facelis apiculata* Cass., nom. illeg. pro *Gnaphalium retusum* Lam., *F. retusa* (Lam.) Sch. Bip. var. *andicola* (Nees) Beauverd, *F. retusa* (Lam.) Sch. Bip. var. *candelabrum* Beauverd, *F. retusa* (Lam.) Sch. Bip. var. *patula* Beauverd, *F. retusa* (Lam.) Sch. Bip. fo. *congesta* Beauverd, *F. retusa* (Lam.) Sch. Bip. fo. *gigantea* Beauverd, *F. retusa* (Lam.) Sch. Bip. fo. *laxa* Beauverd, *F. retusa* (Lam.) Sch. Bip. fo. *nana* Beauverd, *F. retusa* (Lam.) Sch. Bip. fo. *planifolia* Beauverd, *Helichrysum retusum* Spreng., *Leptalea apiculata* (Cass.) D. Don ex Hook. and Arn., *Pteropogon chilense* Fisch. and Meyer, nom. nud., *P. andicola* Nees].
- Jalcophila* M.O. Dillon and Sagást., Brittonia 38(2): 162. 1986. Type species: *J. peruviana* M.O. Dillon and Sagást.
- Four species, S. America (Andes of Colombia, Ecuador, Peru, and Bolivia): *Jalcophila boliviensis* Anderb. and S.E. Freire, Brittonia 42: 139. 1990 (= *Gamochoa boliviensis* (Anderb. and S.E. Freire) M.O. Dillon and Sagást.); *J. colombiana* S. Díaz and Veléz-Nauer, Revista Acad. Colomb. Ci. Exact. 19(72): 25. 1994; *J. ecuadoriensis* M.O. Dillon and Sagást., Brittonia 38(2): 165. 1986; *J. peruviana* M.O. Dillon and Sagást., Brittonia 38(2): 163. 1986.
- Loricaria* Wedd., Chlor. And. 1: 165, t. 27 A, B, C. 1856. Lectotype (designated by Cuatrecasas, 1954: 152): *L. thuyoides* (Lam.) Sch. Bip.
- = *Tafalla* D. Don, Edinb. N. Phil. Journ.: 273. 1831, non Ruiz and Pav. 1794. Type: no stated.
- Twenty two species, S. America (Andes from Colombia to Bolivia): *Loricaria anceps* Sch.Bip., Bonplandia 8: 259. 1860; *L. antisanensis* Cuatrec., Feddes Repert. Spec. Nov. Regni Veg. 56: 157. 1954; *L. azuayensis* Cuatrec., Feddes Repert. Spec. Nov. Regni Veg. 56: 158. 1954; *L. cinerea* D.J.N. Hind, Kew Bull. 59(4): 541. 2005; *L. colombiana* Cuatrec., Trab. Mus. Nac. Ci. Nat., Ser. Bot. 29: 33,

Fig. 12. 1935; *L. complanata* (Sch. Bip.) Wedd., Chlor. And. 1: 167. 1856 (= *Baccharis complanata* Sch. Bip.); *L. ferruginea* (Ruiz and Pav.) Wedd., Chlor. And. 1: 166. 1856 (= *Molina ferruginea* Ruiz and Pav.); *L. graveolens* (Sch. Bip.) Wedd., Chlor. And. 1: 167. 1856 (= *Baccharis graveolens* Sch. Bip.); *L. ilinissae* (Benth.) Cuatrec., Feddes Repert. Spec. Nov. Regni Veg. 56: 162. 1954 (= *Baccharis illissae* Benth.); *L. lagunillensis* Cuatrec., Feddes Repert. Spec. Nov. Regni Veg. 56: 162. 1954; *L. leptothamna* (Mattf.) Cuatrec., Feddes Repert. Spec. Nov. Regni Veg. 56: 163. 1954 (= *Tafalla leptothamna* Mattf.); *L. lucida* Cuatrec., Feddes Repert. Spec. Nov. Regni Veg. 56: 163. 1954; *L. lycopodinea* Cuatrec., Feddes Repert. Spec. Nov. Regni Veg. 56: 164. 1954; *L. macbridei* Cuatrec., Feddes Repert. Spec. Nov. Regni Veg. 56: 164. 1954; *L. ollgaardii* M.O. Dillon and Sagást., Phytologia 59: 228. 1986; *L. pauciflora* Cuatrec., Feddes Repert. Spec. Nov. Regni Veg. 56: 165. 1954; *L. puracensis* Cuatrec., Feddes Repert. Spec. Nov. Regni Veg. 56: 166. 1954; *L. reticulosa* Kuntze, Revis. Gen. Pl. 1: 352. 1891; *L. scolopendra* Kuntze, Revis. Gen. Pl. 1: 352. 1891; *L. thuyoides* (Lam.) Sch. Bip., Bonplandia 8: 260. 1860 [= *Conyza thujoides* Lam., *Baccharis thujoides* (Lam.) Pers., *Loricaria (Tafalla) microphylla* Hieron., *L. stenophylla* Wedd., *L. stuebelii* Hieron., *L. thuyoides* (Lam.) Sch. Bip., *L. thujoides* (Lam.) Kuntze, *Molina incana* Ruiz and Pav., *Tafalla thuyoides* (Lam.) D. Don; synonyms according to Hind 2011]; *L. thyrsoidea* (Cuatrec.) M.O. Dillon and Sagást., Phytologia 59: 230. 1986; *L. unduaviensis* Cuatrec., Feddes Repert. Spec. Nov. Regni Veg. 56: 170. 1954. (revision needed).

**Lucilia** Cass., Bull. Sci. Soc. Philom. Paris: 32. 1817. Type: *Serratula acutifolia* Poir. = *L. acutifolia* (Poir.) Cass.

= *Oligandra* Less., Syn. Gen. Comp.: 123. 1832. Type: *O. lycopodioides* Less.

= *Pachyrhynchus* DC., Prodr. 6: 255. 1838. Type: *Pachyrhynchus xeranthemoides* DC.

= *Hymenopholis* Gardner, London J. Bot. 7: 88. 1848. Type: *Hymenopholis imbricata* Gardner

Eight species, S. America (S Brazil, Paraguay, Uruguay, N and C Argentina, Andes of Bolivia, Argentina and Chile): *Lucilia acutifolia* (Poir.) Cass., Dict. Scienc. Nat., ed. 2. 27: 264. 1823 (= *Serratula acutifolia* Cass., *L. jamesonii* Baker, *L. lundii* Baker, *L. microphylla* Cass., *Pachyrhynchus xeranthemoides* DC.); *L. eriophora* J. Rémy, in Gay, Fl. Chil. 3: 335. 1848; *L. ferruginea* Baker in Martius, Fl. Bras. 6 (3): 114. 1882; *L. linearifolia* Baker, in Martius, Fl. Bras. 6 (3): 114. 1882; *L. lycopodioides* (Less.) S.E. Freire, Taxon 38: 298. 1989 (= *Oligandra lycopodioides* Less., *Hymenopholis imbricata* Gardner, *L. flagelliformis* Wedd., *L. glomerata* Baker); *L. nitens* Less., Linnaea 5: 363. 1830; *L. recurva* Wedd.; Chlor. And. 1:

156. 1856; *L. tomentosa* Wedd., Chlor. And. 1: 157. 1856 (= *L. squarrosa* Baker).

Doubtful species: *Lucilia saxatilis* V.M. Badillo, Ernstia 50: 9, 1988. According to the original diagnosis which is accompanied by an illustration, is likely referable to genus *Gamochaeta* by its small capitula arranged in glomerules, forming short spikes (vs. capitula arranged in leafy racemes in *Lucilia*), but no details of style branches are found nor description neither illustration. Consequently, until the type of Badillo's name is located or materials can be provided, the identity of *L. saxatilis* is uncertain.

**Micropsis** DC., Prodr. 5: 459. 1836. Type: *M. nana* DC.

Five species, S. America (S Brazil, Paraguay, Uruguay, NE Argentina, and C Chile): *Micropsis australis* Cabrera, Notas Mus. La Plata 3, Bot. 20: 147. 1938; *M. dasycarpa* (Griseb.) Beauverd, Bull. Soc. Bot. Genève, sér. 2, 5: 224. 1913 (= *Filago dasycarpa* Griseb.); *M. nana* DC., Prodr. 5: 460. 1836; *M. ostenii* Beauverd, Bull. Soc. Bot. Genève, sér. 2, 5: 226. 1913 (= *M. bonariensis* Manganaro); *M. spathulata* (Pers.) Cabrera, Notas Mus. La Plata 9, Bot. 46: 254. 1944 (= *Gnaphalium involucratum* Lam., nom. illeg. hom., non Foster, *G. bracteatum* Willd., nom. illeg. hom., non Lamarck, *Evax spathulata* Pers., *Micropsis involucrata* Cabrera).

**Mniodes** (A. Gray) Benth., Gen. Pl. 2(1): 301. 1873. *Antennaria* Gaertn. sect. *Mniodes* A. Gray, Proc. Acad. Arts. 5: 138. 1861. Lectotype (designated by Cuatrecasas, 1954: 3): *M. andina* (A. Gray) Cuatrec.

= *Merope* Wedd., Chlor. And. 1: 160. 1856, pro parte, nom. illeg. [excl. *M. erythraetis* Wedd. = *Gamochaeta erythraetis* (Wedd.) Cabrera], non *Merope* M.J. Roemer 1846 (Rutaceae). Lectotype (designated by Anderberg and Freire, 1991: 189): *M. piptolepis* Wedd.

= *Belloa* pro parte, non J. Rémy, syn. nov.

= *Luciliocline* Anderb. and S.E. Freire, Bot. J. Linn. Soc. 106: 187. 1991. Type: *L. lopezmirandae* (Cabrera) Anderb. and Freire, **syn. nov.**

Seventeen species, S. America (Andes from Venezuela to NW Argentina): *Mniodes andina* (A. Gray) A. Gray ex Cuatrec., Fol. Biol. Andina 1: 3. 1954 (= *Antennaria andina* A. Gray); *M. aretioides* (Sch. Bip.) Cuatrec., Fol. Biol. Andina 1: 3. 1954 [= *Baccharis aretioides* Sch. Bip., *Antennaria aretioides* (Sch. Bip.) A. Gray, *Merope aretioides* (Sch. Bip.) Wedd.]; *M. coarctata* Cuatrec., Fol. Biol. Andina 1: 4. 1954; **Mniodes burkartii** (Cabrera) S.E. Freire, Chemisquy, Anderb. and Urtubey, **comb. nov.** Basionym: *Gnaphalium burkartii* Cabrera, Notas Mus. La Plata, Bot. 13, Bot. no. 56: 10, Fig. 2. 1948 [= *Belloa burkartii* (Cabrera) Cabrera, *Lucilia burkartii* (Cabrera) S.E. Freire, *Luciliocline burkartii* (Cabrera) Anderb. and S.E. Freire]; **Mniodes catamarcensis** (Cabrera) S.E. Freire, Chemisquy, Anderb. and Urtubey, **comb. nov.** Basionym: *Belloa*

*catamarcensis* Cabrera, Bol. Soc. Argent. Bot. 7: 81, Fig. 1. 1958 [=*Lucilia catamarcensis* (Cabrera) S.E. Freire, *Luciliocline catamarcensis* (Cabrera) Anderb. and S.E. Freire]; *Mniodes kunthiana* (DC.) S.E. Freire, Chemisquy, Anderb. and Urtubey, **comb. nov.** Basionym: *Conyza kunthiana* DC., Prodr. 5: 379. 1836, nov. nom. [=*Conyza pusilla* Kunth 1820 non *C. pusilla* Houtt. 1782, *Belloa kunthiana* (DC.) Anderb. and S.E. Freire, *Lucilia conoidea* Wedd., *L. kunthiana* (DC.) Zardini, *Lucilia pusilla* Hieron. 1900 nov. nom., *L. venezualensis* Steyerl., *L. violacea* Wedd., *Merope kunthiana* (DC.) Wedd.]; *Mniodes lehmannii* (Hieron.) S.E. Freire, Chemisquy, Anderb. and Urtubey, **comb. nov.** Basionym: *Lucilia lehmannii* Hieron, Bot. Jahrb. 19(5): 51. 1894 [=*Belloa lehmannii* (Hieron.) Anderb. and S.E. Freire]; *Mniodes longifolia* (Cuatrec. and Aristeg.) S.E. Freire, Chemisquy, Anderb. and Urtubey, **comb. nov.** Basionym: *Lucilia longifolia* Cuatrec. and Aristeg., Fl. Venez. 10(1): 367. 1964 [=*Belloa longifolia* (Cuatrec. and Aristeg.) M.O. Dillon and Sagást., *Luciliocline longifolia* (Cuatrec. and Aristeg.) M.O. Dillon and Sagást.]; *Mniodes lopezmirandae* (Cabrera) S.E. Freire, Chemisquy, Anderb. and Urtubey, **comb. nov.** Basionym: *Belloa lopezmirandae* Cabrera, Bol. Soc. Argent. Bot. 7: 83, Fig. 2. 1958 [=*Lucilia lopezmirandae* (Cabrera) S.E. Freire, *Luciliocline lopezmirandae* (Cabrera) Anderb. and S.E. Freire, *Belloa turneri* Sagást. and M.O. Dillon, *Luciliocline turneri* (Sagást. and M.O. Dillon) M.O. Dillon and Sagást.]; *Mniodes pickeringii* (A.Gray) S.E. Freire, Chemisquy, Anderb. and Urtubey, **comb. nov.** Basionym: *Lucilia pickeringii* A. Gray, Proc. Amer. Acad. Arts 5: 138. 1862 [=*Belloa pickeringii* (A.Gray) Sagást. and M.O. Dillon, *Luciliocline pickeringii* (A.Gray) M.O. Dillon and Sagást.]; *Mniodes piptolepis* (Wedd.) S.E. Freire, Chemisquy, Anderb. and Urtubey, **comb. nov.** Basionym: *Lucilia piptolepis* Wedd., Chlor. And. 1: t. 26, f. B. 1856 [=*Belloa piptolepis* (Wedd.) Cabrera, *Gnaphalium piptolepis* (Wedd.) Griseb., *Luciliocline piptolepis* (Wedd.) M.O. Dillon and Sagást.]; *Mniodes plicatifolia* (Sagást. and M.O. Dillon) S.E. Freire, Chemisquy, Anderb. and Urtubey, **comb. nov.** Basionym: *Belloa plicatifolia* Sagást. and M.O. Dillon, Phytlogia 58: 384, f.3F-K. 1985 [=*Lucilia plicatifolia* (Sagást. and M.O. Dillon) S.E. Freire, *Luciliocline plicatifolia* (Sagást. and M.O. Dillon) M.O. Dillon and Sagást.]; *M. pulvinulata* Cuatrec., Fol. Biol. Andina 1: 5. 1954 (= *M. ferreyrae* Cuatrec.); *Mniodes radians* (Benth.) S.E. Freire, Chemisquy, Anderb. and Urtubey, **comb. nov.** Basionym: *Gnaphalium radians* Benth., Pl. Hartw.: 207, tab. 35b. 1845 [=*Belloa radians* (Benth.) Sagást. and M.O. Dillon, *Lucilia radians* (Benth.) Cuatrec., *Luciliocline radians* (Benth.) M.O. Dillon and Sagást.]; *Mniodes santanica* (Cabrera) S.E. Freire, Chemisquy, Anderb. and Urtubey, **comb. nov.** Basionym: *Gnaphalium santanicum* Cabrera, Notas Mus. La Plata, Bot. 13, Bot. no.

56: 12, Fig. 3. 1948 [=*Belloa santanica* (Cabrera) Cabrera, *Lucilia santanica* (Cabrera) S.E. Freire, *Luciliocline santanica* (Cabrera) Anderb. and S.E. Freire, *Belloa spathulifolia* Sagást. and M.O. Dillon, *Luciliocline spathulifolia* (Sagást. and M.O. Dillon) M.O. Dillon and Sagást.]; *Mniodes schultzii* (Wedd.) S.E. Freire, Chemisquy, Anderb. and Urtubey, **comb. nov.** Basionym: *Merope schultzii* Wedd., Chlor. And. 1: 163. 1856 [=*Belloa cerrateae* (Ferreyra) M.O. Dillon and Sagást., *B. schultzii* (Wedd.) Cabrera, *Lucilia schultzii* (Wedd.) A.Gray, *Luciliocline schultzii* (Wedd.) M.O. Dillon and Sagást., *Mniodes cerrateae* Ferreyra]; *Mniodes subspicata* (Cabrera) S.E. Freire, Chemisquy, Anderb. and Urtubey, **comb. nov.** Basionym: *Belloa subspicata* Wedd., Chlor. And. 1: 159. 1856 [=*Lucilia subspicata* (Wedd.) Hieron., *Luciliocline subspicata* (Wedd.) Anderb.].

Note: *Mniodes tunariensis* (Kuntze) Hieron. ex Webber. = *Novenia acaulis* (Benth. and Hook. f. ex B.D. Jacks.) S.E. Freire and F.H. Hellw.

### Concluding remarks

Our study, using plastid (*rpl32-trnL*, *trnL-F*) and nuclear (ITS and ETS) DNA loci, together with morphological characters, and using a broad sampling of the tribe, suggested that the South American *Lucilia* group sensu Anderberg and Freire (1991) is paraphyletic and that the genera *Antennaria*, *Chionolaena*, *Gamochaeta*, *Loricaria*, *Micropsis*, *Mniodes*, and *Stuckertiella* should be included for the establishment of the monophyly in the group. This mainly American *Lucilia* group s. lat. is diagnosed by having slender pappus bristles that are basally connate or coherent at the base by patent cilia. The phylogeny found here corroborates previous generic circumscription (Anderberg, 1991) of most of its genera, i.e., *Berroa*, *Chevreulia*, *Cuatrecasasiella*, *Facelis*, and *Micropsis*. *Belloa* is recovered as a monotypic genus in correspondence with Dillon's study (2003). *Luciliocline* and the remaining species of *Belloa* sensu Anderberg and Freire (1991) are placed in the genus *Mniodes*. Thirteen new combinations are proposed: *Mniodes burkartii* (Cabrera) S.E. Freire, Chemisquy, Anderb. and Urtubey; *Mniodes catamarcensis* (Cabrera) S.E. Freire, Chemisquy, Anderb. and Urtubey; *Mniodes kunthiana* (DC.) S.E. Freire, Chemisquy, Anderb. and Urtubey; *Mniodes lopezmirandae* (Cabrera) S.E. Freire, Chemisquy, Anderb. and Urtubey; *Mniodes lehmannii* (Hieron.) S.E. Freire, Chemisquy, Anderb. and Urtubey; *Mniodes longifolia* (Cuatrec. and Aristeg.) S.E. Freire, Chemisquy, Anderb. and Urtubey; *Mniodes pickeringii* (A.Gray) S.E. Freire, Chemisquy, Anderb. and Urtubey; *Mniodes piptolepis* (Wedd.) S.E. Freire, Chemisquy, Anderb. and Urtubey; *Mniodes plicatifolia* (Sagást. and

M.O. Dillon) S.E. Freire, Chemisquy, Anderb. and Urtubey; *Mniodes radians* (Benth.) S.E. Freire, Chemisquy, Anderb. and Urtubey; *Mniodes santanica* (Cabrera) S.E. Freire, Chemisquy, Anderb. and Urtubey; *Mniodes schultzii* (Wedd.) S.E. Freire, Chemisquy, Anderb. and Urtubey, and *Mniodes subspicata* (Wedd.) S.E. Freire, Chemisquy, Anderb. and Urtubey. *Lucilia* sensu Anderberg and Freire (1991) is non-monophyletic; future studies employing more variable DNA regions with extensive sampling will be valuable before a recircumscription of *Lucilia* can be proposed. The monotypic genera *Stuckertiella* and *Gamochoetopsis* are closely nested within the large genus *Gamochoeta*; however, greater taxonomic sampling is required before to make taxonomic changes for these genera.

**Acknowledgments** We give special thanks to reviewers for critical reading of the manuscript. The authors are grateful to Cecilia Ezcurra (BCRU), Néstor Bayón (LPAG), Andreas Tribisch (SZU), and Juan C. Ospina (SI) for providing us materials of *Belloa chilensis*, *Gamochoetopsis alpina*, *Gnaphalium uliginosum*, and *Loricaria colombiana*, respectively. We also appreciate the help of the curator of the herbaria BCRU, BHCb, CONC, LP, LPAG, LPB, SZU, MO, SI, SPF for permitting access to their collections. Thanks are due to Jorge A. Hurst for some DNA extractions. Also thanks to Fernando O. Zuloaga, Mauricio Bonifacino, Marcelo Baeza, Juan C. Ospina, and Néstor Bayón, for permission to use their photographs included in Figs. 4 and 5. The research and fieldwork to NW Argentina and Northern Bolivia were supported by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina (PIP 112-200801-02196).

## References

- Anderberg AA (1991) Taxonomy and phylogeny of the tribe Gnaphalieae (Asteraceae). *Opera Bot* 104:1–195
- Anderberg AA, Freire SE (1990a) *Luciliopsis perpusilla* Wedd. is a species of *Chaetanthera* Ruiz and Pavon (Asteraceae). *Taxon* 39:430–432
- Anderberg AA, Freire SE (1990b) *Jalcochila boliviensis*, a new species of South American Asteraceae (Gnaphalieae). *Brittonia* 42:138–141
- Anderberg AA, Freire SE (1991) A cladistic and biogeographic analysis of the *Lucilia* group (Asteraceae, Gnaphalieae). *Bot J Linn Soc* 106:173–198
- Baldwin BG, Markos S (1998) Phylogenetic utility of the external transcribed spacer (ETS) of 18S–26S rDNA: congruence of ETS and ITS trees of *Calycadenia* (Compositae). *Molec Phylogen Evol* 10:449–463
- Bayer RJ, Puttock CF, Kelchner SA (2000) Phylogeny of South African Gnaphalieae (Asteraceae) based on two noncoding chloroplast sequences. *Amer J Bot* 87:259–272
- Bayer RJ, Greber DG, Bagnall NH (2002) Phylogeny of Australian Gnaphalieae (Asteraceae) based on four sequences, four sequences, the *trnL* intron, *trnL/trnF* intergenic spacer, *matK*, and ETS. *Syst Bot* 27:801–814
- Beauverd G (1913a) Contribution à l'étude des Composées 8(2). Le genre *Berroa* extrait des *Lucilia*. *Bull Soc Bot Genève* 2(5):210–212
- Beauverd G (1913b) Contribution à l'étude des Composées 8(3). Le genre *Facelis* Cassini (emend. Beauverd). *Bull Soc Bot Genève* 2(5):212–220
- Beauverd G (1913c) Contribution à l'étude des Composées 8(4). Le genre *Micropsis* DC. (emend. Beauverd). *Bull Soc Bot Genève* 2(5):221–228
- Beauverd G (1913d) Contribution à l'étude des Composées 8(1). Le genre *Stuckertiella* Beauverd. *Bull Soc Bot Genève* 2(5):205–209
- Bergh NG, Linder HP (2009) Cape diversification and repeated out-of-southern-Africa dispersal in paper daisies (Asteraceae-Gnaphalieae). *Molec Phylogen Evol* 51:5–18
- Cabrera AL (1958) El género *Belloa* Rémy. *Bol Soc Argent Bot* 7:79–85
- Chouksanova NA, Sveshnikova LI, Alexandrova TV (1968) Data on karyology of the family Compositae Giseke. *Citologija* 10:198–206
- Cuatrecasas J (1954a) Synopsis der Gattung *Loricaria* Wedd. *Feddes Repert Spec Nov Regni Veg* 56:149–172
- Cuatrecasas J (1954b) El género *Mniodes*. *Folia Biol Andina* 1:17
- Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nat Methods* 9:772
- De Jong DCD, Longpre EK (1963) Chromosome studies in Mexican Compositae. *Rhodora* 65:225–240
- Dillon MO (2000) Classification and phylogeny of the South American Gnaphalieae (Asteraceae). In: Andean Botanical Information System. <http://www.sacha.org/Gnaphalieae/Gnaphalieae.htm>. Accessed September 2013
- Dillon MO (2003) New combinations in *Luciliocline* with notes on South American Gnaphalieae. *Arnaldia* 10:45–60
- Dillon MO, Sagástegui-Alva A (1985) New species and combinations in *Belloa* (Inuleae-Asteraceae). *Phytologia* 58:392–400
- Dillon MO, Sagástegui-Alva A (1986) *Jalcochila*, a new genus of Andean Inuleae (Asteraceae). *Brittonia* 38:162–167
- Dillon MO, Sagástegui-Alva A (1991) Tribe Inuleae. In: Macbride JF et al. (eds) *Flora of Peru, Family Asteraceae: Part V. Fieldiana Bot n.s.* 26:1–70
- Dillon MO, Sagástegui-Alva A (1992) Sinopsis de los géneros de Gnaphaliinae (Asteraceae-Inuleae) de Sudamérica. *Arnaldia* 1:5–91
- Doyle JJ, Dickson EE (1987) Preservation of plant samples for DNA restriction endonuclease analysis. *Taxon* 36:715–722
- Farris JS, Albert VA, Källersjö M, Lipscomb D, Kluge AG (1996) Parsimony jackknifing outperforms neighbor-joining. *Cladistics* 12:99–124
- Fernández Casas J, Fernández Piqueras J (1981) Estudio cariológico de algunas plantas bolivianas. *Anales Jard Bot Madrid* 38:149–152
- Freire SE (1986a) *Novenia*: Nuevo género de Inuleae (Compositae). *Bol Soc Argent Bot* 24:295–304
- Freire SE (1986b) Revisión del género *Lucilia* (Compositae, Inuleae). *Darwiniana* 27:431–490
- Freire SE (1986c) Números cromosómicos en el género *Lucilia* (Compositae, Inuleae). *Bol Soc Argent Bot* 24:411–413
- Freire SE (1987) Nuevos sinónimos y una nueva combinación en el género *Lucilia* (Compositae, Inuleae). *Darwiniana* 28:409–411
- Freire SE (1989) *Oligandra* Less. is *Lucilia* Cass. (Compositae, Inuleae). *Taxon* 38:298–299
- Freire SE (1993) A revision of *Chionolaena* (Compositae, Gnaphalieae). *Ann Missouri Bot Gard* 80:397–438
- Freire SE, Iharlegui L (1997) Sinopsis preliminar del género *Gamochoeta* (Asteraceae, Gnaphalieae). *Bol Soc Argent Bot* 33:23–35
- Galbany-Casals M, Andres-Sanchez S, Garcia-Jacas N, Susanna A, Rico E, Martinez-Ortega MM (2010) How many of Cassini

- anagrams should there be? Molecular systematics and phylogenetic relationships in the *Filago* group (Asteraceae, Gnaphalieae), with special focus on the genus *Filago*. *Taxon* 59:671–1689
- Goloboff PA, Farris JS, Källersjö M, Oxelman B, Ramírez MI, Szumik CA (2003) Improvements to resampling measures of group support. *Cladistics* 19:324–332
- Goloboff PA, Farris JS, Nixon K (2008) TNT, a free program for phylogenetic analysis. *Cladistics* 24:774–786
- Guindon S, Gascuel O (2003) A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Syst Biol* 52:696–704
- Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucl Acids Symp Ser* 41:95–98
- Hind DJN (2011) An annotated preliminary checklist of the Compositae of Bolivia, version 2. <http://www.kew.org/science/tropamerica/boliviacompositae> and <http://www.kew.org/science/tropamerica/boliviacompositae/checklist.pdf>. Accessed 7 March 2014
- Huelsenbeck JP, Ronquist F (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17:754–755
- Jørgensen CA, Sørensen TH, Westergaard M (1958) The flowering plants of Greenland. A taxonomical and cytological survey. *Biol Skr Vidensk Selskab* 9(4):1–72
- Juel HO (1900) Vergleichende Untersuchungen über typische und parthenogenetische Fort-pflanzung bei der Gattung *Antennaria*. *Kg Svenska Vet Ak Handl* 33(5):1–59
- Katoh K, Misawa K, Kuma K-I, Miyata T (2002) MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Res* 30:3059–3066
- Lewis PO (2001) A likelihood approach to estimating phylogeny from discrete morphological character data. *Syst Biol* 50:913–925
- Loeuille B, Deble L, Nakajima JN (2011) Four new species of *Chionolaena* (Asteraceae: Gnaphalieae) from south-eastern Brazil. *Kew Bull* 66:263–272
- Löve A, Löve D (1982a) IOPB chromosome number reports 75. *Taxon* 31:344–360
- Löve A, Löve D (1982b) IOPB chromosome number reports 77. *Taxon* 31:766–768
- Merxmüller H, Leins P, Roessler H (1977) Inuleae-systematic review. In: Heywood VH, Harborne JB, Turner BL (eds) *The biology and chemistry of the Compositae*. Academic Press, London, pp 577–602
- Moore DM (1981) Chromosome numbers of Fuegian angiosperms. *Bol Soc Brot* 53:995–1012
- Nesom GL (1990a) Taxonomic status of *Gamochoeta* (Asteraceae: Inuleae) and the species of the United States. *Phytologia* 68:186–198
- Nesom GL (1990b) An additional species of *Gnaphaliothamnus* (Asteraceae: Inuleae) and further evidence for the integrity of the genus. *Phytologia* 69(1):1–3
- Nesom GL (1990c) Taxonomy of *Gnaphaliothamnus* (Asteraceae: Inuleae). *Phytologia* 68(5):366–381
- Nesom GL (2001) New combinations in *Chionolaena* (Asteraceae: Gnaphalieae). *Sida* 19:849–852
- Nixon KC, Carpenter JM (1996) On simultaneous analysis. *Cladistics* 12:221–241
- Packer JG, McPherson GD (1974) Chromosome numbers in some vascular plants from northern Alaska. *Can J Bot* 52:1095–1099
- Rémy EJ (1847) *Compuestas, Belloa*. In: Gay C (ed) *Historia física y política de Chile, Botánica* 3(3). En casa del autor, Paris, pp 336–338
- Robinson H (1985) In honor of the botanical career of José Cuatrecasas. In: *Flora Neotropica*, 2 Supplement. Brunelliaceae. pp 13–16
- Ronquist F, Huelsenbeck JP (2003) MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574
- Shaw J, Lickey EB, Schilling EE, Small RL (2007) Comparison of whole chloroplast genome sequences to choose noncoding regions for phylogenetic studies in angiosperms: the tortoise and the hare III. *Amer J Bot* 94:275–288
- Smitsen RD, Galbany-Casals M, Breitwieser I (2011) Ancient allopolyploidy in the everlasting daisies (Asteraceae: Gnaphalieae): complex relationships among extant clades. *Taxon* 60:649–662
- Spooner DM, De Jong DCD, Sun BY, Stuessy TF, Gengler KM, Nesom GL, Berry PE (1995) Chromosome counts of Compositae from Ecuador and Venezuela. *Ann Missouri Bot Gard* 82:596–602
- Taberlet P, Gielly L, Pautou G, Bouvet J (1991) Universal primers for amplification of three non-coding regions of chloroplast DNA. *Pl Molec Biol* 17:105–1109
- Turner BL, Powell AM, Cuatrecasas J (1967) Chromosome numbers in Compositae. XI Peruvian species. *Ann Missouri Bot Gard* 54:172–177
- Urbanska-Worytkiewicz K (1967) Cytological Investigations in *Antennaria* Gaertn. from North Scandinavia. *Acta Boreal*, A 22:1–14
- Ward J, Bayer RJ, Breitwieser I, Smitsen R, Galbany-Casals M, Unwin M (2009) Gnaphalieae. In: Funk VA, Susanna A, Stuessy TF, Bayer RJ (eds) *Systematics, Evolution, and Biogeography of Compositae*. International Association for Plant Taxonomy, Vienna, pp 539–588
- White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Shinsky JJ, White TJ (eds) *PCR protocols: a guide to methods and applications*. Academic Press, San Diego, pp 315–322
- Wilgenbusch JC, Warren DL, Swofford DL (2004) AWTY: a system for graphical exploration of MCMC convergence in Bayesian phylogenetic inference. <http://ceb.csit.fsu.edu/awty>. Accessed 2 November 2013