# Morphological and molecular analyses of South American Microliabum (Compositae, Liabeae, Paranepheliinae) and reinstatement of Austroliabum 

Short title: Morphological and molecular analyses of Microliabum (Compositae, Liabeae)

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#### Abstract

The small Neotropical tribe Liabeae (Compositae) is currently classified in four subtribes: Liabinae, Munnoziinae, Paranepheliinae, and Sinclairiinae. As currently accepted, Paranepheliinae includes seven genera, Chionoppapus, Erato, Microliabum, Paranephelius, Philoglossa, Pseudonoseris, and Stephanbeckia, distributed especially throughout the Andes from Venezuela and Colombia to Argentina. Our research focuses in the genus Microliabum, which inhabits extra-Andean enviroments from Bolivia to central Argentina. The wide concept of Microliabum and its phylogenetic position within Paranepheliinae is controversial. Bayesian and maximum parsimony analyses of ribosomal nuclear ITS and plastid trnL-F suggest that both subgenera described within Microliabum are monophyletic. However, Microliabum, without the subgenus Austroliabum, is close to Stephanbeckia. A statistical analysis (PCoA) supports separation of the subgenera, and morphology mainly based on traits of the involucre and florets permits to establish new taxonomical circumscriptions. Thus, the reinstatement of Austroliabum, the more southern Liabean genus, is here proposed. The genus includes three endemic species from Sub-Andean and Pampean Hills in central and northwestern Argentina. Austroliabum is characterized by white-tomentose or woolly pubescence on stems and abaxial leaf surfaces, acrodromous leaf venation, campanulate involucres, coriaceous and adpressed phyllaries in usually five series, outer phyllaries shorter than the inner ones, style branches of disc florets shorter than the pubescent part on shaft below the bifurcation point, style pubescence on shaft below the bifurcation point of disc florets at least three times longer than the


branches of the style, persistent 2 -seriate pappus with outer series of scales and inner series of barbellate bristles, and achenes pubescent on the ribs. In addition, a revision of Microliabum s. str., with three species, is carried out.

KEYWORDS: Asteraceae; ITS; Liabeae; morphology; phylogeny; South America; trnL-F.

Liabeae are a phylogenetically derived small tribe within Compositae (Panero \& al., 2014; Mandel \& al., 2017) with 21 genera and 165 species (Gutiérrez, 2010; Funk \& al., 2012; Gutiérrez \& Katinas, 2015a). This Neotropical tribe is distributed mainly in the Andes where its origin was postulated, especially in Central and northern Andes (Funk \& al., 1996; Dillon \& al., 2009; Funk \& al. 2012). However, some Liabean genera inhabit non-Andean areas: (1) Mexico and Central America (e.g., Liabellum Rydb., Sinclairia Hook. \& Arn., Sinclairiopsis Rydb.); (2) The Caribbean [i.e., Liabum Adans., particularly Liabum umbellatum (L.) Sch.Bip.], and (3) central and northwestern Argentina in the Sub-Andean Hills ("Sierras Subandinas") and the Pampean Hills ("Sierras Pampeanas") (i.e., Microliabum Cabrera; Funk \& al., 2012; Gutiérrez, 2015a; Gutiérrez \& Katinas, 2015). The Pampean Hills have a different orogeny (e.g., Rapela \& al., 2001; Martino, 2003; Grosse \& al., 2009), floristic composition (Cabrera \& Willink, 1980), and geobiotic origins (Martínez \& al., 2016) from the Andes.

Four subtribes are currently recognized within Liabeae: Liabinae, Munnoziinae, Paranepheliinae, and Sinclairinae (Dillon \& al., 2009; Funk \& al., 2012; Pruski, 2012). Paranepheliinae are formed by seven genera: Chionopappus Benth., Erato DC., Microliabum, Paranephelius Poepp., Philoglossa DC., Pseudonoseris H.Rob. \& Brettell, and Stephanbeckia H.Rob. \& V.A.Funk. According to Funk \& al. (2012), two evolutionary lineages could be recognized: one is formed by Chionopappus, Erato and Philoglossa, and the other by Microliabum, Paranephelius, Pseudonoseris, and Stephanbeckia. Morphologically, the subtribe is characterized usually by the presence of latex (except Chionopappus and Stephanbeckia), short style branches in the disc florets (except Paranephelius and Pseudonoseris), and three-veined leaf venation (except Erato, Paranephelius, and Pseudonoseris; Funk \& al., 2012; Gutiérrez \& Luna, 2013).

Paranepheliinae are entirely South American in distribution with the exception of one species of Erato in Central America (Moran \& Funk, 2006; Funk \& al., 2012). Soejima et al. (2008) dated the origins of the Pseudonoseris-Paranephelius clade in the Miocene (approximately 13 million years ago [Ma]). Thus, Paranephelius and Pseudonoseris diversified well after the significant central Andean uplifts (Oligocene, ca. 30 Ma ), perhaps concurrently with major northern Andean orogeny (PliocenePleistocene, ca. 3-5 Ma; Soejima \& al., 2008). From a biogeographic standpoint, Microliabum is an
interesting genus because some of its species reach the southernmost distribution of the tribe (Gutiérrez \& Novara, 2009; Gutiérrez, 2015). It is formed by five or six species (e.g. Robinson, 1990; Cabrera \& al., 1999; Funk \& al., 2012; Gutiérrez, 2008a; Gutiérrez, 2015a) growing in open areas in mid-elevation wet forest or in high-elevation Andean habitats in the north of its range, and seasonally dry scrub associated to hills in the south.

The first Microliabum species were originally described under Liabum Adans. (Table 1), and the first comprehensive analysis of most of the current species of Microliabum was made by Cabrera (1947), who described the northwestern Argentinian genus Liabellum (Cabrera, 1954). Soon after, he changed the name to Microliabum (Cabrera, 1955) because the former was a later homonym of a Mexican genus, Liabellum (Rydberg, 1927). Thus, the monotypic genus Microliabum was originally named for one of its most distinctive traits, the small size. However, the diagnostic character was the paleaceous pappus in two series. Later on, Robinson and Brettell (1974) described the genus Angelianthus nom. superfl. (Table 1). From the beginning, Cabrera (1954) recognized the morphological affinity between Microliabum and Liabum s.l. However, on the basis of the paleaceous pappus, Cabrera (1978) and Cabrera \& Iharlegui (1999) kept Microliabum separate from the broad circumscription of Liabum postulated by classic botanists (e.g. Bentham, 1873). Thus, Microliabum was never treated as a synonym or section of Liabum, contrarily to other Liabean genera, i.e. Andromachia Humb. \& Bonpl., Chysactinium Kunth, Erato, Kastnera Sch.Bip., Munnozia Ruiz \& Pav., Oligactis (Kunth) Cass., Paranephelius, Sinclairia, Starkea Willd. (Gutiérrez \& Katinas, 2015).

On the other hand, genus Austroliabum H.Rob. \& Brettell, which is currently considered a synonym of Microliabum, was originally described to accommodate four species (Table 1) segregated from Liabum (Robinson \& Brettell, 1974). Robinson (1983) made only small taxonomical changes, but seven years later (Robinson, 1990) he proposed a recircumscription of Microliabum with six species (Table 1). As a result of this new taxonomic treatment, Microliabum expanded its earliest restricted morphological description from a single species with reduced habit and broadened pappus to several species up to 2 m tall and capillary inner pappus. At the same time, the genus expanded its restricted distribution in northwestern Argentina to a wider distribution in southern and central South America. In addition, Robinson (1990) classified Microliabum in two subgenera, Austroliabum and Microliabum, with three species each.

Phylogenetic relationships of Microliabum within Liabeae have been contradictory. For example, Microliabum was classically placed in subtribe Liabinae (Robinson, 1983; Funk, 1985; Funk \& al., 2007), sister to the Mexican and Central American genera Liabellum and Sinclairia (including

Megaliabum Rydb. and Sinclairiopsis) based on morphology but with weak support (Bremer, 1994; Funk \& al., 1996). Later on, in a preliminary phylogenetic analysis based on the nuclear gen ITS, Microliabum was weakly supported as a basally branching monophyletic genus sister to a clade composed of Sinclairia, Oligactis, Dillandia V.A.Funk \& H.Rob., and Liabum (Gutiérrez \& al., 2007). According to this study, Microliabum was suggested to be an ancestral genus within classical Liabinae. On the other hand, Microliabum was proposed, based on ITS and $\operatorname{trnL}$-trnF sequences, to be close to Paranephelius and Pseudonoseris (Soejima \& al., 2008), both from the classical Paranepheliinae. This latest relationship was confirmed in a phylogenetic study based on nuclear and plastid DNA sequences, and Microliabum was included in a recircumscription of Paranepheliinae together with Paranephelius and Pseudonoseris, plus Chionopappus, Philoglossa, and Erato (Dillon \& al., 2009). In this latest phylogeny, Microliabum resulted surprisingly as sister to Stephanbeckia, which was recently described from southern Bolivia (Robinson \& Funk, 2011; Funk \& al., 2012).

Until now, there is no agreement on the number of species of Microliabum (e.g., Robinson, 1990; Cabrera \& al., 1999; Funk \& al., 2012; Gutiérrez, 2008a, Gutiérrez, 2015a), and an unequivocal phylogeny is yet not available. Besides, phylogenetic relationships of Microliabum to Liabeae or Paranepheliinae are contradictory, probably due to limited sampling in previous phylogenetic studies. Thereafter, we have gathered a comprehensive sample of the genus and we have carried out analyses of nuclear-ribosomal and plastid DNA, and a thorough morphological survey including a statitistical analysis, with the following goals: (1) To evaluate the monophyly of Microliabum and its subgenera, and the position of the genus within Paranepheliinae; and (2) to review in depth the taxonomy, morphology, and geographical distribution of Microliabum and its species.

## MATERIALS AND METHODS

Sampling strategy. - For the DNA analyses, the ingroup included all species of Microliabum: M. candidum (Griseb.) H.Rob., M. eremophilum (Cabrera) H.Rob., M. glanduliferum (Cabrera) H.Rob. (subgenus Austroliabum), and M. humile (Cabrera) Cabrera, M. mulgediifolium (Musch1.) H.Rob. and M. polymnioides (R.E.Fr.) H.Rob. (subgenus Microliabum). Species of subgenus Austroliabum and M. humile were included in a phylogeny for the first time. Sequence data of Cacosmia Kunth, Chionopappus, Chrysactinium, Dillandia, Erato, Ferreyranthus H.Rob. \& Brettell, Liabellum, Liabum, Megaliabum, Munnozia, Oligactis, Paranephelius, Philoglossa, Pseudonoseris, Sampera V.A.Funk \& H.Rob., Sinclairia, Sinclairiopsis, and Stephanbeckia from the four subtribes of Liabeae were mainly obtained from GenBank (including previously unpublished data of Munnozia hastifolia (Poepp.) H. Rob. \& Brettell and Paranephelius asperifolius (Muschl.) H. Rob. \& Brettell), and used as
ingroup too (Appendix 1). Moquinia racemosa (Spreng.) DC. and Pseudostifftia kingii H.Rob. (Moquinieae), and Distephanus barus (Humbert) H.Rob. (Vernonieae) were included as outgroups. Voucher data, source and GenBank accession numbers are given in Appendix 1. DNA regions were selected based on previous molecular works (H.-G. Kim \& al., 2003; Funk \& al., 2004; Funk \& al., 2012).

DNA extraction, amplification and sequencing. - Total genomic DNA was extracted following the CTAB method of Doyle \& Dickson (1987) as modified by Cullings (1992) from silica-gel-dried leaves collected in the field or from herbarium material. For difficult extractions, DNeasy extraction Kit (Qiagen Inc., Hilden, Germany) was used, following the manufacturer's instructions.
$n r D N A$ ITS region strategy. -The ITS region was amplified by polymerase chain reaction (PCR). The amplification primers were ITS1, ITS2, ITS3 and ITS4 (White \& al., 1990), 17SE and 26SE (Sun \& al., 1994). For some species, the ITS region was amplified completely using ITS1 (forward) and ITS4 (reverse) primers or 17SE (f) and 26SE (r) primers. In case of low-quality DNA, the ITS1 and ITS2 fragments were amplified separately using ITS1 (f) and ITS2 (r) primers for the ITS1, and ITS3 (f) and ITS4 (r) primers for the ITS2. The PCR reactions were performed in a $25 \mu 1$ reaction volume containing $3 \mu \mathrm{l}$ of diluted genomic DNA, $2,5 \mu \mathrm{l}$ of $10 \times$ AmpliTaq buffer, $2,5 \mu \mathrm{l}$ of $2.5 \mathrm{mM} \mathrm{MgCl} 2,2,5$ $\mu \mathrm{l}$ of 0.2 mM dNTPs, $1 \mu \mathrm{l}$ of $0.2 \mu \mathrm{M}$ of each primer, $0.5 \mu \mathrm{l}$ of DMSO (Sigma-Aldrich, St. Luis, MO, USA), $5 \mu \mathrm{l}$ of TBT (Samarakoon, 2013) and $6.7 \mu \mathrm{l}$ of purified water and $0.3 \mu \mathrm{l}$ of AmpliTaq DNA polymerase (Applied Biosystems, Foster City, CA, USA) for both regions. The cycling profile included an initial denaturation step at $94^{\circ} \mathrm{C} / 2 \mathrm{~min}$ followed by 35 cycles of $94^{\circ} \mathrm{C} / 1 \mathrm{~min} 30 \mathrm{~s}, 55^{\circ} \mathrm{C} / 2$ $\min$ (for ITS1, ITS2, ITS3 and ITS4 primers) or $57^{\circ} \mathrm{C} / 2 \mathrm{~min}$ (for 17 SE and 26 SE ), $72^{\circ} \mathrm{C} / 3 \mathrm{~min}$, and ended with $72^{\circ} \mathrm{C} / 15 \mathrm{~min}$ and $4^{\circ} \mathrm{C}$ thereafter for the ITS region. Purification of the PCR product was conducted with ExoSAP-IT (USB Corp., Cleveland, Ohio, USA) or with also the QIAquick® purification kit (Qiagen Inc.). The amplified DNA segments were sequenced directly using BigDye Terminator Cycle Sequencing v.3.1 (Applied Biosystems), following the manufacturer's protocol at the University of Florida ICBR Core Facility on an ABI 3730xl capillary sequencer (Applied Biosystems) or at Macrogen Inc., Europe.
$c p D N A$ amplification strategies. - The forward primers trnL-c, trnL-e, and the reverse trnL-f, $\operatorname{trnL}-\mathrm{d}$ (Taberlet et al., 1991) were used for amplifying the $\operatorname{trnL}$ intron and the $\operatorname{trnL}-F$ intergenic spacer. The PCR reactions were performed under the same conditions as nuclear regions, replacing DMSO by BSA.

The PCR procedure included a warm start at $95^{\circ} \mathrm{C}$ for 1 min 35 s . Thirty-five cycles of amplification were carried out: 1 min denaturation at $93^{\circ} \mathrm{C}, 58^{\circ} \mathrm{C}$ annealing for $1 \mathrm{~min}, 72^{\circ} \mathrm{C}$ extension
for 1 min , and a final extension for 10 min at $72^{\circ} \mathrm{C}$. Purification and sequencing were performed as for the ITS region, but with the corresponding primers.

Phylogenetic analyses. - Nucleotide sequences were edited using Bioedit v7.0.5.3 (Hall, 1999) and aligned visually by sequential pairwise comparison (Swofford and Olsen, 1990) or using the program MUSCLE (Edgar, 2004) with manual correction. The only incongruences between datasets involved species unrelated to Microliabum sensu lato, and combination of datasets seemed adequate as proposed by Funk \& al. (2012). Thereafter, three datasets were analyzed: ITS ( 92 accessions), $\operatorname{trnL}$ - $F$ ( 87 accessions), and ITS + trnL-F (87 accessions). Data matrices are available at http://www.ibb.bencsic.es/public, folder Microliabum.

Parsimony analysis of the datasets involved heuristic searches conducted with PAUP v4.0a147 (Swofford, 2002) using tree-bisection-reconnection (TBR) branch swapping with character states specified as unordered and unweighted. Indels were treated as missing data in all datasets. All mostparsimonious trees (MPTs) were saved. To locate other potential islands of MPTs (Maddison, 1991), we performed 10,000 replications with random taxon addition, also with TBR branch swapping. Bootstrap analyses (BS) were performed (Felsenstein, 1985) with 100 replicates with simple addition and TBR branch swapping for ITS, and ITS + trnL-F datasets. For bootstrapping $\operatorname{trnL}-F$ dataset the tree limit of PAUP was reached very quickly and thereafter we followed the approach of Lidén et al. (1997), using 1000 replicates, random taxon addition with 20 replicates, and no branch swapping. Internodes with $\mathrm{BS} \geq 75 \%$ were considered statistically significant. For the strict consensus tree consistency index (CI) and retention index (RI) are given excluding uninformative characters (Electr. Suppl.: Table S\#1). Bayesian inference of the three datasets was calculated using MrBayes v3.2.1 (Ronquist et al., 2012). The best available model of molecular evolution required for Bayesian estimations of phylogeny was selected for all datasets using Akaike information criteria (AIC) as implemented in the software MrModeltest v3.7 (Posada \& Crandall, 1998). The best fitting models were the symmetrical model with gamma distribution and number of invariant sites (SYM $+\Gamma+\mathrm{I}$; Zharkikh, 1994) for ITS, and the general time-reversible model with gamma distribution and number of invariant sites (GTR $+\Gamma+\mathrm{I}$; Gu \& al., 1995) for $\operatorname{trnL}-F$. For the analyses of the combined datasets (ITS $+\operatorname{trnL} L-F$ ), data were partitioned and the adequate model was assigned to each partition.

Bayesian inference analyses were initiated with random starting trees and were run for $30 \times 10^{6}$ generations in two independent runs of four Metropolis-coupled chains in the three datasets. We saved one out of every 1,000 generations, resulting in 30,000 sampled trees. For ensuring that the Markov chain Monte Carlo (MCMC) reached stationarity, we used Tracer 1.7.1 (Rambaut et al., 2018) for checking that the Efective Sample Size (ESS) was higher than 200 after discarding the first $25 \%$ of trees as burn-in. Internodes with posterior probabilities $\geq 0.95$ were considered statistically significant.

Taxonomic and morphologic analyses. More than 300 specimens (including types and images) deposited in BA, BAA, BAB, BAF, CORD, CTES, GH, GOET, HSB, JUA, K, LIL, LP, MCNS, MO, NY, S, SI, and US (Thiers, 2018) were studied. Other specimens were examined as digital images available through online resources of several herbaria and the JSTOR Global Plants web site (http://plants.jstor.org). In addition, field work for this study was conducted at several sites in the range of the geographical distribution of Microliabum throughout Argentina (Catamarca, Córdoba, Jujuy, La Rioja, Salta, San Luis, and Tucumán provinces) from 2006 to 2011, 2016, 2018 and 2019 (see specimens examined for each species). All species were collected with the exception of $M$. humile. Voucher specimens were deposited in BA, LP, and MCNS. Descriptions are based on herbarium specimens and field observations, with specimens having been collected by the authors. The data derived from the specimens were supplemented by information from the literature and databases.

Samples were obtained from living plants (cultivated in greenhouse or collected in field trips) and herbarium specimens. In the case of dry materials for microscopic examination, vegetative and reproductive parts were rehydrated, cleared, stained with $2 \%$ safranin, and mounted on microscope slides (Zarlavsky, 2014). Drawings were made using a Wild M5 stereomicroscope and an Olympus CH2 microscope with a camera-lucida attachment. Drawings of species were made on the base of herborized specimens and compared to field observations for the all species excepting M. humile. Light microscope photographs were taken with a Nikon Coolpix S10 camera. For scanning electron microscopy (SEM) studies, critical point drying was applied to dehydrated material, or dry material was placed directly on the stubs and coated with gold. Samples were scanned and photographed in a Jeol JSM-T 100 SEM (at La Plata Museum) or Philips XL-30 SEM (at Argentine Museum of Natural Sciences). In some cases, low-vacuum scanning electron microscopy was performed.

All the species of Microliabum were macro- and micromorphologically analyzed. Whenever possible, over 20 specimens for each species were measured. Two capitula at the same maturity stage and at least two to five florets (disc and ray) per specimen were analyzed. Macroscopical observations were made on living plants during field trips as well as on those cultivated in La Plata. In addition, specimens of some species from Paranephelius and Pseudonoseris were analysed. In the particular case of Stephanbeckia, data were obtained from the original description and high quality digital images of types.

Terminology for morphology follows Ramayya (1962), Harris \& Wolf Harris (1994), Bremer (1994), and Ash et al. (1999).

Multivariate analyses. In order to analyze morphometric variation among the species of Microliabum, we took measurements from 72 individuals of 55 herbarium specimens (including types and additional collections) (Appendix 2) for 30 characters (six vegetative and 24 reproductive; five quanlitative and 25 quantitative): (1) plant height, (2) petiolate/inconspicuously petiolate or sessile leaf, (3) petiole length, (4) petiole width, (5) leaf lamina length, (6) leaf lamina width, (7) number of capitula, (8) length of the capitula peduncle, (9) involucre height, (10) involucre width, (11) number of phyllaries series, (12) outer phyllary length, (13) outer phyllary width, (14) inner phyllary length, (15) inner phyllary width, (16) consistency of outer phyllaries, (17) number of ray florets series, (18) ray florets corolla length, (19) ray florets corolla limb length, (20) ray florets corolla limb width, (21) disc florets corolla length, (22) disc floret corolla limb width, (23) style branches length of disc florets, (24) achene length, (25) achene width, (26) pubescence of achene, (27) outer pappus length, (28) outer pappus type, (29) inner pappus length, and (30) inner pappus type.

Plant and leaf characters (1--6). - Plant height was measured from the base of the main stem to the apical part of the plant including the inflorescence. Petiole length was measured from the base of the petiole to the base of leaf lamina. In some cases, given the gradual winged character of the petiole, the base of the leaf lamina was defined in the point where the margin conspicuously changes its direction. Petiole width was measured at its broadest point. Leaf lamina length was measured from the base of the lamina to its apex. In the particular case of inconspicuously petiotale or sessile leaves, the lamina length was measured as the total length of the leaf. Leaf lamina width was measured at its broadest point.

Inflorescence characters (7--16): - Number of capitula was counted in each terminal reproductive branch. Length of the inflorescence peduncle was measured in terminal capitula. Involucre height was measured from the apex of the longest phyllary up to the insertion of the receptacle on the peduncle and involucre width at its broadest point. Phyllaries chosen to carry out the measures were the most external and the most internal of the involucre. Phyllary length was measured between the base of the phyllary and its apex, and its width was measured at its broadest point. Consistency of outer phyllaries was classified in coriaceous or herbaceous.

Ray floret characters (17--20). - Ray florets series were classified in 1-seriate or 2-seriate. Ray florets corolla length was measured from the limb apex up to the insertion of the corolla tube on the ovary or achene. Limb length was measured from the notch of the corolla to the limb apex. Limb width was measured at its broadest point.

Disc floret characters (21--23). - Disc florets corolla length was measured from the apex of lobes to the insertion of the corolla tube on the ovary or achene. Limb width was measured at its broadest point. Style branches length were measured from their apex to the bifurcation point of the style.

Achene and pappus characters (24-30). - Length and width of the fruit were measured. Length of the achene was measured from the achene base (i.e. carpopodium) up to the insertion of the pappus. Width of the achene was measured at its broadest point. Achene pubescence was classified in trichomes on ribs or covering all the surface. The outer series of pappus was classified in two types of elements: scale or paleaceous scale. On the other hand, the inner series of pappus was classified in two types of elements: bristle or paleaceous scale. Pappus length in each series was measured from the base up to the apex of the longest element.

Selected characters mentioned above were included in the multivariate analysis. Characters such as the number of phyllaries and the number of florets were not included in the multivariate analysis to avoid damage to herbarium specimens. All specimens were studied by direct observation and by a stereomicroscope Wild Heerbrugg; measurements for quantitative characters were taken using a digital caliper and a calibrated ocular micrometer.

We performed a Principal Coordinate Analysis (PCoA) to find the phenetic relationships among the specimens in an ordination space (Kapplan \& Marhold, 2012) using the Gower distance coefficient (Gower, 1971). Statistical analyses were carried out using the software PAST (Hammer et al., 2001).

## RESULTS

## Molecular results

Numerical results of the molecular study of the two regions and details of the three dataset analyses are shown in Electr. Suppl.: Table S\#1. Parsimony and Bayesian analyses yielded coincident topologies and we are showing the Bayesian phylograms in Figs. 1, 2 and Electr. Suppl.: Fig S\#1.

In the analyses of the three datasets (ITS, $\operatorname{trnL} L-F+$ ITS and $\operatorname{trn} L-F$ ), Liabeae was a monophyletic tribe with high support ( $\mathrm{PP}=1,1,1 ; \mathrm{BS}=100,91,100$ respectively) and in general subtribal classification is recognized with some differences to previous phylogenies, in particular regarding subtribes Liabineae and Paranepheliinae.

According to our analyses, Liabinae showed two main clades each one with high support. One includes species of Ferreyranthus ( $\mathrm{PP}=1,1, \ldots ; \mathrm{BS}=100 \%, 100 \%, \ldots$ ), and the other includes genera Dillandia, Liabum, Oligactis, and Sampera (PP = 1, 1, ...; BS $=87 \%, 92 \%, \ldots$ ). However, relationships between these two clades were unresolved. In particular, the analyses showed a monophyletic clade including Liabum and Sampera nested within the former ( $\mathrm{PP}=1,0.94,1 ; \mathrm{BS}=$ $97, \ldots, 100)$. The phylogenetic location of Cacosmia was contradictory, with affinities with either Liabinae or with Sinclairiinae depending on the marker used. Sinclairinae was a well-supported clade based on posterior probability values ( $\mathrm{PP}=0.92,1,1: \mathrm{BS}=\ldots, 97 \%, 97 \%$ ). Within this subtribe, the analyses showed two clades each one highly supported with ITS and ITS + trnL-F: Sinclairiopsis
clade ( $\mathrm{PP}=1, \ldots, 1 ; \mathrm{BS}=100, \ldots, 100$ ) and a clade with Liabellum, Megaliabum, and Sinclairia (PP $=1, \ldots, 1 ; \mathrm{BS}=100, \ldots, 100)$. Monophyly of Munnoziinae was obtained on the basis of the ITS and ITS $+\operatorname{trnL} L-F$ datasets with high support $(\mathrm{PP}=1,1 ; \mathrm{BS}=81,92$ respectively), however, the $\operatorname{trnL}-F$ dataset did not resolve the phylogenetic relationships nor showed the monophyly of this subtribe. Within Munnoziinae, all the analyses showed Chysactinium to be nested inside Munnozia.

In the case of current Paranepheliinae, genera from this subtribe are placed in different clades (Figs. 1 and 2). Microliabum s.l. (Clade A and Clade C) is placed among Liabeae in a clade that includes the genera Chionopappus, Chrysactinium, Erato, Munnozia, Paranephelius, Philoglossa, Pseudonoseris, and Stephanbeckia. This clade, that brings together the genera of current Munnoziinae and Paranepheliinae, has high support in the analyses of the three datasets: $\mathrm{PP}=0.97,1,1 ; \mathrm{BS}=\ldots$, $79 \%$, $97 \%$; Figs. 1, 2; Electr. Suppl.: Fig S\#1.

However, Microliabum is not monophyletic: subgenera Austroliabum (Clade A) and Microliabum (Clade C) are placed in different clades (Figs. 1, 2; Electr. Suppl.: Fig S\#1). Monophyly of subgenera Austroliabum and Microliabum is equally supported ( $\mathrm{PP}=1$ in the three datasets; $\mathrm{BS}=100 \%, 100 \%$, 81\%). Subgenus Austroliabum is grouped with Paranephelius and Pseudonoseris without support from ITS and the ITS + trnL-F datasets (Figs. 1, 2). Subgenus Microliabum is grouped in a clade with Stephanbeckia (Clade B) with high support ( $\mathrm{PP}=1$ in the three datasets; BS $=99 \%, 100 \%, 99 \%$ ).

The individual species in the subgenus Austroliabum clade show no resolution, whilst the Microliabum clade are well-defined at the species level. It is important to highlight the phylogenetic position of M. humile (the type species of genus Microliabum) within the clade of the subgenus Microliabum; according to the analysis this species forms a clade with M. mulgediifolium from ITS with high support ( $\mathrm{PP}=1 ; \mathrm{BS} 96 \%$; Fig. 1) and molecularly it is very differentiated.

## Morphological results

A detailed comparative morphological analysis between subgenera Austroliabum and Microliabum was undertaken in order to compare it with our phylogenetic results.

Habit, stem, latex and pseudostipules. Species of Microliabum are usually annual, biennial or perennial herbs, rarely subshrubs (Fig. 3 A-B). Plants may be tall, usually up to 2 m in height, less often very reduced, up to 15 cm .

Two patterns of branching and phylotaxis are identified: (1) few-branched or unbranched small herbs with leaves clustered at the base of the main stem (i.e. M. humile), (2) tall branched or unbranched herbs or rarely subshrubs, with only one or few stems, with leaves spread along stems ( $M$. mulgediifolium, M. polymnioides, and all the species of subgenus Austroliabum). In the last type, stems are ascendant or decumbent (subgenus Austroliabum; Fig. 3 A) or erect (especially subgenus

Microliabum; Fig. 3 B). Pubescence varies among glandular-hirsute (Fig. 3 C), arachnoid, whitetomentose or woolly, with the same main type of trichome found on the leaves (see below).

The occurrence of latex has been considered one of the diagnostic characters of Liabeae. Microliabum mulgediifolium and M. polymnioides show abundant white latex (Fig. 3 C) when cutting main stems, branches and also leaves and peduncles in the wild. However, these species show little latex in greenhouse. On the contrary, species of subgenus Austroliabum show always little latex in field and greenhouse. Plants are sticky, especially M. glanduliferum.

Pseudostipules are elements on the nodes arising at each side of the leaf base. In Microliabum, they are completely absent (i.e. M. humile), absent only from several nodes, or very conspicuous (Fig. 3 D-F). When present, they are foliaceous and show different degrees of development among species, individuals or nodes. They can be opposite, sometimes subalternate, free (Fig. 3 D, F) or fused (Fig. 3 E). In species with winged petioles, pseudostipules are continuous with the wings (Fig. 3 F ). They are subglabrous or arachnoid-pubescent adaxially and white-tomentose or woolly abaxially.

Leaves. Leaves are usually opposite and decussate, sometimes clustered at the base of the stem (i.e. M. humile) and subalternate toward the apex in reproductive branches. They are sessile or inconspicuously petiolate (i.e., M. humile and rarely in some specimens of M. eremophilum and M. mulgediifolium), short-petiolate or long-petiolate (subgenus Austroliabum up to $1--6 \mathrm{~cm}$ long, and $M$. mulgediifolium and M. polymnioides up to $10-15 \mathrm{~cm}$ long) (Fig. 3 G-I). The inconspicuous type of petiole is a gradual extension of the leaf lamina toward the leaf base, wider near the lamina and narrowing to the stem. Petioles may be wingless (Fig. $3 \mathrm{G}, \mathrm{I}$ ) or completely winged with narrow or wide wings (Fig. $3 \mathrm{~F}, \mathrm{H}$ ), continuous or not with the pseudostipules; when continuous, the petiole wings are very well demarcated from the leaf lamina base and have the same width throughout. Wing margins may be mucronate-serrate or serrulate, irregularly toothed or erose.

Leaf laminas may be ovate or sub-triangular in shape (Fig. 3 G-I). Apices are usually acute and lamina bases show considerable variation: they are predominantly cuneate but they may also be decurrent, rounded, cordate, truncate or sagittate. Leaf margins may be mucronate-serrate or serrulate (subgenus Austroliabum, M. humile), or irregularly toothed or erose (i.e., M. mulgediifolium and M. polymnioides).

Venation in Microliabum is usually actinodromous, 3-veined, but in M. humile and some small individuals of $M$. mulgediifolium and M. polymnioides it is inconspicuous.

Leaf pubescence (including phyllaries) and trichomes. There is usually a marked difference in the amount of pubescence on the adaxial versus the abaxial surface of the lamina (Fig. 3 G-I). Adaxial leaf surface is glabrescent (Fig. 3 H ) or hirsute, sometimes mixed with a white-arachnoid and evanescent
indumentum (Fig. 3 G, Fig. 4 A), and abaxial leaf surface is usually white-tomentose to woolly (Fig. 3 I), sometimes brownish in dried specimens. In some specimens, the tomentum is mixed with conspicuous glandular trichomes, which may be distributed along the main veins, leaf margins or across the surface of the lamina.

Phyllaries are internally glabrous and externally glabrescent, glandular-hirsute, sometimes mixed with an arachnoid and evanescent indumentum, or white-tomentose to woolly. Trichomes can be classified into four main types (Fig. 4 A-D):
(a) Simple conical trichomes (Fig. 4 A ): These trichomes have a simple foot and a uniseriate body. The body is entire, (1--)2--3-celled, conical, pointed and rounded at the apex. They are present in Microliabum subgenus Austroliabum.
(b) Aseptate-flagellate trichomes (Fig. 4 A-D): These trichomes have a simple foot and a uniseriate body. The stalk is $2--6$-celled with conical or cylindrical cells. The head is 1 -celled, very long, coiled, flagellate, pointed and rounded at the apex. These trichomes usually produce hirsute, arachnoid, tomentose and woolly pubescence. In Microliabum subgenus Austroliabum the stalk is shorter, with more narrow cylindrical cells, than in subgenus Microliabum.
(c) Biseriate glandular trichomes with a big stalk (Fig. 4 A-C): The foot is 2-celled and the body biseriate with sub-opposite or alternate cells in each row. The stalk is 3--7-celled in each row and the head is, demarcated from the stalk or continuous with it, 2--4-celled in each row; the two terminal cells are slightly distinct like a vesicle.
(d) Biseriate glandular trichomes without stalk or with a reduced one (Fig. 4 D ): They are similar to trichomes described under (c) but the stalk is lacking or reduced and they are 1--2-celled in each row. The head is $2--3$-celled in each row with the two terminal cells slightly distinct like a vesicle. These trichomes usually are found in Microliabum subgenus Austroliabum on the lower surface below tomentum.

Inflorescences, capitula, involucres and phyllaries. Microliabum shows few or many capitula grouped in a terminal alternate branched corymbiform secondary inflorescence (also called capitulescence). Particularly, M. humile has commonly a single capitulum or several in terminal branches but not grouped. Only one capitulum is rarely present in the other species during early developmental stages. Capitula are pendulous (i.e. M. mulgediifolium), erect or ascendent (rest of species) with short or long peduncles between $0.5--10 \mathrm{~cm}$ long (Fig. 5 A-B). Peduncles are whitetomentose or woolly (Fig. 5 A), hirsute, usually with conspicuous glandular trichomes (Fig. 5 B; see trichome's type c above), sometimes absent.

Involucre and phyllaries traits (e.g. shape of involucre, phyllaries series, phyllaries positios of outer series, phyllaries size, and number of phyllaries) were important features of macromorphology
for taxonomical purposes because these easily differentiated and/or grouped among subgenera Austroliabum and Microliabum, and related genera.

Involucre is campanulate in subgenus Austroliabum (Fig. 5 A ) or hemispherical in subgenus Microliabum (Fig. 5 B). Phyllaries are organized in 4--6 series, usually five, in subgenus Austroliabum (Fig. 5 A) or 2--4, usually three, in subgenus Microliabum (Fig. 5 B) and are from few to numerous, 15--25 in M. humile to 45--75 in subgenus Autroliabum and M. mulgediifolium and M. polymnioides. From the outer series to the inner, there is a gradual transition. However, inner phyllaries are longer than the outer ones in subgenus Austroliabum, and, on the contrary, inner phyllaries are shorter than the outer ones in subgenus Microliabum. Phyllaries are mainly ovate, long-ovate or oblong, rarely obovate in shape, with acute or attenuate apices. In the case of the subgenus Austroliabum, phyllaries are coriaceous and adpressed throughout all the stages of its development (Fig. $5 \mathrm{~A}, \mathrm{C}$ ). On the contrary, in subgenus Microliabum they are mainly herbaceous with the outer ones exserted (Fig. 5 B, D), and the innermost ones membranaceous and reduced, sometimes inconspicuous. They are hirsute with glandular-tipped trichomes (Fig. 4 C), white-arachnoid, tomentose or woolly.

Receptacle is flat or slightly convex, naked and foveolate.

Florets. Capitula are conspicuously radiate (Fig. 5 E-F) and heterogamous, having ray florets with true ray corollas and disc florets with tubular funnelform corollas. The number of florets per capitulum varies greatly from 25--195: subgenus Austroliabum shows 65--115, subgenus Microliabum (except M. humile) 145--195, and M. humile 25--30. Disc florets are approximately as many as ray florets (i.e., M. humile, subgenus Austroliabum). However, in M. mulgediifolium and M. polymnioides the quantity of disc florets is in general almost the double of ray florets.

Ray florets are pistillate, fertile, without staminodia. There is only one series of ray florets in subgenus Austroliabum (Fig. 5 E) and in M. humile, or two rows in M. mulgediifolium and M. polymnioides (Fig. 5 F ). The number of ray florets varies approximately from 10-75 per capitulum: subgenus Austroliabum has 25--50, subgenus Microliabum (except M. humile) 35--75, and M. humile 10--15(--18). Ray florets have true ray corollas with limbs narrowly elliptic, oblong or obovate in shape, 4 -veined and conspicuously 3 -dentate at the apex. These corollas are usually yellow or rarely slightly orange, and pubescent (excepting some specimens of M. humile with glabrous corollas). Styles of the ray florets are bifid, with filiform, curly or curved branches, narrowly obtuse at the apex, longer than styles branches of the disc florets. Externally, the branches are glabrous; internally, the branches are completely covered by stigmatic papillae. The styles lack a nectary at the base.

Disc florets are hermaphrodite and fertile, and they vary widely from 15--125 per capitulum: in the case of subgenus Austroliabum variation was less than in subgenus Microliabum, from 40--65. Disc florets are 100--125 in M. mulgediifolium and M. polymnioides, and approximately 15 in $M$.
humile. Corollas are tubular funnelform, deeply 5-lobed, usually yellow or rarely slightly orange and pubescent at least on the lobes (i.e., some specimens of $M$. humile).

True ray and tubular corollas may be glabrous or pubescent with glandular trichomes, particularly on upper part of the tube and basal part of limb or throat, limb apex of true ray corollas, and on the lobes of tubular corollas. Papillae are also present on lobes apices of tubular corollas. Trichomes may be divided into two following types:
(a) Simple biseriate trichomes or simple biseriate glandular trichomes without a conspicuous head (Fig. 6 A): these are entire, with $3--5$ long cells in two rows with thin or thick walls. They are usually found on the external side of both true ray and tubular corollas, particularly on upper part of the tube and basal part of limb or throat, limb apex of true ray corollas, and lobes of tubular corollas, near the apex.
(b) Simple biseriate glandular trichomes with a conspicuous head (Fig. 6 A): these are differentiated into stalk and head; the stalk has 2--5 short cells in two rows, and the head 2--3 cells in two rows, of varied length but those of terminal tier often relatively larger, with thin walls. They are found on the external side of true ray and tubular corollas.

The anthers are pale yellowish, linear, shortly calcarate and caudate. Apical appendages are smooth, flat, ovate, and apically rounded. The anther tails are papillose (e.g. M. candidum) or rounded (e.g. M. humile). Styles are broadest at the base (stylopodium) and the two style branches are shorter (from 0.2 mm to 1.1 mm long) than the pubescent part on shaft below the bifurcation point, either straight or curved and divergent at maturity (Fig. 6 B-C); in the case of subgenus Austroliabum, length of style branches is $0.5--1.1 \mathrm{~mm}$ long, and in sugenus Microliabum is $0.2--1 \mathrm{~mm}$ long. Externally, the branches are hispidulous, with sweeping hairs formed by conical elements pointing toward the apex (Fig. 6 C). Sweeping hairs extend down on the style shaft from the bifurcation point to distance more than the length of the style branches. The inner surfaces of the branches have each one a continuous stigmatic surface with papillae (Fig. 6 C). Styles have a short nectary, not or scarcely lobed, at the base.

Achenes. Achenes of ray and disc florets are morphologically similar in subgenera Austroliabum and Microliabum (Fig. 6 D-E): they are cylindrical, ellipsoid or obconic, generally with a conspicuous annular carpopodium at the base, widened in the pappus insertion area, faintly to markedly 8 --10costate, and pubescent. Pubescence is formed by typical twin hairs usually with its cells completely united on their longitudinal walls or sometimes the cells are apically diverging (Fig. 6 F). Twin hairs are mainly on ribs in subgenus Austroliabum (Fig. $6 \mathrm{D}, \mathrm{F}$ ) or they usually cover all the achene surface in subgenus Microliabum (Fig. 6 E).

Pappus. Pappus is 2-seriate and heteromorphic, formed by different types of elements in outer and inner series with the outer elements always conspicuously shorter than the inner. These elements can be scales or bristles (Fig. 6 D-E, G-J). Scales are planate elements, ovate, elliptic or obovate in shape, with decurrent or convex bases, acute, rounded or obtuse apices, and erose or serrulate margins. Sometimes scales are paleaceous, i.e. paleae-like, when they resemble rudimentary bracts. On the other hand, bristles are stiff hair-like elements, thin or broadened, with barbellate margins. Within subgenus Austroliabum, the outer series of the pappus is formed by few, short (up to $0.3-1 \mathrm{~mm}$ long), scales (Fig. 6 D, G), elliptic or obovate in shape, with rounded or obtuse apices, and erose margins; in contrast, within subgenus Microliabum, the outer series is formed by few, short (up to $0.6-1.2 \mathrm{~mm}$ long), paleaceous scales (Fig. $6 \mathrm{E}, \mathrm{H}$ ), elliptic or ovate in shape, with acute, rounded or obtuse apices, and serrulate margins. The inner series of subgenus Austroliabum always consists of numerous, long (ca. 7 mm long), barbellate bristles. Similar elements are present in the inner series of Microliabum mulgediifolium and M. polymnioides (Fig. 6 I). These elements are shorter (approximately 4.5 mm long) barbellate bristles, and sometimes they are broadened with long barbellate margins in specimens of $M$. mulgediifolium. Finally, M. humile has the inner series consisting of few, long (usually 2 mm long) paleaceous scales (Fig. 6 J), ovate in shape, with acute apices and serrulate margins. Thus, morphological variation is greater among species of subgenus Microliabum.

Outer and inner series are usually persistent in subgenus Austroliabum, and the inner series is easily deciduous in subgenus Microliabum. The pappus is yellowish, brownish or orange, and generally the color varies within a species, and between living plants and dried specimens.

Some important characters from a taxonomic point of view of genera Paranephelius, Pseudonoseris (closely related to Microliabum subgenus Austroliabum) and Stephanbeckia (to Microliabum subgenus Microliabum) are comparatively analyzed in Table 2. The selected characters have been mainly used in previous works to circumscribe Liabean genera and the subgenera of Microliabum.

## Multivariate Analyses

Morphological and morphometric variation is shown in Table 3 and Electr. Suppl.: Table S\#2. The Principal Coordinates Analysis (PCoA) recovered two well-defined groups when the two principal coordinates were plotted (Fig. 7). The first three coordinates accounted for $68.64 \%$ of the total variance $(38.82 \%, 26.63 \%$, and $3.19 \%$, respectively). One group includes the three species of Microliabum subgenus Austroliabum, and the other group the three species of M. subgenus Microliabum. In the last group individuals of $M$. humile were differentiated from the individuals of $M$.
mulgediifolium and M. polymnioides. The two groups are in agreement with the results obtained in our phylogenetic analyses (Figs. 1, 2; Electr. Suppl.: Fig S\#1).

## DISCUSSION

## Monophyly of the subgenera and relationships of Microliabum within Paranepheliinae

In our work both subgenera of Microliabum are monophyletic with high support, as originally established by Robinson (1990). However, the current genus Microliabum is not a natural group because subgenus Microliabum is strongly supported as sister to Stephanbeckia. On the other hand, the evolutionary position of Microliabum subgenus Austroliabum within Paranepheliinae remains unclear. It is associated with Paranephelius and Pseudonoseris without support. Circumscription of Austroliabum at genus level as proposed by Robinson \& Brettell (1974), and then by Robinson (1983), including M. mulgediifolium and M. polymnioides is here rejected based on our phylogenetic and multivariate analyses. On the contrary, the treatment made later by Robinson (1990) considering M. candidum, M. eremophilum and M. glanduliferum within subgenus Austroliabum is here confirmed.

According to our analyses, monophyly of Paranepheliinae is neither supported nor refused by our results since there is lack of resolution in the clade consisting of Munnoziinae and Paranepheliinae. Our results on Paranepheliinae and Munnoziinae agree with Funk \& al. (2012).

Morphological affinities between subgenus Austroliabum and the Paranephelius-Pseudonoseris clade, and between subgenus Microliabum and Stephanbeckia

Regarding our morphological study, Microliabum subgenus Austroliabum and Paranephelius and Pseudonoseris share vegetative and reproductive features. In the case of vegetative traits, only one, the lower leaf pubescence, can be highlighted because these taxa share a white-tomentose or woolly abaxial pubescence. On the other hand, reproductive characters shared among Microliabum subgenus Austroliabum and Paranephelius and Pseudonoseris are many. The most important of them for taxonomical purposes are: number of phyllaries series (i.e. four to six), position of the outer series of phyllaries (i.e. adpressed), phyllaries length (i.e. gradually increasing length with the inner phyllaries longer than the outer ones), series of the ray florets (i.e. only one series), series of pappus (i.e. two series), type of inner pappus (i.e. barbellate bristles), and usually persistent elements of pappus. According to our results, two characters of the analysed taxa are especially useful in taxonomy because they are only shared among Microliabum subgenus Austroliabum and Paranephelius and Pseudonoseris: four to six series of phyllaries and usually persistent pappus.

Concerning morphological affinities between Microliabum subgenus Microliabum and Stephanbeckia, they share mainly reproductive features. For example, type of capitula (i.e. pedunculate), number of phyllaries series (i.e. 2--4, usually three), number of phyllaries (i.e. 40--75),
comparative length of style branches of disc florets (i.e. shorter than the pubescent part on shaft below the bifurcation point) and comparative length of style pubescence on shaft below the bifurcation point of disc florets (i.e. at least three times longer than the branches of the style), and pappus elements usually deciduous. In M. humile (part of M. subgenus Microliabum) the phyllaries are much fewer. However, only two of these characters are exclusively shared by these taxa: number of phyllaries series and pappus elements usually deciduous.

## Morphological differences between subgenera Austroliabum and Microliabum

According to our work, based on morphology and a multivariate analysis, the main differences between subgenera Austroliabum and Microliabum are given by both qualitative and quantitative reproductive characters: shape of involucre, number of series, position, comparative length, and consistency of phyllaries, number of series of ray florets, number of disc florets, achenes pubescence, and type and dehiscence of pappus' elements (Table 2). However, some vegetative characters such as the petiole length and its width should not be discarded if the average measures are considered (Table $3)$.

Many features that have been used in previous works (Robinson \& Brettell, 1974; Robinson, 1983, 1990) are here considered as useless, or at least imprecise or incorrect, for distinguishing subgenera Austroliabum and Microliabum because they are variable and overlap: for example, habit ("coarse" vs. "minute" herbs, respectively), type of inner pappus elements ("capillary" vs. "broad laminate"), number of phyllaries ("50--75" vs. "10--40"), number of phyllaries series ("3--4" vs." $1--$ 2 "), comparative length of phyllaries ("gradated series" vs. "subequal"), pubescence of disc corolla throats ("hirsute outside" vs. "glabrous"), pappus color ("rusty yellow" vs. "withish"), shape of pappus outer elements ("narrow, shortly setiform or minutely squamiform" vs."broadly squamiform"), shape of pappus inner elements ("capillary" vs. "minimally to strongly flattened or broadened"), and teeth type and distribution on pappus inner elements ("spreading equally on lateral and outer surfaces" vs. "stronger toward sides, reduced on inner surface and less reduced on outer surface").

Other features belonging to the involucre are confirmed, with modifications, to be of systematic value for distinguishing subgenera Austroliabum and Microliabum: for example, phyllaries features such as number of series (4--6 series, usually five in subgenus Austroliabum vs. 2--4 series, usually three in subgenus Microliabum), and comparative length (inner phyllaries longer than outer ones vs. inner phyllaries shorter than outer ones, respectively), including quantitative characters (Tables 2, 3). Moreover, some characters habe been found here for the first time to be diagnostic like shape of involucre (campanulate vs. hemispherical, respectively), position of outer phyllaries (adpressed vs. exserted), and consistency of phyllaries (coriaceous vs. herbaceous or membranaceous). In addition, other morphometric characters analyzed in our work could provide differences to properly
circumscribe and differentiate subgenera Austroliabum and Microliabum; for example, width of the involucre ( 1.08 cm vs. 1.75 cm , respectively), length of the outer phyllaries ( 4.21 mm vs. 7.78 mm ) and length of inner ones ( 7.92 mm vs. 5.5 mm ) (Table 3).

On the other hand, new floral features are detected in our work for separating the subgenera: series of ray florets, number of ray florets, number of disc florets, ratio between rays and disc florets, length of disc florets corolla, and length of style branches of disc florets. For example, subgenus Austroliabum shows rays in only one series vs. subgenus Microliabum mainly in two series (M. humile is the exception with only one series like subgenus Austroliabum), $25--50$ ray florets vs. 10--25 or $35-$ 75 (subg. Austroliabum and subg. Microliabum, respectively), 40--65 disc florests vs. 15 or 100--125, ca. 7 mm long of disc florets corolla vs. ca. 4.5 mm long, and ca. 0.8 mm long of style branches of disc florets vs. ca. 0.5 mm long (Tables 2, 3). In the case of the achenes, subgenus Austroliabum shows twin hairs especially on the ribs, while in subgenus Microliabum the twin hairs cover densely the complete surface.

One of the most important systematic features of Microliabum is the type of pappus (e.g. Cabrera, 1954; Robinson \& Brettell, 1974; Robinson, 1983). This character was originally used to separate Microliabum from the rest of the Liabean genera or, later on, to recognize morphological affinities among species of M. subgenus Austroliabum and M. subgenus Microliabum (e.g. Robinson, 1983; Robinson, 1990). Both subgenera share some pappus traits like elements in two conspicuous series, and the outer elements shorter than the inner ones. However, several characters allow to differentiate and circumscribe both subgenera. In subgenus Austroliabum the outer series of pappus are formed by scales with erose margins and the inner series by barbellate bristles. On the other hand, subgenus Microliabum shows the outer series of paleaceous scales with serrulate margins and the inner ones of barbellate bristles (i.e. M. mulgediifolium and M. polymnioides) or paleaceous scales (i.e. M. humile). It is important to note that among the barbellate bristles and paleaceous scales of the inner series, intermediate forms appear as long barbellate and planate elements (some specimens of $M$. mulgediifolium). Some morphometric characters of the pappus contribute to the separation between subgenera; for example, the outer series of pappus is approximately 0.6 mm long in subgenus Austroliabum vs ca. 0.8 mm long in subgenus Microliabum. On the contrary, the inner series is ca. 7 mm long in the former subgenus vs ca. 4 mm long in the last subgenus (Table 3). In relation with pappus traits, morphological differences between M. subgenus Austroliabum and M. subgenus Microliabum found in our work are as important as the differences displayed among other genera of Liabeae (Robinson, 1983; Funk \& al., 1996; Robinson \& Funk, 2011).

Based on the phylogeny of Microliabum obtained with molecular data, our thorough comparative morphological study, and the multivariate analysis, we propose the reinstatement of the genus

Austroliabum as an independent genus of Liabeae. Secondarily, it results in a genus Microliabum s. str. with three species. Our study confirms, without doubts, M. humile as relative to M. mulgediifolium and M. polymnioides. Many of its particular morphological characteristics (for example its reduced habit) may be related to its extreme adaptations to the high altitudes and rigorous climates it inhabits.

Our work recognizes all the genera that are currently part of subtribes Munnoziinae and Paranepheliinae (e.g. Soejima et al., 2008; Dillon et al., 2009; Funk et al., 2012) as only one phylogenetic lineage within Liabeae, but it is not conclusive about the circumscription of each subtribe and relationships among genera. We herein propose to include the resurrected genus Austroliabum within the current Paranepheliinae given its morphological affinities with the other genera of this subtribe, in particular with Paranephelius and Pseudonoseris.

Finally, new challenges in order to understand the evolution of Liabeae may include a greater sampling of species for resolving phylogenetic relationships among genera and, especially, to perform phylogeographical studies that may explain the causes of the geographical distribution of South American Liabean taxa that have conquered environments beyond the Andes such as Austroliabum.

## TAXONOMIC TREATMENT

In light of new evidence, a new morphological key to current Paranepheliinae is necessary considering a reestablished genus Austroliabum and a genus Microliabum in a restricted sense.

1. Abaxial leaf surfaces subglabrous and green; leaves and stems with stiff trichomes with enlarged
bases ................................................................................................. 2
2. Leaves actinodromous 5 --9-veined; achenes 4 -sided, 4-ribbed; pappus present Erato
3. Leaves actinodromous 3-veined; achenes 2-sided, 2-ribbed; pappus absent ...... Philoglossa 1. Abaxial leaf surfaces white-tomentose or woolly; leaves and stems without stiff trichomes with
enlarged bases ............................................................................................ 3
4. Pappus of plumose bristles ............................................................................ 4
5. Shrubs or subshrubs; receptacles paleaceous; achenes prismatic, 8--10-ribbed; pappus persistent Chionopappus
6. Herbs; receptacles naked; achenes compressed, 2-ribbed; pappus deciduous

Stephanbeckia
3. Pappus of barbellate bristles or scales ............................................................. 5
5. Involucres hemispherical; phyllaries $2-4$-seriate, mainly 3 -seriate, decreasing in length, outer series longer than inner, exserted, herbaceous or membranaceous; achenes densely pubescent with trichomes usually on the all surface; outer pappus of
paleaceous scales, inner of barbellate bristles or paleaceous scales, deciduous
$\qquad$
5. Involucres campanulate; phyllaries 4--6-seriate, mainly 5-seriate, gradually increasing in length, outer series shorter than inner, adpressed, coriaceous; achenes pubescent with trichomes usually on ribs or glabrous; pappus of barbellate bristles, or outer pappus of scales and inner of barbellate bristles, persistent


#### Abstract

6. Pseudostipules present; leaves acrodromous, 3-veined; disc florets with style branches shorter than the pubescent part on shaft below the bifurcation point

Austroliabum


> 6. Pseudostipules absent; leaves pinnate; disc florets with style branches longer than the pubescent part on shaft below the bifurcation point ........... 7
7. Capitula sessile or subsessile; achenes glabrous ...... Paranephelius
7. Capitula pedunculate; achenes sparsely pubescent ... Pseudonoseris

Austroliabum H.Rob. \& Brettell emend. D.G.Gut., N.Garcia, Susanna \& M.A.Grossi, Phytologia 28: 48, $1974 \equiv$ Microliabum subgenus Austroliabum (H.Rob. \& Brettell) H.Rob., Syst. Bot. 15: 743, 1990. - TYPE: Austroliabum candidum (Griseb.) H.Rob. \& Brettell $\equiv$ Liabum candidum Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 203. 1879.

Annual, biannual or perennial herbs, rarely subshrubs to 1.5 m tall, loosely branched or sometimes unbranched, with inconspicuous or scarce latex. Stems erect, ascendent or decumbent, with appressed dense white-tomentose pubescence or woolly and hirsute with spreading stipitate glandular trichomes; nodes without sheath, pseudostipules opposite, fused or free, sometimes alternate in upper branches, rarely connected to petiole wings, herbaceous. Leaves opposite, less often alternate in upper branches, conspicuously petiolate with winged or wingless petioles; laminas narrowly or broadly ovate or triangular, bases truncate, cordate or cuneate, apices acute or attenuate, margins subentire, dentate or serrate, mucronulate; acrodromous, 3-veined, main pair of lateral veins reaching the middle of the lamina; surfaces flat, hirsute adaxially usually mixed with white-arachnoid pubescence, greenish or whitish, densely white-tomentose or woolly abaxially, sometimes with stipitate glandular trichomes on main veins. Capitula heterogamous, radiate, few or many, terminal, in an alternate branched corymbiform capitulescence, rarely a single terminal capitulum, pedunculate with peduncles erect, densely white-tomentose or woolly. Involucres campanulate, 4--6-seriate, usually 5-seriate; phyllaries 45--70, imbricate, gradually increasing in length, outer shorter, ovate or narrowly ovate, adpressed, coriaceous, white-tomentose, sometimes with stipitate glandular trichomes, inner oblong or narrowly ovate, adpressed, coriaceous, glabrescent; receptacles flat to slightly convex, foveolate, naked. Florets

65--115, all fertile. Ray florets 25--50, 1-seriate, pistillate, without staminodia; corollas true ray, yellow, rare slightly orange, pubescent with glandular trichomes on outer surface, limbs obovate or elliptical, 4-veined, apices 3-dentate; styles filiform, style branches filiform, curved, with papillae on inter and outer surface. Disc florets 40--65, bisexual; corollas tubular, funnelform, yellow, rare slightly orange, deeply 5-lobed, lobes narrowly ovate, with glandular trichomes on the outer surface; anthers yellow, linear, shortly calcarate and shortly caudate; apical appendages ovate, flat; styles filiform, with sweeping hairs externally from the middle of the style shaft up to the apices, style branches shorter than the pubescent part on shaft below the bifurcation point, filiform, curved at maturity, stylopods enlarged, globose; nectaries disciform, not lobed. Achenes obovoid o obconical, 8--10-ribbed, pubescent with twin hairs usually on ribs, carpopodia conspicuous; pappus distinctly 2 -seriate, outer series of scales, margins erose, inner series of bristles barbellate, fine, persistent. Chromosome number: $2 n=14$ (Bernardello, 1986).

Robinson \& Brettell (1974) mixed diagnostic characteristics from Austroliabum and Microliabum when describing Austroliabum, and the description has to be amended. According to the protologue, Austroliabum included originally species with phyllaries equal or subequal and inner pappus series mostly easily deciduous (Robinson \& Brettell, 1974). Actually, these traits belong only to Microliabum. Austroliabum has phyllaries in 4--6 series, usually five, gradually increasing in length and persistent inner pappus.

Distribution and Habitat. Austroliabum is distributed from northwestern to central Argentina (Fig. 8 A). All species grow in environments of non-Andean mountains: the Pampean ranges ("Sierras Pampeanas", also called "Sierras de Córdoba" and "Sierras de San Luis") and the Sub-Andean ranges ("Sierras Subandinas", for example "Sierras de La Rioja"). The Sierras Pampeanas are a chain of mountains that rise sharply from the surrounding pampa region of Northwest Argentina. They run parallel to the Andes and have a temperate and semi-arid climate. The northern east slope is covered by rainforests, due to high humidity in this subtropical zone. The stretch within Córdoba and San Luis provinces enjoys a Mediterranean-type climate. From a phytogeographical point of view, Austroliabum inhabits in the Chacoan (Serrano and Western districts) Biogeographical Province (Cabrera \& Willink, 1980), in open areas in mid-elevation forest or seasonally dry scrub.

## Key to species of Austroliabum

1. Plants strongly glutinous; stems and petioles hirsute with densely spreading, conspicuous glandtipped trichomes and white tomentum
A. glanduliferum
2. Plants not glutinous, rarely slightly glutinous; stems and petioles with dense white tomentum or wool; spreading gland-tipped trichomes absent or rarely inconspicuous hidden below tomentum 2
3. Stems and abaxial leaf surfaces densely white-tomentose or woolly; petioles wingless or slightly winged in the upper part; laminas ovate or subtriangular up to 8 cm wide; capitula on peduncles up to 4 cm long
A. candidum
4. Stems and abaxial leaf surfaces slightly white-tomentose; petioles widely winged; laminas narrowly ovate or subtriangular up to 6 cm wide; capitula on peduncles up to 10 cm long
A. eremophilum
5. Austroliabum candidum (Griseb.) H.Rob. \& Brettell, Phytologia 28: 49. $1974 \equiv$ Liabum candidum Griseb. in Abh. Königl. Ges. Wiss. Göttingen 24: 203. 1879 [Symb. fl. argent.: 203. 1879] $\equiv$ Microliabum candidum (Griseb.) H.Rob., Syst. Bot. 15: 743. 1990. - TYPE: Argentina. Córdoba: Punilla department, "An einem Felsen zwischen Cosquín und Santa María [de Punilla]", 27 Jan 1876, G. Hieronymus 280 (lectotype: GOET 001801 [photo!], designated by Gutiérrez [2015: 292]; isolectotypes: CORD 00006499!, CORD 00006500!, F 0076427F [photo!], GOET 001802 [photo!]). Type loc.: "C [Córdoba]: in rupibus pr [prope] S [Santa] María". Fig. 9.
$=$ Liabum auriculatum Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 202. 1879 [Symb. fl. argent.: 202. 1879]. - TYPE: Argentina. Córdoba: Punilla department, "Sierra [de] Achala, nordl[ich] von der Cuesta de Copina", 20 Feb 1877, G. Hieronymus 641 (holotype: GOET 001803 [photo!]; isotypes: BAF! [without barcode]; CORD 00006498!). Type loc.: "C [Córdoba]: S [Sierra de] Achala".
$=$ Liabum subcirrhosum S.F.Blake, J. Wash. Acad. Sci. 17: 293. $1927 \equiv$ Liabum candidum Griseb. var. subcirrhosum (S.F.Blake) Cabrera, Bol. Soc. Argent. Bot. 2: 95. 1947. - TYPE: Argentina. Catamarca: Andalgalá department, La Playa, 12 Feb 1917, P. Jörgensen 1673 (holotype: US 00122753 [photo!]).

Annual, biennial or perennial herbs, rarely subshrubs, up to 1.5 m tall, with latex scarce in stems and leaves. Stems erect, ascendent or decumbent, terete, not costate, not or densely branched, densely and persistently white-tomentose or woolly, usually without spreading gland-tipped trichomes or rarely present and then inconspicuous and hidden below tomentum; pseudostipules fused or free, herbaceous. Leaves opposite, scattered along the stem and secondary branches, herbaceous, petiolate; petioles 1--6 $\mathrm{x} 0.1--0.2 \mathrm{~cm}$, wingless or slightly wingled in upper part, white-tomentose or woolly usually without spreading gland-tipped trichomes; laminas $4--12.5 \times 1.5--8 \mathrm{~cm}$, ovate or triangular bases truncate, cuneate or slightly cordate, apices acute, margins evenly serrate or dentate, mucronulate, acrodromous, 3 -veined, with the pair of lateral veins reaching the middle of the lamina, surfaces flat, hirsute or
white-arachnoid pubescent and greenish adaxially, densely white-tomentose or woolly abaxially. Capitula few or many, terminal, in a lax corymbiform capitulescence, pedunculate, peduncles $0.5-4$ cm long, densely white-tomentose or woolly. Involucres $0.8-1.3 \times 0.8-1.3 \mathrm{~cm}$, campanulate, 4--6seriate, usually 5 -seriate, all series adpressed; phyllaries $55--65$, imbricate, coriaceous, outer 3--6.2 x $0.8--1.5 \mathrm{~mm}$, ovate, apices acute or attenuate, hirsute with glandular-tipped trichomes and densely white-tomentose, inner $6--10.2 \times 0.7--1.2 \mathrm{~mm}$, narrowly ovate or oblong, apices acute or attenuate, glabrescent. Ray florets $30-50$, 1 -seriate, pistillate, fertile; corolla 1--1.7 cm long, true ray, yellow, pubescent with glandular-tipped trichomes; tubes $5.6--7 \times 0.2--0.3 \mathrm{~mm}$, pubescent above; limbs 5-$11.5 \times 0.7--1.3 \mathrm{~mm}$, narrowly oblong or obovate, 4 -veined, apices 3 -dentate, pubescent below. Disc florets $50--65$, bisexual, fertile; corolla $5.5--8.5 \mathrm{~mm}$ long, tubular, funnelform, yellow, tube and throat gradually differentiate, 5 -lobed, with glandular-tipped trichomes; tube plus throat $5.2--5.5 \mathrm{~mm}$ long, tubes $0.2--0.3 \mathrm{~mm}$ wide, pubescent above; throats $0.6-1.2 \mathrm{~mm}$ wide, pubescent below; lobes $1.5-1.7$ x ca. 0.3 mm , apically pubescent; style branches $0.5--1.1 \mathrm{~mm}$ long. Achenes $1.3--2.4 \times 0.5--1 \mathrm{~mm}$, obovoid or obconical 8--10-ribbed, pubescent mostly on ribs. Pappus 2 -seriate, outer series up to 0.3 -0.7 mm long, of scales, inner series up to $5.3--9.4 \mathrm{~mm}$ long, of bristles barbellate, fine, persistent. Chromosome number: $2 n=14$ (Bernardello, 1986).

Distribution and Habitat. This species is endemic in central and northwestern Argentina, between $500-2000 \mathrm{~m}$ (Fig. 8 A ). It inhabits slopes, hills, valleys, seldom in canyons ("barrancas"), in scrub, grasslands, dry and sunny places, sometimes in damp grassy places.

Phenology. Plants with flowering capitula have been collected from November to June, mostly in summer and early autumn.

Common Names and Uses. "Margarita de las sierras" (Grossi \& al., 2012), "piojera" (in sched. Dominguez 133, BAF). It was mentioned as species of potential pharmacological interest: sesquiterpenes in aerial organs of the plant and flavonoids in leaves and florets (Ariza Espinar, 2006). Austroliabum candidum has been proposed for cultivation as ornamental because of the beautiful yellow corollas and the whitish pubescence of stems and leaves (Cabrera, 1947; Parodi \& Dimitri, 1972; Gutiérrez, 2017).

Job (in sched. Job 497, LP) mentioned white flowers; however, the common color in the genus is yellow, and we could not find another specimen kept at herbaria or field observations with this color. Specimen Slanis et al. 811 (LIL) with winged petioles shows an uncommon trait within A. candidum, however, the other features fit accurately with this species. On the other hand, according to Grossi \&
al. (2012), it could be an endangered species because its population traits. However, ecological, reproductive and distributional studies are necessary.

In the protologue of Liabum subcirrhosum, Blake (1927) indicated as type the specimen "Jörgensen 1673 " with date " 12 Feb 1917" kept at US ("type no. 922182"). There is only one specimen deposited in US that fits accuratelly with the protologue. This material is the holotype (US 922182 barcode 00122753 ). On the other hand, many specimens with the same collector and collector number were found but with different dates: BA 24737 [20 Dec 1916], GH [26 Feb 1917 and 15 Feb 1916, two sheets], LIL 26626 [15 Feb 1916], SI 000925 [Feb 1916]. These materials can be considered as original materials but not duplicates of the holotype.

Representative Specimens Examined. ARGENTINA. Catamarca: Andalgalá department: La Playa, Feb 1916, Jörgensen 1673 (SI); idem, 15 Feb 1916, Jörgensen 1673 (GH, LIL); idem, 20 Dec 1916, Jörgensen 1673 (BA); idem, 26 Feb 1917, Jörgensen 1673 (GH); Faldes de [Río] Yacuchuyo, Jan 1881, Schickendantz 287 (LP); Cuesta de Mina Capillitas, 2000 m, 30 Jan 1974, Cabrera el al. 24787 (LP). Belén department: Ambato, El Potrero, 15 Mar 1909, Castillon s.n. (Lillo 9213) (LIL 26635); Ambato, El Crestón, 25 Mar 1909, Castillon 1248 (Lillo 9214) (LIL); Ambato, Quebrada de El Rincón, 5 Feb 1910, Castillon 1641 (LIL); [Los] Nacimientos, May 1910, Castillon 1435 (LIL); Pomán department: Pomán, Dec 1909, Spegazzini s.n. (BAB 28207, 28950); desde Pomán a la falda del cerro Ambato, 10 Jan 1910, Spegazzini s.n. (LP ex LPS 10052). Córdoba: Calamuchita department: Sierra Chica, valle de Los Reartes, without date, Castellanos s.n. (BA 24741); valle de Los Reartes, Sierra Chica, 24 Apr 1917, Castellanos 220 (SI); V. [valle] [Los] Reartes, 1917--1919, Castellanos s.n. (SI 9440); Embalse Río Tercero, 12 Jan 1940, Burkart 10496 (LP, SI); Embalse Río Tercero, 24 Apr 1945, Lauro s.n. (BAB 66473); Embalse del Río Tercero, 20 Feb/5 Mar 1964, Roig 4978 (SI); Dique Los Molinos, 27 Jan 1969, Krapovickas \& Cristóbal 14725 (CTES, LP); Embalse Río Tercero, 27 Nov 1998, Delucchi 2144 (LP); Villa del Dique, Embalse Río Tercero, Cerro de los Enamorados, $32^{\circ} 10^{\prime} 36.8^{\prime \prime} \mathrm{S}, 64^{\circ} 25^{\prime} 17.8^{\prime \prime}$ W, $566 \mathrm{~m}, 30$ Jan 2006, D. Gutiérrez \& Di Paola 375 (BA); Capital department: in montanis prope Córdoba, Jan 1881, Spegazzini s.n. (LP s.n., ex LPS 10051); Córdoba, Feb 1896, Stuckert 632 (BAF); Córdoba, without date, Castellanos s.n. (SI 9441); Córdoba, Dec 1899, Domínguez 133 (BAF); Colón department: Sierra Chica, entre el dique San Roque y Casabamba [Casa Bamba], 1 Jun 1910, Kutz s.n. (SI 9442); Villa Allende, Jun 1939, Lahitte 60462 (LP); Ascochinga, 14 Mar 1944, O'Donell \& Rodríguez 871 (LIL); Unquillo, 25 Dec 1947, Meyer 12952 (LIL); La Granja, 6 Jan 1950, Borsini 1188 (LIL); Agua de Oro, Sierra Chica, 4 Feb 1951, Castellanos s.n. (LIL 386907); Cabana, 26 Feb 1957, Caro 2537 (BAF); La Calera, 31 Jan 1958, Lanfranchi 1430 (LP); entre La Granja y Agua de Oro, $31^{\circ} 2^{\prime} 46.1^{\prime \prime} \mathrm{S} 64^{\circ} 16^{\prime} 45.5^{\prime \prime} \mathrm{W}, 723 \mathrm{~m}$,

27 Jan 2006, D. Gutiérrez \& Di Paola 281, 282, 283 (BA, LP); entre La Calera y el puente del dique San Roque, 27 Jan 2006, D. Gutiérrez \& Di Paola 284, 285 (BA); Agua de Oro, 31² $2^{\prime} 75.3^{\prime \prime} \mathrm{S} 64^{\circ}$ 16'81.6" W, 724 m, 9 Apr 2008, D. Gutiérrez et al. 404 (BA, LP); alrededores de Villa Animí, entre El Manzano y Agua de Oro, ruta E53, 14 Mar 2009, D. Gutiérrez 1001 (BA, LP); alrededores de El Manzano, entre El Manzano y Agua de Oro, ruta E53, 30 $4^{\prime} 23.2^{\prime \prime} \mathrm{S} 64^{\circ} 17^{\prime} 46.5^{\prime \prime} \mathrm{W}, 736 \mathrm{~m}, 15$ Mar 2009, D. Gutiérrez 1009 (BA, LP); El Pueblito, entre El Pueblito y Salsipuedes, ruta E53, $31^{\circ} 6^{\prime}$ $46.7^{\prime \prime} \mathrm{S} 64^{\circ} 17^{\prime} 35.6^{\prime \prime} \mathrm{W}, 15$ Mar 2009, D. Gutiérrez 1016 (BA, LP); Cruz de Eje department: entre Capilla del Monte y San Marcos Sierra, después del mirador, $30^{\circ} 47^{\prime} 38.3^{\prime \prime} \mathrm{S}, 64^{\circ} 37^{\prime} 41.6^{\prime \prime} \mathrm{W}, 767$ m, 28 Jan 2006, D. Gutiérrez \& Di Paola 337 (BA, LP); General San Martín department: Villa María, 19 Apr 1939, Navarro 84 (BAB). Punilla department: La Falda, Sierra Chica, 1000 m, 11 Apr 1918, Osten 10390 (BAF); 23 Apr 1917, Osten 10376 (BAF); Uritorco, 27 jan 1922, Castellanos s.n. (BA 24740); alrededores de La Falda, Jan 1936, Job 497 (LP); Cosquín, Pan de Azúcar, 1000--1200 m, Jan-Feb 1936, Rodrigo 553 (LP); Carlos Paz, monte La Ballena, 900 m, 18 Feb 1939, Bridarolli 622 (LP); La Falda, 16 Mar 1939, Dawson 433 (LP); San Antonio de Aredondo, Mar 1940, Gautier 13 (BAB); camino a San Marcos [Sierra], 9 Mar 1941, Nicora 17662a,b (SI); La Falda, 7 Feb 1947, Villafañe 755 (LIL); Molinari, $\pm 750 \mathrm{~m}, 18$ Apr 1947, J. Gutiérrez 150 (LIL); La Falda a El Cuadrado, 22 Jan 1948, de la Sota 498 (LIL); La Falda, 12 Jan 1950, de la Sota 1554 (LIL); Tanti, 13 Jan 1950, de la Sota 1592 (LIL); La Estancita, 17 Jan 1950, de la Sota 1713 (LIL); El Cuadrado, 22 Feb 1950, de la Sota 2071 (LIL); Pan de Azúcar, 26 Feb 1950, de la Sota 2251 (LIL); San Marcos Sierra, 24 Jan 1951, de la Sota 4113 (LIL); near Capilla del Monte, path up cerro Uritorco, $30^{\circ} 51^{\prime} \mathrm{S} 64^{\circ} 30^{\prime} \mathrm{W}$, 1550 m, 23 Jan 1966, Hawkes et al. 3290 (K, LP); Carlos Paz, Sierra Chica, falda W, 6 Feb 1966, Ariza Espinar 2149 (CTES); Villa Carlos Paz, 16 Apr 1977, Gautier 8570 (LP); entre Santa María de Punilla y Villa Caerio, ruta 34, km 28, $31^{\circ} 18^{\prime} 29.7^{\prime \prime} \mathrm{S} 64^{\circ} 27^{\prime} 50,3^{\prime \prime} \mathrm{W}, 674 \mathrm{~m}, 27 \mathrm{Jan} 2006, D$. Gutiérrez \& Di Paola 293 (BA); entre Capilla del Monte y San Marcos Sierra, antes del mirador, $30^{\circ}$ $50^{\prime} 12.6^{\prime \prime}$ S $64^{\circ} 34^{\prime} 44.5^{\prime \prime}$ W, $901 \mathrm{~m}, 28$ Jan 2006, D. Gutiérrez \& Di Paola 333 (BA); Río Cuarto department: Achiras, 21 Jan 1932, King 193 (LP); Río Seco department: Cerro Colorado, 5 May 1956, Caro 2002 (BAF); San Alberto department: Dique La Viña, 23 Mar 1947, Terribile 730 (LIL); San Javier department: Paso de la Peña, 19[27], Castellanos s.n. (BA 11856); San Javier, Quebrada del Tigre, 1200 m, 1940, Bridarolli 1596 (LP); San Javier, cuesta del cerro Champaquí, 20 Jan 1967, Fabris \& Pérez Moreau 6800 (BAB, LP); Santa María department: Without locality, 31 Mar 1894, Without collector 2288 (LIL 26627); [La] Ochoa [near Malagueño], Sierra Chica, 29 Mar 1899, Stuckert 6693 (BA, BAF, SI); Cumbre Chica, 1000 m, Mar 1930, King 639 (LP); Alta Gracia, Puesto El Cura, 27 Jan 1944, Pierotti s.n. (LIL 100642); Peñón del Aguila, 1900 m, 28 Apr 1946, Pierotii 5071 (LIL); [Cerro] Ochoa, Sierra Chica, 11 Mar 1954, Hunziker 8985 (LP); Embalse Los Molinos, 21 Feb 1965, Cabrera et al. 16553 (LP); Embalse Los Molinos, 2 Apr 1973, Cabrera et al.

23808 (LP); ruta 34, entre 1 y 4 km al norte del paredón del dique Los Molinos, $600-700 \mathrm{~m}, 18$ Jan 1992, Novara \& Bruno 10540 (LIL, S); entre Los Reartes y Ciudad de América, cerca de Ciudad de América, 20 km antes de la ruta Alta Gracia-Villa General Belgrano, $31^{\circ} 47^{\prime} 17,5^{\prime \prime} \mathrm{S} 64^{\circ} 30^{\prime} 47,5^{\prime \prime}$ W, 30 Jan 2006, D. Gutiérrez \& Di Paola 393 (BA); Dique Los Molinos, Villa Ciudad de América y Villa de la Merced, $31^{\circ} 48^{\prime} 58.1^{\prime \prime}$ S $64^{\circ} 30^{\prime} 62.2^{\prime \prime}$ W, $822 \mathrm{~m}, 9$ Apr 2008, D. Gutiérrez et al. 419 (BA, LP); Totoral department: Sarmiento, 30 Jan 1951, de la Sota 4248 (LIL); Probably Colón-Punilla-Santa María departments: Sierra Chica, Feb 1925, 1600 m, Lossen 146 (SI); La Rioja: Sanagasta department: Dique Los Sauces, faldas del Velazco, 1100 m, 17 Feb 1944, Hunziker 4842 (LIL, LP); San Luis: Juan Martín de Pueyrredón (= La Capital) department: [El] Volcán, saliendo del pueblo hacia Trapiche, 7 Feb 1999, Seijo 1754 (CTES); Coronel Pringles department: Pampa del Alto Grande, Feb 1931, Gez s.n. (BA 31/229); General Pedernera department: El Morro, 1913, Pastore 29 (SI); Junín department: Merlo, Piedra Blanca, 1000 m, 8 Feb 1947, Digilio \& Grassi 2127 (CTES, LIL); El Rincón, Sierra de los Comechingones, 8 Feb 1956, Caro 1757 (BAF); Sierra de Comechingones, falda O, frente a El Rincón, 8 Feb 1956, Hunziker 11757 (CORD); Merlo, Mal Paso, $32^{\circ} 19^{\prime} 49^{\prime \prime} \mathrm{S} 64^{\circ} 59^{\prime} 36.2^{\prime \prime} \mathrm{W}, 976 \mathrm{~m}, 29$ Jan 2006, D. Gutiérrez \& Di Paola 361 (BA); alrededores de Merlo, camino al Filo, Jan 2011, D. Gutiérrez \& Quijano 1020 (BA); Libertador General San Martin department: [Cerro] Intihuasi, Mar 1937, Pastore 2041 (SI); without department, Fries s.n. (Jul 1878, Miers 888) (K). Tucumán: Faimallá department: Quebrada de Lules, 30 Aug 1949, Sás 64 (LP); Chicligasta department: Cuesta del Clarillo [RN 65, border of Catamarca-Tucumán], 10 Apr 2002, Slanis et al. 811 (LIL).
2. Austroliabum eremophilum (Cabrera) H.Rob. \& Brettel, Phytologia 28: 49. $1974 \equiv$ Liabum eremophilum Cabrera in Bol. Soc. Argent. Bot. 2: 96. $1947 \equiv$ Microliabum eremophilum (Cabrera) H.Rob., Syst. Bot. 15: 744. 1990. - TYPE. ARGENTINA. Salta: Cafayate department, Sierra del Cajón, El Alisal, 2800 m, 17 Jan 1914, D. Rodriguez 1294 (lectotype: LP 000299!, designated as holotype by Freire \& Iharlegui in Darwiniana 38: 324. 2000; isolectotypes: CORD 00005457!, LP $000300!$, LP 000301!, SI 000912!). Fig. 10.

Annual or perennial herbs, rarely subshrubs, up to 1 m tall, with with scarce latex in stems and leaves. Stems erect, ascendent or decumbent, terete, not costate, slightly branched, densely and persistently white-tomentose, rarely with glandular-tipped trichomes hidden below the tomentum; pseudostipules free or fused, usually continuing with petiole wings, herbaceous. Leaves opposite, scattered along the stem and secondary branches, herbaceous, petiolate, rarely sessile; petioles $1--2 \times 0.2--0.4 \mathrm{~cm}$, usually winged with wide wings, margins entire, rarely with glandular-tipped trichomes; laminas 4.5--12 x $0.5--3.5(--6) \mathrm{cm}$, narrowly ovate or narrowly subtriangular, sometimes ovate or subtriangular; base
usually decurrent, sometimes cuneate, rounded or cordate, apices acute or attenuate, margins slightly dentate or entire, mucronulate, acrodromous, 3-veined, with the pair of lateral veins reaching the middle of the lamina, surfaces flat, hirsute, greenish adaxially, white-tomentose abaxially. Capitula few, terminal, in a lax corymbiform capitulescence, pedunculate, peduncles $2.5-10 \mathrm{~cm}$ long, rarely shorter, white-tomentose with glandular-tipped trichomes. Involucres $0.8-1.3 \times 0.9--1.5 \mathrm{~cm}$, campanulate, 4--6-seriate, usually 5 -seriate, all series adpressed, phyllaries $55--70$, imbricate, coriaceous, outer $3--6.5 \times 1--1.5 \mathrm{~mm}$, ovate, apices acute or attenuate, hirsute with glandular-tipped trichomes and densely white-arachnoid, greenish, inner $7--10 \times 0.6-1.2 \mathrm{~mm}$, narrowly ovate or oblong, apices acute or attenuate, slightly glandular-pubescent or glabrescent, greenish. Ray florets 35-$-40(--50), 1$-seriate, pistillate, fertile; corollas $1--2 \mathrm{~cm}$ long, true ray, yellow or slightly orange, pubescent with glandular-tipped trichomes; tubes $6.5--10 \times 0.3--0.6 \mathrm{~mm}$, pubescent above; limbs $6--12$ x $1.4-2 \mathrm{~mm}$, narrowly elliptical or obovate, 4 -veined, apices 3 -dentate. Disc florets 40--50, bisexual, fertile; corollas $5.5--9 \mathrm{~mm}$ long, tubular, funnelform, yellow or slightly orange, tube and throat gradually differentiate, 5-lobed, pubescent with glandular-tipped trichomes; tube plus throat 5.8--6.3 mm long, tubes ca. 0.5 mm wide, pubescent above; throats $0.6--1 \mathrm{~mm}$ wide, pubescent below; lobes $2.5--3 \mathrm{x}$ ca. 0.3 mm , apices pubescent; style branches $0.5--1 \mathrm{~mm}$ long. Achenes $1.4--2.5 \times 0.5--1 \mathrm{~mm}$, obovoid or obconical, 8 --10-ribbed, pubescent mostly on ribs. Pappus 2 -seriate, outer series up to 0.3 --$0.5(--1) \mathrm{mm}$ long, of scales, inner series up to $4.2--7(--8) \mathrm{mm}$ long, of bristles, barbellate, fine persistent. Chromosome number unknown.

Distribution and Habitat. This species is endemic of Sub-Andean Hills, especially Calchaquíes (also known as del Cajón) mountains and around Los Sauces dam in northwestern Argentina at 850--3000 m (Fig. 8. A). It inhabits high elevations associated with woods of Alnus acuminata Kunth ("aliso del cerro") and lower valleys.

Common Name. It was mentioned as "cepa de caballo sin espinas" in a label (Droglietti s.n., LIL 157716). However, the Spanish common name "cepa caballo" (English "spiny clotbur") refers to the widespread distributed species Xanthium spinosum L. (Asteraceae).

Phenology. Plants with flowering capitula have been collected from January to April, in summer and early autumn.

Original specimens were collected from 1912 to 1916 in mountains named Sierra del Cajón (currently Sierra de Quilmes) in northwestern Tucumán and southwestern Salta provinces. In addition, the protologue indicates "El Alisal". There is a town in southeastern Salta with this name but very far
from that mountains. Probably, "El Alisal" does not refer to a town name but an environment with trees of Alnus acuminata Kunth (common name: "aliso", "aliso del cerro"). An original label in handwriting (in a material kept at BAF) supports this view because it says "alisal" in lowercase. This point of view agrees with Cabrera (1993: 450, 459, 469).

In the protologue of $L$. eremophilum, Cabrera (1947) indicated as type the gathering D. Rodriguez 1294 with date " 17 Jan 1914" kept at LP and isotypes in LIL and SI. However, the unique specimen found in LIL (LIL 001804) actually is from "16 Jan 1914". On the other hand, those in BAB (without barcode) and BAF (without barcode) were labelled as collected by F. M. Rodríguez since brothers Demetrio and Francisco Manuel Rodríguez used to put the same collector number, and indistinctly their names, for different date collection (e.g., Cabrera, 1993: 469). As a result, we considered the specimens mentioned above plus BA 24736 [15 Jan 1914], BAB [16 Jan 1914], and BAF [12 Jan 1914] as paratypes. Because the lectoype was designated with date " 17 Jan 1914", duplicates are only deposited in CORD, LP and SI. In addition, gatherings Castillón 3435 and Lillo 18035 are paratypes, too.

Representative Specimens Examined. ARGENTINA. Catamarca: Ancasti department: without locality, Feb 1910, Spegazzini s.n. (BAB 29202, 29203). Belén department, Las Cuevas, $4000 \mathrm{~m}, 2$ Apr 1946, Droglietti s.n. (LIL 157716); wihout department: wihout locality, Jan-Feb 1910, Spegazzini s.n. (BAB 34007). La Rioja: Sanagasta department, La Rioja, dique [Los Sauces], 2 Mar 1941, Burkart 12624 (SI, LP); Capital department, Quebrada Los Sauces, Dique [Los Sauces], Feb 1939, Rodrigo 2079 (LP); Quebrada del Sauce, national rd 75, 7 km to monument of Facundo Quiroga, 700 m, 14 Apr 1975, Okada 6110 (SI); Quebrada de Los Sauces, Dique de Los Sauces, RP 1, 12.5 km SE de Sanagasta, $850 \mathrm{~m}, 11$ Apr 2008, D. Gutiérrez et al. 500 (BA, LP, S); RN 75, S of Sanagasta and NW of La Rioja, $29^{\circ} 23^{\prime} 13^{\prime \prime} \mathrm{S} 66^{\circ} 58^{\prime} 41.6^{\prime \prime} \mathrm{W}, 877 \mathrm{~m}, 8$ Mar 2016, Funk \& Bonifacino 13257 (LP). Salta: Cafayate department, Sierra del Cajón, El Alisal, $2800 \mathrm{~m}, 12$ Jan 1914, F. Rodríguez 1294 (BAF); ídem, 15 Jan 1914, D. Rodríguez 1294 (BA); ídem, 16 Jan 1914, D. Rodríguez 1294 (LIL); ídem, F. Rodriguez 1294 (BAB). Tucumán: Tafí del Valle department, Cumbres Calchaquíes, Machoguañusco, 3000 m, 4 Feb 1914, Castillón 3435 (CORD, LIL); Tafí, Jan 1912, Lillo 18035 (CORD, LIL); ruta a Tafí del Valle, Km 40, 21 Mar 1987, Xifreda \& Maldonado 655 (SI).
3. Austroliabum glanduliferum (Cabrera) D.G.Gut., N.Garcia, Susanna \& M.A.Grossi, nov. comb. $\equiv$ Liabum candidum Griseb. var. glanduliferum Cabrera in Bol. Soc. Argent. Bot. 2: 96. $1947 \equiv$ Microliabum glanduliferum (Cabrera) H.Rob., Syst. Bot. 15: 744, 1990. - TYPE: Argentina. San

Luis: Juan Martín de Pueyrredón (= La Capital) department, Estancia Grande, 16 Jan 1911, F. Pastore 124 (lectoype: SI [without barcode; missing], designated as type by Robinson in Syst. Bot. 15: 744. 1990; LP 000297! designated as holotype by Freire \& Iharlegui in Darwiniana 38: 324. 2000). Fig. 11.

Annual or perennial herbs, rarely subshrubs, up to 0.6 m tall, with scarce latex in stems and leaves. Stems erect, ascendent or decumbent, slightly branched, terete, not costate, densely and persistently white-tomentose and with very dense pubescence of glandular-tipped trichomes; pseudostipules free or fused, herbaceous. Leaves opposite, scattered along the stem and secondary branches, herbaceous, petiolate; petioles $1.5--3 \times 0.1--0.2 \mathrm{~cm}$, wingless or slightly winged in upper part, rare narrowly winged with margin entire, dense and persistently white-tomentose and with dense pubescence of glandular-tipped trichomes; laminas $3.5--7.5 \times 2--5(--6.6) \mathrm{cm}$, ovate or triangular, bases truncate or cuneate, sometimes slightly decurrent, apices acute, margins dentate, denticulate or serrate, mucronulate, acrodromous, 3 -veined, with the pair of lateral veins reaching the middle of the lamina, surfaces flat, hirsute and greenish, sometimes with lax white-arachnoid pubescence adaxially, densely white-tomentose with glandular-tipped trichomes abaxially. Capitula many or few, terminal in a lax corymbiform capitulescence, pedunculate, peduncles $0.7--4.5 \mathrm{~cm}$ long, erect, densely white-tomentose mixed with numerous glandular-tipped trichomes. Involucres $0.9-1.3 \times 0.9--1.5 \mathrm{~cm}$, campanulate, $4-$ 6 -seriate, usually 5 -seriate, all series adpressed, phyllaries 45-65, imbricate, coriaceous, outer 3.5--6 x $1--1.6 \mathrm{~mm}$, ovate, apices acute or attenuate, densely pubescent with glandular-tipped trichomes and white-tomentose, inner $7.2-11 \times 0.7--1.1 \mathrm{~mm}$, narrowly ovate or oblong, apices acute or attenuate, slightly pubescent above with glandular-tipped trichomes, glabrescent below. Ray florets $25--35(--40)$, 1 -seriate, pistillate, fertile; corolla $0.9-1.9 \mathrm{~cm}$ long, true ray yellow, pubescent with glandular-tipped trichomes; tubes $4.5--6 \times 0.5-0.6 \mathrm{~mm}$, pubescent above; limbs $5--12 \times 0.4-1.5 \mathrm{~mm}$, narrowly elliptical or obovate, 4-veined, apices 3-dentate. Disc florets 40--55(--60), bisexual, fertile; corolla 6.5--9.9 mm long, tubular, funnelform, yellow, tube and throat gradually differentiate, 5-lobed, pubescent with glandular-tipped trichomes, tube plus throat $5.5--5.8 \mathrm{~mm}$ long, tubes $0.4--0.7 \mathrm{~mm}$ wide, pubescent above, throats $0.6-1.4 \mathrm{~mm}$ wide, pubescent below, lobes $2--2.8 \times 0.4--0.5 \mathrm{~mm}$, apices pubescent; style branches $0.5--1 \mathrm{~mm}$ long. Achenes $1.2--2 \times 0.5--0.8 \mathrm{~mm}$, obovoid or obconical, 8 -10 -ribbed, densely pubescent mostly on ribs. Pappus 2 -seriate, outer series up to $0.5-1 \mathrm{~mm}$ long, of scales, inner series up to $6.8-8.6 \mathrm{~mm}$ long, of bristles barbellate, fine, persistent. Chromosome number unknown.

Distribution and Habitat. This species is endemic in central Argentina in Pampean Hills, between 800 to 1350 m (Fig. 8 A). It inhabits rocky soils, hills, slopes, valleys, grasslands, scrublands, and canyons near rivers.

Phenology. Plants with flowering capitula have been collected from December to March, in summer.

Originally, Cabrera (1947) described this species as a variety of Liabum candidum because of the conspicuous glandular trichomes. Robinson (1990) elevated this variety to species rank of Microliabum using mainly this trait. Cabrera and Iharlegui (1999) kept it as a variety under Liabum candidum. Cabrera et al. (1999) pointed out that the presence of conspicuous glandular trichomes was a feature highly variable and included this variety as a synonym of Microliabum candidum. Gutiérrez (2008) followed this point of view in a catalogue. Recently, Gutiérrez (2015) considered it a current well-defined species under Microliabum based on new collections, field work, and a detailed morphological study. Thus, we follow this last point of view.

In the original description of var. glanduliferum, Cabrera (1947) designed the gathering Pastore 124 as type ("tipo") kept at SI and LP, meaning syntypes. In the protologue, this author also cited many paratypes in BA, CORD, LP and SI. Robinson (1990) cited the specimen kept at SI as type, meaning the lectotype. To the contrary, Freire \& Iharlegui (2000) wrongly mentioned that the type specimen kept at LP was the holotype. Since the lectotype kept at SI was missing (M. Belgrano, pers. comm.), the selection of the specimen kept at LP as holotype made by Freire and Iharlegui can be considered as a lectotype designation for the name Liabum candidum Griseb. var. glanduliferum Cabrera.

Representative Specimens Examined. ARGENTINA. Córdoba: Calamuchita department, La Cruz de Silveira, 26 Jan 1885, Kurtz 139 (CORD); Minas department, Cerro de Criosu [?], 20 Feb 1876, Hieronymus s.n. (CORD); Pocho department, Sierra de Mogigasta, 19 Feb 1922, Castellanos s.n. (BA 24738); entre La Palmas y La Mudana, 16 Feb 1952, Hunziker 9783 (CORD, CTES, LP); falda norte del Cerro Yerba Buena, 17 Feb 1952, Hunziker 9824 (CORD); Sierra de Pocho, falda oeste, frente a Chancaní, en las inmediaciones de la ruta provincial 28 (ex nacional 20), 6 Jan 1955, Hunziker 10562 (CORD); Sierra de Pocho, Los Túneles, 6 Dec 1958, Burkart 20859 (SI); Pocho-San Alberto departments, Sierra de Pocho, 11 Mar 1921, Castellanos s.n. (LIL 36422); Punilla department, Sierra Chica, falda oeste, Carlos Paz, 2 Jan 1966, Ariza Espinar 2109 (CORD). San Luis: Ayacucho department, inmediaciones del Dique Luján, 800 m, 17--20 Feb 1960, Hunziker \& Cocuссі 14965 (CORD); Ayacucho-Coronel Pringles-La Capital departments, entre Cerro [Valle] de Piedra y San Francisco [del Monte de Oro], 1925, Deletang-Guiñazu s.n. (BAB); AyacuchoLibertador General San Martín departments, Quebrada del Río Quines, 12 Mar 1882, Galander s.n. (CORD); Quebrada del Río de Quines, 16 Feb 1925, Castellanos s.n. (BA 25/1064); Coronel Pringles department, nacimiento del Río Quinto, 22 Jan 1969, Roig 5633 (CORD); Loma Alta, entre

Los Membrillos y Paso del Rey, 1350 m, 20 Feb 1979, Anderson et al. 3582 (CORD); Embalse La Florida, a 7.2 km al E del empalme de RP 17 con RP $39,33^{\circ} 6^{\prime} 35.8^{\prime \prime} \mathrm{S} 66^{\circ} 0^{\prime} 13.3^{\prime \prime} \mathrm{W}, 1034 \mathrm{~m}, 10$ Apr 2008, D. Gutiérrez et al. 467 (BA, LP); idem, $33^{\circ} 6^{\prime} 36.95^{\prime \prime} \mathrm{S} 66^{\circ} 0^{\prime} 8.08^{\prime \prime} \mathrm{W}$, 29 Nov 2016, D. Gutiérrez et al. 1151 (BA). Juan Martín de Pueyrredón (= La Capital) department, Intihuasi [Inti Huasi], Mar 1937, Pastore 2041 (SI); Cerro El Lince, 1050 m, 19 Feb 1971, Anderson 2143 (CORD); Junín department, El Talita [Talita], 50 km al W de Santa Rosa [de Conlara], 29 Jan 1944, Burkart 13987 (SI). Without department, Quebrada del Salado, Bebida de Las Vacas, 9 Mar 1882, Galander s.n. (CORD, F); Sierras de San Luis, Cuesta de los Picazos, 21 Feb 1925, Castellanos s.n. (BA 25/1111).

Microliabum Cabrera, Bol. Soc. Argent. Bot. 5: $211.1955 \equiv$ Liabellum Cabrera, Not. Mus. La Plata 17: 76. 1954, nom illeg. (not Liabellum Rydb.). — TYPE: Microliabum humile (Cabrera) Cabrera (= Liabellum humile Cabrera) $\equiv$ Angelianthus H.Rob. \& Brettell, Phytologia 28: 48. 1974.

Annual or biannual herbs, rarely subshrubs, from 3 cm (including pedunculate capitula) up to 2 m tall, lax branched or unbranched, usually with conspicuous latex in stems and leaves. Stems erect, with appressed densely or sparcely white-tomentose pubescence or hirsute-pubescent with spreading stipitate glandular trichomes, rarely glabrescent; nodes without sheath, pseudostipules present or absent, if present free or fused, herbaceous. Leaves opposite, sometimes grouped at the plant base, petiolate, inconspicuously petiolate or sessile; petioles if present usually winged; laminas narrowly or broadly ovate or triangular, bases truncate, cordate, cuneate or decurrent, sometimes hastate, apices acute or attenuate, margins evenly or unevenly dentate or serrate, mucronulate, acrodromous, 3veined, main pair of lateral veins reaching the middle of the lamina; surfaces flat, glabrous, glabrescent or hirsute, greenish, usually mixed with white-arachnoid pubescence adaxially, whitetomentose abaxially. Capitula heterogamous, radiate, few or many, in a terminal alternate branched corymbiform capitulescence, sometimes a single terminal capitulum, pedunculate, peduncles erect or nutant. Involucres hemispherical, 2--4-seriate, usually 3-seriate, phyllaries 15--25 (M. humile) or 45-75 (M. mulgediifolium, M. polymnioides), subimbricate, decreasing in length, outer longer, oblong or narrowly ovate, exserted, herbaceous, with glandular-tipped trichomes, inner narrowly ovate, adpressed, herbaceous, with glandular-tipped trichomes, innermost narrowly ovate or obovate, sometimes inconspicuous, reduced, membranaceous, glabrescent; receptacles flat to slightly convex, foveolate, naked. Florets ca. 25--30 (M. humile) or 145--195 (M. mulgediifolium, M. polymnioides), yellow, rare slightly orange, all fertile. Ray florets ca. 10-15 (M. humile) or 35--75 (M. mulgediifolium, M. polymnioides), 1--2-seriate, pistillate, without staminodia, corollas true ray, pubescent with glandular trichomes on outer surface, limbs obovate or elliptical, 4-veined, apices 3-
dentate; styles filiform, style branches curved, with papillae on inner surfaces. Disc florets ca. 15 ( $M$. humile) or 100--125 (M. mulgediifolium, M. polymnioides), bisexual, corollas tubular, funnelform, lobes long, narrowly ovate, with glandular trichomes on outer surface; anthers linear, shortly calcarate and shortly caudate, yellow, apical appendages ovate, flat; styles filiform with sweeping hairs externally from the middle of their stalks up to the apices, style branches shorter than the pubescent part on shaft below the bifurcation point, filiform, curved at maturity, stylopods enlarged, globose, nectaries not lobed. Achenes obovoid or obconical, 8 --10-ribbed, carpopodia conspicuous, pubescent on all the surface. Pappus distinctly 2 -seriate, outer series of scales, paleaceous, margins serrulate, deciduous or persistent, inner series of scales, paleaceous (M. humile) or bristles babellate, fine or slightly broadened (M. mulgediifolium, M. polymnioides), margins serrulate, deciduous. Chromosome number: $2 n=12$ (Rozenblum \& al., 1985).

Distribution and Habitat. Microliabum is distributed from central Bolivia to northwestern Argentina (Fig. 8 B). Species grow in the Sub-Andean Hills ("Sierras Subandinas"), the Eastern Cordillera of the Andes, and the High Cordillera. It is distributed in the Chacoan (Western districts), Yungas, and High Andean biogeographical provinces (Cabrera \& Willink, 1980). Microliabum inhabits open areas in mid-elevation forest, wet forest or seasonally dry scrub, and one species grows in alpine habitats.

## Key to species of Microliabum

1. Small plants up to 15 cm tall; leaves grouped at the base, sessile; phyllaries $15--25$; ray florets 10 --$15(--18), 1$-seriate, and disc florets ca. 15; pappus with inner series of paleaceous scales up to 1.8-2.6 mm long M. humile 1. Plants up to 2 m tall; leaves scattered along the stems and secondary branches, petiolate; phyllaries 45--75; ray florets $35-75$, 2 -seriate, and disc florets $100-125$; pappus with inner series of barbellate bristles up to $2.9-6 \mathrm{~mm}$ 2. Slender herbs; erect or nutant capitula in a lax corymbiform capitulescence; slightly
broadened bristles of inner series of pappus ................................. M. mulgedifolium 2. Stout herbs, rarely subshrubs; erect capitula in a dense or lax corymbiform capitulescence; fine bristles of inner series of pappus $\qquad$ . M. polymnioides 1. Microliabum humile (Cabrera) Cabrera, Bol. Soc. Argent. Bot. 5: 211. $1955 \equiv$ Liabellum humile Cabrera in Notas Mus. La Plata, Bot. 17: 78. $1954 \equiv$ Angelianthus humilis (Cabrera) H.Rob. \& Brettell, Phytologia 28: 48. 1974. — TYPE: Argentina. Jujuy: Tilcara department, Río Estancia Vieja,
cerca de Abra Mayo, 3300 m, 21 Mar 1952, E. Petersen \& J. Hjerting 45 (holotype: LIL 001806!; isotype: LP 000296!). Fig. 12.

Small annual herbs, up to 15 cm tall. Stems erect or ascendent, slender, terete, not costate, unbranched or scarsely branched, slightly tomentose, rarely with glandular-tipped trichomes, without pseudostipules. Leaves opposite, few, grouped at base of the plant, herbaceous, sessile; laminas 1--3.7 x $0.3--1 \mathrm{~cm}$, narrowly ovate, bases decurrent, apices acute, margins entire, slightly serrate or dentate, mucronulate, acrodromous, 3 -veined, with the pair of lateral veins reaching the middle of the lamina, sometimes veins inconspicuous, surfaces flat, glabrescent, greenish adaxially, white-tomentose abaxially. Capitula few, terminal in a lax corymbiform capitulescence or not grouped, or a single capitulum, pedunculate, peduncles $0.8-4 \mathrm{~cm}$ long, erect or ascendent, densely pubescent with glandular-tipped trichomes. Involucres $5--8 \times 9$--16 mm, hemispherical, 2--3-seriate; phyllaries $15-\mathrm{-}$ 25 , subimbricate, decreasing in length, outer longer, $4.2--7.3 \times 0.8--2.1 \mathrm{~mm}$, ovate or oblong herbaceous, apices acute, hirsute with glandular-tipped trichomes, sometimes white-arachnoid at the base, inner 3.1--5.5 x 1--2.3 mm, narrowly ovate or obovate herbaceous or menbranaceous, apices acute or attenuate, slightly hirsute with glandular-tipped trichomes or glabrescent. Ray florets 10--15(--18), 1 -seriate, pistillate, fertile; corolla $4.4-7 \mathrm{~mm}$ long, true ray, yellow, slightly pubescent with glandular-tipped trichomes or glabrescent, tubes $0.7--0.9 \times 0.2-0.4 \mathrm{~mm}$, limbs $3.2--5 \times 0.5--1.1 \mathrm{~mm}$, narrowly elliptical or ovate, 4-veined, apices 3-dentate, sometimes entire or 2-dentate. Disc florets ca. 15, bisexual, fertile; corolla $2.1-2.8 \mathrm{~mm}$ long, tubular, funnelform, 5 -lobed, yellow, tube and throat gradually differentiate, slightly pubescent or glabrescent, tube plus throat $1.7-1.9 \mathrm{~mm}$ long, tubes $0.3-$ -0.4 mm wide, glabrous, throats $0.5--1 \mathrm{~mm}$ wide, glabrous, lobes $1--1.5 \times 0.2-0.3 \mathrm{~mm}$, apices pubescent; style branches $0.2-0.4 \mathrm{~mm}$ long. Achenes $1.1-2.2 \times 0.4-1 \mathrm{~mm}$, obovoid or obconical, $8-$ ribbed, pubescent. Pappus distinctly 2 -seriate, outer up to $0.6-0.8 \mathrm{~mm}$ long, of $8-10$ scales paleaceous, inner up to $2.2--2.6 \mathrm{~mm}$ long, of 8 scales, paleaceous, easily deciduous. Chromosome number unknown.

Phenology. Plants with flowering capitula have been collected in March to April, in autumn.

Distribution and Habitat. This species is endemic in northwestern Argentina between 3300--3400 m (Fig. 8 B). It inhabits high mountains near rivers, slopes and valleys.

Representative Specimens Examined. ARGENTINA. Jujuy: Doctor Manuel Belgrano department, entre León y Nevado de Chañi, La Peña, Mar 1963, Fabris et al. 4169 (LP). Salta: Santa Victoria department, Cuesta de Santa Cruz, $22^{\circ} 9^{\prime}$ S $65^{\circ} 2^{\prime}$ W, 3400 m, 27 Apr 1974, Okada 5953 (LP, US).
2. Microliabum mulgediifolium (Muschl.) H.Rob., Syst. Bot. 15: 743. $1990 \equiv$ Liabum mulgediifolium Muschl. in Bot. Jahrb. Syst. 50, 2/3, Beibl. 111: 85. $1913 \equiv$ Austroliabum mulgediifolium (Muschl.) H.Rob. \& Brettell, Phytologia 28: 49. 1974. - TYPE: Bolivia. Tarija: Aniceto Arce prov., "Camacho, K. Fiebrig 2870" (holotype B [destroyed], photo FM 18116!; lectotype: K 000037288 [photo!] [designated by Robinson, 1990: 473]; isolectotype [fragment of K], US 00122729 [photo!]). Fig. 13.

Annual, biennial or perennial herbs up to 2 m tall, rarely smaller up to 7 cm . Stems erect, slender, terete, not costate, few or many-branched, hirsute with glandular-tipped trichomes or glabrescent, pseudostipules free or fused, or absent, herbaceous. Leaves opposite, scattered along the main stem and secondary branches, herbaceous, conspicuously petiolate, rarely sessile; petiole $0.8-10.4 \times 0.1--$ 1.6 cm , widely winged, wings margin unevenly dentate; laminas $2.2--22 \times 1.2--19 \mathrm{~cm}$, widely subtriangular or subtriangular, bases cuneate or cuneate-hastate, apices acute, margins widely dentate or serrate, mucronulate, acrodromous, 3 -veined, main pair of lateral veins reaching the middle of the lamina, surfaces flat, lax hirsute and greenish adaxially, white-tomentose abaxially. Capitula many, terminal in a lax corymbiform capitulescence, rarely few or with a single capitulum, pedunculate, peduncles $1.1--8 \mathrm{~cm}$ long, usually nutant, densely hirsute with glandular-tipped trichomes. Involucres $0.5--1.1 \times 1--2.4 \mathrm{~cm}$, hemispherical, $2--4$-seriate, usually 3 -seriate, outer series conspicuously exserted, phyllaries 45--75, rarely lesser, subimbricate, herbaceous, outer $4.4-12 \times 1--1.8 \mathrm{~mm}$, ovate, apices acute or attenuate, densely hirsute with glandular-tipped trichomes, inner 4.4--6.5 x 0.7--1.4 mm , narrowly ovate or oblong, apices acute or attenuate, hirsute with glandular-tipped trichomes, sometimes glabrescent, innermost inconspicuous, reduced, membranaceous, glabrescent. Ray florets $35-60$, 2 -seriate, pistillate, fertile, corolla $0.7-1.6 \mathrm{~cm}$ long, true ray, yellow, pubescent with glandular-tipped trichomes, tubes $5--7.5 \times 0.3--0.4 \mathrm{~mm}$, pubescent, limbs $4.5-11 \times 0.8--1.5 \mathrm{~mm}$, narrowly elliptical or obovate, 4 -veined, pubescent below, apices 3-dentate. Disc florets 110-125, bisexual, fertile, corolla $3.1--6.5 \mathrm{~mm}$ long, tubular, funnelform, tube and throat gradually diferenciate, deeply 5 -lobed, yellow, pubescent with glandular-tipped trichomes, tube plus throat $6-6.8 \mathrm{~mm}$ long, tubes $0.4--0.5 \mathrm{~mm}$ wide, pubescent, throats $0.6--1.1 \mathrm{~mm}$ wide, pubescent, lobes $2--2.3 \times 0.4--0.5 \mathrm{~mm}$, pubescent; style branches $0.3-0.6 \mathrm{~mm}$ long. Achenes $1--2.2 \times 0.5--0.7 \mathrm{~mm}$, obovoid or obconical, 8 -10 -ribbed, pubescent. Pappus distinctly 2 -seriate, outer up to $0.4-0.8 \mathrm{~mm}$ long, of scales, paleaceous, inner up to $2.9--4.7 \mathrm{~mm}$ long, of bristles barbellate, slightly broadened, easily deciduous. Chromosome number unknown.

Distribution and Habitat. This species occurs in southern Bolivia near the border of Argentina, and northwestern Argentina, between 1250--1450 m (Fig. 8 B). It inhabits Yungan and usually Chacoan environments in roadsides, slopes, mountains or edges of forests. One label indicates that a specimen was collected in silty-sandy soil with pH 6.8 .

Phenology. Plants with flowering capitula have been collected in March to May, from the end of summer to the end of the autumn.

Originally, this species was known only from the department of Tarija in Bolivia (Robinson, 1990). However, it was recently found in the province of Salta, northwestern Argentina (Gutiérrez \& Novara, 2009; Gutiérrez, 2015a). This species is easily differentiated from M. polymnioides because of its slender stems, lax few or many-headed capitulescences with usually nutant capitula on long peduncles, and pappus usually with slightly broadened inner pappus elements. However, some traits (i.e., slender stems and nutant capitula) are not very conspicuous in dry specimens.
This species commonly grows in populations of many individuals. Since these individuals start to grow from spring to summer, each plant reaches different height when blooming at the end of summer or autumn. Plants are usually $1.5-2 \mathrm{~m}$ tall, but in the same population some plants just reach as little as 7 cm with few capitula or only one capitulum. Specimen Meyer 22237 (LIL) shows a small habit and uncommon distribution at 3340 m of M . mulgediifolium, however, the other features fit accurately with this species.
On the other hand, it is important to mention that we counted more phyllaries and florets than previous descriptions (phyllaries $45--75$ vs. 10--40, ray florets $35--60$ and disc florets $110--125$ vs. ca. 25 and ca. 32--36, respectively). In the case of phyllaries number, we found inconspicuous inner membranous phyllaries that have not been cited by previous botanists.

Representative Specimens Examined. ARGENTINA. Jujuy: Valle Grande department: San Francisco, 14 Apr 1972, Cabrera \& Fabris 22653 (LP). Salta: Capital department: Salta, Cerro San Bernardo, 1400 m, 14 Apr 1988, Novara 7945 (MCNS, S); Salta, Cerro San Bernardo, 1400--1450 m, 10 Apr 1996, Novara et al. 10868 (CORD, CTES, MCNS); ciudad de Salta, Cerro San Bernardo, $24^{\circ}$ $48^{\prime} 19,6^{\prime \prime}$ S $65^{\circ} 23^{\prime} 38,7^{\prime \prime}$ W, 1373 m , 15 Apr 2008, D. Gutiérrez et al. 554 (BA, LP). La Caldera department: Ruta 9 km 1614, 1200 m, 4 Apr 1999, Novara \& Bruno 11279 (MCNS); pasando 1--5 km (al N) del puente del río Wierna, $1300 \mathrm{~m}, 26$ Apr 1999, De la Fuente \& Lusvarghi s.n. (MCNS 1280); camino de cornisa a Jujuy, ruta 9, km 1612--1616, entre Vaqueros y La Calderilla, a 10 km de Salta capital, 1250--1350 m, 30 Apr 2000, De la Fuente \& Lusvarghi 1364 (CORD, MCNS); La Caldera, ruta nacional 9, entre Vaqueros y La Calderilla, a lo largo del río Caldera, $24^{\circ} 39^{\prime} 43.4^{\prime \prime} \mathrm{S}$
$65^{\circ} 22^{\prime} 53.0^{\prime \prime} \mathrm{W}, 1260 \mathrm{~m}, 16$ Apr 2008, D. Gutiérrez et al. 573 (BA, LP); ruta 9, entre Vaqueros y La Calderilla, 23--25 Apr 2010, D. Gutiérrez et al. 1017 (BA). Santa Victoria department: Lizoite, 3340 m, 5 Apr 1940, Meyer 22237 (LIL). BOLIVIA. Tarija department: Aniceto Arce prov., ruta Bermejo-Tarija, 8 km SE de La Mamora, 14 May 1971, Krapovickas et al. 18758 (CTES, LP); Cercado prov., de Tarija a Iscayachi, 2000--3000 m, 20 Mar 1982, Kiesling et al. 3817 (SI); Eustaquio Méndez prov., Sama, 2950 m, 7 May 1988, Ehrich 544 (LPB, SI, US).
3. Microliabum polymnioides (R.E.Fr.) H.Rob., Syst. Bot. 15: 473. $1990 \equiv$ Liabum polymnioides R.E.Fr. in Ark. Bot. 5: 24. $1906 \equiv$ Austroliabum polymnioides (R.E.Fr.) H.Rob. \& Brettell, Phytologia 28: 49. 1974. - TYPE: Argentina. Jujuy: [Santa Bárbara department,] quinta prope Laguna de la Brea [Laguna La Brea] in nemore Citri raro, 2 Jun 1901, R. E. Fries 74 (holotype: S S-R-3243!). Fig. 14.

Annual, biennial or perennial herbs, sometimes subshrubs, $0.5--2 \mathrm{~m}$ tall, rarely short herb up to 20 cm tall. Stems erect, stout, terete, not costate, few or many-branched, hirsute with glandular-tipped trichomes, usually mixed with densely white-tomentose pubescence; pseudostipules free or fused, or absent, herbaceous. Leaves opposite, scattered along the main stem and secondary branches, herbaceous, conspicuously petiolate; petiole $3-14 \times 0.3-1.8 \mathrm{~cm}$, wingless or widely winged, wings margin unevenly dentate; laminas $7.7-28 \times 5--23.7 \mathrm{~cm}$, widely subtriangular or subtriangular, bases cuneate or cuneate-hastate, apices acute, margins widely dentate or serrate, mucronulate, acrodromous, 3 -veined, with the main pair of lateral veins reaching the middle of the lamina, surfaces flat, lax hirsute adaxially, greenish and densely white-tomentose abaxially. Capitula many, sometimes few, terminal, in a densely corymbiform capitulescence, pedunculate, peduncles ( $0.5--) 2.5--8 \mathrm{~cm}$ long, erect, hirsute with glandular-tipped trichomes sometimes mixed with white-tomentose pubescence. Involucres $0.8--1.6 \times 1.5--3 \mathrm{~cm}$, hemispherical, (2--)3--4-seriate, outer series conspicuously exserted, phyllaries $60--65$, subimbricate, herbaceous, outer $6.3-15 \times 1--2.5 \mathrm{~mm}$, narrowly oblong or ovate, apices acute, densely hirsute with glandular-tipped trichomes, inner $4.5--8.1 \times 0.8-1.6 \mathrm{~mm}$, narrowly ovate, apices attenuate or acute, densely hirsute with glandular-tipped trichomes, rarely glabrescent, innermost inconspicuous, reduced, membranaceous, glabrescent. Ray florets 50--75, 2-seriate, pistillate, fertile; corolla $0.7-2.2 \mathrm{~cm}$ long, true ray yellow, pubescent with glandular-tipped trichomes, tubes $3.5--4 \times 0.3--0.4 \mathrm{~mm}$, limbs $4--15.5 \times 0.8--2.2 \mathrm{~mm}$, narrowly obovate or elliptical, (3--)4-veined, apices 3 -dentate. Disc florets 100--125, bisexual, fertile; corolla $5--7 \mathrm{~mm}$ long, tubular, funnelform, tube and throat gradually differentiate, 5-lobed, yellow, rare slightly orange, tube plus throat 4.2-4.5 mm long, tubes $0.2--0.5 \mathrm{~mm}$ wide, pubescent or glabrous, throats $0.5--1.2 \mathrm{~mm}$ wide, pubescent or glabrous, lobes $1.5-1.8 \times 0.3--0.4 \mathrm{~mm}$, pubescent; style branches $0.4-1 \mathrm{~mm}$ long. Achenes $1--1.8 \mathrm{x}$ $0.3--0.8 \mathrm{~mm}$, obovoid or obconical 8 --10-ribbed, pubescent. Pappus distinctly 2 -seriate, outer up to
$0.6-1.2 \mathrm{~mm}$ long, of scales, paleaceous, inner up to $4--6 \mathrm{~mm}$ long, of bristles barbellate, fine, easily deciduous. Chromosome number: $2 n=12$ (Rozenblum \& al., 1985).

Distribution and Habitat. This species occurs in central and southeastern Bolivia to northwestern Argentina, between 450--2300 m (Fig. 8 B). It inhabits Yungan and usually Chacoan wet or slightly dry enviroments, slopes near running water or rivers, river beaches, rain forests, edges of forests or woodlands, streams or rivers, shady woods, mountains and valleys, river canyons, quebradas, disturbed ground, roadsides, train tracks, secondary succession environments. Sometimes, it is an invasive species of roadsides and embankments near rivers.

Common Name: "flor del río" (in sched. Bellomo 344, LIL).

Phenology. Plants with flowering capitula have been collected from the end of the autumn to the beginning of the spring, from April to June.

It was mentioned on some labels to be as tall as 3 m (i. e., Krapovickas et al. 26652, CTES, SI; Pedersen 16127, CTES) but it does not seem to grow that tall. We counted more phyllaries than previous works ( $60-65$ vs. 10--40, respectively) since we found inconspicuous inner membranous phyllaries that have not been cited by previous botanists. On the contrary, we counted less ray florets than the original description (up to 75 vs. 60--100, respectively). Specimen Pierotti 1155 (LIL) with slender herbs shows an uncommon trait within M. polymnioides, however, the other features fit accurately with this species. On the other hand, the corollas have been cited as yellow on several specimen labels and in our observations in field trips. However, it has been noted as orange on labels (e.g., Calcagnini 117, BAB). It is very aromatic (Eyerdam \& Beetle 2260, K).

Robinson (1990) cited that the holotype of M. polymnioides was kept at UPS. However, there are no type specimens of M. polymnioides deposited in UPS (M. Hjertson, pers. comm.), and the types are actually conserved in S. In that work, "Quinta" was cited as the type locality; however, this word in Spanish means just farm. Actually, according to the type label, this type material was collected in La Brea lagoon, near the intersection of Routes 1 and 6 in Salta in a citrus farm.

Representative Specimens Examined. ARGENTINA. Catamarca: Paclín department: Balcozna [Balcosna], 1250 m, 17 Jan 1928, Venturi 7073 (GH, SI). Jujuy: Capital department: alrededores de [San Salvador de] Jujuy, Yala, 8 May 1962, Cabrera et al. 14391 (LP); Quebrada de Jaire, camino a Tiracsi [Tiraxi], 20 May 1962, Cabrera el al. 14686 (LP); río de Las Capillitas [Capillas], 24 Jul 1963,

Cabrera 15879 (LP); camino a Tiraxi, 10 Jun 1980, Medán \& Tortosa 77 (LIL); RN 9, antes de León, debajo del puente, 17 Apr 2008, D. Gutiérrez et al. 580 (BA, LP, S). Ledesma department, Sierra de Calilegua, 750 m, 9 Sep 1927, Venturi 5210 (LIL, SI); near río San Lorenzo, Leach Estates near Calilegua, 800 m, 18 Oct 1938, Eyerdam \& Beetle 22608 (K); El Mirador, Ledesma, Aug 1940, Ringuelet 122 (LP); Calilegua, 460 m, 15 Oct 1963, Fabris 4420 (LP); Yuto, El Bananal, 500 m, 19 Oct 1963, Fabris 4536 (BAB, LP); camino a Valle Grande, a orilla del río Las Cañas, 7 Aug 1969, Legname \& Cuezzo 7100 (LIL); puente arroyo Yuto, 30 Aug 1970, Cabrera 20818 (LP); camino de Ledesma a Pichanal, arroyo Yuto, 5 Oct 1974, Legname \& Cuezzo 10448 (LIL); camino a Valle Grande, río Aguas Negras, 30 Oct 1974, Cabrera et al. 25707 (LP, SI); 10--20 km de Libertador General San Martín, camino a Valle Grande, 9 Nov 1974, Krapovickas et al. 26652 (CTES, SI); Calilegua, Sep 1976, Cabrera et al. 27924 (SI); Parque Nacional Calilegua, Aug 1980, Martelli 1899 (LIL); arroyo Yuto, sobre ruta 34, 450 m, 27 Nov 1981, Legname \& López 8818 (LIL); arroyo Aguas Negras, 450 m, 26 Aug 1980, Legname et al. 8324 (LIL); camino a Valle Grande, entre ruta 34 y río Aguas Negras, 13 Jun 1983, Cabrera 33898 (SI); arroyo Yuto, 14 Jun 1983, Cabrera et al. 33935 (SI); Parque Nacional Calilegua, 19 Jun 1983, Rotman 738 (CTES, LIL); Parque Nacional Calilegua, 1000 m, 28 Feb 1986, Iudica \& Ramadori 288 (SI); Parque Nacional Calilegua, paralelo al río Aguas Negras, 600--800 m, 11 Sep 1991, Guaglianone et al. 2530 (CTES, SI); Parque Nacional Calilegua, río Jordán, 11 Dec 1991, Xifreda \& Sanso 1117 (SI); Parque Nacional Calilegua, 21 Sep 1997, Dematteis \& Seijo 807 (CTES, LIL); Parque Nacional Calilegua, camino desde arroyo Tres Cruces hasta arroyo Aguas Negras, RP 83, $23^{\circ} 46^{\prime} \mathrm{S} 64^{\circ} 50^{\prime} \mathrm{W}, 550-1100 \mathrm{~m}, 7$ Nov 1998, Ahumada \& Castellón 8817 (LP); Parque Nacional Calilegua, $23^{\circ} 43^{\prime} 31.2^{\prime \prime} \mathrm{S} 64^{\circ} 51^{\prime} 5.8^{\prime \prime} \mathrm{W}, 864 \mathrm{~m}, 20 \mathrm{Apr}$ 2008, D. Gutiérrez et al. 605 (BA). Santa Bárbara department: Vinalito, Yuto, 7 Jul 1937, Cabrera 4050 (SI); Santa Bárbara Range, Quebrada de las Termas, 80 km South of San Pedro de Jujuy, 1500 m, 8 Oct 1938, Eyerdam \& Beetle 22468 (K). Tumbaya department: Volcán, 2200 m, 13 Dec 1918, Castillon 6512 (LIL); estación Volcán, quebradas orientales, $2200 \mathrm{~m}, 13$ Dec 1918, Castillon 6592 (LIL). Valle Grande department: alrededores de Valle Grande, 15 May 1972, Cabrera \& Fabris 22687 (LP); camino a Valle Grande, río Jordán, 1500 m, 8 Oct 1973, Legname \& Cuezzo 9584 (LIL).

Salta: Anta department: Parque Nacional El Rey, Cerro Maldonado, Sierra González, Jun 1934, Ragonese 153 (BA); Parque Nacional El Rey, 5 Jul 1979, Brown et al. 839 (SI). La CandelariaRosario de la Frontera departments: Sierra de la Candelaria, río Nogalito, 1500 m, 6 Apr 1925, Venturi 3753 (LIL, SI). Chicoana department: camino a Cachi, Quebrada de Escoipe, 27 Mar 1979, Cabrera et al. 30697 (CTES, SI); camino a Cachi, 27 Mar 1979, Cabrera et al. 30699 (CTES, SI); Los Laureles, pasando Pulares hacia PN Los Cardones, RP 33, $25^{\circ} 10^{\prime} 12.8^{\prime \prime} \mathrm{S} 65^{\circ} 49^{\prime} 46.2^{\prime \prime} \mathrm{W}, 1368 \mathrm{~m}$, 14 Apr 2008, D. Gutiérrez et al. 566 (BA, LP). General Güemes department: Quisto, 20 km al E de General Güemes, 27 Aug 1982, Novara 2840 (SI). General José de San Martín department:

Tartagal, 14 Jun 1934, Meyer 930 (BA, LIL); [Campamento] Vespucio, 13 Aug 1937, Cabrera 4158 (LP); Quebrada Yariguarenda, sub-quebrada Peña de la Virgen, 4 Jul 1944, Schulz \& Varela 5201 (CTES); Quebrada Virgen-Tartagal, 4 Jul 1944, Schulz \& Varela 5201 (LIL); [Las] Tablillas, 24 Nov 1946, Rial Alberti s.n. (BAB 72360); [Campamento] Vespucio, May 1971, de González Montaner 17 (SI); Tartagal, ca. 400 m, 10 Sep 1983, Novara 3587 (CTES, LP, SI). General José de San MartínOrán departments: Río Bermejo, gran chaco salteño, 11 jul 1902, Calcagnini 117 (BAB). Orán department: Orán, 338 m, 27 Jul 1913, Jorgensen s.n. (BAB 37202); Cerro Tablada, 2400 m, 4 Apr 1915, Pierotti 1155 (LIL); Alambique, 27 Jun 1944, Ruiz Huidobro s.n. (LIL 363697); márgenes de río Pescado, 7 Nov 1946, Rial Alberti s.n. (BAB 72343); camino a Los Toldos, 15 km del puente Agua Blanca, 29 Aug 1968, Legname \& Cuezzo 5755 (LIL); a 3 km del puente internacional de Agua Blanca, hacia la Quebrada El Arasayal, 5 Aug 1969, Legname \& Cuezzo 7121 (LIL); camino a finca Yaculika, a 5 km del puente internacional, río Bermejo, $480 \mathrm{~m}, 6$ Nov 1975, Schiavone et al. 11928, 11947 (LIL); arroyo Arasayal, 550 m, 20 Nov 1976, Giusti et al. 12099 (LIL); camino a Isla de Cañas, 20 km de Orán, próximo a Vado Hondo, $500 \mathrm{~m}, 17$ Sep 1982, Legname et al. 8783 (LIL); RN 50, antes de llegar a Aguas Blancas, 650 m, 13 Sep 1999, Muruaga et al. 303 (LIL); quinta del río Santa María, Willink 111 (LIL). Santa Victoria department: path between Santa Victoria and San Felipe by río Lizoite, $22^{\circ} 16^{\prime} \mathrm{S} 64^{\circ} 58^{\prime} \mathrm{W}, 2300 \mathrm{~m}, 14$ Mar 1966, Hawkes et al. 3852 (K). Tucumán: Burruyacu department: Sierra de Medina, 900 m, 25 Oct 1923, Venturi 2558 (BAB); Sierra del Nogalito, 1450 m, 11 Apr 1991, Aceñolaga et al. s.n. (Proyecto Fitosociología del Aliso 041) (LIL 596587). Capital department: alrededores de [San Miguel de] Tucumán, Oct 1902, Baer 52 (BA, BAF [circa Tucumán]); circa [San Miguel de] Tucumán, Baer 53 (BAF). Faimallá department: Quebrada de Lules, camino al dique, $600 \mathrm{~m}, 23$ Sep 1923, Venturi 2558 (BA, BAB, SI); La Quebrada, Lules, 13 May 1945, Ortiz s.n. (LIL 123370, 123372); Quebrada de Lules, 9 Sep 1945, Villa 495 (LIL 139590); Quebrada de Lules, 30 Aug 1949, Sás 64 (LIL). J.B. Alberti departmanet: RP 18, entre bifurcación RP 1 y RP 18, próximo al límite con Catamarca, cerca de Balcosna, $27^{\circ} 50^{\prime} 7.8^{\prime \prime} \mathrm{S} 65^{\circ}$ 48'37.4' W, 1401 m, 12 Apr 2008, D. Gutiérrez et al. 540 (BA); camino río Singuil, RP 308, entre Las Higueras y Dique Escaba, $27^{\circ} 39^{\prime} 11.0^{\prime \prime} \mathrm{S} 65^{\circ} 44^{\prime} 59.6^{\prime \prime} \mathrm{W}, 568 \mathrm{~m}, 12$ Apr 2008, D. Gutiérrez et al. 548 (BA). Lules department: Lules, 15 Jul 1911, Lizer s.n. (SI 9443); de La Reducción a Potrero de las Tablas, Dec 1988, Slanis 136 (LIL); camino a Potrero de Las Tablas, aprox. 17 km de ruta 38, 550 m, 24 Nov 1993, Figueroa Romero et al. 760 (LIL); ca. Lules, $26^{\circ} 54^{\prime} 41.07^{\prime \prime} \mathrm{S} 65^{\circ} 19^{\prime} 42.09^{\prime \prime}$ W, 12 Apr 2008, D. Gutiérrez et al. 549 (BA). Río Chico department: Quebrada de Marapa, 600 m , 7 Jul 1945, Castellanos s.n. (LIL 114970). Tafí department: Quebrada Lules, camino al dique, 800 m, 29 Sep 1920, Venturi 942 (BA, SI); Quebrada de Lules, 21 Jul 1934, Clos 5537 (BAB); Yerba Buena, camino a San Javier, 520 m, 12 Aug 1941, Rohmerz 32 (LIL); Quebrada de Lules, 30 Nov 1945, Villa 592, 615 (LIL). Trancas department: Río del Potrero, 28 Apr 1945, Bellomo s.n. (LIL

173311, NY); [probable, río] Potrero, 1400 m, 8 May 1946, Bellomo 344 (LIL); río Vipos, $600 \mathrm{~m}, 3$ May 1921, Schreiter s.n. (GH, LIL 76118). Yerba Buena department: ladera de San Javier, 5 Jun 1949, Soriano \& Banett 3647 (BAB). Without department: without locality, 1902, Baer s.n. (SI 15584). BOLIVIA. Cochabamba: Chapare prov., Locotal, $1600 \mathrm{~m}, 27$ Feb 1929, Steinbach 9430 (LIL). Chuquisaca: Hernando Siles prov., [Ruta 6, entre Monteagudo y Padilla], $19^{\circ} 31^{\prime} 40^{\prime \prime} \mathrm{S} 64^{\circ} 9^{\prime}$ $41^{\prime \prime}$ W, $1647 \mathrm{~m}, 13$ Oct 2008, Lliully et al. 1516 (HSB, MO); Belisario Boeto prov., [Potreros], $19^{\circ} 4^{\prime}$ 39" S $64^{\circ} 5^{\prime} 30^{\prime \prime}$ W, 1772 m , 20 Jun 2009, Peñaranda 1470 (HSB, MO, NY). Chuquisaca-Santa Cruz: Cordillera prov., finca Guacareta [probably Huacareta in Chuquisaca dept., Hernando Siles prov., near the border with Santa Cruz dept., Cordillera prov.], 22 Sep 1982, Cabrera \& M. Gutiérrez 33681 (MO, SI). Tarija: Burdet O'Connor prov., ruta Tarija-Villa Montes, bajada de San Simón, 15 km E de Entre Ríos, 22 May 1971, Krapovickas et al. 19117 (CTES, LIL, SI); Aniceto Arce prov., El Salado, 700 m, 24 Aug 1971, Nuesser 13 (CTES, LIL); Aniceto Arce prov., de Pozos del Bermejo a Emboruzú, a 56 km de Bermejo, 18 Oct 1980, Zuloaga et al. 1050 (SI); Gran Chaco prov., Villamontes, 13 km hacia Tarija, en la quebrada del río Pilcomayo, $470 \mathrm{~m}, 26$ Oct 1983, Beck \& Liberman 9767 (SI); Gran Chaco prov., Yacuiba, 18--24 km hacia Palos Blancos, Serranía de Caraparí, 800--1230 m, 24 Sep 1985, Beck et al. 11582 (SI).

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## AUTHOR CONTRIBUTION STATEMENT

D.G.G. conceived the presented research. D.G.G. designed and directed the morphological study; N.G.-J. and A.S. designed and directed the molecular study; D.G.G. performed morphological study; D.G.G. and M.A.G. performed the statistical analysis of morphological quantitative characters; D.G.G., N.G.-J., A.S. and M.A.G. performed molecular analyses; D.G.G. took the lead in writing the manuscript. All authors provided critical feedback and helped shaping the research, analyses, and manuscript.

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# Morphological and molecular analyses of South American Microliabum (Compositae, Liabeae, Paranepheliinae) and reinstatement of Austroliabum 

Short title: Morphological and molecular analyses of Microliabum (Compositae, Liabeae)

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#### Abstract

The small Neotropical tribe Liabeae (Compositae) is currently classified in four subtribes: Liabinae, Munnoziinae, Paranepheliinae, and Sinclairiinae. As currently accepted, Paranepheliinae includes seven genera, Chionoppapus, Erato, Microliabum, Paranephelius, Philoglossa, Pseudonoseris, and Stephanbeckia, distributed especially throughout the Andes from Venezuela and Colombia to Argentina. Our research focuses in the genus Microliabum, which inhabits extra-Andean enviroments from Bolivia to central Argentina. The wide concept of Microliabum and its phylogenetic position within Paranepheliinae is controversial. Bayesian and maximum parsimony analyses of ribosomal nuclear ITS and plastid trnL-F suggest that both subgenera described within Microliabum are monophyletic. However, Microliabum, without the subgenus Austroliabum, is close to Stephanbeckia. A statistical analysis (PCoA) supports separation of the subgenera, and morphology mainly based on traits of the involucre and florets permits to establish new taxonomical circumscriptions. Thus, the reinstatement of Austroliabum, the more southern Liabean genus, is here proposed. The genus includes three endemic species from Sub-Andean and Pampean Hills in central and northwestern Argentina. Austroliabum is characterized by white-tomentose or woolly pubescence on stems and abaxial leaf surfaces, acrodromous leaf venation, campanulate involucres, coriaceous and adpressed phyllaries in usually five series, outer phyllaries shorter than the inner ones, style branches of disc florets shorter than the pubescent part on shaft below the bifurcation point, style pubescence on shaft below the bifurcation point of disc florets at least three times longer than the


branches of the style, persistent 2 -seriate pappus with outer series of scales and inner series of barbellate bristles, and achenes pubescent on the ribs. In addition, a revision of Microliabum s. str., with three species, is carried out.

KEYWORDS: Asteraceae; ITS; Liabeae; morphology; phylogeny; South America; trnL-F.

Liabeae are a phylogenetically derived small tribe within Compositae (Panero \& al., 2014; Mandel \& al., 2017) with 21 genera and 165 species (Gutiérrez, 2010; Funk \& al., 2012; Gutiérrez \& Katinas, 2015a). This Neotropical tribe is distributed mainly in the Andes where its origin was postulated, especially in Central and northern Andes (Funk \& al., 1996; Dillon \& al., 2009; Funk \& al. 2012). However, some Liabean genera inhabit non-Andean areas: (1) Mexico and Central America (e.g., Liabellum Rydb., Sinclairia Hook. \& Arn., Sinclairiopsis Rydb.); (2) The Caribbean [i.e., Liabum Adans., particularly Liabum umbellatum (L.) Sch.Bip.], and (3) central and northwestern Argentina in the Sub-Andean Hills ("Sierras Subandinas") and the Pampean Hills ("Sierras Pampeanas") (i.e., Microliabum Cabrera; Funk \& al., 2012; Gutiérrez, 2015a; Gutiérrez \& Katinas, 2015). The Pampean Hills have a different orogeny (e.g., Rapela \& al., 2001; Martino, 2003; Grosse \& al., 2009), floristic composition (Cabrera \& Willink, 1980), and geobiotic origins (Martínez \& al., 2016) from the Andes.

Four subtribes are currently recognized within Liabeae: Liabinae, Munnoziinae, Paranepheliinae, and Sinclairinae (Dillon \& al., 2009; Funk \& al., 2012; Pruski, 2012). Paranepheliinae are formed by seven genera: Chionopappus Benth., Erato DC., Microliabum, Paranephelius Poepp., Philoglossa DC., Pseudonoseris H.Rob. \& Brettell, and Stephanbeckia H.Rob. \& V.A.Funk. According to Funk \& al. (2012), two evolutionary lineages could be recognized: one is formed by Chionopappus, Erato and Philoglossa, and the other by Microliabum, Paranephelius, Pseudonoseris, and Stephanbeckia. Morphologically, the subtribe is characterized usually by the presence of latex (except Chionopappus and Stephanbeckia), short style branches in the disc florets (except Paranephelius and Pseudonoseris), and three-veined leaf venation (except Erato, Paranephelius, and Pseudonoseris; Funk \& al., 2012; Gutiérrez \& Luna, 2013).

Paranepheliinae are entirely South American in distribution with the exception of one species of Erato in Central America (Moran \& Funk, 2006; Funk \& al., 2012). Soejima et al. (2008) dated the origins of the Pseudonoseris-Paranephelius clade in the Miocene (approximately 13 million years ago [Ma]). Thus, Paranephelius and Pseudonoseris diversified well after the significant central Andean uplifts (Oligocene, ca. 30 Ma ), perhaps concurrently with major northern Andean orogeny (PliocenePleistocene, ca. 3-5 Ma; Soejima \& al., 2008). From a biogeographic standpoint, Microliabum is an
interesting genus because some of its species reach the southernmost distribution of the tribe (Gutiérrez \& Novara, 2009; Gutiérrez, 2015). It is formed by five or six species (e.g. Robinson, 1990; Cabrera \& al., 1999; Funk \& al., 2012; Gutiérrez, 2008a; Gutiérrez, 2015a) growing in open areas in mid-elevation wet forest or in high-elevation Andean habitats in the north of its range, and seasonally dry scrub associated to hills in the south.

The first Microliabum species were originally described under Liabum Adans. (Table 1), and the first comprehensive analysis of most of the current species of Microliabum was made by Cabrera (1947), who described the northwestern Argentinian genus Liabellum (Cabrera, 1954). Soon after, he changed the name to Microliabum (Cabrera, 1955) because the former was a later homonym of a Mexican genus, Liabellum (Rydberg, 1927). Thus, the monotypic genus Microliabum was originally named for one of its most distinctive traits, the small size. However, the diagnostic character was the paleaceous pappus in two series. Later on, Robinson and Brettell (1974) described the genus Angelianthus nom. superfl. (Table 1). From the beginning, Cabrera (1954) recognized the morphological affinity between Microliabum and Liabum s.l. However, on the basis of the paleaceous pappus, Cabrera (1978) and Cabrera \& Iharlegui (1999) kept Microliabum separate from the broad circumscription of Liabum postulated by classic botanists (e.g. Bentham, 1873). Thus, Microliabum was never treated as a synonym or section of Liabum, contrarily to other Liabean genera, i.e. Andromachia Humb. \& Bonpl., Chysactinium Kunth, Erato, Kastnera Sch.Bip., Munnozia Ruiz \& Pav., Oligactis (Kunth) Cass., Paranephelius, Sinclairia, Starkea Willd. (Gutiérrez \& Katinas, 2015).

On the other hand, genus Austroliabum H.Rob. \& Brettell, which is currently considered a synonym of Microliabum, was originally described to accommodate four species (Table 1) segregated from Liabum (Robinson \& Brettell, 1974). Robinson (1983) made only small taxonomical changes, but seven years later (Robinson, 1990) he proposed a recircumscription of Microliabum with six species (Table 1). As a result of this new taxonomic treatment, Microliabum expanded its earliest restricted morphological description from a single species with reduced habit and broadened pappus to several species up to 2 m tall and capillary inner pappus. At the same time, the genus expanded its restricted distribution in northwestern Argentina to a wider distribution in southern and central South America. In addition, Robinson (1990) classified Microliabum in two subgenera, Austroliabum and Microliabum, with three species each.

Phylogenetic relationships of Microliabum within Liabeae have been contradictory. For example, Microliabum was classically placed in subtribe Liabinae (Robinson, 1983; Funk, 1985; Funk \& al., 2007), sister to the Mexican and Central American genera Liabellum and Sinclairia (including

Megaliabum Rydb. and Sinclairiopsis) based on morphology but with weak support (Bremer, 1994; Funk \& al., 1996). Later on, in a preliminary phylogenetic analysis based on the nuclear gen ITS, Microliabum was weakly supported as a basally branching monophyletic genus sister to a clade composed of Sinclairia, Oligactis, Dillandia V.A.Funk \& H.Rob., and Liabum (Gutiérrez \& al., 2007). According to this study, Microliabum was suggested to be an ancestral genus within classical Liabinae. On the other hand, Microliabum was proposed, based on ITS and $\operatorname{trnL}$-trnF sequences, to be close to Paranephelius and Pseudonoseris (Soejima \& al., 2008), both from the classical Paranepheliinae. This latest relationship was confirmed in a phylogenetic study based on nuclear and plastid DNA sequences, and Microliabum was included in a recircumscription of Paranepheliinae together with Paranephelius and Pseudonoseris, plus Chionopappus, Philoglossa, and Erato (Dillon \& al., 2009). In this latest phylogeny, Microliabum resulted surprisingly as sister to Stephanbeckia, which was recently described from southern Bolivia (Robinson \& Funk, 2011; Funk \& al., 2012).

Until now, there is no agreement on the number of species of Microliabum (e.g., Robinson, 1990; Cabrera \& al., 1999; Funk \& al., 2012; Gutiérrez, 2008a, Gutiérrez, 2015a), and an unequivocal phylogeny is yet not available. Besides, phylogenetic relationships of Microliabum to Liabeae or Paranepheliinae are contradictory, probably due to limited sampling in previous phylogenetic studies. Thereafter, we have gathered a comprehensive sample of the genus and we have carried out analyses of nuclear-ribosomal and plastid DNA, and a thorough morphological survey including a statitistical analysis, with the following goals: (1) To evaluate the monophyly of Microliabum and its subgenera, and the position of the genus within Paranepheliinae; and (2) to review in depth the taxonomy, morphology, and geographical distribution of Microliabum and its species.

## MATERIALS AND METHODS

Sampling strategy. - For the DNA analyses, the ingroup included all species of Microliabum: M. candidum (Griseb.) H.Rob., M. eremophilum (Cabrera) H.Rob., M. glanduliferum (Cabrera) H.Rob. (subgenus Austroliabum), and M. humile (Cabrera) Cabrera, M. mulgediifolium (Musch1.) H.Rob. and M. polymnioides (R.E.Fr.) H.Rob. (subgenus Microliabum). Species of subgenus Austroliabum and M. humile were included in a phylogeny for the first time. Sequence data of Cacosmia Kunth, Chionopappus, Chrysactinium, Dillandia, Erato, Ferreyranthus H.Rob. \& Brettell, Liabellum, Liabum, Megaliabum, Munnozia, Oligactis, Paranephelius, Philoglossa, Pseudonoseris, Sampera V.A.Funk \& H.Rob., Sinclairia, Sinclairiopsis, and Stephanbeckia from the four subtribes of Liabeae were mainly obtained from GenBank (including previously unpublished data of Munnozia hastifolia (Poepp.) H. Rob. \& Brettell and Paranephelius asperifolius (Muschl.) H. Rob. \& Brettell), and used as
ingroup too (Appendix 1). Moquinia racemosa (Spreng.) DC. and Pseudostifftia kingii H.Rob. (Moquinieae), and Distephanus barus (Humbert) H.Rob. (Vernonieae) were included as outgroups. Voucher data, source and GenBank accession numbers are given in Appendix 1. DNA regions were selected based on previous molecular works (H.-G. Kim \& al., 2003; Funk \& al., 2004; Funk \& al., 2012).

DNA extraction, amplification and sequencing. - Total genomic DNA was extracted following the CTAB method of Doyle \& Dickson (1987) as modified by Cullings (1992) from silica-gel-dried leaves collected in the field or from herbarium material. For difficult extractions, DNeasy extraction Kit (Qiagen Inc., Hilden, Germany) was used, following the manufacturer's instructions.
$n r D N A$ ITS region strategy. -The ITS region was amplified by polymerase chain reaction (PCR). The amplification primers were ITS1, ITS2, ITS3 and ITS4 (White \& al., 1990), 17SE and 26SE (Sun \& al., 1994). For some species, the ITS region was amplified completely using ITS1 (forward) and ITS4 (reverse) primers or 17SE (f) and 26SE (r) primers. In case of low-quality DNA, the ITS1 and ITS2 fragments were amplified separately using ITS1 (f) and ITS2 (r) primers for the ITS1, and ITS3 (f) and ITS4 (r) primers for the ITS2. The PCR reactions were performed in a $25 \mu 1$ reaction volume containing $3 \mu \mathrm{l}$ of diluted genomic DNA, $2,5 \mu \mathrm{l}$ of $10 \times$ AmpliTaq buffer, $2,5 \mu \mathrm{l}$ of $2.5 \mathrm{mM} \mathrm{MgCl} 2,2,5$ $\mu \mathrm{l}$ of 0.2 mM dNTPs, $1 \mu \mathrm{l}$ of $0.2 \mu \mathrm{M}$ of each primer, $0.5 \mu \mathrm{l}$ of DMSO (Sigma-Aldrich, St. Luis, MO, USA), $5 \mu \mathrm{l}$ of TBT (Samarakoon, 2013) and $6.7 \mu \mathrm{l}$ of purified water and $0.3 \mu \mathrm{l}$ of AmpliTaq DNA polymerase (Applied Biosystems, Foster City, CA, USA) for both regions. The cycling profile included an initial denaturation step at $94^{\circ} \mathrm{C} / 2 \mathrm{~min}$ followed by 35 cycles of $94^{\circ} \mathrm{C} / 1 \mathrm{~min} 30 \mathrm{~s}, 55^{\circ} \mathrm{C} / 2$ $\min$ (for ITS1, ITS2, ITS3 and ITS4 primers) or $57^{\circ} \mathrm{C} / 2 \mathrm{~min}$ (for 17 SE and 26 SE ), $72^{\circ} \mathrm{C} / 3 \mathrm{~min}$, and ended with $72^{\circ} \mathrm{C} / 15 \mathrm{~min}$ and $4^{\circ} \mathrm{C}$ thereafter for the ITS region. Purification of the PCR product was conducted with ExoSAP-IT (USB Corp., Cleveland, Ohio, USA) or with also the QIAquick® purification kit (Qiagen Inc.). The amplified DNA segments were sequenced directly using BigDye Terminator Cycle Sequencing v.3.1 (Applied Biosystems), following the manufacturer's protocol at the University of Florida ICBR Core Facility on an ABI 3730xl capillary sequencer (Applied Biosystems) or at Macrogen Inc., Europe.
$c p D N A$ amplification strategies. - The forward primers trnL-c, trnL-e, and the reverse trnL-f, $\operatorname{trnL}-\mathrm{d}$ (Taberlet et al., 1991) were used for amplifying the $\operatorname{trnL}$ intron and the $\operatorname{trnL}-F$ intergenic spacer. The PCR reactions were performed under the same conditions as nuclear regions, replacing DMSO by BSA.

The PCR procedure included a warm start at $95^{\circ} \mathrm{C}$ for 1 min 35 s . Thirty-five cycles of amplification were carried out: 1 min denaturation at $93^{\circ} \mathrm{C}, 58^{\circ} \mathrm{C}$ annealing for $1 \mathrm{~min}, 72^{\circ} \mathrm{C}$ extension
for 1 min , and a final extension for 10 min at $72^{\circ} \mathrm{C}$. Purification and sequencing were performed as for the ITS region, but with the corresponding primers.

Phylogenetic analyses. - Nucleotide sequences were edited using Bioedit v7.0.5.3 (Hall, 1999) and aligned visually by sequential pairwise comparison (Swofford and Olsen, 1990) or using the program MUSCLE (Edgar, 2004) with manual correction. The only incongruences between datasets involved species unrelated to Microliabum sensu lato, and combination of datasets seemed adequate as proposed by Funk \& al. (2012). Thereafter, three datasets were analyzed: ITS ( 92 accessions), $\operatorname{trnL}$ - $F$ ( 87 accessions), and ITS + trnL-F (87 accessions). Data matrices are available at http://www.ibb.bencsic.es/public, folder Microliabum.

Parsimony analysis of the datasets involved heuristic searches conducted with PAUP v4.0a147 (Swofford, 2002) using tree-bisection-reconnection (TBR) branch swapping with character states specified as unordered and unweighted. Indels were treated as missing data in all datasets. All mostparsimonious trees (MPTs) were saved. To locate other potential islands of MPTs (Maddison, 1991), we performed 10,000 replications with random taxon addition, also with TBR branch swapping. Bootstrap analyses (BS) were performed (Felsenstein, 1985) with 100 replicates with simple addition and TBR branch swapping for ITS, and ITS + trnL-F datasets. For bootstrapping $\operatorname{trnL}-F$ dataset the tree limit of PAUP was reached very quickly and thereafter we followed the approach of Lidén et al. (1997), using 1000 replicates, random taxon addition with 20 replicates, and no branch swapping. Internodes with $\mathrm{BS} \geq 75 \%$ were considered statistically significant. For the strict consensus tree consistency index (CI) and retention index (RI) are given excluding uninformative characters (Electr. Suppl.: Table S\#1). Bayesian inference of the three datasets was calculated using MrBayes v3.2.1 (Ronquist et al., 2012). The best available model of molecular evolution required for Bayesian estimations of phylogeny was selected for all datasets using Akaike information criteria (AIC) as implemented in the software MrModeltest v3.7 (Posada \& Crandall, 1998). The best fitting models were the symmetrical model with gamma distribution and number of invariant sites (SYM $+\Gamma+\mathrm{I}$; Zharkikh, 1994) for ITS, and the general time-reversible model with gamma distribution and number of invariant sites (GTR $+\Gamma+\mathrm{I}$; Gu \& al., 1995) for $\operatorname{trnL}-F$. For the analyses of the combined datasets (ITS $+\operatorname{trnL} L-F$ ), data were partitioned and the adequate model was assigned to each partition.

Bayesian inference analyses were initiated with random starting trees and were run for $30 \times 10^{6}$ generations in two independent runs of four Metropolis-coupled chains in the three datasets. We saved one out of every 1,000 generations, resulting in 30,000 sampled trees. For ensuring that the Markov chain Monte Carlo (MCMC) reached stationarity, we used Tracer 1.7.1 (Rambaut et al., 2018) for checking that the Efective Sample Size (ESS) was higher than 200 after discarding the first $25 \%$ of trees as burn-in. Internodes with posterior probabilities $\geq 0.95$ were considered statistically significant.

Taxonomic and morphologic analyses. More than 300 specimens (including types and images) deposited in BA, BAA, BAB, BAF, CORD, CTES, GH, GOET, HSB, JUA, K, LIL, LP, MCNS, MO, NY, S, SI, and US (Thiers, 2018) were studied. Other specimens were examined as digital images available through online resources of several herbaria and the JSTOR Global Plants web site (http://plants.jstor.org). In addition, field work for this study was conducted at several sites in the range of the geographical distribution of Microliabum throughout Argentina (Catamarca, Córdoba, Jujuy, La Rioja, Salta, San Luis, and Tucumán provinces) from 2006 to 2011, 2016, 2018 and 2019 (see specimens examined for each species). All species were collected with the exception of $M$. humile. Voucher specimens were deposited in BA, LP, and MCNS. Descriptions are based on herbarium specimens and field observations, with specimens having been collected by the authors. The data derived from the specimens were supplemented by information from the literature and databases.

Samples were obtained from living plants (cultivated in greenhouse or collected in field trips) and herbarium specimens. In the case of dry materials for microscopic examination, vegetative and reproductive parts were rehydrated, cleared, stained with $2 \%$ safranin, and mounted on microscope slides (Zarlavsky, 2014). Drawings were made using a Wild M5 stereomicroscope and an Olympus CH2 microscope with a camera-lucida attachment. Drawings of species were made on the base of herborized specimens and compared to field observations for the all species excepting M. humile. Light microscope photographs were taken with a Nikon Coolpix S10 camera. For scanning electron microscopy (SEM) studies, critical point drying was applied to dehydrated material, or dry material was placed directly on the stubs and coated with gold. Samples were scanned and photographed in a Jeol JSM-T 100 SEM (at La Plata Museum) or Philips XL-30 SEM (at Argentine Museum of Natural Sciences). In some cases, low-vacuum scanning electron microscopy was performed.

All the species of Microliabum were macro- and micromorphologically analyzed. Whenever possible, over 20 specimens for each species were measured. Two capitula at the same maturity stage and at least two to five florets (disc and ray) per specimen were analyzed. Macroscopical observations were made on living plants during field trips as well as on those cultivated in La Plata. In addition, specimens of some species from Paranephelius and Pseudonoseris were analysed. In the particular case of Stephanbeckia, data were obtained from the original description and high quality digital images of types.

Terminology for morphology follows Ramayya (1962), Harris \& Wolf Harris (1994), Bremer (1994), and Ash et al. (1999).

Multivariate analyses. In order to analyze morphometric variation among the species of Microliabum, we took measurements from 72 individuals of 55 herbarium specimens (including types and additional collections) (Appendix 2) for 30 characters (six vegetative and 24 reproductive; five quanlitative and 25 quantitative): (1) plant height, (2) petiolate/inconspicuously petiolate or sessile leaf, (3) petiole length, (4) petiole width, (5) leaf lamina length, (6) leaf lamina width, (7) number of capitula, (8) length of the capitula peduncle, (9) involucre height, (10) involucre width, (11) number of phyllaries series, (12) outer phyllary length, (13) outer phyllary width, (14) inner phyllary length, (15) inner phyllary width, (16) consistency of outer phyllaries, (17) number of ray florets series, (18) ray florets corolla length, (19) ray florets corolla limb length, (20) ray florets corolla limb width, (21) disc florets corolla length, (22) disc floret corolla limb width, (23) style branches length of disc florets, (24) achene length, (25) achene width, (26) pubescence of achene, (27) outer pappus length, (28) outer pappus type, (29) inner pappus length, and (30) inner pappus type.

Plant and leaf characters (1--6). - Plant height was measured from the base of the main stem to the apical part of the plant including the inflorescence. Petiole length was measured from the base of the petiole to the base of leaf lamina. In some cases, given the gradual winged character of the petiole, the base of the leaf lamina was defined in the point where the margin conspicuously changes its direction. Petiole width was measured at its broadest point. Leaf lamina length was measured from the base of the lamina to its apex. In the particular case of inconspicuously petiotale or sessile leaves, the lamina length was measured as the total length of the leaf. Leaf lamina width was measured at its broadest point.

Inflorescence characters (7--16): - Number of capitula was counted in each terminal reproductive branch. Length of the inflorescence peduncle was measured in terminal capitula. Involucre height was measured from the apex of the longest phyllary up to the insertion of the receptacle on the peduncle and involucre width at its broadest point. Phyllaries chosen to carry out the measures were the most external and the most internal of the involucre. Phyllary length was measured between the base of the phyllary and its apex, and its width was measured at its broadest point. Consistency of outer phyllaries was classified in coriaceous or herbaceous.

Ray floret characters (17--20). - Ray florets series were classified in 1-seriate or 2-seriate. Ray florets corolla length was measured from the limb apex up to the insertion of the corolla tube on the ovary or achene. Limb length was measured from the notch of the corolla to the limb apex. Limb width was measured at its broadest point.

Disc floret characters (21--23). - Disc florets corolla length was measured from the apex of lobes to the insertion of the corolla tube on the ovary or achene. Limb width was measured at its broadest point. Style branches length were measured from their apex to the bifurcation point of the style.

Achene and pappus characters (24-30). - Length and width of the fruit were measured. Length of the achene was measured from the achene base (i.e. carpopodium) up to the insertion of the pappus. Width of the achene was measured at its broadest point. Achene pubescence was classified in trichomes on ribs or covering all the surface. The outer series of pappus was classified in two types of elements: scale or paleaceous scale. On the other hand, the inner series of pappus was classified in two types of elements: bristle or paleaceous scale. Pappus length in each series was measured from the base up to the apex of the longest element.

Selected characters mentioned above were included in the multivariate analysis. Characters such as the number of phyllaries and the number of florets were not included in the multivariate analysis to avoid damage to herbarium specimens. All specimens were studied by direct observation and by a stereomicroscope Wild Heerbrugg; measurements for quantitative characters were taken using a digital caliper and a calibrated ocular micrometer.

We performed a Principal Coordinate Analysis (PCoA) to find the phenetic relationships among the specimens in an ordination space (Kapplan \& Marhold, 2012) using the Gower distance coefficient (Gower, 1971). Statistical analyses were carried out using the software PAST (Hammer et al., 2001).

## RESULTS

## Molecular results

Numerical results of the molecular study of the two regions and details of the three dataset analyses are shown in Electr. Suppl.: Table S\#1. Parsimony and Bayesian analyses yielded coincident topologies and we are showing the Bayesian phylograms in Figs. 1, 2 and Electr. Suppl.: Fig S\#1.

In the analyses of the three datasets (ITS, $\operatorname{trnL} L-F+$ ITS and $\operatorname{trn} L-F$ ), Liabeae was a monophyletic tribe with high support ( $\mathrm{PP}=1,1,1 ; \mathrm{BS}=100,91,100$ respectively) and in general subtribal classification is recognized with some differences to previous phylogenies, in particular regarding subtribes Liabineae and Paranepheliinae.

According to our analyses, Liabinae showed two main clades each one with high support. One includes species of Ferreyranthus ( $\mathrm{PP}=1,1, \ldots ; \mathrm{BS}=100 \%, 100 \%, \ldots$ ), and the other includes genera Dillandia, Liabum, Oligactis, and Sampera (PP = 1, 1, ...; BS $=87 \%, 92 \%, \ldots$ ). However, relationships between these two clades were unresolved. In particular, the analyses showed a monophyletic clade including Liabum and Sampera nested within the former ( $\mathrm{PP}=1,0.94,1 ; \mathrm{BS}=$ $97, \ldots, 100)$. The phylogenetic location of Cacosmia was contradictory, with affinities with either Liabinae or with Sinclairiinae depending on the marker used. Sinclairinae was a well-supported clade based on posterior probability values ( $\mathrm{PP}=0.92,1,1: \mathrm{BS}=\ldots, 97 \%, 97 \%$ ). Within this subtribe, the analyses showed two clades each one highly supported with ITS and ITS + trnL-F: Sinclairiopsis
clade ( $\mathrm{PP}=1, \ldots, 1 ; \mathrm{BS}=100, \ldots, 100$ ) and a clade with Liabellum, Megaliabum, and Sinclairia (PP $=1, \ldots, 1 ; \mathrm{BS}=100, \ldots, 100)$. Monophyly of Munnoziinae was obtained on the basis of the ITS and ITS $+\operatorname{trnL} L-F$ datasets with high support $(\mathrm{PP}=1,1 ; \mathrm{BS}=81,92$ respectively), however, the $\operatorname{trnL}-F$ dataset did not resolve the phylogenetic relationships nor showed the monophyly of this subtribe. Within Munnoziinae, all the analyses showed Chysactinium to be nested inside Munnozia.

In the case of current Paranepheliinae, genera from this subtribe are placed in different clades (Figs. 1 and 2). Microliabum s.l. (Clade A and Clade C) is placed among Liabeae in a clade that includes the genera Chionopappus, Chrysactinium, Erato, Munnozia, Paranephelius, Philoglossa, Pseudonoseris, and Stephanbeckia. This clade, that brings together the genera of current Munnoziinae and Paranepheliinae, has high support in the analyses of the three datasets: $\mathrm{PP}=0.97,1,1 ; \mathrm{BS}=\ldots$, $79 \%$, $97 \%$; Figs. 1, 2; Electr. Suppl.: Fig S\#1.

However, Microliabum is not monophyletic: subgenera Austroliabum (Clade A) and Microliabum (Clade C) are placed in different clades (Figs. 1, 2; Electr. Suppl.: Fig S\#1). Monophyly of subgenera Austroliabum and Microliabum is equally supported ( $\mathrm{PP}=1$ in the three datasets; $\mathrm{BS}=100 \%, 100 \%$, 81\%). Subgenus Austroliabum is grouped with Paranephelius and Pseudonoseris without support from ITS and the ITS + trnL-F datasets (Figs. 1, 2). Subgenus Microliabum is grouped in a clade with Stephanbeckia (Clade B) with high support ( $\mathrm{PP}=1$ in the three datasets; BS $=99 \%, 100 \%, 99 \%$ ).

The individual species in the subgenus Austroliabum clade show no resolution, whilst the Microliabum clade are well-defined at the species level. It is important to highlight the phylogenetic position of M. humile (the type species of genus Microliabum) within the clade of the subgenus Microliabum; according to the analysis this species forms a clade with M. mulgediifolium from ITS with high support ( $\mathrm{PP}=1 ; \mathrm{BS} 96 \%$; Fig. 1) and molecularly it is very differentiated.

## Morphological results

A detailed comparative morphological analysis between subgenera Austroliabum and Microliabum was undertaken in order to compare it with our phylogenetic results.

Habit, stem, latex and pseudostipules. Species of Microliabum are usually annual, biennial or perennial herbs, rarely subshrubs (Fig. 3 A-B). Plants may be tall, usually up to 2 m in height, less often very reduced, up to 15 cm .

Two patterns of branching and phylotaxis are identified: (1) few-branched or unbranched small herbs with leaves clustered at the base of the main stem (i.e. M. humile), (2) tall branched or unbranched herbs or rarely subshrubs, with only one or few stems, with leaves spread along stems ( $M$. mulgediifolium, M. polymnioides, and all the species of subgenus Austroliabum). In the last type, stems are ascendant or decumbent (subgenus Austroliabum; Fig. 3 A) or erect (especially subgenus

Microliabum; Fig. 3 B). Pubescence varies among glandular-hirsute (Fig. 3 C), arachnoid, whitetomentose or woolly, with the same main type of trichome found on the leaves (see below).

The occurrence of latex has been considered one of the diagnostic characters of Liabeae. Microliabum mulgediifolium and M. polymnioides show abundant white latex (Fig. 3 C) when cutting main stems, branches and also leaves and peduncles in the wild. However, these species show little latex in greenhouse. On the contrary, species of subgenus Austroliabum show always little latex in field and greenhouse. Plants are sticky, especially M. glanduliferum.

Pseudostipules are elements on the nodes arising at each side of the leaf base. In Microliabum, they are completely absent (i.e. M. humile), absent only from several nodes, or very conspicuous (Fig. 3 D-F). When present, they are foliaceous and show different degrees of development among species, individuals or nodes. They can be opposite, sometimes subalternate, free (Fig. 3 D, F) or fused (Fig. 3 E). In species with winged petioles, pseudostipules are continuous with the wings (Fig. 3 F ). They are subglabrous or arachnoid-pubescent adaxially and white-tomentose or woolly abaxially.

Leaves. Leaves are usually opposite and decussate, sometimes clustered at the base of the stem (i.e. M. humile) and subalternate toward the apex in reproductive branches. They are sessile or inconspicuously petiolate (i.e., M. humile and rarely in some specimens of M. eremophilum and M. mulgediifolium), short-petiolate or long-petiolate (subgenus Austroliabum up to $1--6 \mathrm{~cm}$ long, and $M$. mulgediifolium and M. polymnioides up to $10-15 \mathrm{~cm}$ long) (Fig. 3 G-I). The inconspicuous type of petiole is a gradual extension of the leaf lamina toward the leaf base, wider near the lamina and narrowing to the stem. Petioles may be wingless (Fig. $3 \mathrm{G}, \mathrm{I}$ ) or completely winged with narrow or wide wings (Fig. $3 \mathrm{~F}, \mathrm{H}$ ), continuous or not with the pseudostipules; when continuous, the petiole wings are very well demarcated from the leaf lamina base and have the same width throughout. Wing margins may be mucronate-serrate or serrulate, irregularly toothed or erose.

Leaf laminas may be ovate or sub-triangular in shape (Fig. 3 G-I). Apices are usually acute and lamina bases show considerable variation: they are predominantly cuneate but they may also be decurrent, rounded, cordate, truncate or sagittate. Leaf margins may be mucronate-serrate or serrulate (subgenus Austroliabum, M. humile), or irregularly toothed or erose (i.e., M. mulgediifolium and M. polymnioides).

Venation in Microliabum is usually actinodromous, 3-veined, but in M. humile and some small individuals of $M$. mulgediifolium and M. polymnioides it is inconspicuous.

Leaf pubescence (including phyllaries) and trichomes. There is usually a marked difference in the amount of pubescence on the adaxial versus the abaxial surface of the lamina (Fig. 3 G-I). Adaxial leaf surface is glabrescent (Fig. 3 H ) or hirsute, sometimes mixed with a white-arachnoid and evanescent
indumentum (Fig. 3 G, Fig. 4 A), and abaxial leaf surface is usually white-tomentose to woolly (Fig. 3 I), sometimes brownish in dried specimens. In some specimens, the tomentum is mixed with conspicuous glandular trichomes, which may be distributed along the main veins, leaf margins or across the surface of the lamina.

Phyllaries are internally glabrous and externally glabrescent, glandular-hirsute, sometimes mixed with an arachnoid and evanescent indumentum, or white-tomentose to woolly. Trichomes can be classified into four main types (Fig. 4 A-D):
(a) Simple conical trichomes (Fig. 4 A ): These trichomes have a simple foot and a uniseriate body. The body is entire, (1--)2--3-celled, conical, pointed and rounded at the apex. They are present in Microliabum subgenus Austroliabum.
(b) Aseptate-flagellate trichomes (Fig. 4 A-D): These trichomes have a simple foot and a uniseriate body. The stalk is $2--6$-celled with conical or cylindrical cells. The head is 1 -celled, very long, coiled, flagellate, pointed and rounded at the apex. These trichomes usually produce hirsute, arachnoid, tomentose and woolly pubescence. In Microliabum subgenus Austroliabum the stalk is shorter, with more narrow cylindrical cells, than in subgenus Microliabum.
(c) Biseriate glandular trichomes with a big stalk (Fig. 4 A-C): The foot is 2-celled and the body biseriate with sub-opposite or alternate cells in each row. The stalk is 3--7-celled in each row and the head is, demarcated from the stalk or continuous with it, 2--4-celled in each row; the two terminal cells are slightly distinct like a vesicle.
(d) Biseriate glandular trichomes without stalk or with a reduced one (Fig. 4 D ): They are similar to trichomes described under (c) but the stalk is lacking or reduced and they are 1--2-celled in each row. The head is $2--3$-celled in each row with the two terminal cells slightly distinct like a vesicle. These trichomes usually are found in Microliabum subgenus Austroliabum on the lower surface below tomentum.

Inflorescences, capitula, involucres and phyllaries. Microliabum shows few or many capitula grouped in a terminal alternate branched corymbiform secondary inflorescence (also called capitulescence). Particularly, M. humile has commonly a single capitulum or several in terminal branches but not grouped. Only one capitulum is rarely present in the other species during early developmental stages. Capitula are pendulous (i.e. M. mulgediifolium), erect or ascendent (rest of species) with short or long peduncles between $0.5--10 \mathrm{~cm}$ long (Fig. 5 A-B). Peduncles are whitetomentose or woolly (Fig. 5 A), hirsute, usually with conspicuous glandular trichomes (Fig. 5 B; see trichome's type c above), sometimes absent.

Involucre and phyllaries traits (e.g. shape of involucre, phyllaries series, phyllaries positios of outer series, phyllaries size, and number of phyllaries) were important features of macromorphology
for taxonomical purposes because these easily differentiated and/or grouped among subgenera Austroliabum and Microliabum, and related genera.

Involucre is campanulate in subgenus Austroliabum (Fig. 5 A ) or hemispherical in subgenus Microliabum (Fig. 5 B). Phyllaries are organized in 4--6 series, usually five, in subgenus Austroliabum (Fig. 5 A) or 2--4, usually three, in subgenus Microliabum (Fig. 5 B) and are from few to numerous, 15--25 in M. humile to 45--75 in subgenus Autroliabum and M. mulgediifolium and M. polymnioides. From the outer series to the inner, there is a gradual transition. However, inner phyllaries are longer than the outer ones in subgenus Austroliabum, and, on the contrary, inner phyllaries are shorter than the outer ones in subgenus Microliabum. Phyllaries are mainly ovate, long-ovate or oblong, rarely obovate in shape, with acute or attenuate apices. In the case of the subgenus Austroliabum, phyllaries are coriaceous and adpressed throughout all the stages of its development (Fig. $5 \mathrm{~A}, \mathrm{C}$ ). On the contrary, in subgenus Microliabum they are mainly herbaceous with the outer ones exserted (Fig. 5 B, D), and the innermost ones membranaceous and reduced, sometimes inconspicuous. They are hirsute with glandular-tipped trichomes (Fig. 4 C), white-arachnoid, tomentose or woolly.

Receptacle is flat or slightly convex, naked and foveolate.

Florets. Capitula are conspicuously radiate (Fig. 5 E-F) and heterogamous, having ray florets with true ray corollas and disc florets with tubular funnelform corollas. The number of florets per capitulum varies greatly from 25--195: subgenus Austroliabum shows 65--115, subgenus Microliabum (except M. humile) 145--195, and M. humile 25--30. Disc florets are approximately as many as ray florets (i.e., M. humile, subgenus Austroliabum). However, in M. mulgediifolium and M. polymnioides the quantity of disc florets is in general almost the double of ray florets.

Ray florets are pistillate, fertile, without staminodia. There is only one series of ray florets in subgenus Austroliabum (Fig. 5 E) and in M. humile, or two rows in M. mulgediifolium and M. polymnioides (Fig. 5 F ). The number of ray florets varies approximately from 10-75 per capitulum: subgenus Austroliabum has 25--50, subgenus Microliabum (except M. humile) 35--75, and M. humile 10--15(--18). Ray florets have true ray corollas with limbs narrowly elliptic, oblong or obovate in shape, 4 -veined and conspicuously 3 -dentate at the apex. These corollas are usually yellow or rarely slightly orange, and pubescent (excepting some specimens of M. humile with glabrous corollas). Styles of the ray florets are bifid, with filiform, curly or curved branches, narrowly obtuse at the apex, longer than styles branches of the disc florets. Externally, the branches are glabrous; internally, the branches are completely covered by stigmatic papillae. The styles lack a nectary at the base.

Disc florets are hermaphrodite and fertile, and they vary widely from 15--125 per capitulum: in the case of subgenus Austroliabum variation was less than in subgenus Microliabum, from 40--65. Disc florets are 100--125 in M. mulgediifolium and M. polymnioides, and approximately 15 in $M$.
humile. Corollas are tubular funnelform, deeply 5-lobed, usually yellow or rarely slightly orange and pubescent at least on the lobes (i.e., some specimens of $M$. humile).

True ray and tubular corollas may be glabrous or pubescent with glandular trichomes, particularly on upper part of the tube and basal part of limb or throat, limb apex of true ray corollas, and on the lobes of tubular corollas. Papillae are also present on lobes apices of tubular corollas. Trichomes may be divided into two following types:
(a) Simple biseriate trichomes or simple biseriate glandular trichomes without a conspicuous head (Fig. 6 A): these are entire, with $3--5$ long cells in two rows with thin or thick walls. They are usually found on the external side of both true ray and tubular corollas, particularly on upper part of the tube and basal part of limb or throat, limb apex of true ray corollas, and lobes of tubular corollas, near the apex.
(b) Simple biseriate glandular trichomes with a conspicuous head (Fig. 6 A): these are differentiated into stalk and head; the stalk has 2--5 short cells in two rows, and the head 2--3 cells in two rows, of varied length but those of terminal tier often relatively larger, with thin walls. They are found on the external side of true ray and tubular corollas.

The anthers are pale yellowish, linear, shortly calcarate and caudate. Apical appendages are smooth, flat, ovate, and apically rounded. The anther tails are papillose (e.g. M. candidum) or rounded (e.g. M. humile). Styles are broadest at the base (stylopodium) and the two style branches are shorter (from 0.2 mm to 1.1 mm long) than the pubescent part on shaft below the bifurcation point, either straight or curved and divergent at maturity (Fig. 6 B-C); in the case of subgenus Austroliabum, length of style branches is $0.5--1.1 \mathrm{~mm}$ long, and in sugenus Microliabum is $0.2--1 \mathrm{~mm}$ long. Externally, the branches are hispidulous, with sweeping hairs formed by conical elements pointing toward the apex (Fig. 6 C). Sweeping hairs extend down on the style shaft from the bifurcation point to distance more than the length of the style branches. The inner surfaces of the branches have each one a continuous stigmatic surface with papillae (Fig. 6 C). Styles have a short nectary, not or scarcely lobed, at the base.

Achenes. Achenes of ray and disc florets are morphologically similar in subgenera Austroliabum and Microliabum (Fig. 6 D-E): they are cylindrical, ellipsoid or obconic, generally with a conspicuous annular carpopodium at the base, widened in the pappus insertion area, faintly to markedly 8 --10costate, and pubescent. Pubescence is formed by typical twin hairs usually with its cells completely united on their longitudinal walls or sometimes the cells are apically diverging (Fig. 6 F). Twin hairs are mainly on ribs in subgenus Austroliabum (Fig. $6 \mathrm{D}, \mathrm{F}$ ) or they usually cover all the achene surface in subgenus Microliabum (Fig. 6 E).

Pappus. Pappus is 2-seriate and heteromorphic, formed by different types of elements in outer and inner series with the outer elements always conspicuously shorter than the inner. These elements can be scales or bristles (Fig. 6 D-E, G-J). Scales are planate elements, ovate, elliptic or obovate in shape, with decurrent or convex bases, acute, rounded or obtuse apices, and erose or serrulate margins. Sometimes scales are paleaceous, i.e. paleae-like, when they resemble rudimentary bracts. On the other hand, bristles are stiff hair-like elements, thin or broadened, with barbellate margins. Within subgenus Austroliabum, the outer series of the pappus is formed by few, short (up to $0.3-1 \mathrm{~mm}$ long), scales (Fig. 6 D, G), elliptic or obovate in shape, with rounded or obtuse apices, and erose margins; in contrast, within subgenus Microliabum, the outer series is formed by few, short (up to $0.6-1.2 \mathrm{~mm}$ long), paleaceous scales (Fig. $6 \mathrm{E}, \mathrm{H}$ ), elliptic or ovate in shape, with acute, rounded or obtuse apices, and serrulate margins. The inner series of subgenus Austroliabum always consists of numerous, long (ca. 7 mm long), barbellate bristles. Similar elements are present in the inner series of Microliabum mulgediifolium and M. polymnioides (Fig. 6 I). These elements are shorter (approximately 4.5 mm long) barbellate bristles, and sometimes they are broadened with long barbellate margins in specimens of $M$. mulgediifolium. Finally, M. humile has the inner series consisting of few, long (usually 2 mm long) paleaceous scales (Fig. 6 J), ovate in shape, with acute apices and serrulate margins. Thus, morphological variation is greater among species of subgenus Microliabum.

Outer and inner series are usually persistent in subgenus Austroliabum, and the inner series is easily deciduous in subgenus Microliabum. The pappus is yellowish, brownish or orange, and generally the color varies within a species, and between living plants and dried specimens.

Some important characters from a taxonomic point of view of genera Paranephelius, Pseudonoseris (closely related to Microliabum subgenus Austroliabum) and Stephanbeckia (to Microliabum subgenus Microliabum) are comparatively analyzed in Table 2. The selected characters have been mainly used in previous works to circumscribe Liabean genera and the subgenera of Microliabum.

## Multivariate Analyses

Morphological and morphometric variation is shown in Table 3 and Electr. Suppl.: Table S\#2. The Principal Coordinates Analysis (PCoA) recovered two well-defined groups when the two principal coordinates were plotted (Fig. 7). The first three coordinates accounted for $68.64 \%$ of the total variance $(38.82 \%, 26.63 \%$, and $3.19 \%$, respectively). One group includes the three species of Microliabum subgenus Austroliabum, and the other group the three species of M. subgenus Microliabum. In the last group individuals of $M$. humile were differentiated from the individuals of $M$.
mulgediifolium and M. polymnioides. The two groups are in agreement with the results obtained in our phylogenetic analyses (Figs. 1, 2; Electr. Suppl.: Fig S\#1).

## DISCUSSION

## Monophyly of the subgenera and relationships of Microliabum within Paranepheliinae

In our work both subgenera of Microliabum are monophyletic with high support, as originally established by Robinson (1990). However, the current genus Microliabum is not a natural group because subgenus Microliabum is strongly supported as sister to Stephanbeckia. On the other hand, the evolutionary position of Microliabum subgenus Austroliabum within Paranepheliinae remains unclear. It is associated with Paranephelius and Pseudonoseris without support. Circumscription of Austroliabum at genus level as proposed by Robinson \& Brettell (1974), and then by Robinson (1983), including M. mulgediifolium and M. polymnioides is here rejected based on our phylogenetic and multivariate analyses. On the contrary, the treatment made later by Robinson (1990) considering M. candidum, M. eremophilum and M. glanduliferum within subgenus Austroliabum is here confirmed.

According to our analyses, monophyly of Paranepheliinae is neither supported nor refused by our results since there is lack of resolution in the clade consisting of Munnoziinae and Paranepheliinae. Our results on Paranepheliinae and Munnoziinae agree with Funk \& al. (2012).

Morphological affinities between subgenus Austroliabum and the Paranephelius-Pseudonoseris clade, and between subgenus Microliabum and Stephanbeckia

Regarding our morphological study, Microliabum subgenus Austroliabum and Paranephelius and Pseudonoseris share vegetative and reproductive features. In the case of vegetative traits, only one, the lower leaf pubescence, can be highlighted because these taxa share a white-tomentose or woolly abaxial pubescence. On the other hand, reproductive characters shared among Microliabum subgenus Austroliabum and Paranephelius and Pseudonoseris are many. The most important of them for taxonomical purposes are: number of phyllaries series (i.e. four to six), position of the outer series of phyllaries (i.e. adpressed), phyllaries length (i.e. gradually increasing length with the inner phyllaries longer than the outer ones), series of the ray florets (i.e. only one series), series of pappus (i.e. two series), type of inner pappus (i.e. barbellate bristles), and usually persistent elements of pappus. According to our results, two characters of the analysed taxa are especially useful in taxonomy because they are only shared among Microliabum subgenus Austroliabum and Paranephelius and Pseudonoseris: four to six series of phyllaries and usually persistent pappus.

Concerning morphological affinities between Microliabum subgenus Microliabum and Stephanbeckia, they share mainly reproductive features. For example, type of capitula (i.e. pedunculate), number of phyllaries series (i.e. 2--4, usually three), number of phyllaries (i.e. 40--75),
comparative length of style branches of disc florets (i.e. shorter than the pubescent part on shaft below the bifurcation point) and comparative length of style pubescence on shaft below the bifurcation point of disc florets (i.e. at least three times longer than the branches of the style), and pappus elements usually deciduous. In M. humile (part of M. subgenus Microliabum) the phyllaries are much fewer. However, only two of these characters are exclusively shared by these taxa: number of phyllaries series and pappus elements usually deciduous.

## Morphological differences between subgenera Austroliabum and Microliabum

According to our work, based on morphology and a multivariate analysis, the main differences between subgenera Austroliabum and Microliabum are given by both qualitative and quantitative reproductive characters: shape of involucre, number of series, position, comparative length, and consistency of phyllaries, number of series of ray florets, number of disc florets, achenes pubescence, and type and dehiscence of pappus' elements (Table 2). However, some vegetative characters such as the petiole length and its width should not be discarded if the average measures are considered (Table $3)$.

Many features that have been used in previous works (Robinson \& Brettell, 1974; Robinson, 1983, 1990) are here considered as useless, or at least imprecise or incorrect, for distinguishing subgenera Austroliabum and Microliabum because they are variable and overlap: for example, habit ("coarse" vs. "minute" herbs, respectively), type of inner pappus elements ("capillary" vs. "broad laminate"), number of phyllaries ("50--75" vs. "10--40"), number of phyllaries series ("3--4" vs." $1--$ 2 "), comparative length of phyllaries ("gradated series" vs. "subequal"), pubescence of disc corolla throats ("hirsute outside" vs. "glabrous"), pappus color ("rusty yellow" vs. "withish"), shape of pappus outer elements ("narrow, shortly setiform or minutely squamiform" vs."broadly squamiform"), shape of pappus inner elements ("capillary" vs. "minimally to strongly flattened or broadened"), and teeth type and distribution on pappus inner elements ("spreading equally on lateral and outer surfaces" vs. "stronger toward sides, reduced on inner surface and less reduced on outer surface").

Other features belonging to the involucre are confirmed, with modifications, to be of systematic value for distinguishing subgenera Austroliabum and Microliabum: for example, phyllaries features such as number of series (4--6 series, usually five in subgenus Austroliabum vs. 2--4 series, usually three in subgenus Microliabum), and comparative length (inner phyllaries longer than outer ones vs. inner phyllaries shorter than outer ones, respectively), including quantitative characters (Tables 2, 3). Moreover, some characters habe been found here for the first time to be diagnostic like shape of involucre (campanulate vs. hemispherical, respectively), position of outer phyllaries (adpressed vs. exserted), and consistency of phyllaries (coriaceous vs. herbaceous or membranaceous). In addition, other morphometric characters analyzed in our work could provide differences to properly
circumscribe and differentiate subgenera Austroliabum and Microliabum; for example, width of the involucre ( 1.08 cm vs. 1.75 cm , respectively), length of the outer phyllaries ( 4.21 mm vs. 7.78 mm ) and length of inner ones ( 7.92 mm vs. 5.5 mm ) (Table 3).

On the other hand, new floral features are detected in our work for separating the subgenera: series of ray florets, number of ray florets, number of disc florets, ratio between rays and disc florets, length of disc florets corolla, and length of style branches of disc florets. For example, subgenus Austroliabum shows rays in only one series vs. subgenus Microliabum mainly in two series (M. humile is the exception with only one series like subgenus Austroliabum), $25--50$ ray florets vs. 10--25 or $35-$ 75 (subg. Austroliabum and subg. Microliabum, respectively), 40--65 disc florests vs. 15 or 100--125, ca. 7 mm long of disc florets corolla vs. ca. 4.5 mm long, and ca. 0.8 mm long of style branches of disc florets vs. ca. 0.5 mm long (Tables 2, 3). In the case of the achenes, subgenus Austroliabum shows twin hairs especially on the ribs, while in subgenus Microliabum the twin hairs cover densely the complete surface.

One of the most important systematic features of Microliabum is the type of pappus (e.g. Cabrera, 1954; Robinson \& Brettell, 1974; Robinson, 1983). This character was originally used to separate Microliabum from the rest of the Liabean genera or, later on, to recognize morphological affinities among species of M. subgenus Austroliabum and M. subgenus Microliabum (e.g. Robinson, 1983; Robinson, 1990). Both subgenera share some pappus traits like elements in two conspicuous series, and the outer elements shorter than the inner ones. However, several characters allow to differentiate and circumscribe both subgenera. In subgenus Austroliabum the outer series of pappus are formed by scales with erose margins and the inner series by barbellate bristles. On the other hand, subgenus Microliabum shows the outer series of paleaceous scales with serrulate margins and the inner ones of barbellate bristles (i.e. M. mulgediifolium and M. polymnioides) or paleaceous scales (i.e. M. humile). It is important to note that among the barbellate bristles and paleaceous scales of the inner series, intermediate forms appear as long barbellate and planate elements (some specimens of $M$. mulgediifolium). Some morphometric characters of the pappus contribute to the separation between subgenera; for example, the outer series of pappus is approximately 0.6 mm long in subgenus Austroliabum vs ca. 0.8 mm long in subgenus Microliabum. On the contrary, the inner series is ca. 7 mm long in the former subgenus vs ca. 4 mm long in the last subgenus (Table 3). In relation with pappus traits, morphological differences between M. subgenus Austroliabum and M. subgenus Microliabum found in our work are as important as the differences displayed among other genera of Liabeae (Robinson, 1983; Funk \& al., 1996; Robinson \& Funk, 2011).

Based on the phylogeny of Microliabum obtained with molecular data, our thorough comparative morphological study, and the multivariate analysis, we propose the reinstatement of the genus

Austroliabum as an independent genus of Liabeae. Secondarily, it results in a genus Microliabum s. str. with three species. Our study confirms, without doubts, M. humile as relative to M. mulgediifolium and M. polymnioides. Many of its particular morphological characteristics (for example its reduced habit) may be related to its extreme adaptations to the high altitudes and rigorous climates it inhabits.

Our work recognizes all the genera that are currently part of subtribes Munnoziinae and Paranepheliinae (e.g. Soejima et al., 2008; Dillon et al., 2009; Funk et al., 2012) as only one phylogenetic lineage within Liabeae, but it is not conclusive about the circumscription of each subtribe and relationships among genera. We herein propose to include the resurrected genus Austroliabum within the current Paranepheliinae given its morphological affinities with the other genera of this subtribe, in particular with Paranephelius and Pseudonoseris.

Finally, new challenges in order to understand the evolution of Liabeae may include a greater sampling of species for resolving phylogenetic relationships among genera and, especially, to perform phylogeographical studies that may explain the causes of the geographical distribution of South American Liabean taxa that have conquered environments beyond the Andes such as Austroliabum.

## TAXONOMIC TREATMENT

In light of new evidence, a new morphological key to current Paranepheliinae is necessary considering a reestablished genus Austroliabum and a genus Microliabum in a restricted sense.

1. Abaxial leaf surfaces subglabrous and green; leaves and stems with stiff trichomes with enlarged
bases ................................................................................................. 2
2. Leaves actinodromous 5 --9-veined; achenes 4 -sided, 4-ribbed; pappus present Erato
3. Leaves actinodromous 3-veined; achenes 2-sided, 2-ribbed; pappus absent ...... Philoglossa 1. Abaxial leaf surfaces white-tomentose or woolly; leaves and stems without stiff trichomes with
enlarged bases ............................................................................................ 3
4. Pappus of plumose bristles ............................................................................ 4
5. Shrubs or subshrubs; receptacles paleaceous; achenes prismatic, 8--10-ribbed; pappus persistent Chionopappus
6. Herbs; receptacles naked; achenes compressed, 2-ribbed; pappus deciduous

Stephanbeckia
3. Pappus of barbellate bristles or scales ............................................................. 5
5. Involucres hemispherical; phyllaries $2-4$-seriate, mainly 3 -seriate, decreasing in length, outer series longer than inner, exserted, herbaceous or membranaceous; achenes densely pubescent with trichomes usually on the all surface; outer pappus of
paleaceous scales, inner of barbellate bristles or paleaceous scales, deciduous
$\qquad$
5. Involucres campanulate; phyllaries 4--6-seriate, mainly 5-seriate, gradually increasing in length, outer series shorter than inner, adpressed, coriaceous; achenes pubescent with trichomes usually on ribs or glabrous; pappus of barbellate bristles, or outer pappus of scales and inner of barbellate bristles, persistent


#### Abstract

6. Pseudostipules present; leaves acrodromous, 3-veined; disc florets with style branches shorter than the pubescent part on shaft below the bifurcation point

Austroliabum


> 6. Pseudostipules absent; leaves pinnate; disc florets with style branches longer than the pubescent part on shaft below the bifurcation point ........... 7
7. Capitula sessile or subsessile; achenes glabrous ...... Paranephelius
7. Capitula pedunculate; achenes sparsely pubescent ... Pseudonoseris

Austroliabum H.Rob. \& Brettell emend. D.G.Gut., N.Garcia, Susanna \& M.A.Grossi, Phytologia 28: 48, $1974 \equiv$ Microliabum subgenus Austroliabum (H.Rob. \& Brettell) H.Rob., Syst. Bot. 15: 743, 1990. - TYPE: Austroliabum candidum (Griseb.) H.Rob. \& Brettell $\equiv$ Liabum candidum Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 203. 1879.

Annual, biannual or perennial herbs, rarely subshrubs to 1.5 m tall, loosely branched or sometimes unbranched, with inconspicuous or scarce latex. Stems erect, ascendent or decumbent, with appressed dense white-tomentose pubescence or woolly and hirsute with spreading stipitate glandular trichomes; nodes without sheath, pseudostipules opposite, fused or free, sometimes alternate in upper branches, rarely connected to petiole wings, herbaceous. Leaves opposite, less often alternate in upper branches, conspicuously petiolate with winged or wingless petioles; laminas narrowly or broadly ovate or triangular, bases truncate, cordate or cuneate, apices acute or attenuate, margins subentire, dentate or serrate, mucronulate; acrodromous, 3-veined, main pair of lateral veins reaching the middle of the lamina; surfaces flat, hirsute adaxially usually mixed with white-arachnoid pubescence, greenish or whitish, densely white-tomentose or woolly abaxially, sometimes with stipitate glandular trichomes on main veins. Capitula heterogamous, radiate, few or many, terminal, in an alternate branched corymbiform capitulescence, rarely a single terminal capitulum, pedunculate with peduncles erect, densely white-tomentose or woolly. Involucres campanulate, 4--6-seriate, usually 5-seriate; phyllaries 45--70, imbricate, gradually increasing in length, outer shorter, ovate or narrowly ovate, adpressed, coriaceous, white-tomentose, sometimes with stipitate glandular trichomes, inner oblong or narrowly ovate, adpressed, coriaceous, glabrescent; receptacles flat to slightly convex, foveolate, naked. Florets

65--115, all fertile. Ray florets 25--50, 1-seriate, pistillate, without staminodia; corollas true ray, yellow, rare slightly orange, pubescent with glandular trichomes on outer surface, limbs obovate or elliptical, 4-veined, apices 3-dentate; styles filiform, style branches filiform, curved, with papillae on inter and outer surface. Disc florets 40--65, bisexual; corollas tubular, funnelform, yellow, rare slightly orange, deeply 5-lobed, lobes narrowly ovate, with glandular trichomes on the outer surface; anthers yellow, linear, shortly calcarate and shortly caudate; apical appendages ovate, flat; styles filiform, with sweeping hairs externally from the middle of the style shaft up to the apices, style branches shorter than the pubescent part on shaft below the bifurcation point, filiform, curved at maturity, stylopods enlarged, globose; nectaries disciform, not lobed. Achenes obovoid o obconical, 8--10-ribbed, pubescent with twin hairs usually on ribs, carpopodia conspicuous; pappus distinctly 2 -seriate, outer series of scales, margins erose, inner series of bristles barbellate, fine, persistent. Chromosome number: $2 n=14$ (Bernardello, 1986).

Robinson \& Brettell (1974) mixed diagnostic characteristics from Austroliabum and Microliabum when describing Austroliabum, and the description has to be amended. According to the protologue, Austroliabum included originally species with phyllaries equal or subequal and inner pappus series mostly easily deciduous (Robinson \& Brettell, 1974). Actually, these traits belong only to Microliabum. Austroliabum has phyllaries in 4--6 series, usually five, gradually increasing in length and persistent inner pappus.

Distribution and Habitat. Austroliabum is distributed from northwestern to central Argentina (Fig. 8 A). All species grow in environments of non-Andean mountains: the Pampean ranges ("Sierras Pampeanas", also called "Sierras de Córdoba" and "Sierras de San Luis") and the Sub-Andean ranges ("Sierras Subandinas", for example "Sierras de La Rioja"). The Sierras Pampeanas are a chain of mountains that rise sharply from the surrounding pampa region of Northwest Argentina. They run parallel to the Andes and have a temperate and semi-arid climate. The northern east slope is covered by rainforests, due to high humidity in this subtropical zone. The stretch within Córdoba and San Luis provinces enjoys a Mediterranean-type climate. From a phytogeographical point of view, Austroliabum inhabits in the Chacoan (Serrano and Western districts) Biogeographical Province (Cabrera \& Willink, 1980), in open areas in mid-elevation forest or seasonally dry scrub.

## Key to species of Austroliabum

1. Plants strongly glutinous; stems and petioles hirsute with densely spreading, conspicuous glandtipped trichomes and white tomentum
A. glanduliferum
2. Plants not glutinous, rarely slightly glutinous; stems and petioles with dense white tomentum or wool; spreading gland-tipped trichomes absent or rarely inconspicuous hidden below tomentum 2
3. Stems and abaxial leaf surfaces densely white-tomentose or woolly; petioles wingless or slightly winged in the upper part; laminas ovate or subtriangular up to 8 cm wide; capitula on peduncles up to 4 cm long
A. candidum
4. Stems and abaxial leaf surfaces slightly white-tomentose; petioles widely winged; laminas narrowly ovate or subtriangular up to 6 cm wide; capitula on peduncles up to 10 cm long
A. eremophilum
5. Austroliabum candidum (Griseb.) H.Rob. \& Brettell, Phytologia 28: 49. $1974 \equiv$ Liabum candidum Griseb. in Abh. Königl. Ges. Wiss. Göttingen 24: 203. 1879 [Symb. fl. argent.: 203. 1879] $\equiv$ Microliabum candidum (Griseb.) H.Rob., Syst. Bot. 15: 743. 1990. - TYPE: Argentina. Córdoba: Punilla department, "An einem Felsen zwischen Cosquín und Santa María [de Punilla]", 27 Jan 1876, G. Hieronymus 280 (lectotype: GOET 001801 [photo!], designated by Gutiérrez [2015: 292]; isolectotypes: CORD 00006499!, CORD 00006500!, F 0076427F [photo!], G [phote!], GOET 001802 [photo!]). Type loc.: "C [Córdoba]: in rupibus pr [prope] S [Santa] María". Fig. 9.
= Liabum auriculatum Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 202. 1879 [Symb. fl. argent.: 202. 1879]. - TYPE: Argentina. Córdoba: Punilla department, "Sierra [de] Achala, nordl[ich] von der Cuesta de Copina", 20 Feb 1877, G. Hieronymus 641 (holotype: GOET 001803 [photo!]; isotypes: BAF! [without barcode]; CORD 00006498!). Type loc.: "C [Córdoba]: S [Sierra de] Achala".
$=$ Liabum subcirrhosum S.F.Blake, J. Wash. Acad. Sci. 17: 293. $1927 \equiv$ Liabum candidum Griseb. var. subcirrhosum (S.F.Blake) Cabrera, Bol. Soc. Argent. Bot. 2: 95. 1947. - TYPE: Argentina. Catamarca: Andalgalá department, La Playa, 12 Feb 1917, P. Jörgensen 1673 (holotype: US 00122753 [photo!]; isetypes: BA 24737 ! [20 Dec 1916], F [photo!, fragment of St], GH [photer!, La Playa, 26 Feb 1917 and 15 Feb 1916, two sheets], LlL 26626! [15 Feb 1916], SI 000925! [1915, Feb 1916]).

Annual, biennial or perennial herbs, rarely subshrubs, up to 1.5 m tall, with latex scarce in stems and leaves. Stems erect, ascendent or decumbent, terete, not costate, not or densely branched, densely and persistently white-tomentose or woolly, usually without spreading gland-tipped trichomes or rarely present and then inconspicuous and hidden below tomentum; pseudostipules fused or free, herbaceous. Leaves opposite, scattered along the stem and secondary branches, herbaceous, petiolate; petioles 1--6 $\mathrm{x} 0.1--0.2 \mathrm{~cm}$, wingless or slightly wingled in upper part, white-tomentose or woolly usually without spreading gland-tipped trichomes; laminas $4--12.5 \times 1.5--8 \mathrm{~cm}$, ovate or triangular bases truncate,
cuneate or slightly cordate, apices acute, margins evenly serrate or dentate, mucronulate, acrodromous, 3 -veined, with the pair of lateral veins reaching the middle of the lamina, surfaces flat, hirsute or white-arachnoid pubescent and greenish adaxially, densely white-tomentose or woolly abaxially. Capitula few or many, terminal, in a lax corymbiform capitulescence, pedunculate, peduncles $0.5--4$ cm long, densely white-tomentose or woolly. Involucres $0.8-1.3 \times 0.8-1.3 \mathrm{~cm}$, campanulate, 4--6seriate, usually 5 -seriate, all series adpressed; phyllaries $55--65$, imbricate, coriaceous, outer 3--6.2 x $0.8--1.5 \mathrm{~mm}$, ovate, apices acute or attenuate, hirsute with glandular-tipped trichomes and densely white-tomentose, inner $6--10.2 \times 0.7-1.2 \mathrm{~mm}$, narrowly ovate or oblong, apices acute or attenuate, glabrescent. Ray florets $30-50$, 1 -seriate, pistillate, fertile; corolla 1--1.7 cm long, true ray, yellow, pubescent with glandular-tipped trichomes; tubes $5.6-7 \times 0.2--0.3 \mathrm{~mm}$, pubescent above; limbs 5-$11.5 \times 0.7--1.3 \mathrm{~mm}$, narrowly oblong or obovate, 4 -veined, apices 3 -dentate, pubescent below. Disc florets $50--65$, bisexual, fertile; corolla $5.5--8.5 \mathrm{~mm}$ long, tubular, funnelform, yellow, tube and throat gradually differentiate, 5 -lobed, with glandular-tipped trichomes; tube plus throat $5.2--5.5 \mathrm{~mm}$ long, tubes $0.2--0.3 \mathrm{~mm}$ wide, pubescent above; throats $0.6-1.2 \mathrm{~mm}$ wide, pubescent below; lobes $1.5--1.7$ x ca. 0.3 mm , apically pubescent; style branches $0.5--1.1 \mathrm{~mm}$ long. Achenes $1.3--2.4 \times 0.5--1 \mathrm{~mm}$, obovoid or obconical 8 --10-ribbed, pubescent mostly on ribs. Pappus 2 -seriate, outer series up to 0.3 -0.7 mm long, of scales, inner series up to $5.3--9.4 \mathrm{~mm}$ long, of bristles barbellate, fine, persistent. Chromosome number: $2 n=14$ (Bernardello, 1986).

Distribution and Habitat. This species is endemic in central and northwestern Argentina, between $500-2000 \mathrm{~m}$ (Fig. 8 A). It inhabits slopes, hills, valleys, seldom in canyons ("barrancas"), in scrub, grasslands, dry and sunny places, sometimes in damp grassy places.

Phenology. Plants with flowering capitula have been collected from November to June, mostly in summer and early autumn.

Common Names and Uses. "Margarita de las sierras" (Grossi \& al., 2012), "piojera" (in sched. Domínguez 133, BAF). It was mentioned as species of potential pharmacological interest: sesquiterpenes in aerial organs of the plant and flavonoids in leaves and florets (Ariza Espinar, 2006). Austroliabum candidum has been proposed for cultivation as ornamental because of the beautiful yellow corollas and the whitish pubescence of stems and leaves (Cabrera, 1947; Parodi \& Dimitri, 1972; Gutiérrez, 2017).

Job (in sched. Job 497, LP) mentioned white flowers; however, the common color in the genus is yellow, and we could not find another specimen kept at herbaria or field observations with this color.

Specimen Slanis et al. 811 (LIL) with winged petioles shows an uncommon trait within A. candidum, however, the other features fit accurately with this species. On the other hand, according to Grossi \& al. (2012), it could be an endangered species because its population traits. However, ecological, reproductive and distributional studies are necessary.

In the protologue of Liabum subcirrhosum, Blake (1927) indicated as type the specimen "Jörgensen 1673 " with date " 12 Feb 1917" kept at US ("type no. 922182 "). There is only one specimen deposited in US that fits accuratelly with the protologue. This material is the holotype (US 922182 barcode 00122753 ). On the other hand, many specimens with the same collector and collector number were found but with different dates: BA 24737 [20 Dec 1916], GH [26 Feb 1917 and 15 Feb 1916, two sheets], LIL 26626 [ 15 Feb 1916], SI 000925 [Feb 1916]. These materials can be considered as original materials but not duplicates of the holotype.

Representative Specimens Examined. ARGENTINA. Catamarca: Andalgalá department: La Playa, Feb 1916, Jörgensen 1673 (SI); idem, 15 Feb 1916, Jörgensen 1673 (GH, LIL); idem, 20 Dec 1916, Jörgensen 1673 (BA); idem, 26 Feb 1917, Jörgensen 1673 (GH); Faldes de [Río] Yacuchuyo, Jan 1881, Schickendantz 287 (LP); Cuesta de Mina Capillitas, 2000 m, 30 Jan 1974, Cabrera el al. 24787 (LP). Belén department: Ambato, El Potrero, 15 Mar 1909, Castillon s.n. (Lillo 9213) (LIL 26635); Ambato, El Crestón, 25 Mar 1909, Castillon 1248 (Lillo 9214) (LIL); Ambato, Quebrada de El Rincón, 5 Feb 1910, Castillon 1641 (LIL); [Los] Nacimientos, May 1910, Castillon 1435 (LIL); Pomán department: Pomán, Dec 1909, Spegazzini s.n. (BAB 28207, 28950); desde Pomán a la falda del cerro Ambato, 10 Jan 1910, Spegazzini s.n. (LP ex LPS 10052). Córdoba: Calamuchita department: Sierra Chica, valle de Los Reartes, without date, Castellanos s.n. (BA 24741); valle de Los Reartes, Sierra Chica, 24 Apr 1917, Castellanos 220 (SI); V. [valle] [Los] Reartes, 1917--1919, Castellanos s.n. (SI 9440); Embalse Río Tercero, 12 Jan 1940, Burkart 10496 (LP, SI); Embalse Río Tercero, 24 Apr 1945, Lauro s.n. (BAB 66473); Embalse del Río Tercero, 20 Feb/5 Mar 1964, Roig 4978 (SI); Dique Los Molinos, 27 Jan 1969, Krapovickas \& Cristóbal 14725 (CTES, LP); Embalse Río Tercero, 27 Nov 1998, Delucchi 2144 (LP); Villa del Dique, Embalse Río Tercero, Cerro de los Enamorados, $32^{\circ} 10^{\prime} 36.8^{\prime \prime}$ S, $64^{\circ} 25^{\prime} 17.8^{\prime \prime}$ W, $566 \mathrm{~m}, 30$ Jan 2006, D. Gutiérrez \& Di Paola 375 (BA); Capital department: in montanis prope Córdoba, Jan 1881, Spegazzini s.n. (LP s.n., ex LPS 10051); Córdoba, Feb 1896, Stuckert 632 (BAF); Córdoba, without date, Castellanos s.n. (SI 9441); Córdoba, Dec 1899, Dominguez 133 (BAF); Colón department: Sierra Chica, entre el dique San Roque y Casabamba [Casa Bamba], 1 Jun 1910, Kutz s.n. (SI 9442); Villa Allende, Jun 1939, Lahitte 60462 (LP); Ascochinga, 14 Mar 1944, O'Donell \& Rodríguez 871 (LIL); Unquillo, 25 Dec 1947, Meyer 12952 (LIL); La Granja, 6 Jan 1950, Borsini 1188 (LIL); Agua de Oro, Sierra Chica, 4 Feb

1951, Castellanos s.n. (LIL 386907); Cabana, 26 Feb 1957, Caro 2537 (BAF); La Calera, 31 Jan 1958, Lanfranchi 1430 (LP); entre La Granja y Agua de Oro, $31^{\circ} 2^{\prime} 46.1^{\prime \prime} \mathrm{S} 64^{\circ} 16^{\prime} 45.5^{\prime \prime} \mathrm{W}, 723 \mathrm{~m}$, 27 Jan 2006, D. Gutiérrez \& Di Paola 281, 282, 283 (BA, LP); entre La Calera y el puente del dique San Roque, 27 Jan 2006, D. Gutiérrez \& Di Paola 284, 285 (BA); Agua de Oro, $31^{\circ} 2^{\prime} 75.3^{\prime \prime} \mathrm{S} 64^{\circ}$ 16'81.6" W, 724 m, 9 Apr 2008, D. Gutiérrez et al. 404 (BA, LP); alrededores de Villa Animí, entre El Manzano y Agua de Oro, ruta E53, 14 Mar 2009, D. Gutiérrez 1001 (BA, LP); alrededores de El Manzano, entre El Manzano y Agua de Oro, ruta E53, $30^{\circ} 4^{\prime} 23.2^{\prime \prime} \mathrm{S} 64^{\circ} 17^{\prime} 46.5^{\prime \prime} \mathrm{W}, 736 \mathrm{~m}, 15$ Mar 2009, D. Gutiérrez 1009 (BA, LP); El Pueblito, entre El Pueblito y Salsipuedes, ruta E53, $31^{\circ} 6^{\prime}$ 46.7오 S $64^{\circ} 17^{\prime} 35.6^{\prime \prime}$ W, 15 Mar 2009, D. Gutiérrez 1016 (BA, LP); Cruz de Eje department: entre Capilla del Monte y San Marcos Sierra, después del mirador, $30^{\circ} 47^{\prime} 38.3^{\prime \prime} \mathrm{S}, 64^{\circ} 37^{\prime} 41.6^{\prime \prime} \mathrm{W}, 767$ m, 28 Jan 2006, D. Gutiérrez \& Di Paola 337 (BA, LP); General San Martín department: Villa María, 19 Apr 1939, Navarro 84 (BAB). Punilla department: La Falda, Sierra Chica, 1000 m, 11 Apr 1918, Osten 10390 (BAF); 23 Apr 1917, Osten 10376 (BAF); Uritorco, 27 jan 1922, Castellanos s.n. (BA 24740); alrededores de La Falda, Jan 1936, Job 497 (LP); Cosquín, Pan de Azúcar, 1000--1200 m, Jan-Feb 1936, Rodrigo 553 (LP); Carlos Paz, monte La Ballena, 900 m, 18 Feb 1939, Bridarolli 622 (LP); La Falda, 16 Mar 1939, Dawson 433 (LP); San Antonio de Aredondo, Mar 1940, Gautier 13 (BAB); camino a San Marcos [Sierra], 9 Mar 1941, Nicora 17662a,b (SI); La Falda, 7 Feb 1947, Villafañe 755 (LIL); Molinari, $\pm 750 \mathrm{~m}, 18$ Apr 1947, J. Gutiérrez 150 (LIL); La Falda a El Cuadrado, 22 Jan 1948, de la Sota 498 (LIL); La Falda, 12 Jan 1950, de la Sota 1554 (LIL); Tanti, 13 Jan 1950, de la Sota 1592 (LIL); La Estancita, 17 Jan 1950, de la Sota 1713 (LIL); El Cuadrado, 22 Feb 1950, de la Sota 2071 (LIL); Pan de Azúcar, 26 Feb 1950, de la Sota 2251 (LIL); San Marcos Sierra, 24 Jan 1951, de la Sota 4113 (LIL); near Capilla del Monte, path up cerro Uritorco, $30^{\circ} 51^{\prime} \mathrm{S} 64^{\circ} 30^{\prime} \mathrm{W}$, 1550 m, 23 Jan 1966, Hawkes et al. 3290 (K, LP); Carlos Paz, Sierra Chica, falda W, 6 Feb 1966, Ariza Espinar 2149 (CTES); Villa Carlos Paz, 16 Apr 1977, Gautier 8570 (LP); entre Santa María de Punilla y Villa Caerio, ruta 34, km 28, $31^{\circ} 18^{\prime} 29.7^{\prime \prime} \mathrm{S} 64^{\circ} 27^{\prime} 50,3^{\prime \prime} \mathrm{W}, 674 \mathrm{~m}, 27 \mathrm{Jan} 2006, D$. Gutiérrez \& Di Paola 293 (BA); entre Capilla del Monte y San Marcos Sierra, antes del mirador, $30^{\circ}$ $50^{\prime} 12.6^{\prime \prime}$ S $64^{\circ} 34^{\prime} 44.5^{\prime \prime}$ W, $901 \mathrm{~m}, 28$ Jan 2006, D. Gutiérrez \& Di Paola 333 (BA); Río Cuarto department: Achiras, 21 Jan 1932, King 193 (LP); Río Seco department: Cerro Colorado, 5 May 1956, Caro 2002 (BAF); San Alberto department: Dique La Viña, 23 Mar 1947, Terribile 730 (LIL); San Javier department: Paso de la Peña, 19[27], Castellanos s.n. (BA 11856); San Javier, Quebrada del Tigre, 1200 m, 1940, Bridarolli 1596 (LP); San Javier, cuesta del cerro Champaquí, 20 Jan 1967, Fabris \& Pérez Moreau 6800 (BAB, LP); Santa María department: Without locality, 31 Mar 1894, Without collector 2288 (LIL 26627); [La] Ochoa [near Malagueño], Sierra Chica, 29 Mar 1899, Stuckert 6693 (BA, BAF, SI); Cumbre Chica, 1000 m, Mar 1930, King 639 (LP); Alta Gracia, Puesto El Cura, 27 Jan 1944, Pierotti s.n. (LIL 100642); Peñón del Aguila, 1900 m, 28 Apr 1946,

Pierotii 5071 (LIL); [Cerro] Ochoa, Sierra Chica, 11 Mar 1954, Hunziker 8985 (LP); Embalse Los Molinos, 21 Feb 1965, Cabrera et al. 16553 (LP); Embalse Los Molinos, 2 Apr 1973, Cabrera et al. 23808 (LP); ruta 34, entre 1 y 4 km al norte del paredón del dique Los Molinos, 600--700 m, 18 Jan 1992, Novara \& Bruno 10540 (LIL, S); entre Los Reartes y Ciudad de América, cerca de Ciudad de América, 20 km antes de la ruta Alta Gracia-Villa General Belgrano, $31^{\circ} 47^{\prime} 17,5^{\prime \prime} \mathrm{S} 64^{\circ} 30^{\prime} 47,5^{\prime \prime}$ W, 30 Jan 2006, D. Gutiérrez \& Di Paola 393 (BA); Dique Los Molinos, Villa Ciudad de América y Villa de la Merced, $31^{\circ} 48^{\prime} 58.1^{\prime \prime} \mathrm{S} 64^{\circ} 30^{\prime} 62.2^{\prime \prime} \mathrm{W}, 822 \mathrm{~m}, 9$ Apr 2008, D. Gutiérrez et al. 419 (BA, LP); Totoral department: Sarmiento, 30 Jan 1951, de la Sota 4248 (LIL); Probably Colón-Punilla-Santa María departments: Sierra Chica, Feb 1925, 1600 m, Lossen 146 (SI); La Rioja: Sanagasta department: Dique Los Sauces, faldas del Velazco, 1100 m, 17 Feb 1944, Hunziker 4842 (LIL, LP); San Luis: Juan Martín de Pueyrredón (= La Capital) department: [El] Volcán, saliendo del pueblo hacia Trapiche, 7 Feb 1999, Seijo 1754 (CTES); Coronel Pringles department: Pampa del Alto Grande, Feb 1931, Gez s.n. (BA 31/229); General Pedernera department: El Morro, 1913, Pastore 29 (SI); Junín department: Merlo, Piedra Blanca, 1000 m, 8 Feb 1947, Digilio \& Grassi 2127 (CTES, LIL); El Rincón, Sierra de los Comechingones, 8 Feb 1956, Caro 1757 (BAF); Sierra de Comechingones, falda O, frente a El Rincón, 8 Feb 1956, Hunziker 11757 (CORD); Merlo, Mal Paso, $32^{\circ} 19^{\prime} 49^{\prime \prime} \mathrm{S} 64^{\circ} 59^{\prime} 36.2^{\prime \prime} \mathrm{W}, 976 \mathrm{~m}, 29$ Jan 2006, D. Gutiérrez \& Di Paola 361 (BA); alrededores de Merlo, camino al Filo, Jan 2011, D. Gutiérrez \& Quijano 1020 (BA); Libertador General San Martin department: [Cerro] Intihuasi, Mar 1937, Pastore 2041 (SI); without department, Fries s.n. (Jul 1878, Miers 888) (K). Tucumán: Faimallá department: Quebrada de Lules, 30 Aug 1949, Sás 64 (LP); Chicligasta department: Cuesta del Clarillo [RN 65, border of Catamarca-Tucumán], 10 Apr 2002, Slanis et al. 811 (LIL).
2. Austroliabum eremophilum (Cabrera) H.Rob. \& Brettel, Phytologia 28: 49. $1974 \equiv$ Liabum eremophilum Cabrera in Bol. Soc. Argent. Bot. 2: 96. $1947 \equiv$ Microliabum eremophilum (Cabrera) H.Rob., Syst. Bot. 15: 744. 1990. - TYPE. ARGENTINA. Salta: Cafayate department, Sierra del Cajón, El Alisal, 2800 m, 17 Jan 1914, D. Rodríguez [or F.M. Rodrígzez] 1294 (lectotype: LP 000299!, designated as holotype by Freire \& Iharlegui in Darwiniana 38: 324. 2000; isolectotypes: BA 24736 ! [15 Jan 1914], BAB! [16 Jan 1914], BAF! [12 Jan 1914, two sheets], CORD 00005457! [17 Jan 1914], LLL 001804! [16 Jan 1914], LP 000300!-[17 Jan 1914], LP 000301!-[17 Jan 1914], SI 000912 ! [17 Jan 1914]). Fig. 10.

Annual or perennial herbs, rarely subshrubs, up to 1 m tall, with with scarce latex in stems and leaves. Stems erect, ascendent or decumbent, terete, not costate, slightly branched, densely and persistently white-tomentose, rarely with glandular-tipped trichomes hidden below the tomentum; pseudostipules
free or fused, usually continuing with petiole wings, herbaceous. Leaves opposite, scattered along the stem and secondary branches, herbaceous, petiolate, rarely sessile; petioles $1--2 \times 0.2--0.4 \mathrm{~cm}$, usually winged with wide wings, margins entire, rarely with glandular-tipped trichomes; laminas 4.5--12 x $0.5--3.5(--6) \mathrm{cm}$, narrowly ovate or narrowly subtriangular, sometimes ovate or subtriangular; base usually decurrent, sometimes cuneate, rounded or cordate, apices acute or attenuate, margins slightly dentate or entire, mucronulate, acrodromous, 3 -veined, with the pair of lateral veins reaching the middle of the lamina, surfaces flat, hirsute, greenish adaxially, white-tomentose abaxially. Capitula few, terminal, in a lax corymbiform capitulescence, pedunculate, peduncles $2.5-10 \mathrm{~cm}$ long, rarely shorter, white-tomentose with glandular-tipped trichomes. Involucres $0.8--1.3 \times 0.9--1.5 \mathrm{~cm}$, campanulate, 4--6-seriate, usually 5 -seriate, all series adpressed, phyllaries $55-70$, imbricate, coriaceous, outer 3--6.5 x 1--1.5 mm, ovate, apices acute or attenuate, hirsute with glandular-tipped trichomes and densely white-arachnoid, greenish, inner $7-10 \times 0.6-1.2 \mathrm{~mm}$, narrowly ovate or oblong, apices acute or attenuate, slightly glandular-pubescent or glabrescent, greenish. Ray florets 35-$-40(--50), 1$-seriate, pistillate, fertile; corollas $1--2 \mathrm{~cm}$ long, true ray, yellow or slightly orange, pubescent with glandular-tipped trichomes; tubes $6.5--10 \times 0.3--0.6 \mathrm{~mm}$, pubescent above; limbs 6--12 x 1.4-2 mm, narrowly elliptical or obovate, 4-veined, apices 3-dentate. Disc florets 40-50, bisexual, fertile; corollas $5.5--9 \mathrm{~mm}$ long, tubular, funnelform, yellow or slightly orange, tube and throat gradually differentiate, 5 -lobed, pubescent with glandular-tipped trichomes; tube plus throat 5.8--6.3 mm long, tubes ca. 0.5 mm wide, pubescent above; throats $0.6--1 \mathrm{~mm}$ wide, pubescent below; lobes $2.5--3 \mathrm{x}$ ca. 0.3 mm , apices pubescent; style branches $0.5--1 \mathrm{~mm}$ long. Achenes $1.4--2.5 \times 0.5--1 \mathrm{~mm}$, obovoid or obconical, 8 --10-ribbed, pubescent mostly on ribs. Pappus 2 -seriate, outer series up to 0.3 --$0.5(--1) \mathrm{mm}$ long, of scales, inner series up to $4.2--7(--8) \mathrm{mm}$ long, of bristles, barbellate, fine persistent. Chromosome number unknown.

Distribution and Habitat. This species is endemic of Sub-Andean Hills, especially Calchaquies (also known as del Cajón) mountains and around Los Sauces dam in northwestern Argentina at 850--3000 m (Fig. 8. A). It inhabits high elevations associated with woods of Alnus acuminata Kunth ("aliso del cerro") and lower valleys.

Common Name. It was mentioned as "cepa de caballo sin espinas" in a label (Droglietti s.n., LIL 157716). However, the Spanish common name "cepa caballo" (English "spiny clotbur") refers to the widespread distributed species Xanthium spinosum L. (Asteraceae).

Phenology. Plants with flowering capitula have been collected from January to April, in summer and early autumn.

Original specimens were collected from 1912 to 1916 in mountains named Sierra del Cajón (currently Sierra de Quilmes) in northwestern Tucumán and southwestern Salta provinces. In addition, the protologue indicates "El Alisal". There is a town in southeastern Salta with this name but very far from that mountains. Probably, "El Alisal" does not refer to a town name but an environment with trees of Alnus acuminata Kunth (common name: "aliso", "aliso del cerro"). An original label in handwriting (in a duplieate-material kept at BAF) supports this view because it says "alisal" in lowercase. This point of view agrees with Cabrera (1993: 450, 459, 469).

In the protologue of $L$. eremophilum, Cabrera (1947) indicated as types the specimens-gathering $D$. Rodríguez 1294 with date "17 Jan 1914" kept at LP and isotypes in LIL, LP, and SI. However, the unique specimen deposited-found in LIL (LIL 001804) actually is from "16 Jan 1914". On the other hand, those in BAB (without barcode) and BAF (without barcode) were labelled as collected by F. M. Rodríguez since brothers Demetrio and Francisco Manuel Rodríguez used to put the same collector number, and indistinctly their names, for different date collection (e.g., Cabrera, 1993: 469). As a result, we considered the specimens mentioned above plus BA_24736 [15 Jan 1914], BAB [16 Jan 1914], and BAF [12 Jan 1914] as-riginal materials paratypes. Because the lectoype was designated with date "17 Jan 1914", duplicates are only deposited in CORD, LP and SI. In addition, gatherings Castillón 3435 and Lillo 18035 are paratypes, too.

Representative Specimens Examined. ARGENTINA. Catamarca: Ancasti department: without locality, Feb 1910, Spegazzini s.n. (BAB 29202, 29203). Belén department, Las Cuevas, $4000 \mathrm{~m}, 2$ Apr 1946, Droglietti s.n. (LIL 157716); wihout department: wihout locality, Jan-Feb 1910, Spegazzini s.n. (BAB 34007). La Rioja: Sanagasta department, La Rioja, dique [Los Sauces], 2 Mar 1941, Burkart 12624 (SI, LP); Capital department, Quebrada Los Sauces, Dique [Los Sauces], Feb 1939, Rodrigo 2079 (LP); Quebrada del Sauce, national rd 75, 7 km to monument of Facundo Quiroga, 700 m, 14 Apr 1975, Okada 6110 (SI); Quebrada de Los Sauces, Dique de Los Sauces, RP 1, 12.5 km SE de Sanagasta, $850 \mathrm{~m}, 11$ Apr 2008, D. Gutiérrez et al. 500 (BA, LP, S); RN 75, S of Sanagasta and NW of La Rioja, $29^{\circ} 23^{\prime} 13^{\prime \prime}$ S $66^{\circ} 58^{\prime} 41.6^{\prime \prime}$ W, $877 \mathrm{~m}, 8$ Mar 2016, Funk \& Bonifacino 13257 (LP). Salta: Cafayate department, Sierra del Cajón, El Alisal, $2800 \mathrm{~m}, 12$ Jan 1914, F. Rodríguez 1294 (BAF); ídem, 15 Jan 1914, D. Rodríguez 1294 (BA); ídem, 16 Jan 1914, D. Rodríguez 1294 (LIL); ídem, F. Rodríguez 1294 (BAB). Tucumán: Tafí del Valle department, Cumbres Calchaquíes, Machoguañusco, 3000 m, 4 Feb 1914, Castillón 3435 (CORD, LIL); Tafí, Jan 1912, Lillo 18035 (CORD, LIL); ruta a Tafí del Valle, Km 40, 21 Mar 1987, Xifreda \& Maldonado 655 (SI).
3. Austroliabum glanduliferum (Cabrera) D.G.Gut., N.Garcia, Susanna \& M.A.Grossi, nov. comb. $\equiv$ Liabum candidum Griseb. var. glanduliferum Cabrera in Bol. Soc. Argent. Bot. 2: 96. $1947 \equiv$ Microliabum glanduliferum (Cabrera) H.Rob., Syst. Bot. 15: 744, 1990. - TYPE: Argentina. San Luis: Juan Martín de Pueyrredón (= La Capital) department, Estancia Grande, 16 Jan 1911, F. Pastore 124 (lectoype: SI [without barcode; missing], designated as type by Robinson in Syst. Bot. 15: 744. 1990; LP 000297! designated as holotype by Freire \& Iharlegui in Darwiniana 38: 324. 2000 LP 000297!.: holotype:SI; isotype: LP 000297!). Fig. 11.

Annual or perennial herbs, rarely subshrubs, up to 0.6 m tall, with scarce latex in stems and leaves. Stems erect, ascendent or decumbent, slightly branched, terete, not costate, densely and persistently white-tomentose and with very dense pubescence of glandular-tipped trichomes; pseudostipules free or fused, herbaceous. Leaves opposite, scattered along the stem and secondary branches, herbaceous, petiolate; petioles $1.5--3 \times 0.1--0.2 \mathrm{~cm}$, wingless or slightly winged in upper part, rare narrowly winged with margin entire, dense and persistently white-tomentose and with dense pubescence of glandular-tipped trichomes; laminas $3.5--7.5 \times 2--5(--6.6) \mathrm{cm}$, ovate or triangular, bases truncate or cuneate, sometimes slightly decurrent, apices acute, margins dentate, denticulate or serrate, mucronulate, acrodromous, 3 -veined, with the pair of lateral veins reaching the middle of the lamina, surfaces flat, hirsute and greenish, sometimes with lax white-arachnoid pubescence adaxially, densely white-tomentose with glandular-tipped trichomes abaxially. Capitula many or few, terminal in a lax corymbiform capitulescence, pedunculate, peduncles $0.7--4.5 \mathrm{~cm}$ long, erect, densely white-tomentose mixed with numerous glandular-tipped trichomes. Involucres $0.9-1.3 \times 0.9-1.5 \mathrm{~cm}$, campanulate, $4-$ 6 -seriate, usually 5 -seriate, all series adpressed, phyllaries $45--65$, imbricate, coriaceous, outer $3.5--6$ x $1--1.6 \mathrm{~mm}$, ovate, apices acute or attenuate, densely pubescent with glandular-tipped trichomes and white-tomentose, inner $7.2--11 \times 0.7--1.1 \mathrm{~mm}$, narrowly ovate or oblong, apices acute or attenuate, slightly pubescent above with glandular-tipped trichomes, glabrescent below. Ray florets $25-35(--40)$, 1 -seriate, pistillate, fertile; corolla $0.9-1.9 \mathrm{~cm}$ long, true ray yellow, pubescent with glandular-tipped trichomes; tubes $4.5--6 \times 0.5--0.6 \mathrm{~mm}$, pubescent above; limbs $5--12 \times 0.4-1.5 \mathrm{~mm}$, narrowly elliptical or obovate, 4-veined, apices 3-dentate. Disc florets 40--55(--60), bisexual, fertile; corolla 6.5--9.9 mm long, tubular, funnelform, yellow, tube and throat gradually differentiate, 5 -lobed, pubescent with glandular-tipped trichomes, tube plus throat $5.5--5.8 \mathrm{~mm}$ long, tubes $0.4--0.7 \mathrm{~mm}$ wide, pubescent above, throats $0.6-1.4 \mathrm{~mm}$ wide, pubescent below, lobes $2--2.8 \times 0.4--0.5 \mathrm{~mm}$, apices pubescent; style branches $0.5--1 \mathrm{~mm}$ long. Achenes $1.2-2 \times 0.5-0.8 \mathrm{~mm}$, obovoid or obconical, 8 -10 -ribbed, densely pubescent mostly on ribs. Pappus 2 -seriate, outer series up to $0.5-1 \mathrm{~mm}$ long, of
scales, inner series up to $6.8--8.6 \mathrm{~mm}$ long, of bristles barbellate, fine, persistent. Chromosome number unknown.

Distribution and Habitat. This species is endemic in central Argentina in Pampean Hills, between 800 to 1350 m (Fig. 8 A). It inhabits rocky soils, hills, slopes, valleys, grasslands, scrublands, and canyons near rivers.

Phenology. Plants with flowering capitula have been collected from December to March, in summer.

Originally, Cabrera (1947) described this species as a variety of Liabum candidum because of the conspicuous glandular trichomes. Robinson (1990) elevated this variety to species rank of Microliabum using mainly this trait. Cabrera and Iharlegui (1999) kept it as a variety under Liabum candidum. Cabrera et al. (1999) pointed out that the presence of conspicuous glandular trichomes was a feature highly variable and included this variety as a synonym of Microliabum candidum. Gutiérrez (2008) followed this point of view in a catalogue. Recently, Gutiérrez (2015) considered it a current well-defined species under Microliabum based on new collections, field work, and a detailed morphological study. Thus, we follow this last point of view.
In the original description of var. glanduliferum, Cabrera (1947) designed aeewrately the specimen gathering Pastore 124 as type ("tipo") kept at SI and LPas type ("tipo"), meaning the holotypesyntypes. In the protologue, this author also cited a duplicate specimen deposited in LP that is an isotype, and-many paratypes in BA, CORD, LP and SI. Robinson (1990) cited the specimen kept at SI as type, meaning the lectotypefollowed this view. To the contrary, Freire \& Iharlegui (2000) wrongly mentioned that the type specimen kept at LP was the holotype. Since the lectotype kept at SI was missing (M. Belgrano, pers. comm.), the selection of the specimen kept at LP as holotype made by Freire and Iharlegui can be considered as a lectotype designation for the name Liabum candidum Griseb. var. glanduliferum Cabrera.

Representative Specimens Examined. ARGENTINA. Córdoba: Calamuchita department, La Cruz de Silveira, 26 Jan 1885, Kurtz 139 (CORD); Minas department, Cerro de Criosu [?], 20 Feb 1876, Hieronymus s.n. (CORD); Pocho department, Sierra de Mogigasta, 19 Feb 1922, Castellanos s.n. (BA 24738); entre La Palmas y La Mudana, 16 Feb 1952, Hunziker 9783 (CORD, CTES, LP); falda norte del Cerro Yerba Buena, 17 Feb 1952, Hunziker 9824 (CORD); Sierra de Pocho, falda oeste, frente a Chancaní, en las inmediaciones de la ruta provincial 28 (ex nacional 20), 6 Jan 1955, Hunziker 10562 (CORD); Sierra de Pocho, Los Túneles, 6 Dec 1958, Burkart 20859 (SI); Pocho-San Alberto departments, Sierra de Pocho, 11 Mar 1921, Castellanos s.n. (LIL 36422); Punilla
department, Sierra Chica, falda oeste, Carlos Paz, 2 Jan 1966, Ariza Espinar 2109 (CORD). San Luis: Ayacucho department, inmediaciones del Dique Luján, $800 \mathrm{~m}, 17--20$ Feb 1960, Hunziker \& Cocucci 14965 (CORD); Ayacucho-Coronel Pringles-La Capital departments, entre Cerro [Valle] de Piedra y San Francisco [del Monte de Oro], 1925, Deletang-Guiñazu s.n. (BAB); AyacuchoLibertador General San Martín departments, Quebrada del Río Quines, 12 Mar 1882, Galander s.n. (CORD); Quebrada del Río de Quines, 16 Feb 1925, Castellanos s.n. (BA 25/1064); Coronel Pringles department, nacimiento del Río Quinto, 22 Jan 1969, Roig 5633 (CORD); Loma Alta, entre Los Membrillos y Paso del Rey, 1350 m, 20 Feb 1979, Anderson et al. 3582 (CORD); Embalse La Florida, a 7.2 km al E del empalme de RP 17 con RP $39,33^{\circ} 6^{\prime} 35.8^{\prime \prime} \mathrm{S} 66^{\circ} 0^{\prime} 13.3^{\prime \prime} \mathrm{W}, 1034 \mathrm{~m}, 10$ Apr 2008, D. Gutiérrez et al. 467 (BA, LP); idem, $33^{\circ} 6^{\prime} 36.95^{\prime \prime} \mathrm{S} 66^{\circ} 0^{\prime} 8.08^{\prime \prime} \mathrm{W}, 29$ Nov 2016, D. Gutiérrez et al. 1151 (BA). Juan Martín de Pueyrredón (= La Capital) department, Intihuasi [Inti Huasi], Mar 1937, Pastore 2041 (SI); Cerro El Lince, 1050 m, 19 Feb 1971, Anderson 2143 (CORD); Junín department, El Talita [Talita], 50 km al W de Santa Rosa [de Conlara], 29 Jan 1944, Burkart 13987 (SI). Without department, Quebrada del Salado, Bebida de Las Vacas, 9 Mar 1882, Galander s.n. (CORD, F); Sierras de San Luis, Cuesta de los Picazos, 21 Feb 1925, Castellanos s.n. (BA 25/1111).

Microliabum Cabrera, Bol. Soc. Argent. Bot. 5: $211.1955 \equiv$ Liabellum Cabrera, Not. Mus. La Plata 17: 76. 1954, nom illeg. (not Liabellum Rydb.). - TYPE: Microliabum humile (Cabrera) Cabrera (= Liabellum humile Cabrera) $\equiv$ Angelianthus H.Rob. \& Brettell, Phytologia 28: 48. 1974.

Annual or biannual herbs, rarely subshrubs, from 3 cm (including pedunculate capitula) up to 2 m tall, lax branched or unbranched, usually with conspicuous latex in stems and leaves. Stems erect, with appressed densely or sparcely white-tomentose pubescence or hirsute-pubescent with spreading stipitate glandular trichomes, rarely glabrescent; nodes without sheath, pseudostipules present or absent, if present free or fused, herbaceous. Leaves opposite, sometimes grouped at the plant base, petiolate, inconspicuously petiolate or sessile; petioles if present usually winged; laminas narrowly or broadly ovate or triangular, bases truncate, cordate, cuneate or decurrent, sometimes hastate, apices acute or attenuate, margins evenly or unevenly dentate or serrate, mucronulate, acrodromous, 3veined, main pair of lateral veins reaching the middle of the lamina; surfaces flat, glabrous, glabrescent or hirsute, greenish, usually mixed with white-arachnoid pubescence adaxially, whitetomentose abaxially. Capitula heterogamous, radiate, few or many, in a terminal alternate branched corymbiform capitulescence, sometimes a single terminal capitulum, pedunculate, peduncles erect or nutant. Involucres hemispherical, 2--4-seriate, usually 3-seriate, phyllaries 15--25 (M. humile) or 45-75 (M. mulgediifolium, M. polymnioides), subimbricate, decreasing in length, outer longer, oblong or
narrowly ovate, exserted, herbaceous, with glandular-tipped trichomes, inner narrowly ovate, adpressed, herbaceous, with glandular-tipped trichomes, innermost narrowly ovate or obovate, sometimes inconspicuous, reduced, membranaceous, glabrescent; receptacles flat to slightly convex, foveolate, naked. Florets ca. 25--30 (M. humile) or 145--195 (M. mulgediifolium, M. polymnioides), yellow, rare slightly orange, all fertile. Ray florets ca. 10--15 (M. humile) or 35--75 (M. mulgediifolium, M. polymnioides), 1--2-seriate, pistillate, without staminodia, corollas true ray, pubescent with glandular trichomes on outer surface, limbs obovate or elliptical, 4-veined, apices 3dentate; styles filiform, style branches curved, with papillae on inner surfaces. Disc florets ca. 15 ( $M$. humile) or 100--125 (M. mulgediifolium, M. polymnioides), bisexual, corollas tubular, funnelform, lobes long, narrowly ovate, with glandular trichomes on outer surface; anthers linear, shortly calcarate and shortly caudate, yellow, apical appendages ovate, flat; styles filiform with sweeping hairs externally from the middle of their stalks up to the apices, style branches shorter than the pubescent part on shaft below the bifurcation point, filiform, curved at maturity, stylopods enlarged, globose, nectaries not lobed. Achenes obovoid or obconical, 8--10-ribbed, carpopodia conspicuous, pubescent on all the surface. Pappus distinctly 2-seriate, outer series of scales, paleaceous, margins serrulate, deciduous or persistent, inner series of scales, paleaceous (M. humile) or bristles babellate, fine or slightly broadened (M. mulgediifolium, M. polymnioides), margins serrulate, deciduous. Chromosome number: $2 n=12$ (Rozenblum \& al., 1985).

Distribution and Habitat. Microliabum is distributed from central Bolivia to northwestern Argentina (Fig. 8 B). Species grow in the Sub-Andean Hills ("Sierras Subandinas"), the Eastern Cordillera of the Andes, and the High Cordillera. It is distributed in the Chacoan (Western districts), Yungas, and High Andean biogeographical provinces (Cabrera \& Willink, 1980). Microliabum inhabits open areas in mid-elevation forest, wet forest or seasonally dry scrub, and one species grows in alpine habitats.

## Key to species of Microliabum

1. Small plants up to 15 cm tall; leaves grouped at the base, sessile; phyllaries $15--25$; ray florets $10--$ $15(-18), 1$-seriate, and disc florets ca. 15; pappus with inner series of paleaceous scales up to 1.8-2.6 mm long
M. humile
2. Plants up to 2 m tall; leaves scattered along the stems and secondary branches, petiolate; phyllaries 45--75; ray florets $35--75$, 2 -seriate, and disc florets $100-125$; pappus with inner series of barbellate bristles up to $2.9--6 \mathrm{~mm}$

> 2. Slender herbs; erect or nutant capitula in a lax corymbiform capitulescence; slightly broadened bristles of inner series of pappus ........................................ M. mulgediifolium fine bristles of inner series of pappus M. polymnioides

1. Microliabum humile (Cabrera) Cabrera, Bol. Soc. Argent. Bot. 5: 211. $1955 \equiv$ Liabellum humile Cabrera in Notas Mus. La Plata, Bot. 17: 78. $1954 \equiv$ Angelianthus humilis (Cabrera) H.Rob. \& Brettell, Phytologia 28: 48. 1974. — TYPE: Argentina. Jujuy: Tilcara department, Río Estancia Vieja, cerca de Abra Mayo, $3300 \mathrm{~m}, 21$ Mar 1952, E. Petersen \& J. Hjerting 45 (holotype: LIL 001806!; isotype: LP 000296!). Fig. 12.

Small annual herbs, up to 15 cm tall. Stems erect or ascendent, slender, terete, not costate, unbranched or scarsely branched, slightly tomentose, rarely with glandular-tipped trichomes, without pseudostipules. Leaves opposite, few, grouped at base of the plant, herbaceous, sessile; laminas 1--3.7 x $0.3--1 \mathrm{~cm}$, narrowly ovate, bases decurrent, apices acute, margins entire, slightly serrate or dentate, mucronulate, acrodromous, 3 -veined, with the pair of lateral veins reaching the middle of the lamina, sometimes veins inconspicuous, surfaces flat, glabrescent, greenish adaxially, white-tomentose abaxially. Capitula few, terminal in a lax corymbiform capitulescence or not grouped, or a single capitulum, pedunculate, peduncles $0.8-4 \mathrm{~cm}$ long, erect or ascendent, densely pubescent with glandular-tipped trichomes. Involucres $5--8 \times 9$--16 mm, hemispherical, 2--3-seriate; phyllaries $15-\mathrm{-}$ 25 , subimbricate, decreasing in length, outer longer, $4.2--7.3 \times 0.8--2.1 \mathrm{~mm}$, ovate or oblong herbaceous, apices acute, hirsute with glandular-tipped trichomes, sometimes white-arachnoid at the base, inner 3.1--5.5 x 1--2.3 mm, narrowly ovate or obovate herbaceous or menbranaceous, apices acute or attenuate, slightly hirsute with glandular-tipped trichomes or glabrescent. Ray florets 10--15(--18), 1 -seriate, pistillate, fertile; corolla $4.4-7 \mathrm{~mm}$ long, true ray, yellow, slightly pubescent with glandular-tipped trichomes or glabrescent, tubes $0.7--0.9 \times 0.2--0.4 \mathrm{~mm}$, limbs $3.2--5 \times 0.5--1.1 \mathrm{~mm}$, narrowly elliptical or ovate, 4-veined, apices 3-dentate, sometimes entire or 2 -dentate. Disc florets ca. 15, bisexual, fertile; corolla $2.1--2.8 \mathrm{~mm}$ long, tubular, funnelform, 5 -lobed, yellow, tube and throat gradually differentiate, slightly pubescent or glabrescent, tube plus throat $1.7-1.9 \mathrm{~mm}$ long, tubes 0.3 --0.4 mm wide, glabrous, throats $0.5--1 \mathrm{~mm}$ wide, glabrous, lobes $1--1.5 \times 0.2-0.3 \mathrm{~mm}$, apices pubescent; style branches $0.2--0.4 \mathrm{~mm}$ long. Achenes $1.1--2.2 \times 0.4-1 \mathrm{~mm}$, obovoid or obconical, 8ribbed, pubescent. Pappus distinctly 2 -seriate, outer up to $0.6-0.8 \mathrm{~mm}$ long, of $8-10$ scales paleaceous, inner up to $2.2--2.6 \mathrm{~mm}$ long, of 8 scales, paleaceous, easily deciduous. Chromosome number unknown.

Phenology. Plants with flowering capitula have been collected in March to April, in autumn.

Distribution and Habitat. This species is endemic in northwestern Argentina between 3300--3400 m (Fig. 8 B). It inhabits high mountains near rivers, slopes and valleys.

Representative Specimens Examined. ARGENTINA. Jujuy: Doctor Manuel Belgrano department, entre León y Nevado de Chañi, La Peña, Mar 1963, Fabris et al. 4169 (LP). Salta: Santa Victoria department, Cuesta de Santa Cruz, $22^{\circ} 9^{\prime}$ S $65^{\circ} 2^{\prime}$ W, 3400 m, 27 Apr 1974, Okada 5953 (LP, US).
2. Microliabum mulgediifolium (Muschl.) H.Rob., Syst. Bot. 15: 743. $1990 \equiv$ Liabum mulgediifolium Muschl. in Bot. Jahrb. Syst. 50, 2/3, Beibl. 111: 85. $1913 \equiv$ Austroliabum mulgediifolium (Muschl.) H.Rob. \& Brettell, Phytologia 28: 49. 1974. - TYPE: Bolivia. Tarija: Aniceto Arce prov., "Camacho, K. Fiebrig 2870" (holotype B [destroyed], photo FM 18116!; lectotype: K 000037288 [photo!] [designated by Robinson, 1990: 473]; isolectotype [fragment of K], US 00122729 [photo!]). Fig. 13.

Annual, biennial or perennial herbs up to 2 m tall, rarely smaller up to 7 cm . Stems erect, slender, terete, not costate, few or many-branched, hirsute with glandular-tipped trichomes or glabrescent, pseudostipules free or fused, or absent, herbaceous. Leaves opposite, scattered along the main stem and secondary branches, herbaceous, conspicuously petiolate, rarely sessile; petiole $0.8-10.4 \times 0.1--$ 1.6 cm , widely winged, wings margin unevenly dentate; laminas $2.2-22 \times 1.2--19 \mathrm{~cm}$, widely subtriangular or subtriangular, bases cuneate or cuneate-hastate, apices acute, margins widely dentate or serrate, mucronulate, acrodromous, 3 -veined, main pair of lateral veins reaching the middle of the lamina, surfaces flat, lax hirsute and greenish adaxially, white-tomentose abaxially. Capitula many, terminal in a lax corymbiform capitulescence, rarely few or with a single capitulum, pedunculate, peduncles $1.1--8 \mathrm{~cm}$ long, usually nutant, densely hirsute with glandular-tipped trichomes. Involucres $0.5--1.1 \times 1--2.4 \mathrm{~cm}$, hemispherical, $2--4$-seriate, usually 3 -seriate, outer series conspicuously exserted, phyllaries 45--75, rarely lesser, subimbricate, herbaceous, outer 4.4--12 x $1-1.8 \mathrm{~mm}$, ovate, apices acute or attenuate, densely hirsute with glandular-tipped trichomes, inner 4.4--6.5 x $0.7-1.4$ mm , narrowly ovate or oblong, apices acute or attenuate, hirsute with glandular-tipped trichomes, sometimes glabrescent, innermost inconspicuous, reduced, membranaceous, glabrescent. Ray florets $35--60$, 2 -seriate, pistillate, fertile, corolla $0.7--1.6 \mathrm{~cm}$ long, true ray, yellow, pubescent with glandular-tipped trichomes, tubes $5--7.5 \times 0.3-0.4 \mathrm{~mm}$, pubescent, limbs $4.5-11 \times 0.8--1.5 \mathrm{~mm}$, narrowly elliptical or obovate, 4 -veined, pubescent below, apices 3-dentate. Disc florets 110--125, bisexual, fertile, corolla $3.1--6.5 \mathrm{~mm}$ long, tubular, funnelform, tube and throat gradually diferenciate, deeply 5 -lobed, yellow, pubescent with glandular-tipped trichomes, tube plus throat $6--6.8 \mathrm{~mm}$ long, tubes $0.4--0.5 \mathrm{~mm}$ wide, pubescent, throats $0.6-1.1 \mathrm{~mm}$ wide, pubescent, lobes $2--2.3 \times 0.4--0.5 \mathrm{~mm}$,
pubescent; style branches $0.3--0.6 \mathrm{~mm}$ long. Achenes $1--2.2 \times 0.5--0.7 \mathrm{~mm}$, obovoid or obconical, 8-10 -ribbed, pubescent. Pappus distinctly 2 -seriate, outer up to $0.4-0.8 \mathrm{~mm}$ long, of scales, paleaceous, inner up to 2.9--4.7 mm long, of bristles barbellate, slightly broadened, easily deciduous. Chromosome number unknown.

Distribution and Habitat. This species occurs in southern Bolivia near the border of Argentina, and northwestern Argentina, between 1250--1450 m (Fig. 8 B). It inhabits Yungan and usually Chacoan environments in roadsides, slopes, mountains or edges of forests. One label indicates that a specimen was collected in silty-sandy soil with pH 6.8 .

Phenology. Plants with flowering capitula have been collected in March to May, from the end of summer to the end of the autumn.

Originally, this species was known only from the department of Tarija in Bolivia (Robinson, 1990). However, it was recently found in the province of Salta, northwestern Argentina (Gutiérrez \& Novara, 2009; Gutiérrez, 2015a). This species is easily differentiated from M. polymnioides because of its slender stems, lax few or many-headed capitulescences with usually nutant capitula on long peduncles, and pappus usually with slightly broadened inner pappus elements. However, some traits (i.e., slender stems and nutant capitula) are not very conspicuous in dry specimens.
This species commonly grows in populations of many individuals. Since these individuals start to grow from spring to summer, each plant reaches different height when blooming at the end of summer or autumn. Plants are usually $1.5--2 \mathrm{~m}$ tall, but in the same population some plants just reach as little as 7 cm with few capitula or only one capitulum. Specimen Meyer 22237 (LIL) shows a small habit and uncommon distribution at 3340 m of M. mulgediifolium, however, the other features fit accurately with this species.

On the other hand, it is important to mention that we counted more phyllaries and florets than previous descriptions (phyllaries 45--75 vs. 10--40, ray florets $35--60$ and disc florets 110--125 vs. ca. 25 and ca. 32--36, respectively). In the case of phyllaries number, we found inconspicuous inner membranous phyllaries that have not been cited by previous botanists.

Representative Specimens Examined. ARGENTINA. Jujuy: Valle Grande department: San Francisco, 14 Apr 1972, Cabrera \& Fabris 22653 (LP). Salta: Capital department: Salta, Cerro San Bernardo, 1400 m, 14 Apr 1988, Novara 7945 (MCNS, S); Salta, Cerro San Bernardo, 1400--1450 m, 10 Apr 1996, Novara et al. 10868 (CORD, CTES, MCNS); ciudad de Salta, Cerro San Bernardo, $24^{\circ}$ $48^{\prime} 19,6^{\prime \prime} \mathrm{S} 65^{\circ} 23^{\prime} 38,7^{\prime \prime} \mathrm{W}, 1373 \mathrm{~m}, 15$ Apr 2008, D. Gutiérrez et al. 554 (BA, LP). La Caldera
department: Ruta 9 km 1614, 1200 m, 4 Apr 1999, Novara \& Bruno 11279 (MCNS); pasando 1--5 km (al N) del puente del río Wierna, $1300 \mathrm{~m}, 26$ Apr 1999, De la Fuente \& Lusvarghi s.n. (MCNS 1280); camino de cornisa a Jujuy, ruta 9, km 1612--1616, entre Vaqueros y La Calderilla, a 10 km de Salta capital, 1250--1350 m, 30 Apr 2000, De la Fuente \& Lusvarghi 1364 (CORD, MCNS); La Caldera, ruta nacional 9, entre Vaqueros y La Calderilla, a lo largo del río Caldera, $24^{\circ} 39^{\prime} 43.4^{\prime \prime} \mathrm{S}$ $65^{\circ} 22^{\prime} 53.0^{\prime \prime} \mathrm{W}, 1260 \mathrm{~m}, 16$ Apr 2008, D. Gutiérrez et al. 573 (BA, LP); ruta 9, entre Vaqueros y La Calderilla, 23--25 Apr 2010, D. Gutiérrez et al. 1017 (BA). Santa Victoria department: Lizoite, 3340 m, 5 Apr 1940, Meyer 22237 (LIL). BOLIVIA. Tarija department: Aniceto Arce prov., ruta Bermejo-Tarija, 8 km SE de La Mamora, 14 May 1971, Krapovickas et al. 18758 (CTES, LP); Cercado prov., de Tarija a Iscayachi, 2000--3000 m, 20 Mar 1982, Kiesling et al. 3817 (SI); Eustaquio Méndez prov., Sama, 2950 m, 7 May 1988, Ehrich 544 (LPB, SI, US).
3. Microliabum polymnioides (R.E.Fr.) H.Rob., Syst. Bot. 15: 473. $1990 \equiv$ Liabum polymnioides R.E.Fr. in Ark. Bot. 5: 24. $1906 \equiv$ Austroliabum polymnioides (R.E.Fr.) H.Rob. \& Brettell, Phytologia 28: 49. 1974. - TYPE: Argentina. Jujuy: [Santa Bárbara department,] quinta prope Laguna de la Brea [Laguna La Brea] in nemore Citri raro, 2 Jun 1901, R. E. Fries 74 (holotype: S S-R-3243!). Fig. 14.

Annual, biennial or perennial herbs, sometimes subshrubs, $0.5-2 \mathrm{~m}$ tall, rarely short herb up to 20 cm tall. Stems erect, stout, terete, not costate, few or many-branched, hirsute with glandular-tipped trichomes, usually mixed with densely white-tomentose pubescence; pseudostipules free or fused, or absent, herbaceous. Leaves opposite, scattered along the main stem and secondary branches, herbaceous, conspicuously petiolate; petiole $3-14 \times 0.3-1.8 \mathrm{~cm}$, wingless or widely winged, wings margin unevenly dentate; laminas $7.7--28 \times 5--23.7 \mathrm{~cm}$, widely subtriangular or subtriangular, bases cuneate or cuneate-hastate, apices acute, margins widely dentate or serrate, mucronulate, acrodromous, 3 -veined, with the main pair of lateral veins reaching the middle of the lamina, surfaces flat, lax hirsute adaxially, greenish and densely white-tomentose abaxially. Capitula many, sometimes few, terminal, in a densely corymbiform capitulescence, pedunculate, peduncles ( $0.5--) 2.5--8 \mathrm{~cm}$ long, erect, hirsute with glandular-tipped trichomes sometimes mixed with white-tomentose pubescence. Involucres $0.8-1.6 \times 1.5--3 \mathrm{~cm}$, hemispherical, (2--)3--4-seriate, outer series conspicuously exserted, phyllaries $60--65$, subimbricate, herbaceous, outer $6.3-15 \times 1--2.5 \mathrm{~mm}$, narrowly oblong or ovate, apices acute, densely hirsute with glandular-tipped trichomes, inner $4.5--8.1 \times 0.8-1.6 \mathrm{~mm}$, narrowly ovate, apices attenuate or acute, densely hirsute with glandular-tipped trichomes, rarely glabrescent, innermost inconspicuous, reduced, membranaceous, glabrescent. Ray florets 50--75, 2-seriate, pistillate, fertile; corolla $0.7--2.2 \mathrm{~cm}$ long, true ray yellow, pubescent with glandular-tipped trichomes, tubes $3.5--4 \times 0.3--0.4 \mathrm{~mm}$, limbs 4--15.5 x $0.8--2.2 \mathrm{~mm}$, narrowly obovate or elliptical, (3--)4-veined,
apices 3-dentate. Disc florets 100--125, bisexual, fertile; corolla 5--7 mm long, tubular, funnelform, tube and throat gradually differentiate, 5 -lobed, yellow, rare slightly orange, tube plus throat 4.2-4.5 mm long, tubes $0.2-0.5 \mathrm{~mm}$ wide, pubescent or glabrous, throats $0.5-1.2 \mathrm{~mm}$ wide, pubescent or glabrous, lobes $1.5-1.8 \times 0.3--0.4 \mathrm{~mm}$, pubescent; style branches $0.4-1 \mathrm{~mm}$ long. Achenes $1--1.8 \mathrm{x}$ $0.3--0.8 \mathrm{~mm}$, obovoid or obconical 8 --10-ribbed, pubescent. Pappus distinctly 2 -seriate, outer up to $0.6-1.2 \mathrm{~mm}$ long, of scales, paleaceous, inner up to $4--6 \mathrm{~mm}$ long, of bristles barbellate, fine, easily deciduous. Chromosome number: $2 n=12$ (Rozenblum \& al., 1985).

Distribution and Habitat. This species occurs in central and southeastern Bolivia to northwestern Argentina, between 450-2300 m (Fig. 8 B). It inhabits Yungan and usually Chacoan wet or slightly dry enviroments, slopes near running water or rivers, river beaches, rain forests, edges of forests or woodlands, streams or rivers, shady woods, mountains and valleys, river canyons, quebradas, disturbed ground, roadsides, train tracks, secondary succession environments. Sometimes, it is an invasive species of roadsides and embankments near rivers.

Common Name: "flor del río" (in sched. Bellomo 344, LIL).

Phenology. Plants with flowering capitula have been collected from the end of the autumn to the beginning of the spring, from April to June.

It was mentioned on some labels to be as tall as 3 m (i. e., Krapovickas et al. 26652, CTES, SI; Pedersen 16127, CTES) but it does not seem to grow that tall. We counted more phyllaries than previous works ( $60-65$ vs. 10--40, respectively) since we found inconspicuous inner membranous phyllaries that have not been cited by previous botanists. On the contrary, we counted less ray florets than the original description (up to 75 vs. 60--100, respectively). Specimen Pierotti 1155 (LIL) with slender herbs shows an uncommon trait within M. polymnioides, however, the other features fit accurately with this species. On the other hand, the corollas have been cited as yellow on several specimen labels and in our observations in field trips. However, it has been noted as orange on labels (e.g., Calcagnini 117, BAB). It is very aromatic (Eyerdam \& Beetle 2260, K).

Robinson (1990) cited that the holotype of M. polymnioides was kept at UPS. However, there are no type specimens of M. polymnioides deposited in UPS (M. Hjertson, pers. comm.), and the types are actually conserved in S. In that work, "Quinta" was cited as the type locality; however, this word in Spanish means just farm. Actually, according to the type label, this type material was collected in La Brea lagoon, near the intersection of Routes 1 and 6 in Salta in a citrus farm.

Representative Specimens Examined. ARGENTINA. Catamarca: Paclín department: Balcozna [Balcosna], 1250 m, 17 Jan 1928, Venturi 7073 (GH, SI). Jujuy: Capital department: alrededores de [San Salvador de] Jujuy, Yala, 8 May 1962, Cabrera et al. 14391 (LP); Quebrada de Jaire, camino a Tiracsi [Tiraxi], 20 May 1962, Cabrera el al. 14686 (LP); río de Las Capillitas [Capillas], 24 Jul 1963, Cabrera 15879 (LP); camino a Tiraxi, 10 Jun 1980, Medán \& Tortosa 77 (LIL); RN 9, antes de León, debajo del puente, 17 Apr 2008, D. Gutiérrez et al. 580 (BA, LP, S). Ledesma department, Sierra de Calilegua, $750 \mathrm{~m}, 9$ Sep 1927, Venturi 5210 (LIL, SI); near río San Lorenzo, Leach Estates near Calilegua, 800 m, 18 Oct 1938, Eyerdam \& Beetle 22608 (K); El Mirador, Ledesma, Aug 1940, Ringuelet 122 (LP); Calilegua, 460 m, 15 Oct 1963, Fabris 4420 (LP); Yuto, El Bananal, 500 m, 19 Oct 1963, Fabris 4536 (BAB, LP); camino a Valle Grande, a orilla del río Las Cañas, 7 Aug 1969, Legname \& Cuezzo 7100 (LIL); puente arroyo Yuto, 30 Aug 1970, Cabrera 20818 (LP); camino de Ledesma a Pichanal, arroyo Yuto, 5 Oct 1974, Legname \& Cuezzo 10448 (LIL); camino a Valle Grande, río Aguas Negras, 30 Oct 1974, Cabrera et al. 25707 (LP, SI); 10--20 km de Libertador General San Martín, camino a Valle Grande, 9 Nov 1974, Krapovickas et al. 26652 (CTES, SI); Calilegua, Sep 1976, Cabrera et al. 27924 (SI); Parque Nacional Calilegua, Aug 1980, Martelli 1899 (LIL); arroyo Yuto, sobre ruta 34, $450 \mathrm{~m}, 27$ Nov 1981, Legname \& López 8818 (LIL); arroyo Aguas Negras, $450 \mathrm{~m}, 26$ Aug 1980, Legname et al. 8324 (LIL); camino a Valle Grande, entre ruta 34 y río Aguas Negras, 13 Jun 1983, Cabrera 33898 (SI); arroyo Yuto, 14 Jun 1983, Cabrera et al. 33935 (SI); Parque Nacional Calilegua, 19 Jun 1983, Rotman 738 (CTES, LIL); Parque Nacional Calilegua, 1000 m, 28 Feb 1986, Iudica \& Ramadori 288 (SI); Parque Nacional Calilegua, paralelo al río Aguas Negras, 600--800 m, 11 Sep 1991, Guaglianone et al. 2530 (CTES, SI); Parque Nacional Calilegua, río Jordán, 11 Dec 1991, Xifreda \& Sanso 1117 (SI); Parque Nacional Calilegua, 21 Sep 1997, Dematteis \& Seijo 807 (CTES, LIL); Parque Nacional Calilegua, camino desde arroyo Tres Cruces hasta arroyo Aguas Negras, RP 83, $23^{\circ} 46^{\prime}$ S $64^{\circ} 50^{\prime}$ W, 550--1100 m, 7 Nov 1998, Ahumada \& Castellón 8817 (LP); Parque Nacional Calilegua, $23^{\circ} 43^{\prime} 31.2^{\prime \prime} \mathrm{S} 64^{\circ} 51^{\prime} 5.8^{\prime \prime} \mathrm{W}, 864 \mathrm{~m}, 20 \mathrm{Apr}$ 2008, D. Gutiérrez et al. 605 (BA). Santa Bárbara department: Vinalito, Yuto, 7 Jul 1937, Cabrera 4050 (SI); Santa Bárbara Range, Quebrada de las Termas, 80 km South of San Pedro de Jujuy, 1500 m, 8 Oct 1938, Eyerdam \& Beetle 22468 (K). Tumbaya department: Volcán, $2200 \mathrm{~m}, 13$ Dec 1918, Castillon 6512 (LIL); estación Volcán, quebradas orientales, $2200 \mathrm{~m}, 13$ Dec 1918, Castillon 6592 (LIL). Valle Grande department: alrededores de Valle Grande, 15 May 1972, Cabrera \& Fabris 22687 (LP); camino a Valle Grande, río Jordán, $1500 \mathrm{~m}, 8$ Oct 1973, Legname \& Cuezzo 9584 (LIL). Salta: Anta department: Parque Nacional El Rey, Cerro Maldonado, Sierra González, Jun 1934, Ragonese 153 (BA); Parque Nacional El Rey, 5 Jul 1979, Brown et al. 839 (SI). La CandelariaRosario de la Frontera departments: Sierra de la Candelaria, río Nogalito, 1500 m, 6 Apr 1925,

Venturi 3753 (LIL, SI). Chicoana department: camino a Cachi, Quebrada de Escoipe, 27 Mar 1979, Cabrera et al. 30697 (CTES, SI); camino a Cachi, 27 Mar 1979, Cabrera et al. 30699 (CTES, SI); Los Laureles, pasando Pulares hacia PN Los Cardones, RP 33, $25^{\circ} 10^{\prime} 12.8^{\prime \prime} \mathrm{S} 65^{\circ} 49^{\prime} 46.2^{\prime \prime} \mathrm{W}, 1368 \mathrm{~m}$, 14 Apr 2008, D. Gutiérrez et al. 566 (BA, LP). General Güemes department: Quisto, 20 km al E de General Güemes, 27 Aug 1982, Novara 2840 (SI). General José de San Martín department: Tartagal, 14 Jun 1934, Meyer 930 (BA, LIL); [Campamento] Vespucio, 13 Aug 1937, Cabrera 4158 (LP); Quebrada Yariguarenda, sub-quebrada Peña de la Virgen, 4 Jul 1944, Schulz \& Varela 5201 (CTES); Quebrada Virgen-Tartagal, 4 Jul 1944, Schulz \& Varela 5201 (LIL); [Las] Tablillas, 24 Nov 1946, Rial Alberti s.n. (BAB 72360); [Campamento] Vespucio, May 1971, de González Montaner 17 (SI); Tartagal, ca. 400 m, 10 Sep 1983, Novara 3587 (CTES, LP, SI). General José de San MartínOrán departments: Río Bermejo, gran chaco salteño, 11 jul 1902, Calcagnini 117 (BAB). Orán department: Orán, 338 m, 27 Jul 1913, Jorgensen s.n. (BAB 37202); Cerro Tablada, $2400 \mathrm{~m}, 4$ Apr 1915, Pierotti 1155 (LIL); Alambique, 27 Jun 1944, Ruiz Huidobro s.n. (LIL 363697); márgenes de río Pescado, 7 Nov 1946, Rial Alberti s.n. (BAB 72343); camino a Los Toldos, 15 km del puente Agua Blanca, 29 Aug 1968, Legname \& Cuezzo 5755 (LIL); a 3 km del puente internacional de Agua Blanca, hacia la Quebrada El Arasayal, 5 Aug 1969, Legname \& Cuezzo 7121 (LIL); camino a finca Yaculika, a 5 km del puente internacional, río Bermejo, $480 \mathrm{~m}, 6$ Nov 1975, Schiavone et al. 11928, 11947 (LIL); arroyo Arasayal, $550 \mathrm{~m}, 20$ Nov 1976, Giusti et al. 12099 (LIL); camino a Isla de Cañas, 20 km de Orán, próximo a Vado Hondo, $500 \mathrm{~m}, 17$ Sep 1982, Legname et al. 8783 (LIL); RN 50, antes de llegar a Aguas Blancas, 650 m , 13 Sep 1999, Muruaga et al. 303 (LIL); quinta del río Santa María, Willink 111 (LIL). Santa Victoria department: path between Santa Victoria and San Felipe by río Lizoite, $22^{\circ} 16^{\prime} \mathrm{S} 64^{\circ} 58^{\prime} \mathrm{W}, 2300 \mathrm{~m}, 14$ Mar 1966, Hawkes et al. 3852 (K). Tucumán: Burruyacu department: Sierra de Medina, 900 m, 25 Oct 1923, Venturi 2558 (BAB); Sierra del Nogalito, 1450 m, 11 Apr 1991, Aceñolaga et al. s.n. (Proyecto Fitosociologia del Aliso 041) (LIL 596587). Capital department: alrededores de [San Miguel de] Tucumán, Oct 1902, Baer 52 (BA, BAF [circa Tucumán]); circa [San Miguel de] Tucumán, Baer 53 (BAF). Faimallá department: Quebrada de Lules, camino al dique, $600 \mathrm{~m}, 23$ Sep 1923, Venturi 2558 (BA, BAB, SI); La Quebrada, Lules, 13 May 1945, Ortiz s.n. (LIL 123370, 123372); Quebrada de Lules, 9 Sep 1945, Villa 495 (LIL 139590); Quebrada de Lules, 30 Aug 1949, Sás 64 (LIL). J.B. Alberti departmanet: RP 18, entre bifurcación RP 1 y RP 18, próximo al límite con Catamarca, cerca de Balcosna, $27^{\circ} 50^{\prime} 7.8^{\prime \prime} \mathrm{S} 65^{\circ}$ 48' $37.4^{\prime \prime}$ W, $1401 \mathrm{~m}, 12$ Apr 2008, D. Gutiérrez et al. 540 (BA); camino río Singuil, RP 308, entre Las Higueras y Dique Escaba, $27^{\circ} 39^{\prime} 11.0^{\prime \prime} \mathrm{S} 65^{\circ} 44^{\prime} 59.6^{\prime \prime} \mathrm{W}, 568 \mathrm{~m}, 12$ Apr 2008, D. Gutiérrez et al. 548 (BA). Lules department: Lules, 15 Jul 1911, Lizer s.n. (SI 9443); de La Reducción a Potrero de las Tablas, Dec 1988, Slanis 136 (LIL); camino a Potrero de Las Tablas, aprox. 17 km de ruta 38, 550 m, 24 Nov 1993, Figueroa Romero et al. 760 (LIL); ca. Lules, $26^{\circ} 54^{\prime} 41.07^{\prime \prime} \mathrm{S} 65^{\circ} 19^{\prime} 42.09^{\prime \prime}$

W, 12 Apr 2008, D. Gutiérrez et al. 549 (BA). Río Chico department: Quebrada de Marapa, 600 m , 7 Jul 1945, Castellanos s.n. (LIL 114970). Tafí department: Quebrada Lules, camino al dique, 800 m, 29 Sep 1920, Venturi 942 (BA, SI); Quebrada de Lules, 21 Jul 1934, Clos 5537 (BAB); Yerba Buena, camino a San Javier, 520 m, 12 Aug 1941, Rohmerz 32 (LIL); Quebrada de Lules, 30 Nov 1945, Villa 592, 615 (LIL). Trancas department: Río del Potrero, 28 Apr 1945, Bellomo s.n. (LIL 173311, NY); [probable, río] Potrero, 1400 m, 8 May 1946, Bellomo 344 (LIL); río Vipos, $600 \mathrm{~m}, 3$ May 1921, Schreiter s.n. (GH, LIL 76118). Yerba Buena department: ladera de San Javier, 5 Jun 1949, Soriano \& Banett 3647 (BAB). Without department: without locality, 1902, Baer s.n. (SI 15584). BOLIVIA. Cochabamba: Chapare prov., Locotal, 1600 m, 27 Feb 1929, Steinbach 9430 (LIL). Chuquisaca: Hernando Siles prov., [Ruta 6, entre Monteagudo y Padilla], $19^{\circ} 31^{\prime} 40^{\prime \prime} \mathrm{S} 64^{\circ} 9^{\prime}$ $41^{\prime \prime}$ W, $1647 \mathrm{~m}, 13$ Oct 2008, Lliully et al. 1516 (HSB, MO); Belisario Boeto prov., [Potreros], $19^{\circ} 4^{\prime}$ 39" S $64^{\circ} 5^{\prime} 30^{\prime \prime}$ W, 1772 m , 20 Jun 2009, Peñaranda 1470 (HSB, MO, NY). Chuquisaca-Santa Cruz: Cordillera prov., finca Guacareta [probably Huacareta in Chuquisaca dept., Hernando Siles prov., near the border with Santa Cruz dept., Cordillera prov.], 22 Sep 1982, Cabrera \& M. Gutiérrez 33681 (MO, SI). Tarija: Burdet O'Connor prov., ruta Tarija-Villa Montes, bajada de San Simón, 15 km E de Entre Ríos, 22 May 1971, Krapovickas et al. 19117 (CTES, LIL, SI); Aniceto Arce prov., El Salado, 700 m, 24 Aug 1971, Nuesser 13 (CTES, LIL); Aniceto Arce prov., de Pozos del Bermejo a Emboruzú, a 56 km de Bermejo, 18 Oct 1980, Zuloaga et al. 1050 (SI); Gran Chaco prov., Villamontes, 13 km hacia Tarija, en la quebrada del río Pilcomayo, $470 \mathrm{~m}, 26$ Oct 1983, Beck \& Liberman 9767 (SI); Gran Chaco prov., Yacuiba, 18--24 km hacia Palos Blancos, Serranía de Caraparí, 800--1230 m, 24 Sep 1985, Beck et al. 11582 (SI).

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## AUTHOR CONTRIBUTION STATEMENT

D.G.G. conceived the presented research. D.G.G. designed and directed the morphological study; N.G.-J. and A.S. designed and directed the molecular study; D.G.G. performed morphological study; D.G.G. and M.A.G. performed the statistical analysis of morphological quantitative characters; D.G.G., N.G.-J., A.S. and M.A.G. performed molecular analyses; D.G.G. took the lead in writing the manuscript. All authors provided critical feedback and helped shaping the research, analyses, and manuscript.

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## AUTHOR CONTRIBUTION STATEMENT

D.G.G. conceived the presented research. D.G.G. designed and directed the morphological study; N.G.-J. and A.S. designed and directed the molecular study; D.G.G. performed morphological study; D.G.G. and M.A.G. performed the statistical analysis of morphological quantitative characters; D.G.G., N.G.-J., A.S. and M.A.G. performed molecular analyses; D.G.G. took the lead in writing the manuscript. All authors provided critical feedback and helped shaping the research, analyses, and manuscript.

Table 1. Taxonomic history of Microliabum and Austroliabum

|  | Cabrera, 1947 | $\begin{aligned} & \text { Cabrera, 1954, } \\ & 1955 \end{aligned}$ | $\begin{aligned} & \hline \text { Robinson \& } \\ & \text { Brettell, } 1974 \\ & \hline \end{aligned}$ | Cabrera, 1978 | $\begin{aligned} & \hline \text { Robinson, } \\ & 1983 \\ & \hline \end{aligned}$ | Robinson, 1990 | Robinson, 1990 | $\begin{aligned} & \hline \text { Cabrera \& } \\ & \text { Iharlegui, } 1999 \\ & \hline \end{aligned}$ | Cabrera et al., 1999 | Gutiérrez, 2008a | $\begin{aligned} & \hline \text { Gutiérrez, } \\ & \text { 2015a } \\ & \hline \end{aligned}$ | This work |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Liabum auriculatum (Grisebach, 1879) | Liabum candidum var. candidum | Not treated | Not treated | Not treated | Austroliabum candidum | Subgenus Austroliabum | Microliabum candidum | Liabum candidum var. candidum | Microliabum candidum | Microliabum candidum | Microliabum candidum | Austroliabum candidum |
| Liabum candidum (Grisebach, 1879) | Liabum candidum var. candidum | Not treated | Austroliabum candidum | Not treated | Austroliabum candidum |  | Microliabum candidum | Liabum candidum var. candidum | Microliabum candidum | Microliabum candidum | Microliabum candidum | Austroliabum candidum |
| Liabum <br> subcirrhosum <br> (Blake, 1927) | Liabum candidum var. subcirrhosum | Not treated | Not treated | Not treated | Austroliabum candidum |  | Microliabum candidum | Liabum candidum var. subcirrhosum | Microliabum candidum | Microliabum candidum | Microliabum candidum | Austroliabum candidum |
| - | Liabum candidum var glanduliferum | Not treated | Not treated | Not treated | Not treated |  | Microliabum glanduliferum | Liabum candidum var. glanduliferum | Microliabum candidum | Microliabum candidum | Microliabum glanduliferum | Austroliabum glanduliferum |
|  | Liabum eremophilum | Not treated | Austroliabum eremophilum | Not treated | Austroliabum eremophilum |  | Microliabum eremophilum | Liabum eremophilum | Microliabum eremophilum | Microliabum eremophilum | Microliabum eremophilum | Austroliabum eremophilum |
| Liabum polymnioides (Fries, 1906) | Liabum polymnioides | Not treated | Austroliabum polymnioides | Liabum polymnioides | Austroliabum polymnioides | $\begin{aligned} & \hline \text { Subgenus } \\ & \text { Microliabum } \end{aligned}$ | Microliabum polymnioides | Liabum polymnioides | Microliabum polymnioides | Microliabum polymnioides | Microliabum polymnioides | Microliabum polymnioides |
| Liabum <br> mulgedifolium <br> (Muschler, <br> 1913) | Not treated | Not treated | Austroliabum mulgediifolium | Not treated | Austroliabum polymnioides |  | Microliabum mulgediifolium | Not treated | Not treated | Not treated | Microliabum mulgediifolium | Microliabum mulgediifolium |
| - | Not treated | Microliabum humile (三 Liabellum humile) | Angelianthus humilis | Microliabum humile | Microliabum humile |  | Microliabum humile | Microliabum humile | Microliabum humile | Microliabum humile | Microliabum humile | Microliabum humile |

Table 2. Morphological characters, number of species, geographical distribution, and environment of Microliabum subgenus Austroliabum, subgenus Microliabum, Paranephelius, Pseudonoseris, and Stephanbeckia. *In the case of Stephanbeckia, its pappus is not differentiated between outer and inner elements.

| Genera and subgenera/ Characters | Microliabum subgen. <br> Austroliabum | Microliabum subgen. <br> Microliabum | Paranephelius | Pseudonoseris | Stephanbeckia |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Species number | 3 | 3 | 7 | 2 | 1 |
| Habit | Caulescent herb or subshrub | Caulescent herb, rarely subshrub or small caulescent herb | Acaulescent herb, rarely small caulescent herb | Small caulescent herb | Small caulescent herb |
| Latex | Present | Present | Present | Present | Absent |
| Pseudostipules | Present | Present or absent | Absent | Absent | Absent |
| Grouping of the leaves | Sparse | Sparse or crowded | Rosulate, rarely crowded | Usually crowded | Crowded |
| Phylotaxis | Opposite (alternate in inflorescence) | Opposite (alternate in inflorescence) | Opposite or subopposite | Opposite | Opposite or subopposite |
| Leaf venation | Actinodromous | Actinodromous | Pinnate | Pinnate | Actinodromous |
| Adaxial leaf pubescence | Hirsute and whitearachnoid | Hirsute and whitearachnoid,or glabrescent | Hirsute and whitearachnoid, or glabrescent | Glabrescent, hirsute or arachnoid | Glabrescent |
| Abaxial leaf pubescence | Densely whitetomentose or woolly | Densely whitetomentose, rarely woolly | Densely whitetomentose or woolly | Densely whitetomentose or woolly | Densely whitetomentose |
| Type of secondary inflorescence (= capitulescence) | Corymbiform, few to many-headed, rarely a single capitulum | Corymbiform, few to many-headed, or a single capitulum | A single capitulum, rarely scapose, 2--3headed | Subscapose, fewheaded | Few-headed |
| Pedunculate/Sessil e capitulum | Pedunculate | Pedunculate | Sessile or subsessile | Pedunculate | Pedunculate |
| Shape of the involucre | Campanulate | Hemispherical | Campanulate | Campanulate | Campanulate |
| Number of phyllaries series | 4--6, usually 5 | 2--4, usually 3 | 4 | 4-5 | 2--3 |
| Disposition of outer phyllaries | Adpressed | Exserted | Adpressed | Adpressed | Adpressed |
| Phyllaries lenght | Gradually increasing, with inner phyllaries longer than the outer | Gradually increasing, with inner phyllaries shorter than the outer | Gradually increasing, with inner phyllaries longer than the outer | Gradually increasing, with inner phyllaries longer than the outer | Gradually increasing, with inner phyllaries longer than the outer |
| Number of phyllaries | 45--70 | 10--25, 45--75 | 40--50 | Ca. 40 | 25--30 |
| Type of receptacle | Areolate | Areolate | Areolate, fimbriate | Areolate | Areolate, fimbriate |
| Number of ray florets series | 1-seriate | 1--2-seriate | 1-seriate | 1-seriate | 1-seriate |
| Ray florets number | 25--50 | 10--15, 35--75 | 20--35 | 12--25 | Ca. 15 |
| Disc florets number | 40--65 | Ca. 15, 100--125 | 20--35 | 25--55 | 25--30 |
| Comparative length of style branches of disc florets | Shorter than the pubescent part on shaft below the bifurcation point | Shorter than the pubescent part on shaft below the bifurcation point | Longer than the pubescent part on shaft below the bifurcation point | Longer than the pubescent part on shaft below the bifurcation point | Shorter than the pubescent part on shaft below the bifurcation point |
| Comparative length of style pubescence on shaft below the bifurcation point of disc florets | At least three times longer than the branches of the style | At least three times longer than the branches of the style | At least three times shorter than the branches of the style | At least three times shorter than the branches of the style | At least three times longer than the branches of the style |
| Number of achene ribs | 8--10 | 8--10 | 10 | 10 | 2 |


| Achene <br> pubescence | Pubescent on ribs | Pubescent on all <br> the surface | Glabrous | Pubescent on all <br> the surface | Glabrous |
| :--- | :--- | :--- | :--- | :--- | :--- |
| Number of pappus <br> series | 2 | 2 | 2 | 2 | 1 |
| Type of pappus <br> outer series | Scales | Paleaceous scales | Barbellate bristles | Barbellate bristles <br> or scales | Plumose bristles* |
| Type of pappus <br> inner series | Barbellate bristles | Barbellate bristles, <br> or paleaceous <br> scales | Barbellate bristles | Barbellate bristles |  |
| Deciduous/Persist <br> ent pappus | Persistent | Deciduous | Persistent | Persistent | Deciduous |
| Habitat | Hills | Mountains and <br> hills, | Mountains | Mountains | Mountains |
| Country <br> distribution | Central and <br> northwestern <br> Argentina | Northwestern <br> Argentina and <br> Bolivia | Extreme <br> northwestern <br> Argentina, <br> Bolivia, and Peru | Bolivia and Peru | Southern Bolivia |

Table S1. Characteristics of data matrices and substitution models applied in the Bayesian and Parsimony analyses.

|  | ITS | $\boldsymbol{t r n L} \boldsymbol{- F}$ | ITS + trnL-F |
| :--- | :--- | :--- | :--- |
| Number of Taxa | 92 | 87 | 87 |
| Total Characters | 665 | 884 | 1547 |
| Number informative characters | 297 | 59 | 355 |
| Replicates MP | 10,000 | 10,000 | 10,000 |
| MP trees | $3525(42$ island $)$ | $12(1$ island $)$ | $17134(19$ islands $)$ |
| Number of steps | 1072 | 75 | 0.4883 |
| Consistency index (CI) | 0.4701 | 0.8667 | 0.8526 |
| Retention index (RI) | 0.8470 | GTR + I + |  |
| Bayes model |  | SYM |  |

Table S\#2. Measures and codifications for the Principal Coordinate Analysis (PCoA). Characters: plant height [m] (1), petiolate $[=1]$ inconspicuously petiolate or sessile leaf $[=0](2)$, petiole length [cm] (3), petiole width [cm] (4), leaf lamina length $[\mathrm{cm}]$ (5), leaf lamina width [cm] (6), number of capitula (7), length of the capitula peduncle [cm] (8), involucre height $[\mathrm{cm}]$ (9), involucre width $[\mathrm{cm}]$ (10), number of phyllaries series (11), outer phyllary length [mm] (12), outer phyllary width [mm] (13), inner phyllary length [mm] (14), inner phyllary width [mm] (15), consistency of outer phyllaries [coriaceous $=1$; herbaceous $=0$ ] (16), number of ray florets series $(17)$, ray florets corolla length [mm] (18), ray florets corolla limb length [mm] (19), ray florets corolla limb width [mm] (20), disc florets corolla length [mm] (21), disc floret corolla limb width [mm] (22), style branches length of disc florets [mm] (23), achene length [mm] (24), achene width $[\mathrm{mm}]$ (25), pubescence of achene [trichomes on ribs $=0$; covering all the surface $=1$ ] (26), outer pappus length [mm] (27), outer pappus type [scales $=1$; paleaceous scales $=0$ ] (28), inner pappus length [mm] (29), and inner pappus type [bristles $=1$; paleaceous scales $=0](30)$.

|  | Characters | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| M. candidum | Individual $1$ | 0.63 | 1 | 3.4 | 0.1 | 6.4 | 3.6 | 10 | 2.2 | 1 | 1.1 | 5 | 6.2 | 1.5 | 10 | 1 | 1 | 1 | 9.5 | 5.5 | 1 | 5.7 | 0.7 | 0.8 | 2 | 0.6 | 0 | 0.4 | 1 | 5.3 | 1 |
|  | 2 | 0.32 | 1 | 2.6 | 0.2 | 9.3 | 5.2 | 17 | 2.1 | 1.1 | 1.1 | 5 | 4.5 | 1.5 | 8.1 | 0.7 | 1 | 1 | 13 | 8 | 0.7 | 7 | 0.8 | 0.9 | 2 | 0.7 | 0 | 0.5 | 1 | 7.6 | 1 |
|  | 3 | 1.02 | 1 | 5.9 | 0.2 | 11.8 | 8.2 | 10 | 2 | 1 | 1 | 5 | 4.8 | 1.3 | 7.4 | 0.8 | 1 | 1 | 13.7 | 9.7 | 1.2 | 7.6 | 0.6 | 1.1 | 2.4 | 0.9 | 0 | 0.5 | 1 | 9.4 | 1 |
|  | 4 | 0.33 | 1 | 4.5 | 0.2 | 12.6 | 7 | 15 | 3.9 | 1 | 0.9 | 6 | 3.5 | 1 | 6.6 | 1 | 1 | 1 | 14.9 | 9.9 | 1.1 | 8.2 | 1 | 0.8 | 2.4 | 0.9 | 0 | 0.6 | 1 | 7.5 | 1 |
|  | 5 | 0.4 | 1 | 2.3 | 0.1 | 5 | 3.2 | 13 | 1.1 | 0.8 | 1.2 | 5 | 3.7 | 1.2 | 6.6 | 0.9 | 1 | 1 | 13 | 10 | 1.2 | 7 | 0.8 | 0.8 | 1.6 | 0.8 | 0 | 0.6 | 1 | 6.9 | 1 |
|  | 6 | 0.29 | 1 | 1.9 | 0.1 | 7.7 | 4 | 6 | 1.6 | 1.3 | 1.2 | 5 | 5 | 1.5 | 10.2 | 1.2 | 1 | 1 | 15 | 8 | 1 | 8.2 | 0.8 | 1 | 2.4 | 1 | 0 | 0.7 | 1 | 7.1 | 1 |
|  | 7 | 1 | 1 | 3.2 | 0.1 | 8 | 6.5 | 19 | 1.9 | 0.9 | 1.2 | 5 | 3.7 | 1.5 | 7 | 1 | 1 | 1 | 13 | 10 | 1 | 5.5 | 0.6 | 0.7 | 2.3 | 0.7 | 0 | 0.5 | 1 | 5.6 | 1 |
|  | 8 | 1 | 1 | 2 | 0.1 | 5.7 | 2.8 | 17 | 2.5 | 0.8 | 1.1 | 5 | 3.5 | 1 | 6.6 | 1 | 1 | 1 | 12.5 | 8.5 | 1.3 | 6.1 | 0.6 | 0.8 | 1.5 | 0.6 | 0 | 0.5 | 1 | 6.4 | 1 |
|  | 9 | 1 | 1 | 3 | 0.15 | 8.4 | 4 | 12 | 3.7 | 1 | 1.2 | 5 | 4.2 | 1.3 | 8.3 | 1.1 | 1 | 1 | 11 | 6 | 0.8 | 7.1 | 0.9 | 0.6 | 2.2 | 0.6 | 0 | 0.6 | 1 | 7.2 | 1 |
|  | 10 | 1 | 1 | 1.5 | 0.15 | 7.7 | 4.1 | 12 | 1.7 | 1 | 1 | 5 | 3 | 1.4 | 7.5 | 1 | 1 | 1 | 10 | 6 | 0.9 | 7.2 | 0.9 | 0.8 | 1.4 | 0.7 | 0 | 0.4 | 1 | 8.5 | 1 |
|  | 11 | 1 | 1 | 3.1 | 0.1 | 6.5 | 4.1 | 18 | 1.7 | 0.9 | 0.8 | 5 | 4 | 0.9 | 6.3 | 0.9 | 1 | 1 | 15 | 11.5 | 0.9 | 6.9 | 0.7 | 0.7 | 1.9 | 0.7 | 0 | 0.5 | 1 | 5.5 | 1 |
|  | 12 | 1 | 1 | 2.9 | 0.1 | 8.1 | 3.8 | 13 | 1.6 | 0.9 | 1.1 | 4 | 4.5 | 1.5 | 8.3 | 0.9 | 1 | 1 | 11.5 | 7 | 1.1 | 7.8 | 1 | 0.8 | 1.3 | 0.6 | 0 | 0.7 | 1 | 7.6 | 1 |
|  | 13 | 0.39 | 1 | 2 | 0.1 | 6.5 | 4.1 | 10 | 1.5 | 1 | 1.3 | 5 | 4.4 | 1.3 | 7.3 | 0.8 | 1 | 1 | 15 | 10 | 0.7 | 8.4 | 1.1 | 0.9 | 1.7 | 0.8 | 0 | 0.7 | 1 | 8.2 | 1 |
|  | 14 | 0.4 | 1 | 3.6 | 0.2 | 11.4 | 5.3 | 17 | 3.1 | 1 | 1.2 | 5 | 4.3 | 0.8 | 9.2 | 1.2 | 1 | 1 | 13 | 8 | 0.7 | 7.5 | 0.8 | 0.9 | 2.2 | 0.6 | 0 | 0.5 | 1 | 8.8 | 1 |
|  | 15 | 0.49 | 1 | 1.7 | 0.15 | 6.3 | 3.9 | 7 | 1.6 | 1 | 1.2 | 5 | 4 | 1.2 | 8 | 1.1 | 1 | 1 | 11 | 6 | 0.7 | 8 | 0.8 | 1 | 1.5 | 0.7 | 0 | 0.5 | 1 | 8.2 | 1 |
|  | 16 | 0.32 | 1 | 1.2 | 0.1 | 4 | 2.4 | 11 | 1.8 | 0.8 | 0.9 | 5 | 3.5 | 1 | 6 | 1 | 1 | 1 | 10.6 | 6.1 | 0.8 | 6.5 | 0.7 | 0.6 | 1.5 | 0.7 | 0 | 0.5 | 1 | 6 | 1 |
|  | 17 | 1 | 1 | 4.2 | 0.1 | 9.8 | 6 | 12 | 2.7 | 0.9 | 1.1 | 5 | 4 | 1.1 | 8.1 | 0.8 | 1 | 1 | 10 | 6 | 0.9 | 6.8 | 0.7 | 0.8 | 1.8 | 0.5 | 0 | 0.4 | 1 | 7.6 | 1 |
|  | 18 | 0.33 | 1 | 1.9 | 0.15 | 5.4 | 4.2 | 10 | 1.1 | 0.8 | 1.2 | 5 | 4.1 | 1.5 | 7.5 | 0.9 | 1 | 1 | 17 | 11 | 0.8 | 7.7 | 0.6 | 1 | 2.2 | 0.9 | 0 | 0.5 | 1 | 6.5 | 1 |
|  | 19 | 0.32 | 1 | 3.1 | 0.1 | 6.9 | 5.2 | 9 | 2.7 | 0.9 | 1.1 | 6 | 4.1 | 1.4 | 7 | 0.9 | 1 | 1 | 13.5 | 8.5 | 1.3 | 8.5 | 0.7 | 0.5 | 1.5 | 0.6 | 0 | 0.5 | 1 | 7.5 | 1 |
|  | 20 | 0.5 | 1 | 1.7 | 0.15 | 4.5 | 2.8 | 6 | 1.6 | 0.8 | 0.9 | 5 | 3.5 | 1.3 | 8.1 | 1.1 | 1 | 1 | 10 | 5 | 1 | 5.6 | 0.7 | 0.7 | 2.1 | 0.8 | 0 | 0.5 | 1 | 6.4 | 1 |
| M. eremophilum | 21 | 0.3 | 1 | 2.1 | 0.2 | 8.6 | 5.8 | 12 | 2.1 | 0.8 | 0.9 | 5 | 4.5 | 1 | 7.1 | 0.6 | 1 | 1 | 14 | 10.5 | 1.5 | 5.5 | 1 | 0.5 | 1.5 | 0.5 | 0 | 0.4 | 1 | 5.8 | 1 |
|  | 22 | 0.5 | 1 | 1.2 | 0.4 | 7.6 | 2.9 | 12 | 3.4 | 0.9 | 1.1 | 6 | 3.8 | 1.2 | 8.3 | 1.1 | 1 | 1 | 14.5 | 9 | 1.2 | 5.7 | 0.6 | 0.7 | 2 | 1 | 0 | 0.4 | 1 | 6.4 | 1 |
|  | 23 | 0.36 | 1 | 1.5 | 0.2 | 4.5 | 1.8 | 14 | 4.7 | 0.9 | 1 | 5 | 3 | 1.3 | 7.3 | 0.8 | 1 | 1 | 10.5 | 6.5 | 1.1 | 7 | 0.6 | 0.5 | 2.5 | 1 | 0 | 0.4 | 1 | 4.9 | 1 |
|  | 24 | 0.65 | 0 | 0 | 0.4 | 7.9 | 1.8 | 5 | 5 | 1 | 1 | 6 | 5 | 1.3 | 8.5 | 1 | 1 | 1 | 12.6 | 6 | 1.1 | 5.5 | 0.6 | 1 | 2.3 | 0.6 | 0 | 0.9 | 1 | 6.9 | 1 |
|  | 25 | 1 | 1 | 1.9 | 0.4 | 12.1 | 5.9 | 10 | 2.8 | 1.1 | 1.2 | 5 | 4.6 | 1.1 | 7.8 | 0.8 | 1 | 1 | 13 | 9.5 | 1 | 6.8 | 1 | 0.7 | 1.4 | 0.5 | 0 | 0.3 | 1 | 4.2 | 1 |
| M. glanduliferum | 26 | 0.31 | 1 | 1.7 | 0.1 | 3.9 | 2.6 | 10 | 3 | 1.1 | 1.1 | 5 | 5.2 | 1.1 | 9.5 | 0.8 | 1 | 1 | 18 | 12 | 1.1 | 8.7 | 1 | 1 | 1.4 | 0.6 | 0 | 0.6 | 1 | 6.9 | 1 |
|  | 27 | 0.33 | 1 | 2.9 | 0.1 | 7.5 | 6.6 | 13 | 1.9 | 1 | 1.3 | 5 | 5.4 | 1.6 | 9 | 0.8 | 1 | 1 | 14.5 | 8.4 | 1.5 | 7.5 | 1.1 | 0.5 | 1.2 | 0.6 | 0 | 0.6 | 1 | 7 | 1 |
|  | 28 | 0.5 | 1 | 2.7 | 0.1 | 6.6 | 4.1 | 10 | 1.6 | 1 | 0.9 | 5 | 4 | 1.2 | 7.2 | 0.8 | 1 | 1 | 13 | 8 | 1.4 | 7.2 | 0.8 | 0.8 | 2 | 0.7 | 0 | 0.5 | 1 | 7.7 | 1 |
|  | 29 | 0.5 | 1 | 2.3 | 0.1 | 5.4 | 4.2 | 12 | 1.2 | 1 | 1 | 5 | 4.1 | 1.3 | 7.6 | 0.9 | 1 | 1 | 13 | 8 | 1.4 | 7.2 | 0.8 | 0.8 | 2 | 0.7 | 0 | 1 | 1 | 8.6 | 1 |
|  | 30 | 0.32 | 1 | 1.3 | 0.1 | 6.6 | 4.8 | 12 | 1.8 | 0.9 | 1.1 | 5 | 3.5 | 1.1 | 7.6 | 1.1 | 1 | 1 | 16 | 10 | 1.3 | 7.7 | 1 | 0.7 | 1.3 | 0.7 | 0 | 0.6 | 1 | 6.8 | 1 |
|  | 31 | 0.27 | 1 | 2.2 | 0.1 | 5.2 | 3.5 | 5 | 0.8 | 1.1 | 1 | 6 | 4.5 | 1.3 | 9.2 | 1 | 1 | 1 | 9.1 | 5 | 0.4 | 7.8 | 0.6 | 0.7 | 1.2 | 0.8 | 0 | 0.7 | 1 | 8 | 1 |
|  | 32 | 0.24 | 1 | 1.4 | 0.1 | 4.1 | 2.6 | 3 | 0.7 | 1 | 0.9 | 5 | 3.9 | 1.5 | 7.8 | 1 | 1 | 1 | 10.5 | 6 | 0.5 | 6.5 | 0.7 | 0.8 | 1.5 | 0.5 | 0 | 0.8 | 1 | 7.2 | 1 |


| M. humile | 33 | 0.65 | 1 | 2.5 | 0.2 | 5.4 | 4.1 | 16 | 64.5 | 1.1 | 1.2 | 5 | 5 | 1.2 | 10.2 | 1.1 | 1 | 1 | 19 | 7 | 1.5 | 9.9 | 1 | 1 | 1.7 | 0.7 | 0 | 0.9 | 1 | 8.5 | 1 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  | 34 | 0.03 | 0 | 0 | 0 | 1.6 | 0.5 | 2 | 20.8 | 0.5 | 0.9 | 2 | 5 | 0.8 | 4.5 | 2.1 | 0 | 1 | 4.5 | 3.2 | 0.8 | 2.8 | 1 | 0.3 | 1.5 | 0.5 | 1 | 0.6 | 0 | 1.8 | 0 |
|  | 35 | 0.034 | 0 | 0 | 0 | 1.7 | 0.5 |  | 41.5 | 0.6 | 1 | 2 | 5.1 | 1.6 | 4.8 | 2.3 | 0 | 1 | 5 | 3.8 | 1 | 2.5 | 0.7 | 0.2 | 2.1 | 0.8 | 1 | 0.7 | 0 | 2.6 | 0 |
|  | 36 | 0.046 | 0 | 0 | 0 | 1.5 | 0.5 |  | 43.2 | 0.6 | 1.1 | 3 | 5.1 | 1.2 | 4 | 1.7 | 0 | 1 | 7 | 5 | 0.6 | 2.3 | 0.6 | 0.3 | 2 | 0.6 | 1 | 0.6 | 0 | 2 | 0 |
|  | 37 | 0.057 | 0 | 0 | 0 | 2.4 | 0.7 |  | 63.1 | 0.6 | 1.2 | 3 | 7.3 | 2.1 | 4.1 | 1.6 | 0 | 1 | 6 | 4.5 | 0.8 | 2.5 | 0.9 | 0.2 | 2.2 | 0.7 | 1 | 0.8 | 0 | 2 | 0 |
|  | 38 | 0.054 | 0 | 0 | 0 | 2.3 | 0.4 |  | 41.5 | 0.6 | 1.2 | 3 | 5 | 1.6 | 3.1 | 1.2 | 0 | 1 | 5.5 | 4 | 1.1 | 2.6 | 0.9 | 0.3 | 2 | 0.6 | 1 | 0.7 | 0 | 1.9 | 0 |
|  | 39 | 0.069 | 0 | 0 | 0 | 2 | 0.7 |  | $8 \quad 2.1$ | 0.6 | 1.4 | 3 | 4.2 | 1.8 | 3.5 | 1 | 0 | 1 | 5 | 3.5 | 0.8 | 2.3 | 1 | 0.2 | 1.9 | 0.6 | 1 | 0.7 | 0 | 2.4 | 0 |
|  | 40 | 0.06 | 0 | 0 | 0 | 2.4 | 0.5 |  | 31.1 | 0.7 | 1.3 | 3 | 4.6 | 1.7 | 3.7 | 1.5 | 0 | 1 | 4.4 | 3.4 | 1 | 2.3 | 0.5 | 0.3 | 1.3 | 0.4 | 1 | 0.8 | 0 | 1.9 | 0 |
|  | 41 | 0.034 | 0 | 0 | 0 | 1.4 | 0.3 |  | 31.2 | 0.6 | 1.2 | 2 | 4.8 | 1.1 | 5 | 2 | 0 | 1 | 4.5 | 3.7 | 0.7 | 2.1 | 0.6 | 0.2 | 2.1 | 0.7 | 1 | 0.6 | 0 | 1.8 | 0 |
|  | 42 | 0.053 | 0 | 0 | 0 | 2.3 | 0.7 | 8 | $8 \quad 2.2$ | 0.8 | 1.6 | 2 | 7.3 | 1.5 | 5.4 | 1.8 | 0 | 1 | 6 | 4.5 | 1 | 2.6 | 0.6 | 0.2 | 2.2 | 0.7 | 1 | 0.6 | 0 | 2.4 | 0 |
|  | 43 | 0.087 | 0 | 0 | 0 | 3.7 | 1 | 14 | $4 \quad 2.4$ | 0.8 | 1.6 | 2 | 5 | 1.2 | 4.5 | 1.3 | 0 | 1 | 4.9 | 3.4 | 0.6 | 2.8 | 0.8 | 0.4 | 1.6 | 0.7 | 1 | 0.7 | 0 | 2.4 | 0 |
|  | 44 | 0.096 | 0 | 0 | 0 | 3.1 | 0.8 | 13 | $3 \quad 2.4$ | 0.7 | 1.5 | 3 | 4.5 | 1.2 | 4 | 2.2 | 0 | 1 | 4.8 | 3.5 | 0.7 | 2.5 | 0.6 | 0.3 | 1.8 | 0.6 | 1 | 0.7 | 0 | 2.4 | 0 |
| M. mulgediifolium | 45 | 0.07 | 1 | 1.8 | 0.3 | 6.7 | 3.2 | 3 | 31.1 | 1.1 | 1.9 | 4 | 6.6 | 1.5 | 5 | 1.2 | 0 | 2 | 13.5 | 10 | 1.5 | 5 | 0.8 | 0.5 | 1.2 | 0.6 | 1 | 0.7 | 0 | 4.5 | 1 |
|  | 46 | 1.75 | 1 | 10.4 | 1.6 | 19.2 | 18.7 | 20 | 07.7 | 1.1 | 2.4 | 3 | 12 | 1 | 4.6 | 0.9 | 0 | 2 | 15 | 11 | 1.2 | 6.5 | 0.9 | 0.5 | 1.4 | 0.6 | 1 | 0.7 | 0 | 4.3 | 1 |
|  | 47 | 2 | 1 | 5.1 | 1 | 16.7 | 11.4 | 17 | 76.1 | 0.6 | 1.6 | 3 | 9.2 | 1.8 | 6.3 | 1.1 | 0 | 2 | 13 | 9 | 0.9 | 6 | 1 | 0.5 | 1.5 | 0.7 | 1 | 0.7 | 0 | 4 | 1 |
|  | 48 | 0.9 | 1 | 7.4 | 1.1 | 12.6 | 11.9 | 7 | $7 \quad 3.5$ | 1.1 | 2.4 | 2 | 11 | 1.3 | 5.4 | 0.8 | 0 | 2 | 15.5 | 11 | 1 | 5.1 | 0.6 | 0.6 | 1.4 | 0.5 | 1 | 0.8 | 0 | 4.4 | 1 |
|  | 49 | 0.21 | 1 | 1.7 | 0.5 | 4 | 3.5 | 12 | 23.6 | 0.8 | 1.4 | 3 | 6.2 | 1.3 | 4.7 | 0.9 | 0 | 2 | 8.3 | 5.3 | 0.8 | 3.4 | 0.9 | 0.3 | 1.4 | 0.7 | 1 | 0.4 | 0 | 3.3 | 1 |
|  | 50 | 0.08 | 1 | 0.8 | 0.3 | 2.2 | 1.8 | 3 | $3 \quad 2.8$ | 0.7 | 1.1 | 2 | 5.1 | 1.4 | 4.4 | 1.1 | 0 | 2 | 9.9 | 6.9 | 1.5 | 4.6 | 0.8 | 0.3 | 1.2 | 0.6 | 1 | 0.6 | 0 | 2.9 | 1 |
|  | 51 | 0.23 | 1 | 2.3 | 0.3 | 4.2 | 3.8 | 15 | $5 \quad 2.7$ | 0.9 | 1.4 | 3 | 5.8 | 1 | 4.5 | 0.8 | 0 | 2 | 11 | 6.7 | 0.9 | 4.5 | 0.9 | 0.4 | 1 | 0.6 | 1 | 0.7 | 0 | 3.2 | 1 |
|  | 52 | 0.16 | 0 | 0 | 0 | 2.9 | 1.2 | 16 | 63.1 | 0.8 | 1.3 | 3 | 4.4 | 1.2 | 4.4 | 1.1 | 0 | 2 | 6.5 | 4.5 | 0.8 | 3.1 | 0.8 | 0.3 | 1.8 | 0.7 | 1 | 0.7 | 0 | 3 | 1 |
|  | 53 | 0.15 | 1 | 0.8 | 0.1 | 2.3 | 1.2 | 9 | 94.9 | 1 | 1.4 | 3 | 6.6 | 1.5 | 5.9 | 1.4 | 0 | 2 | 11 | 7.8 | 1.5 | 4.7 | 1.1 | 0.5 | 2.2 | 0.7 | 1 | 0.7 | 0 | 3.4 | 1 |
| M. <br> polymnioides | 54 | 2 | 1 | 13.2 | 1.1 | 28.2 | 23.7 | 21 | 16.5 | 1.4 | 2.2 | 4 | 12 | 2 | 6.6 | 1.2 | 0 | 2 | 16 | 12.5 | 2.2 | 5.8 | 0.9 | 0.6 | 1.1 | 0.5 | 1 | 0.8 | 0 | 4.9 | 1 |
|  | 55 | 0.49 | 1 | 13.1 | 1 | 19.4 | 17.6 | 10 | $0 \quad 3.9$ | 1.1 | 1.8 | 3 | 8.8 | 1.9 | 5 | 0.8 | 0 | 2 | 11 | 7.5 | 2 | 6.6 | 1 | 0.8 | 1.1 | 0.5 | 1 | 1 | 0 | 4.6 | 1 |
|  | 56 | 0.79 | 1 | 7.7 | 0.4 | 10.6 | 9.2 | 23 | 33.6 | 0.9 | 1.5 | 4 | 6.3 | 1 | 5.2 | 0.9 | 0 | 2 | 11 | 7.2 | 1.3 | 5 | 0.6 | 0.8 | 1.4 | 0.6 | 1 | 0.6 | 0 | 5.5 | 1 |
|  | 57 | 0.55 | 1 | 3.8 | 0.6 | 7.7 | 6.7 | 14 | 43.9 | 1.1 | 1.6 | 3 | 6.5 | 1.5 | 5.2 | 1.5 | 0 | 2 | 7.3 | 4 | 1.2 | 5 | 0.6 | 0.3 | 1 | 0.3 | 1 | 0.6 | 0 | 4.1 | 1 |
|  | 58 | 1.8 | 1 | 8.1 | 1 | 13.9 | 16.5 | 20 | 07.7 | 1.2 | 2.3 | 4 | 10.5 | 2.1 | 7.5 | 1.3 | 0 | 2 | 18 | 13 | 1.2 | 6.1 | 0.9 | 0.9 | 1.4 | 0.6 | 1 | 1.1 | 0 | 5.2 | 1 |
|  | 59 | 2 | 1 | 3.4 | 0.6 | 10.2 | 10.1 | 21 | 15.2 | 0.9 | 1.7 | 3 | 8 | 1.2 | 7 | 1.1 | 0 | 2 | 13.3 | 9.3 | 1.6 | 5.3 | 0.7 | 0.4 | 1.4 | 0.6 | 1 | 0.9 | 0 | 4.4 | 1 |
|  | 60 | 0.33 | 1 | 4.3 | 0.4 | 9.9 | 10 | 22 | 24.1 | 0.9 | 1.8 | 4 | 7.7 | 1.4 | 7.9 | 1.2 | 0 | 2 | 11.5 | 7.5 | 1 | 5.2 | 0.8 | 0.7 | 1.1 | 0.5 | 1 | 1.2 | 0 | 4.9 | 1 |
|  | 61 | 0.25 | 1 | 5.3 | 0.6 | 9.5 | 6.7 |  | 64.6 | 1.3 | 3 | 3 | 8.9 | 1.4 | 4.5 | 0.8 | 0 | 2 | 18.5 | 15 | 1.2 | 6 | 1.2 | 0.6 | 1.5 | 0.7 | 1 | 0.6 | 0 | 4.6 | 1 |
|  | 62 | 0.3 | 1 | 6.6 | 0.8 | 11.9 | 9.7 | 12 | 23.9 | 1.2 | 2.1 | 3 | 8.8 | 1.8 | 7.6 | 1 | 0 | 2 | 19 | 13.5 | 1.8 | 6.6 | 1 | 0.8 | 1.5 | 0.6 | 1 | 0.8 | 0 | 4.5 | 1 |
|  | 63 | 0.4 | 1 | 14.9 | 1 | 19 | 21.6 | 10 | 04.7 | 1 | 2.2 | 4 | 10.2 | 2 | 6.2 | 1.5 | 0 | 2 | 19 | 13 | 1.5 | 6 | 0.7 | 0.8 | 1.2 | 0.6 | 1 | 0.6 | 0 | 5.4 | 1 |
|  | 64 | 0.32 | 1 | 5.7 | 0.5 | 12.8 | 8.2 | 10 | 03.9 | 1.3 | 3 | 4 | 15 | 2 | 5.2 | 0.8 | 0 | 2 | 18 | 13.4 | 1.6 | 6 | 1 | 0.5 | 1.1 | 0.5 | 1 | 0.8 | 0 | 5 | 1 |
|  | 65 | 0.39 | 1 | 11.9 | 1 | 17.1 | 17.6 | 14 | 44.2 | 0.9 | 1.7 | 4 | 8 | 1.7 | 6.1 | 0.9 | 0 | 2 | 10 | 5.8 | 0.8 | 6.1 | 0.7 | 0.8 | 1 | 0.5 | 1 | 1 | 0 | 4.8 | 1 |
|  | 66 | 1 | 1 | 3.2 | 0.6 | 12.3 | 13.6 | 25 | 55.2 | 1.2 | 1.9 | 3 | 8.5 | 1.4 | 7.5 | 1.4 | 0 | 2 | 22.5 | 15.5 | 1.7 | 6 | 0.8 | 0.6 | 1.8 | 0.6 | 1 | 1 | 0 | 5.9 | 1 |
|  | 67 | 1 | 1 | 4.5 | 0.7 | 10.7 | 12.3 | 22 | 24.6 | 1.2 | 2 | 4 | 8.5 | 1.6 | 6.1 | 0.9 | 0 | 2 | 18 | 13.3 | 1.4 | 5.5 | 0.5 | 0.7 | 1.3 | 0.6 | 1 | 0.8 | 0 | 5.9 | 1 |
|  | 68 | 2 | 1 | 3.2 | 1.7 | 10.2 | 8.6 | 17 | 75.8 | 1.6 | 2.4 | 4 | 9.5 | 2.2 | 7 | 1.2 | 0 | 2 | 20 | 15 | 1.7 | 6.3 | 0.8 | 0.7 | 1.4 | 0.8 | 1 | 1 | 0 | 6 | 1 |
|  | 69 | 0.8 | 1 | 8.3 | 1.8 | 12.2 | 9.2 |  | $7 \quad 2.5$ | 0.8 | 1.7 | 3 | 8.8 | 1.9 | 6.2 | 1.2 | 0 | 2 | 18.5 | 1.5 | 1.5 | 6 | 1.2 | 1 | 1 | 0.6 | 1 | 0.7 | 0 | 4.9 | 1 |
|  | 70 | 0.8 | 1 | 10.6 | 1.3 | 13.6 | 11.3 | 12 | 23.5 | 1.4 | 2.2 | 4 | 9.5 | 1.8 | 5.7 | 1.3 | 0 | 2 | 15 | 10.5 | 1.5 | 5.8 | 0.6 | 0.6 | 1.1 | 0.5 | 1 | 0.8 | 0 | 5 | 1 |
|  | 71 | 0.5 | 1 | 4.5 | 0.3 | 10.3 | 5 | 30 | 08.6 | 0.9 | 2.5 | 4 | 12 | 2.5 | 8 | 1.2 | 0 | 2 | 8 | 4.6 | 0.8 | 6.2 | 0.9 | 0.6 | 1.6 | 0.7 | 1 | 1.1 | 0 | 4.6 | 1 |
|  | 72 | 0.51 | 1 | 9.4 | 0.6 | 13.8 | 12.8 | 13 | 35.3 | 0.9 | 1.9 | 4 | 11 | 1.7 | 8.1 | 1.6 | 0 | 2 | 9 | 5.2 | 0.8 | 5.9 | 0.7 | 0.8 | 1.2 | 0.6 | 1 | 1.2 | 0 | 4.5 | 1 |

Legends
Fig. 1. Majority-rule consensus tree resulting from Bayesian analysis of the 28 Paranepheliinae and 63 of Liabinae, Munnoziinae, Sinclairiinae, and outgroup samples from the ITS region. The ingroup included Microliabum subgenus Austroliabum, Microliabum subgenus Microliabum, and Chionopappus, Erato, Paranephelius, Philoglossa, Pseudonoseris, and Stephanbeckia. In addition, Cacosmia, Dillandia, Ferreyranthus, Liabum, Oligactis, and Sampera (Liabinae), Chrysactinium and Munnozia (Munnoziinae), and Liabellum, Megaliabum, Sinclairia, and Sinclairiopsis (Sinclairinae) were included as ingroup. The outgroups were formed by species of tribes Moquinieae (Moquinia and Pseudostifftia) and Vernonieae (Distephanus). Numbers above branches are posterior probability values; below branches, parsimony bootstrap percentages.

Fig. 2. Majority-rule consensus tree resulting from the Bayesian analysis of the 24 Paranepheliinae and 63 of Liabinae, Munnoziinae, Sinclairiinae, and outgroup samples of the combined ITS and trnL-F regions. The ingroup included Microliabum subgenus Austroliabum, Microliabum subgenus Microliabum, and Chionopappus, Erato, Paranephelius, Philoglossa, Pseudonoseris, and Stephanbeckia. In addition, Cacosmia, Dillandia, Ferreyranthus, Liabum, Oligactis, and Sampera (Liabinae), Chrysactinium and Munnozia (Munnoziinae), and Liabellum, Megaliabum, Sinclairia, and Sinclairiopsis (Sinclairiinae) were included as ingroup. The outgroups were formed by species of tribes Moquinieae (Moquinia and Pseudostifftia) and Vernonieae (Distephanus). Numbers above branches are posterior probability values; below branches, parsimony bootstrap percentages.

Fig. 3. A, D-E, G, I. Microliabum candidum. B, C, F, H. M. mulgediifolium. A-B. Plant. C. Crosssection of stem with latex. D. Free pseudostipules. E. Fused pseudostipules. F. Free pseudostipules prolongated as wings of the petioles. G-H. Adaxial leaf surface. I. Abaxial leaf surface. a. White latex. b. Pseudostipule. c. Wing of petiole. Photos: D.G. Gutiérrez.

Fig. 4. A. Adaxial leaf surface of M. candidum. B. Adaxial leaf surface of M. polymnioides. C. Lateral view of phyllary in M. candidum. D. Abaxial leaf surface of M. candidum. a. Simple conical trichome. b. Aseptate-flagellate trichome. c. Biseriate glandular trichome with a big stalk. d. Biseriate glandular trichome with a short stalk. A, C-D: M. candidum (Gutiérrez \& Di Paola 281, BA); B: M. polymnioides (Gutiérrez et al. 580, BA).

Fig. 5. A, C, E. Microliabum candidum. B, D, F. M. mulgediifolium. A-B. Lateral view of a capitulum. C-D. Upper view of capitula in early stages of development. F-G. Upper view of a capitulum. a. Outer phyllary. Photos: D.G. Gutiérrez.

Fig. 6. A. Trichomes in a corolla's lobe of disc floret. B. Apical part of a style of disc floret. C. Detail of style branches of disc floret showing sweeping hairs, papillae, and pollen. D-E. Achene with pappus. F. Twin hairs of achene. G. Scales of outer series of pappus. H. Paleaceous scales of outer series of pappus. I. Barbellate bristles of inner series of pappus. J. Paleaceous scales of inner series of pappus. a. Simple biseriate glandular trichome with a conspicuous head. b. Simple biseriate glandular trichome without a head. c. Papillae. d. Stomes. e. Style branches. f. Pubescent shaft of style. g. Stigmatic papillae. h. Sweeping hair. i. pollen grain. j. Carpopodium. k. Twin hairs. 1. Depressed area between ribs. m. Scale. n. Bristle. o. Paleaceous scale. p. A twin hair in detail with divergent apical cells. A-D, F-G: M. candidum (Gutiérrez \& Di Paola 281, BA); E, H-I: M. polymnioides (Gutiérrez et al. 580, BA); J: M. humile (Fabris et al. 4169, LP).

Fig. 7. Principal coordinate analysis (PCoA). Plot of mean value of 72 individuals of 52 specimens on the first two principal coordinates. $\mathrm{PC} 1=38.82 \%, \mathrm{PC} 2=26.64 \%, \mathrm{PC} 3=3.19 \%$. Microliabum
candidum (red plus), M. eremophilum (violet circle), M. glanduliferum (blue asterisk), M. humile (light blue triangle), M. mulgediifolium (green ex), and M. polymnioides (red rectangle).

Fig. 8. Maps of distribution. A: Austroliabum. B: Microliabum.

Fig. 9. Austroliabum candidum. A. Reproductive branch. B. Central stem with leaves. C. Involucre, showing pappus of florets. D. Outer phyllary. E. Inner phyllary. F. Ray floret (without ovary and pappus). G. Disc floret (without ovary and pappus). H. Achene and pappus. Gutiérrez \& Di Paola 281 (BA).

Fig. 10. Austroliabum eremophilum. A. Reproductive branch, with capitula on fruiting stage. B. Involucre, showing pappus of florets. C. Outer phyllary. D. Inner phyllary. E. Ray floret (without ovary and pappus). F. Disc floret (without ovary and pappus). G. Achene and pappus. Rodriguez 1294 (LP).

Fig. 11. Austroliabum glanduliferum. A. Reproductive branch. B. Involucre, showing pappus of florets. C. Outer phyllary. D. Inner phyllary. E. Ray floret (without ovary and pappus). F. Disc floret (without ovary and pappus). G. Achene and pappus. Gutiérrez et al. 467 (BA).

Fig. 12. Microliabum humile. A. Plant. B. Involucre, showing pappus and a ray floret. C. Outer phyllary. D. Inner phyllary. E. Ray floret (without ovary and pappus). F. Disc floret (without ovary and pappus). G. Achene and pappus. Fabris et al. 4169 (LP).

Fig. 13. Microliabum mulgediifolium. A. Reproductive branch. B. Small plant. C. Central stem with leaves. D. Involucre. E. Outer phyllary. F. Inner phyllary. G. Innermost phyllary. H. Ray floret
(without ovary and pappus). I. Disc floret (without ovary and pappus). J. Achene and pappus. Gutiérrez et al. 554 (BA).

Fig. 14. Microliabum polymnioides. A. Reproductive branch. B. Leave. C. Involucre. D. Outer phyllary. E. Inner phyllary. F. Innermost phyllary. G. Ray floret (without ovary and pappus). H. Disc floret (without ovary and pappus). I. Achene and pappus. Gutiérrez et al. 580 (BA).


## Outgroups



Microliabum subgenus Microliabum



Figure
Click hellentozia hastiflia n NB37750



Chrysactinium acaule Ne3z7 58 Munnozial yrata sn837157


Paranepheliinae
E Erato costaricensis. NN837166
Chionopapppus benthamii N833777
Chionoppopus benthami NB7776
Paranephelius asperifolius Jne3z714
Paranephelius asperifolius Mk867794*

- Pseudonoseris discolor NN837171 - Pseudonosesis szyszylowiczii NB37172

Paranephelius unifornus AB355508
Microliabum
subgenus subgenus
Austroliabum
Microliabum polymnioides JNB37169


Microliabum subgenus Microliabum


## ${ }_{100}$ Liabum sp. . bNoellatitu

14 Liabum asclepiadeum JNB37134
LLiabum kingii NB37137


Liabinae

## Outgroups








Figure
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Figure
Click here to access/download;Figure;FIGURE 7_GRAY.pdf






(2)



Figure
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Appendix 1. Voucher information and GenBank accession number for taxa used in the present study.
Species, country, province, locality, date, voucher specimen, and Gen Bank accession numbers for ITS and trnL-F, respectively. Newly generated sequences are indicated by an asterisk $\left(^{*}\right)$ and lacking sequences by a dash ( - ). Previously published sequences are indicated by a superscript: ${ }^{1}=$ Funk \& al., 2004; ${ }^{2}=$ Soejima \& al., 2008; ${ }^{3}=$ Funk \& al., 2012. New identifications of voucher are indicated by a superscript: ${ }^{4}=$ Gutiérrez, 2008b; ${ }^{5}=$ Funk \& al., 2012; ${ }^{6}=$ Gutiérrez, 2015b; ${ }^{7}=$ Gutiérrez \& Katinas, 2015.
INGROUP LIABEAE, PARANEPHELIINAE: Chionopappus benthamii S.F.Blake, Peru: Cajamarca, 14 Jul 1991, Sagástegui 14448 \& al. (F), JN837176 ${ }^{3}$, JN837266 ${ }^{3}$. C. benthamii S.F.Blake, Peru: Ancash, 3 Nov 2007, Leiva 4169 \& al. (US), JN837177 ${ }^{3}$, JN8372673. Erato costaricensis E.Moran \& V.A.Funk, Costa Rica: San José, 18 Aug 1994, Kress (Funk \& Zermoglio) 4814 (US), JN837166³, JN837256 ${ }^{3}$. E. polymnioides DC., Ecuador: Morona-Santiago, 26 Oct 1995, Funk 11455 \& Torracchi (US), JN837164 ${ }^{3}$, JN837254 ${ }^{3}$.E. sodiroi (Hieron.) H.Rob., Ecuador: Chimborazo, 5 Jul 1992, Panero 2930 (US), JN837165³, JN837255³. Microliabum (Austroliabum) candidum (Griseb.) H.Rob., Argentina, Córdoba, La Granja, 27 Jan 2006, Gutiérrez 281 \& Di Paola (BA), MK867789*, MK869766*. M. (Austroliabum) candidum (Griseb.) H.Rob., Argentina, Córdoba, Dique Los Molinos, 9 Apr 2008, Gutiérrez 419 \& al. (BA), MK867788*, -. M. (Austroliabum) eremophilum (Cabrera) H.Rob., Argentina, La Rioja, Dique Los Sauces, 11 Apr 2008, Gutiérrez 500 \& al. (BA), MK867790*, MK869767*. M. (Austroliabum) glanduliferum (Cabrera) H.Rob., Argentina, San Luis, Embalse La Florida, 10 Apr 2008, Gutiérrez 467 \& al. (BA), sample 2 (130), MK867791*, -. Ibidem, Gutiérrez 467 \& al. (BA), sample 1 (132), MK867792*, MK869768*. M. (Microliabum) humile (Cabrera) Cabrera, Argentina, Salta, Santa Victoria, Cuesta de Santa Cruz, 27 Apr 1974, Okada 5953 (US), MK867787*, -. M. (Microliabum) mulgediifolium (Muschl.) H.Rob., Argentina, Salta, Ciudad de Salta, 15 Apr 2008, Gutiérrez 554 \& al. (BA), MK867783*, MK869764*. M. (Microliabum) mulgediifolium (Muschl.) H.Rob., Argentina, Salta, La Caldera, 16 Apr 2008, Gutiérrez 573 et al. (BA), MK869764*, -. M. (Microliabum) polymnioides (R.E.Fr.) H.Rob., Argentina, Jujuy, PN Calilegua, 20 Apr 2008, Gutiérrez 605 \& al. (BA), sample 1, MK867785*, MK869765*. Ibidem, Gutiérrez 605 \& al. (BA), sample 2, MK867786*, -. Paranephelius asperifolius (Muschl.) H.Rob. \& Brettell, Argentina, Salta, to Santa Victoria, 23-25 Apr 2010, Gutiérrez 1010 \& al. (BA), MK867794*, MK869770*. P. asperifolius (Muschl.) H.Rob. \& Brettell, Argentina: Salta, 6 Jan 1998, Funk 12088 \& Rankin (LP, US), JN8371743³, JN837264³. P. ovatus Wedd., Bolivia: La Paz, 27 Apr 1995, Funk 11393 (LPB, US), JN837173³, JN837263 ${ }^{3}$. P. uniflorus Poepp., Peru: Cajamarca, prov. Contumazá, Sagástegui 17557 ( F ), AB355508², AB355581². Philoglossa mimuloides (Hieron.) H.Rob. \& Cuatrec., Ecuador: Azuay, 25 Oct 1995, Funk 11453 \& Torracchi (US), AY504699 ${ }^{1,3}$, AY504781 $1^{1,3}$. P. mimuloides (Hieron.) H.Rob. \& Cuatrec., Peru: La Libertad, 11 May 2004, Sagástegui 17539 et al. (F), JN837161³, JN837251 ${ }^{3}$. P. peruviana DC., Peru: Lima, 14 Sep 1986, Knapp 8311 (US), JN837163 ${ }^{3}$, JN837253 ${ }^{3}$. P. purpureodisca H.Rob., Peru: Trujillo, 6 Oct 1996, Leiva \& Suarez 1889 (US), JN837162 ${ }^{3}$, JN837252 ${ }^{3}$. Pseudonoseris discolor (Muschl.) H.Rob. \& Brettell, Peru: Puno, 28 May 2005, Quipuscoa \& Caceres 3338 (F), JN837171³, JN837261 ${ }^{3}$. P. szyszylowiczii (Hieron.) H.Rob. \& Brettell, Peru: Amazonas, 22 May 1962, Wurdack 467 (US), JN837172 ${ }^{3}$, JN837262 ${ }^{3}$. Stephanbeckia plumosa H.Rob. \& V.A.Funk, Bolivia: Tarija, 17 Apr 2000, Beck 27047 (LPB, US), JN837167³, JN8372573. LIABINAE: Cacosmia harlingii B.Nord., Ecuador: Loja, 21 Feb 1993, Harling \& Stahl 26577 (US), JN8371203, JN8372103. C. hieronymi H.Rob., Ecuador: Azuay, 24 Oct 1997, Lewis 3645 (US), JN837119³, JN837209³. C. rugosa Kunth, Peru: Amazonas, 1 Jul 1997, Sánchez V. \& Dillon 9083 (F, MO), JN8371183, JN8372083. Dillandia perfoliata (S.F.Blake) V.A.Funk \& H.Rob., Ecuador: Carchi, 20 Jul 1992, Panero 3038 \& Clark (US), JN837125³, JN8372153. Ferreyranthus gentryi H.Rob., Peru: Amazonas, 19 Jul 1995, Sánchez V. 8137 (MO, US), JN8371233', JN837213 ${ }^{3}$. F. rugosus (Ferreyra) H.Rob. \& Brettell, Peru: La Libertad, 18 May 2004, Sagástegui 17569 \& al. (F), JN837121³, JN8372113. F. verbascifolius (Kunth) H.Rob. \& Brettell, Peru: Cajamarca, 11 Jan 1990, Dillon 6099 (F), JN837122 ${ }^{3}$, JN837212 ${ }^{3}$. Liabum asclepiadeum Sch.Bip., Colombia: Putumayo, 2 Jan 1963, Bristol 441 (US), JN837134 ${ }^{3}$, JN837224 ${ }^{3}$. L. asclepiadeum ${ }^{7}$ Sch.Bip. (sub L. bourgeaui Hieron. by Funk \& al., 2012), Costa Rica: San Isidro, 17 Jun 2002, Redden 999 (US), JN837128³, JN837218 ${ }^{3}$. L. floribundum Less., Ecuador: Loja, 23 Jul 1996, Lewis 2460 (US), JN837136 ${ }^{3}$, JN837226 ${ }^{3}$. L. grandiflorum (Kunth) Less., Ecuador: Loja, 1 Jun 2003, Croat \& Menke 89956 (MO), JN837133³, JN837223 ${ }^{3}$. L. igniarium (Bonpl.) Less., Ecuador: Pichincha, 17 Jul 1992, Panero \& Clark 3012 (US), JN837132 ${ }^{3}$, JN837222 ${ }^{3}$. L. kingii H.Rob., Ecuador: Pichincha, 27 Oct 1989, Borchsenius 91419 (US), JN837137³, JN8372273. L. solidagineum (Kunth) Less., Peru: Amazonas, 1 Jul 1997, Sánchez V. \& Dillon 9085 (F), JN8371293, JN8372193. Liabum sp. ${ }^{7}$ (probably L. umbellatum (L.) Sch.Bip.), Cuba: Guantánamo, 15 Mar 2009, Ventosa s.n. (HAC), JN837143 ${ }^{3}$, JN837233 ${ }^{3}$. L. umbellatum ${ }^{7}$ (L.) Sch.Bip. (sub L. barahonense Urb. by Funk \& al., 2012), Dominican Republic: Barahona, 21 Jul 1996, Funk 11464 \& Zermoglio (US), JN837139 ${ }^{3}$, JN8372293. L. umbellatum $^{7}$ (L.) Sch.Bip. (sub L. poiteaui (Cass.) Urb. by Funk \& al., 2012), Dominican Republic: Barahona, 26 Jun 2006, Pruski 4061 \& Ortiz (US), JN837138 ${ }^{3}$, JN837228 ${ }^{3}$. L. umbellatum ${ }^{7}$ (L.) Sch.Bip. (sub L. selleanum Urb. by Funk et al., 2012), Dominican Republic:

Elías Piña, 24 Jun 2003, Acevedo 13366 (US), JN837142 ${ }^{3}$, JN837232 ${ }^{3}$. L. umbellatum $^{7}$ (L.) Sch.Bip. (sub L. subacaule Rydb. by Funk \& al., 2012), Dominican Republic: Santiago, 1 Jun 2004, Acevedo 14178 (US), JN8371413, JN8372313. L. umbellatum (L.) Sch.Bip., Jamaica: St. Andrew, 9 Jul 1996, Funk 11462 \& Zermoglio (US), JN837140³, JN8372303. L. vargasii H.Rob., Peru: Cuzco, 15 Sep 2002, Galiano \& al. 4418 (MO), JN8371353², JN8372253. L. wurdackii Ferreyra, Peru: Amazonas, 7 Jul 1997, Sánchez V. \& Dillon 9094 (F, MO), JN837130³, JN837220³. Oligactis sessiliflora (Kunth) DC., Colombia: Boyaca, 21 Aug 1997, Funk 12031 \& Mendoza (US), JN837124 ${ }^{3}$, JN837214 ${ }^{3}$. O. sessiliflora ${ }^{4}$ (Kunth) DC. (sub L. volubilis (Kunth) Cass. by Funk \& al., 2004), Colombia: Cundinamarca, San Antonio de Tena, 26 Aug 1997, Funk 12042 \& Méndez (MO, US), AY504698 ${ }^{1,3}$, AY504780 ${ }^{1,3}$. Sampera coriacea (Hieron.) V.A.Funk \& H.Rob., Ecuador: Loja, 2 Jun 1984, Ollgaard 74615 (US), JN837127³, JN8372173. S. cuatrecasasii (M.O.Dillon \& Sagást.) V.A.Funk \& H.Rob., Peru: Piura, 20 Oct 2001, Sagástegui 16823 \& al. (F), JN837126 ${ }^{3}$, JN837216 ${ }^{3}$. MUNNOZIINAE: Chrysactinium acaule (Kunth) Wedd., Peru: Amazonas, 12 Nov 2000, Sánchez V. 10327 \& al. (F), JN837158³, JN8372483. C. hieracioides (Kunth) H.Rob. \& Brettell, Peru: Cajamarca, 1 Apr 1987, Becker 1674 \& al. (US), JN837160³, JN8372503. C. hieracioides (Kunth) H.Rob. \& Brettell, Peru: Cajamarca, 1 Mar 1988, Panero 1130 (US), JN837159³, JN837249³. Munnozia campii H.Rob., Ecuador: Morona-Santiago, 26 Oct 1995, Funk 11456 \& Torracchi (US), JN837152³, JN837242³. M. foliosa Rusby, Bolivia: La Paz, 29 Jun 1988, Lewis 88161 (US), JN837144³, JN8372343 ${ }^{3}$ M. fosbergii H.Rob., Colombia: Boyaca, 21 Aug 1997, Funk 12039 \& Mendoza (US), JN837146³, JN837236 ${ }^{3}$. M. gigantea (Rusby) Rusby, Peru: Madre de Dios, 27 Nov 1985, Dillon 9200 (F), AY5046971,3, AY5047391,3. M. hastifolia (Poepp.) H.Rob. \& Brettell, Argentina, Jujuy, PN Calilegua, 20-IV-2008, Gutiérrez \& al. 608 (BA), MK867793*, MK869769*. M. hastifolia (Poepp.) H.Rob. \& Brettell, Colombia: Cundinamarca, 27 Aug 1997, Funk 12050 \& Mendez (US), JN837150³, JN8372403. M. hastifolia ${ }^{6}$ (Poepp.) H.Rob. \& Brettell (sub M. maronii (André) H.Rob. by Funk \& al., 2012), Argentina: Salta, 4 Jan 1998, Funk 12087 \& Rankin (US), JN8371513, JN837241³. M. jussieui (Cass.) H.Rob. \& Brettell, Peru: Piura, 19 Oct 2001, Sagástegui 16768 \& al. (F, HAO), JN837147³, JN837237³. M. lyrata (A. Gray) H.Rob. \& Brettell, Peru: Cajamarca, 10 Mar 1988, Panero 1201 (US), JN837157³, JN837247³. M. nivea (Hieron.) H.Rob. \& Brettell, Ecuador: Tungurahua, 3 Mar 1989, Buitron 464 (US), JN837156³, JN837246³. M. sagasteguii H.Rob., Peru: Cajamarca, 12 May 2004, Sagástegui 17562 \& al. (F), JN837148³, JN8372383. M. senecionidis Benth., Colombia: Boyaca, 21 Aug 1997, Funk 12028 \& Mendoza (LP, US), JN8371493, JN837239 ${ }^{3}$. M. wilburii H.Rob., Costa Rica: Alajuela, 25 Feb 1992, Almeda \& Daniel 7068, (US), JN8371543, JN8372443. M. wilburii H.Rob., Costa Rica: Puntarenas, 14 Aug 1994, Kress (Funk \& Zermoglio) 4802 (US), JN837153 ${ }^{3}$, JN837243 ${ }^{3}$. SINCLAIRIINAE: Liabellum angustissimum (A.Gray) Rydb., Mexico: Jalisco, 23 Sep 2005, Funk 12605 \& al. (US), JN837189³, JN837279³. L. cervinum (B.L.Rob.) Rydb., Mexico: Nayarit, 30 Aug 1957, McVaugh 16583 (US), JN837188³, JN8372783. L. palmeri (A.Gray) Rydb., Mexico: Jalisco, 23 Sep 2005, Funk 12603 \& al. (US), JN837190³, JN837280³. Megaliabum andrieuxii (DC.) Rydb., Mexico: Chiapas, 27 Sep 2005, Funk 12617 \& Montero-Castro (MEXU, US), JN8371913, JN837281³. M. pringlei (B.L.Rob. \& Greenm.) Rydb., Mexico: Jalisco, 23 Sep 2005, Funk 12606 \& al. (MEXU, US), JN837192 ${ }^{3}$, JN837282 ${ }^{3}$. Sinclairia caducifolia (B.L.Rob. \& Bartlett) Rydb., Mexico: Chiapas, 27 Sep 2005, Funk 12614 \& Montero-Castro (US), JN837179³, JN8372693. S. deamii (B.L.Rob. \& Bartlett) Rydb., Mexico: Chiapas, 27 Sep 2005, Funk 12616 \& Montero-Castro (US), JN837180³, JN837270 ${ }^{3}$. S. discolor Hook. \& Arn., Mexico: Chiapas, 29 Sep 2005, Funk 12624 \& Montero-Castro (US), JN8371813, JN8372713. S. glabra (Hemsl.) Rydb., Mexico: Chiapas, 27 Sep 2005, Funk 12618 \& Montero-Castro (US), JN837182 ${ }^{3}$, JN837272 ${ }^{3}$. S. liebmannii (Klatt) Sch.Bip. ex Rydb., Mexico: Colima, 10 Dec 1959, McVaugh \& Koelz 1642 (MICH, US), JN837185³, JN837275³. S. moorei (H.Rob. \& Brettell) H.Rob. \& Brettell, Mexico: Jalisco, 23 Sep 2005, Funk 12607 \& al. (US), JN837183³, JN837273 ${ }^{3}$. S. polyantha (Klatt) Rydb., Costa Rica: Alajuela, 30 Apr 1987, Funk 10106 \& al. (US), JN8371783, JN837268³. S. similis (McVaugh) H.Rob. \& Brettell, Mexico: Jalisco, 24 Sep 2005, Funk 12609 \& al. (US), JN837187³, JN837277³. S. sublobata (B.L.Rob.) Rydb., El Salvador: Usulatán, 29 Jan 1999, Williams 15 (US), JN837184³, JN837274 ${ }^{3}$. S. vagans (S.F.Blake) H.Rob. \& Brettell, Guatemala: Chimaltenango, 27 Nov 1993, Castillo 2073 \& al. (F), JN837186³, JN837276³. Sinclairiopsis ismaelis ${ }^{5}$ (Panero \& Villaseñor) V.A. Funk (sub Sinclairia ismaelis Panero \& Villaseñor by Funk in Funk \& al., 2012), Mexico: Oaxaca, 30 Sep 1993, Panero 3572 (MEXU, US), JN837193³, JN837283 ${ }^{3}$. S. klattii (B.L.Rob. \& Greenm.) Rydb., Mexico: Oaxaca, 30 Oct 1974, Breedlove 39185 (MO, US), JN837194³, JN8372843. — OUTGROUPS: MOQUINIEAE: Moquinia racemosa (Spreng.) DC., Brazil: Bahia, 9 Nov 2007, Roque 1691 (ALCB), JN837117³, JN837207³. Pseudostifftia kingii H.Rob., Brazil: Bahia, 1 Feb 2008, Roque 1754 (ALCB), JN837116³, JN837206³. VERNONIEAE: Distephanus barus (Humbert) H.Rob., Madagascar: Antananarivo, 20 Oct 2009, van Ee 1015 \& al. (US), JN837113³, JN837203³.

Appendix 2. Voucher information for specimens used in the PCoA including species, country, province, department, locality, date, collector with collector number, herbarium, and order number/s. In some cases there were several complete individuals of plants mounted on the same sheet, in other cases one complete or incomplete individual was on a sheet but there were duplicates, and in the majority cases one incomplete individual was on a sheet kept at a single herbarium.

Microliabum (Austroliabum) candidum (Griseb.) H.Rob., Argentina, Catamarca, Andalgalá department, La Playa, 12 Feb 1917, Jörgensen 1673 (BA, isotype) (1); Córdoba, Calamuchita department, Sierra Chica, valle de Los Reartes, without date, Castellanos s.n. (BA 24741) (2); Valle Los Reartes, 1917--1919, Castellanos s.n. (SI 9440) (3); Embalse Río Tercero, 12 Jan 1940, Burkart 10496 (SI) (4); Embalse del Río Tercero, 20 Feb/5 Mar 1964, Roig 4978 (SI) (5); Colón department, Sierra Chica, entre el dique San Roque y Casa Bamba, 1 Jun 1910, Kutz s.n. (SI 9442) (6); entre La Granja y Agua de Oro, 27 Jan 2006, D. Gutiérrez \& Di Paola 281, 282 (BA) (7 and 8, respectively); Agua de Oro, 9 Apr 2008, D. Gutiérrez et al. 404 (BA) (9); alrededores de Villa Animí, 14 Mar 2009, D. Gutiérrez 1001 (BA) (10); alrededores de El Manzano, 15 Mar 2009, D. Gutiérrez 1009 (BA) (11); El Pueblito, 15 Mar 2009, D. Gutiérrez 1016 (BA) (12); Punilla department, Uritorco, 27 Jan 1922, Castellanos s.n. (BA 24740) (13); camino a San Marcos Sierra, 9 Mar 1941, Nicora 17662 (SI) (14); San Javier department, Paso de la Peña, 1927, Castellanos s.n. (BA 11856) (15); Santa María department, Embalse Los Molinos, 2 Apr 1973, Cabrera et al. 23808 (LP) (16); Dique Los Molinos, 9 Apr 2008, D. Gutiérrez et al. 419 (BA) (17); San Luis, Coronel Pringles department, Pampa del Alto Grande, Feb 1931, Gez s.n. (BA 31/229) (18); General Pedernera department, El Morro, 1913, Pastore 29 (SI) (19); Junín department, Merlo, 29 Jan 2006, D. Gutiérrez \& Di Paola 361 (BA) (20). M. (Austroliabum) eremophilum (Cabrera) H.Rob., Argentina, La Rioja, Capital department, Quebrada del Sauce, 14 Apr 1975, Okada 6110 (SI) (21); Quebrada de Los Sauces, Dique de Los Sauces, 11 Apr 2008, D. Gutiérrez et al. 500 (BA) (22); Sanagasta department, dique Los Sauces, 2 Mar 1941, Burkart 12624 (SI) (23); Salta, Cafayate department, Sierra del Cajón, 15 Jan 1914, Rodríguez 1294 (BA, isolectotype) (24); Tucumán, Tafí del Valle department, a Tafí del Valle, 21 Mar 1987, Xifreda \& Maldonado 655 (SI) (25). M. (Austroliabum) glanduliferum (Cabrera) H.Rob., Argentina, Córdoba, Pocho department, Sierra de Mogigasta, 19 Feb 1922, Castellanos s.n. (BA 24738) (26); Sierra de Pocho, Los Túneles, 6 Dec 1958, Burkart 20859 (SI) (27); San Luis, Coronel Pringles department, Embalse La Florida, 10 Apr 2008, D. Gutiérrez et al. 467 (BA) (28); idem, 29 Nov 2016, D. Gutiérrez et al. 1151 (BA) (29); Juan Martín de Pueyrredón department, Estancia Grande, 16 Jan 1911, Pastore 124 (SI, holotype) (30); Inti Huasi, Mar 1937, Pastore 2041 (SI, two individuals) (31 and 32); without department, Sierras de San Luis, Cuesta de los Picazos, 21 Feb 1925, Castellanos s.n. (BA 25/1111) (33). M. (Microliabum) humile (Cabrera) Cabrera, Argentina, Jujuy, Doctor Manuel Belgrano department, entre León y Nevado de Chañi, La Peña, Mar 1963, Fabris et al. 4169 (LP, 11 individuals) ( $\mathbf{3 4}$ to 44). M. (Microliabum) mulgediifolium (Muschl.) H.Rob., Argentina, Salta, Capital department, Salta, ciudad de Salta, 15 Apr 2008, D. Gutiérrez et al. 554 (BA, two individuals) (45 and 46); La Caldera department, La Caldera, 16 Apr 2008, D. Gutiérrez et al. 573 (BA) (47); entre Vaqueros y La Calderilla, 23--25 Apr 2010, D. Gutiérrez et al. 1017 (BA) (48); Bolivia, Tarija department, Cercado prov., de Tarija a Iscayachi, 20 Mar 1982, Kiesling et al. 3817 (SI, three individuals) (49 to 51); Eustaquio Méndez prov., Sama, 7 May 1988, Ehrich 544 (SI, two individuals) (52 and 53). M. (Microliabum) polymnioides (R.E.Fr.) H.Rob., Argentina, Jujuy, Capital department, antes de León, 17 Apr 2008, D. Gutiérrez et al. 580 (BA) (54); Salta, Anta department, Parque Nacional El Rey, Jun 1934, Ragonese 153 (BA) (55); Parque Nacional El Rey, 5 Jul 1979, Brown et al. 839 (SI) (56); Chicoana department, Quebrada de Escoipe, 27 Mar 1979, Cabrera et al. 30697 (SI) (57); Los Laureles, 14 Apr 2008, D. Gutiérrez et al. 566 (BA) (58); General José de San Martín department, Tartagal, 14 Jun 1934, Meyer 930 (BA) (59); Campamento Vespucio, May 1971, González Montaner 17 (SI) (60); Ledesma department, camino a Valle Grande, 9 Nov 1974, Krapovickas et al. 26652 (SI) (61); Calilegua, Sep 1976, Cabrera et al. 27924 (SI) (62); camino a Valle Grande, 13 Jun 1983, Cabrera 33898 (SI) (63); arroyo Yuto, 14 Jun 1983, Cabrera et al. 33935 (SI) (64); Parque Nacional Calilegua, 28 Feb 1986, Iudica \& Ramadori 288 (SI) (65); Tucumán, Faimallá department, Quebrada de Lules, 23 Sep 1923, Venturi 2558 (BA, SI) ( 66 and 67, respectively); J.B. Alberti department, cerca de Balcosna, 12 Apr 2008, D. Gutiérrez et al. 540 (BA) (68); Tafí department, Quebrada Lules, 29 Sep 1920, Venturi 942 (BA, SI) ( 69 and 70, respectively); Bolivia, Chuquisaca-Santa Cruz, Cordillera prov., finca Guacareta, 22 Sep 1982, Cabrera \& M. Gutiérrez 33681 (SI) (71); Tarija, Aniceto Arce prov., a 56 km de Bermejo, 18 Oct 1980, Zuloaga et al. 1050 (SI) (72).

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