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ORIGINAL ARTICLE

New circumscription of the genus *Gamochaeta* (Asteraceae, Gnaphalieae) inferred from nuclear and plastid DNA sequences

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Abstract *Gamochaeta* (tribe Gnaphalieae, Asteraceae) is composed of ca. 60 species primarily distributed in tropical and subtropical America. Within the tribe Gnaphalieae, the genus is characterized by capitula arranged in spikes or head-like clusters, few hermaphroditic central florets, truncate style branches with apical sweeping trichomes, pappus bristles connate at the base into a ring falling as a unit, and achenes with globose twin trichomes. Previous molecular phylogenetic studies have suggested the paraphyly of the genus, but have not provided a basis for redefining generic limits due to incomplete taxon sampling. To address this problem, DNA sequences from the plastid (*trn*L-F) and nuclear (ETS and ITS) genomes were analyzed from a broad taxon sample representing the full range of morphological variation known in the genus. Our results affirm that *Gamochaeta* is paraphyletic as presently circumscribed. Two clades can be recognized: one clade that includes the majority of the species currently assigned to *Gamochaeta* and a second clade that includes *Gamochaetopsis*, *Stuckertiella* and seven species of *Gamochaeta.* We present here a new circumscription of *Gamochaeta*, including two new combinations, *Gamochaeta alpina* and *Gamochaeta peregrina,* and the resurrection of *Gamochaeta capitata*. Our results also show *Omalotheca supina*, *O. norvegica* and *O. sylvatica*, which were placed by some authors in *Gamochaeta* or in *Gnaphalium*, form a monophyletic group distantly related to both genera.

Keywords *Gamochaetopsis* · *Omalotheca* · *Stuckertiella* · ETS · ITS · *trn*L-F

Introduction

Gamochaeta (tribe Gnaphalieae, Asteraceae) is represented by ca. 60 species characterized by their capitula arranged in spikes or head-like clusters, pistillate florets

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outnumbering the hermaphroditic disk florets, truncate style branches with apical sweeping trichomes, pappus bristles connate at the base into a ring that falls as a unit, and achenes with globose twin trichomes (e.g., Cabrera 1961; Anderberg 1991; Bayer et al. 2007; Ward et al. 2009). The greatest diversity is in South America, with ca. 45 species (Cabrera 1963, 1971, 1974, 1978; Aristeguieta 1964; Marticorena and Quezada 1985; Dillon and Sagástegui-Alva 1991a, b; Freire 1998; Deble and Marchiori 2007; Freire and Iharlegui 2008, 2014; Freire et al. 2011; Hind 2011). A few species are native to Central America, e.g., *G. irazuensis*, *G. standleyi* (Pruski 2011), and North America, e.g., *G. argyrinea* and *G. ustulata* (Nesom 1990a, 2004, 2006), and a few species are adventive or naturalized in Asia, Australia, Hawaii, New Zealand, Southern Africa, and Europe, e.g., *Gamochaeta calviceps* and *G. pensylvanica* (Drury 1971; Hilliard 1983; Chen and Bayer 2011; Alford 2012).

Gamochaeta was first proposed as a genus by Weddell (1855) to accommodate five species of *Gnaphalium* L. diagnosed by the presence of pappus bristles connate at the base into a ring, hence the name of the genus (from the Greek *gamos* "connate" and *xaite* "hairs"). In the following years, many authors considered *Gamochaeta* as a section of *Gnaphalium* (Bentham and Hooker 1873; Hoffmann 1890; Wagenitz 1965; Drury 1970, 1971; Merxmüller et al. 1977; Hilliard and Burtt 1981; Webb 1988), whereas others recognized it as a distinct genus (Cabrera 1961; Nesom 1990a, 2004, 2006; Anderberg, 1991; Dillon and Sagástegui-Alva 1991a, b; Freire and Iharlegui 1997, 2014; Bayer et al. 2007; Deble and Marchiori 2007; Chen and Bayer 2011; Hind 2011).

In the first morphological cladistic study of generic relationships in the Gnaphalieae, Anderberg (1991) included a cladogram in which *Gamochaeta* was sister to the "*Lucilia* group" (e.g., *Belloa* J.Rémy, *Chevreulia* Cass., *Facelis* Cass.) and made numerous combinations in *Gamochaeta*. Anderberg's work demonstrated the heterogeneity of *Gnaphalium* as it was circumscribed in many floras (e.g., Rémy 1849; Aristeguieta 1964), as well as by Merxmüller et al. (1977). Anderberg (1991) also recognized many of the segregate genera from *Gnaphalium*, i.e., *Anaphaloides* (Benth.) Kirp., *Euchiton* Cass., *Gamochaeta*, *Gnaphaliothamnus* Kirp., *Homognaphalium* Kirp., and *Pseudognaphalium* Kirp., but still left a rather heterogeneous *Gnaphalium* including *Omalotheca* Cass. and *Synchaeta* Kirp. Different authors have variously recognized the genus *Omalotheca* (including *Synchaeta*) or placed *Omalotheca* species in *Gamochaeta* or *Gnaphalium*. Nesom (1990b) excluded *Omalotheca* from *Gnaphalium* and mentioned that *Omalotheca* was superficially similar to *Gamochaeta* in its spiciform capitulescences. In their treatment for Flora of China, Chen and Bayer (2011) placed some species of *Omalotheca* in *Gamochaeta* (*O. nanchuanensis* (Y.Ling & Y.Q.Tseng) Holub, *O. sylvatica* (L.) Sch.Bip. & F.W.Schultz, *O. norvegica* (Gunnerus) Sch.Bip. & F.W.Schultz) but placed the type species of the genus (*O. supina* (L.) DC.) in *Gnaphalium.* However, Blöch et al. (2010) considered *Omalotheca hoppeana* (W.D.J.Koch) Sch.Bip. & F.W.Schultz, *O. norvegica*, *O. supina* and *O. sylvatica* as *Gnaphalium* species.

More recently, phylogenetic analyses utilizing molecular data have been used to address relationships within the tribe Gnaphalieae. Based on the plastid marker *trn*L-F, Blöch et al. (2010) presented a molecular phylogeny of the Asian-European *Leontopodium* R.Br. ex Cass. and found a relationship between *Gamochaeta* (*G. pensylvanica*), *Antennaria* Gaertn., *Ewartia* Beauverd, *Leucogenes* Beauverd and *Leontopodium.* Based on both nuclear (ETS, ITS) and plastid markers (*rpL*32-*trn*L intergeneric spacer + *trn*L intron + *trn*L-F), Galbany-Casals et al. (2010) recognized the "FLAG clade" including *Filago* Loefl., *Leontopodium*, *Antennaria* and *Gamochaeta*. In a study focused on ancient polyploidy in Gnaphalieae, Smissen et al. (2011) also recovered *Gamochaeta* [*G. coarctata, G. subfalcata*] in the "FLAG clade." More recently, Freire et al. (2015) using DNA sequences from plastid (*rpl*32-*trn*L, *trn*L-F) and nuclear (ITS and ETS) markers, together with morphological characters, presented a cladogram of the South American "*Lucilia* group s.l." in which *Gamochaeta* (three species) formed a well-supported clade together with *Gamochaetopsis* and *Stuckertiella*, hence providing initial evidence that *Gamochaeta*, as currently circumscribed, might not be monophyletic.

The aim of this study is to extend the sampling of *Gamochaeta* to provide a better supported and more reliable phylogenetic hypothesis for generic realignments using one plastid (*trn*L-F) and two nuclear DNA regions (ETS and ITS).

Materials and methods

Ingroup and outgroup

This study includes 33 species of *Gamochaeta* representing ca. 60 % of the species of the genus, all major morphological forms (concolorous and discolorous leaves, spicate and head-like arrangement of capitula) and almost the entire distributional and elevational range of the genus. In order to test the monophyly of *Gamochaeta*, we included 22 species of 13 other genera of Gnaphalieae, ten of them belonging to the FLAG clade and two outside of the FLAG clade. The choice of these genera and species was based on

Table 1 Distinguishing characters of *Gamochaeta*, *Gamochaetopsis*, and *Stuckertiella* (exclusive character in boldface)

	Gamochaeta	*Gamochaetopsis*	*Stuckertiella*
Distribution	North, Central and South America	Southern Andes of Chile and Argentina	Central Andes of Peru, Bolivia and NW Argentina
Habit	Ascendent or erect multistemmed herbs (caespitose)	Caespitose multistemmed herbs	Ascendent multistemmed herbs
Capitula arrangement	Spikes (head-like clusters or solitary)	Head-like clusters	Head-like clusters
No. of ray florets	25–119 (12–20)	9–17	Many
Central florets	Hermaphrodite	Hermaphrodite	**Male**
No. corolla lobes of central florets	5(4)	5	4
Achenial twin hairs	Globose (clavate)	Clavate	Globose

results of previous investigations: (1) Based on Freire et al. (2015), representatives of the sister group of the *Gamochaeta-Stuckertiella* clade such as *Belloa chilensis* (Hook. & Arn.) J.Rémy, *Berroa gnaphalioides* (Less.) Beauverd, *Facelis plumosa* (Wedd.) Sch.Bip., *Jalcophila boliviensis* Anderb. & S.E.Freire, *Jalcophila ecuadoriensis* M.O.Dillon & Sagást. and *Lucilia acutifolia* (Poir.) Cass. were included; (2) based on Galbany-Casals et al. (2010), Smissen et al. (2011), and Freire et al. (2015), other related Gnaphalieae species such as *Antennaria chilensis* J. Rémy, *Filago fuscescens* Pomel, *F. lutescens* Jord., *F. pyramidata* L., *Gnaphalium austroafricanum* Hilliard, *G. declinatum* L.f., *G. uliginosum* L., *Leontopodium alpinum* Cass., *L. microphylum* Hayata, *Omalotheca norvegica, O. supina*, and *O. sylvatica* were included. Trees were rooted with *Achyrocline tomentosa* Rusby, selected from Freire et al. (2015). DNA samples were obtained from silica-preserved leaves and from herbarium specimens. Vouchers are deposited in CONC, LP, LPB, MNCS, MO, SI, SZU, USMS, and W. When no plant material was available, sequences were obtained from GenBank ("Appendix").

Morphological characters and distribution of the species of *Gamochaeta* in Tables 1, 2 and 3 are from the literature and own observations.

DNA extraction, amplification, sequencing, sequence alignment and editing

DNA extraction used the modified CTAB protocol by Doyle and Dickson (1987), adapted for small amounts of plant material. When material preserved in silica gel was not available, DNA was extracted from herbarium specimens using the DNeasy Plant Mini Kit (QIAGEN Inc., Hilden, Germany).

The plastid intergenic spacer *trn*L-F (primers C and F; Taberlet et al. 1991) and nuclear regions ITS (primers ITS4 and ITS5; White et al. 1990) and ETS (primers ETS1 and *18S*-ETS; Bayer et al. 2002 and Baldwin and Markos 1998, respectively) were selected for this study. Reactions were performed in a final volume of 25 µl or rarely in 50 µl. Each reaction contained 50–100 ng of DNA, 1.5 units of Taq polymerase (Invitrogen Life Technologies, São Paulo, Brazil or TaKaRa ExTaq, Otsu, Shiga, Japan), 1 × PCR Buffer, 5 mM $MgCl_2$, 0.2 pmol of each primer and 0.025 mM of each dNTP. In species for which these protocols were unsuccessful, BSA 0.4 % and DMSO 1.6 % or a mixture of trehalose, BSA and polysorbate-20 (Samarakoon et al. 2013) were included to increase the yield of PCR. The annealing temperatures ranged between 48 and 52 °C for the plastid markers and 56–60 °C for the nuclear markers. Final extension at 72 °C for 6 min terminated the reactions. The quality of the PCR products was estimated by electrophoresis and visualized with ethidium bromide under UV light. A negative control with no template was included for each series of amplifications to test for contamination. PCR products were sequenced by Macrogen Inc. (Korea) or Eurofins MWG Operon (Louisville, KY).

Sequences were assembled and edited using the program ChromasPro version 1.34 (Technelysium Pty, Ltd, Tewantin, Australia). Matrices were edited using the program BioEdit (Hall 1999), and sequences were aligned using the application ClustalW, using multiple alignment with the option run ClustalW. Data matrices are deposited at TreeBase (TB2: S19294).

Phylogenetic analyses

Analyses of nuclear and plastid sequences were performed separately and combined. Parsimony analyses were conducted using the program TNT version 1.1 (Goloboff et al. 2008), with all characters equally weighted and considered unordered. Gaps were scored as missing data. In all analyses, parsimony-uninformative characters were omitted. Heuristic searches were performed using 1000 random addition replicates and tree bisection–reconnection (TBR) branch swapping, saving ten trees per replicate. Branch support was assessed with 10,000 parsimony jackknifing replicates (JK; Farris et al. 1996), using ten series of

Table 2 Key morphological characters of the species of **Gamochaeta**, **Gamochaetopsis** and **Stuckertiella** (species used in the analysis in boldface)

Genera ***Gamochaeta***	Plant height (cm)	Leaf blade shape (cauline leaves)	Leaf surfaces	Capitula arrangement	Inflorescence spikes	Inner phyllary apex shape	No. of corolla lobes of central florets	No. of marginal florets	Achenial twin hairs
G. affinis Cabrera	5–12	Linear-obovate	Concolorous	Head-like clusters	–	Acute-apiculate	5	ca. 30	Globose
G. aliena (Hook. & Arn.) Cabrera	16–17	Linear-oblanceolate	Concolorous	Spikes	Continuous (interrupted basally)	Acute	5	ca. 18	Globose
G. ambatensis Ariza	ca. 25	Oblanceolate	Discolorous	Spikes	Continuous (interrupted basally)	Obtuse	5	ca.50	Globose
G. americana (Mill.) Wedd.	15–35	Spathulate	Discolorous	Spikes	Continuous (interrupted basally)	Short acuminate	5	ca. 90	Globose
G. andina (Phil.) Cabrera	3–6	Narrowly linear	Concolorous	Head-like clusters	–	Acute	5	ca. 12	Globose
G. antarctica (Hook. f.) Cabrera	2–4	Obovate	Concolorous	Head-like clusters	–	Acute	5	Many	Globose
G. antillana (Urb.) Anderb.	15–25	Linear- lanceolate (basal)	Concolorous	Spikes	Continuous (interrupted basally)	Subobtuse	5	ca. 77	Globose
G. argentina Cabrera	10–30	Spathulate	Concolorous	Spikes	Interrupted	Acuminate	5	ca. 70	Globose
G. argyrinea G.L.Nesom	12–40	Oblanceolate	Discolorous	Spikes	Continuous (interrupted basally)	Truncate-rounded	5	ca. 118	Globose
G. axillaris (J.Rémy) Cabrera	ca. 15	Oblanceolate	Concolorous	Spikes	Interrupted	Obtuse	5	52–63	Globose
G. badillana (Ariteg.) Anderb.	ca. 4	Linear-lanceolate	Concolorous	Head-like clusters	–	Acute	5	Many	–
G. beckii Urtubey & S.E.Freire	ca. 20	Oblanceolate	Slightly discolorous	Head-like clusters arranged in leafy spikes	–	Short acuminate	5	36–38	Globose
G. berteroana (DC.) Cabrera	ca. 15	Oblanceolate	Concolorous	Spikes	Continuous (interrupted basally)	Acute	5	Many	Globose
G. cabrerae Anderb.	ca. 6	Oblanceolate	Discolorous	Spikes	Continuous	Acute	5	42–45	Globose
G. calviceps (Fernald) Cabrera	20–40	Linear-oblanceolate	Concolorous	Spikes	Continuous (interrupted basally)	Obtuse to rounded	5	ca. 50	Globose
G. camaquaensis Deble	30–60	Spathulate	Concolorous	Spikes	Continuous (interrupted basally)	Acute	5	70–100	Globose

Table 2 continued

Genera ***Gamochaeta***	Plant height (cm)	Leaf blade shape (cauline leaves)	Leaf surfaces	Capitula arrangement	Inflorescence spikes	Inner phyllary apex shape	No. of corolla lobes of central florets	No. of marginal florets	Achenial twin hairs
G. chamissonis (DC.) Cabrera	15–50	Linear-oblanceolate	Concolorous	Spikes	Interrupted	Obtuse	5	27–50	Globose
G. chionesthes G.L.Nesom	Up to 45	Oblanceolate	Discolorous	Spikes	Continuous (interrupted basally)	Acute to acute-acuminate	5	86–119	Globose
G. coarctata (Willd.) Kerguélen	20–50	Spathulate	Discolorous	Spikes	Continuous (interrupted basally)	Obtuse to rounded	5	80–85	Globose
G. depilata (Phil.) Cabrera	5–20	Obovate	Concolorous	Head-like clusters	–	Subacute	5	12–20	Globose
G. deserticola Cabrera	3–10	Oblanceolate	Concolorous	Spikes	Continuous (interrupted basally)	Subacute	5	ca. 25	Globose
G. diffusa Deble & Marchiori	15–30	Oblanceolate	Concolorous to slightly discolorous	Spikes	Interrupted	Obtuse-apiculate	5	40–60	Globose
G. erecta Deble	20–50	Oblanceolate to spathulate	Concolorous to slightly discolorous	Spikes	Interrupted	Acute	5	ca. 70	Globose
G. erythractis (Wedd.) Cabrera	1–6 (10)	Oblanceolate	Concolorous	Spikes	Continuous	Obtuse to subacute	5	ca. 30	Globose
G. falcata (Lam.) Cabrera	10–50	Linear-oblanceolate	Concolorous	Spikes	Continuous	Acute	5	ca. 70	Globose
G. *filaginea* (DC.) Cabrera	15–40	Oblanceolate	Concolorous	Spikes	Continuous (interrupted basally)	Acute	5	ca. 78	Globose
G. foliosa (Phil.) Anderb.	ca. 7	Broadly obovate	Slightly discolorous	Head-like clusters	–	Unknown	5	ca. 49	Oblong
G. *girardiana* Deble & A.S.Olivera	15–45	Oblanceolate	Concolorous	Head-like clusters arranged in leafy spikes	–	Acute	5	40–50	Globose
G. grazielae (Rizzini) Deble	20–50	Oblanceolate	Concolorous	Spikes	Interrupted	Long-acuminate	5	ca. 101	Globose
G. hiemalis Cabrera	30–40	Linear-oblanceolate	Concolorous	Spikes	Continuous	Obtuse	5	30–50	Clavate
G. humilis Wedd.	ca. 10	Oblanceolate	Discolorous	Spikes	Interrupted	Acute	5	35–40	Globose
G. irazuensis G.L.Nesom	ca. 30	Elliptic-oblanceolate	Discolorous	Spikes	Continuous	Acute	5	65–73	Globose

Table 2 continued

Genera ***Gamochaeta***	Plant height (cm)	Leaf blade shape (cauline leaves)	Leaf surfaces	Capitula arrangement	Inflorescence spikes	Inner phyllary apex shape	No. of corolla lobes of central florets	No. of marginal florets	Achenial twin hairs
G. longipedicellata Cabrera	1–4	Oblong-spathulate	Concolorous	Solitary in the axils of the upper leaves	–	Acute	5	ca. 30	Globose
G. lulioana S.E.Freire & Iharl.	ca. 1	Oblong-obovate	Concolorous	Solitary	–	Acute	4	ca. 27	Globose
G. meridensis V.M.Badillo	1–4	Oblanceolate	Concolorous	Head-like clusters	–	Acute	5	Many	Globose
G. monticola (Phil. ex Reiche) Cabrera	2–4	Oblanceolate	Concolorous	Head-like clusters	–	Acute	5	ca. 30	Globose
G. neuquensis Cabrera	5–12	Oblanceolate	Concolorous	Head-like clusters	–	Acute	5	ca.12	Clavate
G. *nigrevestis* Deble & Marchiori	10–20	Oblanceolate	Concolorous	Spikes	Interrupted	Acute	5	50–70	Globose
G. nivalis Cabrera	4–7	Linear-obovate	Concolorous	Head-like clusters	–	Subacute	5	13–15	Globose
G. oligantha (Phil.) L.E.Navas	2–5	Oblanceolate	Concolorous	Head-like clusters	–	Acute	5	Many	Globose
G. paramora (S.F.Blake) Anderb.	7–15	Oblanceolate	Concolorous	Head-like clusters	–	Subacute	5	More than 40	–
G. pensylvanica (Willd.) Cabrera	20–50	Spathulate	Concolorous	Spikes	Continuous (interrupted basally)	Obtuse or subacute	5	70-80	Globose
G. procumbens (Phil.) Cabrera	10–25	Linear-obovate	Concolorous	Head-like clusters	–	Acute or subacute	5	ca. 20	Globose
G. purpurea (L.) Cabrera	20–40	Oblanceolate	Slightly discolorous	Spikes	Continuous (interrupted basally)	Acute	5	70–80	Globose
G. rizzini Cabrera	ca. 35	Oblanceolate	Discolorous	Spikes	Interrupted	Acuminate	5	Many	Globose
G. serpyllifolia Wedd.	10–15	Widely obovate or suborbicular	Concolorous	Head-like clusters	–	Acute	5	ca. 20	Globose
G. simplicicaulis (Willd. ex Spreng.) Cabrera	40–60	Oblanceolate	Discolorous	Spikes	Interrupted	Acuminate	5	ca. 90	Globose
G. sphacelata (Kunth) Cabrera	15–20	Narrowly linear	Concolorous	Spikes	Continuous (interrupted basally)	Acute	5	ca. 30	Globose
G. spiciformis (Sch.Bip.) Cabrera	7–30	Widely obovate	Discolorous	Head-like clusters	–	Obtuse	5	ca. 50	Globose
G. stachydifolia (Lam.) Cabrera	10–40	Spathulate	Concolorous	Spikes	Continuous	Acute	5	ca. 50	Globose

Table 2 continued

Genera ***Gamochaeta***	Plant height (cm)	Leaf blade shape (cauline leaves)	Leaf surfaces	Capitula arrangement	Inflorescence spikes	Inner phyllary apex shape	No. of corolla lobes of central florets	No. of marginal florets	Achenial twin hairs
G. stagnalis (I.M.Johnst.) Anderb.	2.5–30	oblanceolate to oblong-oblanceolate	Concolorous to slightly discolorous	Spikes	Continuous (interrupted basally)	Obtuse to rounded	5	ca. 50	?
G. standleyi (Steyerm.) G.L.Nesom	1–4.5	Elliptic-obovate to oblanceolate	Concolorous	Spike	Continuous	Subacute	5	ca.65	Globose
G. subfalcata (Cabrera) Cabrera	15–35	oblanceolate	Concolorous	Spikes	Continuous (interrupted basally)	Obtuse	5	ca. 100	Globose
G. suffruticosa (Phil.) Anderb.	ca. 10	Linear-oblanceolate	Concolorous	Spikes	Interrupted	Obtuse	5	Unknown	Globose
G. thouarsii (Spreng.) Anderb.	ca. 25	Spathulate	Slightly discolorous	Spikes	Continuous	Unknown	5	Unknown	Globose
G. ustulata (Nutt.) Holub	10–40	Broadly obovate to oblanceolate	Discolorous	Spikes	Usually continuous	Rounded to obtuse	5	Many	?
G. valparadisea (Phil.) Anderb.	10–15	Spathulate	Concolorou	Spikes	Continuous	Acute	5	ca. 50	Globose
G. villarroelii (Phil.) Cabrera	15–20	Oblong-oblanceolate	Concolorous	Spikes	Interrupted	Acute	5	38–49	Globose
Gamochaetopsis Anderb. & S.E.Freire									
G. alpina (Poepp.) Anderb. & S.E.Freire	3–5	Widely obovate or suborbicular	Concolorous	Head-like clusters	–	Acute or subacute	5	9–17	Clavate
Stuckertiella Beauverd									
S. capitata (Wedd.) Beauverd	8–30	Narrowly linear	Concolorous	Head-like clusters	–	Obtuse	4	50–75	Globose
S. peregrina Beauverd	4–15	Linear-obovate	Concolorous	Head-like clusters	–	Obtuse	4	Many	Globose

Table 3 Species of *Gamochaeta* (based on this study) with its distributions (species included in the analysis are in bold face)

Genera/species	Distribution (*adventive or naturalized)
Gamochaeta	
G. affinis	Falkland Islands (=Islas Malvinas)
G. aliena	C and S Chile. 250–2600 m a. s. l.
G. alpina	SW Argentina, S Chile. 1250–1900 m a. s. l.
G. ambatensis	NW Argentina. 2600–2700 m a. s. l.
G. americana	Central and South America. *New Zealand, *Hawaii. 0-3500 m a. s. l.
G. andina	C Chile. ca. 2300 m a. s. l.
G. antarctica	Falkland Islands (=Islas Malvinas)
G. antillana	S Brazil, Cuba, Uruguay, *USA. *Europe, *New Zealand
G. argentina	NE, C Argentina, S. Brazil, Uruguay
G. argyrinea	USA, West Indies, *Hawaii. 0–250 m a. s. l.
G. axillaris	C Chile
G. badillana	Venezuela. ca. 3000 m a. s. l.
G. beckii	Bolivia. ca. 3800 m a. s. l.
G. berteroana	C Chile
G. cabrerae	N and C Peru. 3100–4870 m a. s. l.
G. calviceps	Central and South America, *USA, *Australia, *New Zealand, *Europe, *Asia, *S Africa
G. camaquaensis	S Brazil
G. capitata	NW Argentina, Bolivia, Peru. 2000–3400 m a. s. l.
G. chamissonis	C and S Argentina, Chile. 1000–1800 m a. s. l.
G. chionesthes	USA
G. coarctata	Cosmopolitic. 0–3200 m a. s. l.
G. depilata	S Chile, SW Argentina. 500–2000 m a. s. l.
G. deserticola	NW Argentina and N Chile. 3000–4000 m a. s. l.
G. diffusa	S Brazil
G. erecta	S Brazil, N Uruguay
G. erythractis	NW Argentina, Bolivia, Peru. 3000–4000 m a. s. l.
G. falcata	NE Argentina, S Brazil, Paraguay, Uruguay
G. *filaginea*	NE Argentina, Brazil, Uruguay
G. foliosa	C Chile
G. girardiana	S Brazil
G. grazielae	SE Brazil
G. hiemalis	S and SE Brazil. 1400–1800 m a. s. l.
G. humilis	Bolivia, Chile, Peru. 3560–4000 m a. s. l.
G. irazuensis	Costa Rica. 3030–3430 m a. s. l.
G. longipedicellata	NW Argentina, Bolivia, Chile. 3500–4250 m a. s. l.
G. lulioana	Bolivia, Peru. 4500 m a. s. l.
G. meridensis	Venezuela
G. monticola	S Argentina, C Chile. 400–600 m a. s. l.
G. neuquensis	Argentina, S Chile. 780–1150 m a. s. l.
G. nigrevestis	S and SE Brazil, more than 1000 m a. s. l.
G. nivalis	SW Argentina. C and S Chile, 800–3000 m a. s. l.
G. oligantha	C Chile
G. paramora	Venezuela, probably Colombia. 2900–3500 m a. s. l.
G. pensylvanica	Cosmopolitic
G. peregrina	N and C Argentina
G. procumbens	C and S Chile. ca. 2000 m a. s. l.
G. purpurea	Cosmopolitan. 0-4300 m a. s. l.

Table 3 continued

Genera/species	Distribution (*adventive or naturalized)
G. rizzini	S and SE Brazil
G. serpyllifolia	Argentina, C and S Chile. 700–3200 m a. s. l. Chile
G. simplicicaulis	South America. *Australia, *New Zealand, *USA, *Hawaii. 0–3700 m a. s. l.
G. sphacelata	North and South America. ca. 2200 m a. s. l.
G. spiciformis	SW Argentina, S Chile. 250–1500 m a. s. l.
G. stachydifolia	Argentina, Brazil, Chile. Uruguay. 400–1800 m a. s. l.
G. stagnalis	Guatemala, Mexico, USA. 1000–2500 m a. s. l.
G. standleyi	Guatemala. 3500–4300 m a. s. l.
G. subfalcata	Argentina, Brazil, Chile, Uruguay. *New Zealand, *southern Africa. Up to 4100 m a. s. l.
G. suffruticosa	Chile
G. thouarsii	Tristan da Cunha
G. ustulata	USA, Canada, 0–1100 m a. s. l.
G. valparadisea	C Chile. 0–60 m a. s. l.
G. villarroelii	C Chile. 750–1200 m a. s. l.

random addition sequences, swapped using TBR and holding two optimal trees per series. Consistency index (CI; Kluge and Farris 1969) and retention index (RI; Farris 1989) were calculated as measures of homoplasy.

For each of the four markers, an appropriate model of evolution was selected with JModeltest v.2.1.1 (Darriba et al. 2012) based on the Akaike information criterion, AIC (Akaike 1973; Sugiura 1978; Hurvich and Tsai 1989). The best models were GTR + I+G for ITS; HKY + G for ETS and GTR + G for *trn*L-F. Bayesian inference was performed as implemented in Beast version 1.8.1 (Drummond et al. 2012). With BEAUti v.1.6.2 (Drummond and Rambaut 2007) we created the input file with the nucleotide substitution models mentioned above, empirical base frequencies, four gamma categories, under an uncorrelated lognormal relaxed-clock model (Drummond et al. 2006), and a Yule process of speciation as prior. The MCMC analysis was performed for 10,000,000 generations and sampled every 1000th generation. Convergence of the chains was checked using Tracer v.1.5 (Drummond and Rambaut 2007). All trees obtained prior to convergence were discarded, and trees were summarized in a maximum clade credibility tree in TreeAnnotator v.1.6.2 (Drummond and Rambaut 2007). Trees were visualized and edited using FigTree version 1.4.2 (Rambaut 2014).

Analyses were performed for (1) plastid data only (*trn*L-F), (2) nuclear data only (ITS + ETS), and (3) combined nuclear + plastid data.

Results

Matrices

Sequences of the plastid *trn*L-F region were obtained for 47 taxa, including 27 *Gamochaeta* species, *Gamochaetopsis alpina*, *Stuckertiella capitata* (Wedd.) Beauverd, and ten other genera, *Achyrocline tomentosa* serving as the outgroup. The total length of the sequence ranged from 599 bp in *Gamochaeta grazielae* to 754 bp in *G. andina*, *G. serpyllifollia*, and *Gamochaetopsis alpina*. The aligned matrix consisted of 779 characters, of which 24 were parsimony informative.

Sequences of the nuclear ETS region were obtained for 55 taxa, including 33 *Gamochaeta* species, *Gamochaetopsis alpina* and *Stuckertiella capitata* and 20 other species, including the outgroup. The total length of the sequence ranged from 356 bp in *Leontopodium* to 474 bp in *Omalotheca norvegica* and *Antennaria chilensis*. The aligned matrix consisted of 482 characters, of which 112 were parsimony informative.

Sequences of the nuclear ITS region were obtained for 45 taxa, including 25 *Gamochaeta* species, *Gamochaetopsis alpina* and *Stuckertiella capitata* and 17 other species plus *Achyrocline tomentosa*. The total length of the sequence ranged from 516 bp in *Gamochaeta americana* to 527 bp in *Gnaphalium uliginosum*. The aligned matrix consisted of 532 characters, of which 92 were parsimony informative.

Parsimony and Bayesian analyses showed highly congruent results, with the latter providing more resolved nodes. Consensus trees obtained from the parsimony analyses of nuclear and nuclear + plastid data are illustrated, but some of the more resolved nodes from Bayesian analysis are also shown.

Relationships

The analysis of the plastid marker resulted in a highly polytomized consensus tree (CI 0.87, RI 0.95) due to low character state variability, showing little relevant information. Furthermore, the relationships do not correspond to any proposed hypotheses and even though they are poorly supported we decided to show the data obtained (Fig. 1). The combined analysis of the nuclear markers (hereafter referred to as nuclear analysis) resulted in 175 most parsimonious trees (CI 0.60, RI 0.79), and the combined analysis of the three markers (hereafter referred to as the combined analysis) resulted in 209 most parsimonious trees (CI 0.61, RI 0.79).

The hypothesis of relationships obtained from the nuclear and combined analyses shows that *Gamochaeta*, as currently circumscribed, is paraphyletic, since *Gamochaetopsis* and *Stuckertiella* also appear nested within *Gamochaeta* with 98/97 Jackknife support and a posterior probability of 1.00 (Figs. 2, 3).

The combined data, under Bayesian analysis, show the pair *Omalotheca norvegica-O. sylvatica* (maximum values) distant from *Gamochaeta*, forming a group with *Omalotheca supina* (Fig. 3) but with low support (54/0.91).

In the nuclear and combined analyses, *Gamochaeta* species are divided into two major groups: clade A (99/1.00) including *Gamochaetopsis alpina, Gamochaeta affinis Gamochaeta affinis, Gamochaeta andina*, *Gamochaeta depilata*, *Gamochaeta nivalis, Gamochaeta procumbens*, *Gamochaeta serpyllifolia*, and *Gamochaeta spiciformis*; and clade B (*/0.86, 65/1.00) including all the remaining *Gamochaeta* species (Figs. 2, 3).

Clade A (Fig. 3) is principally characterized by having capitula arranged in head-like clusters (vs. clade B with capitula usually arranged in spikes). In the nuclear analysis *Stuckertiella* is placed as a basal member in the clade B (*/0.84, Fig. 2), and in the combined analysis *Stuckertiella* is placed as a basal member in the clade A (52/0.99, Fig. 3).

In both analyses, clade B showed some internal resolution, with the following clades present: *Gamochaeta ambatensis* + *G. falcata* (85/1.00 Fig. 2; 85/1.00 Fig. 3), principally characterized by having capitula with 50–70 marginal florets, and linear-oblanceolate or oblanceolate leaves (Table 2); *G. filaginea* + *G. pensylvanica* (61/1.00 Fig. 2, 61/1.00 Fig. 3), principally

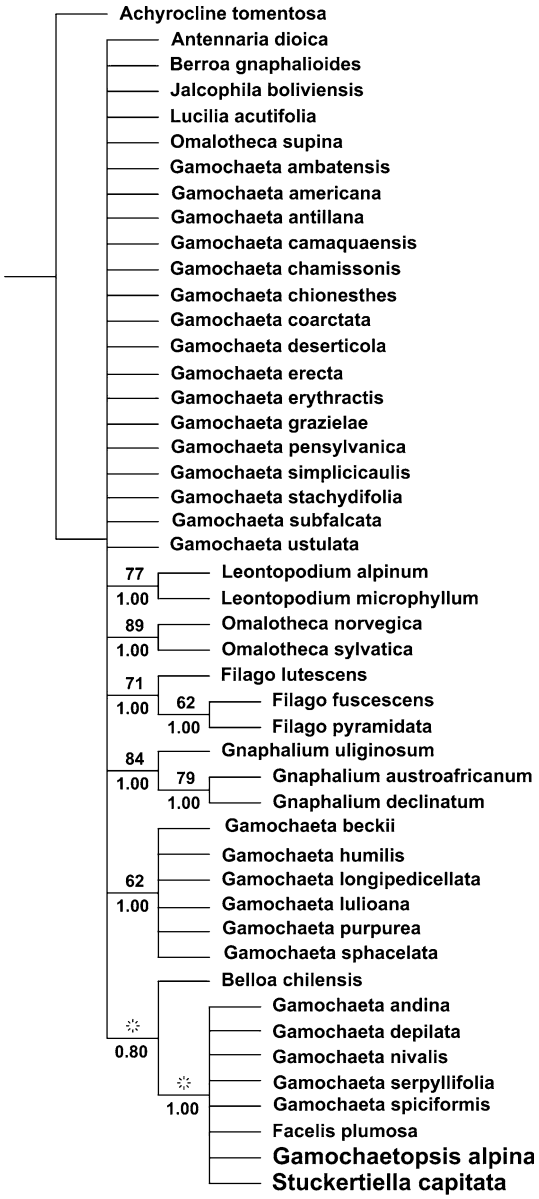

Fig. 1 Strict consensus tree for plastid (*trn*L-F) data obtained under maximum parsimony. *Numbers above* branches are JK values, *numbers below* branches Bayesian PP

characterized by having capitula with 70–80 marginal florets, acute or subacute to obtuse inner phyllaries, and oblanceolate or spathulate leaves (Table 2); *G. argyrinea* + *G. chionesthes* (61/0.98 Fig. 2; 62/0.99 Fig. 3b), principally characterized by having capitula with up 120 marginal florets, and discolorous, oblanceolate leaves (Table 2); *G. humilis* + *G. longipedicellata* + *G. lulioana* (63/0.93 Fig. 2, 63/0.94 Fig. 3c), principally characterized by having caespitose or subcaespitose habit, capitula with 27–40 marginal florets, acute inner phyllaries, and oblanceolate or oblong-obovate to oblong-spathulate leaves (Table 2); and *G. camaquaensis* + *G. erecta* + *G.*

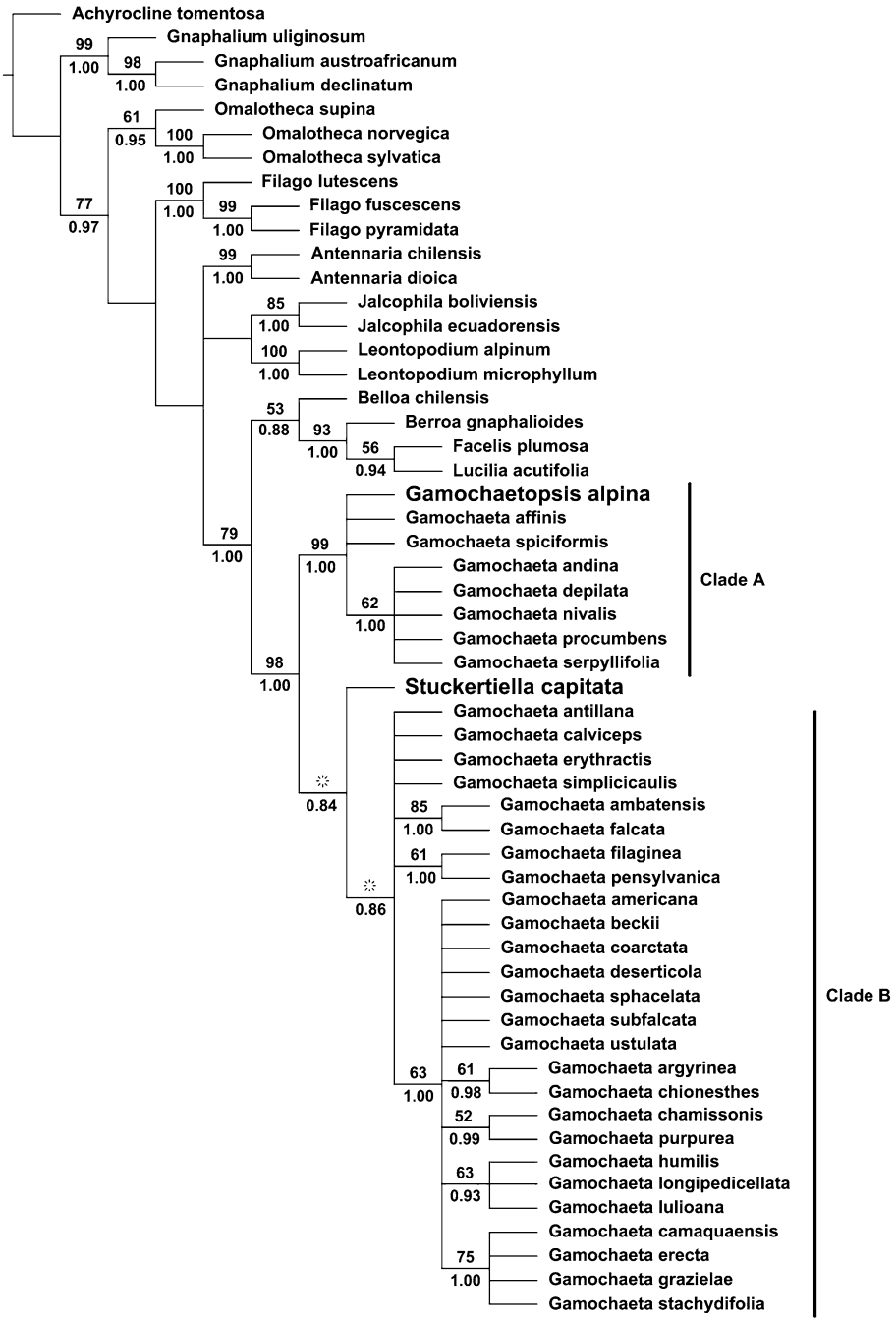

Fig. 2 Strict consensus tree for nuclear (ETS + ITS) data obtained under maximum parsimony. *Numbers above* branches are JK values, *numbers below* branches Bayesian PP

grazielae + *G. stachydifolia* (75/1.00 Fig. 2, 71/1.00 Fig. 3), principally characterized by having capitula with 50–100 marginal florets, acute to acuminate inner phyllaries, and concolorous, oblanceolate to spathulate leaves (Table 2). Other small clades were also present within clade B in each analysis (Figs. 2, 3), e.g., *G. americana* clade (Fig. 3), which comprises *G. americana*, *G. coarctata* and *G. ustulata*, all with strongly discolorous and broadly obovate to spathulate leaves.

The clade *Belloa chilensis*, *Berroa gnaphalioides*, *Facelis plumosa* and *Lucilia acutifolia* is placed as sister group of clades A and B (53/0.88 Fig. 2) in both the nuclear and combined analyses (51/0.88 Fig. 3). They also conform to two morphologically well-defined groups. The genera of the clade of *Belloa chilensis*, *Berroa gnaphalioides*, *Facelis plumosa* and *Lucilia acutifolia* are defined by solitary or few together capitula and elongated (rarely clavate) twin hairs. Conversely, the clade A + B is defined by capitula arranged in head-like clusters or in spiciform inflorescences, and globose (sometimes clavate) twin hairs.

Finally, *Gamochaetopsis alpina* and *Stuckertiella capitata* appear nested within *Gamochaeta* in both analyses

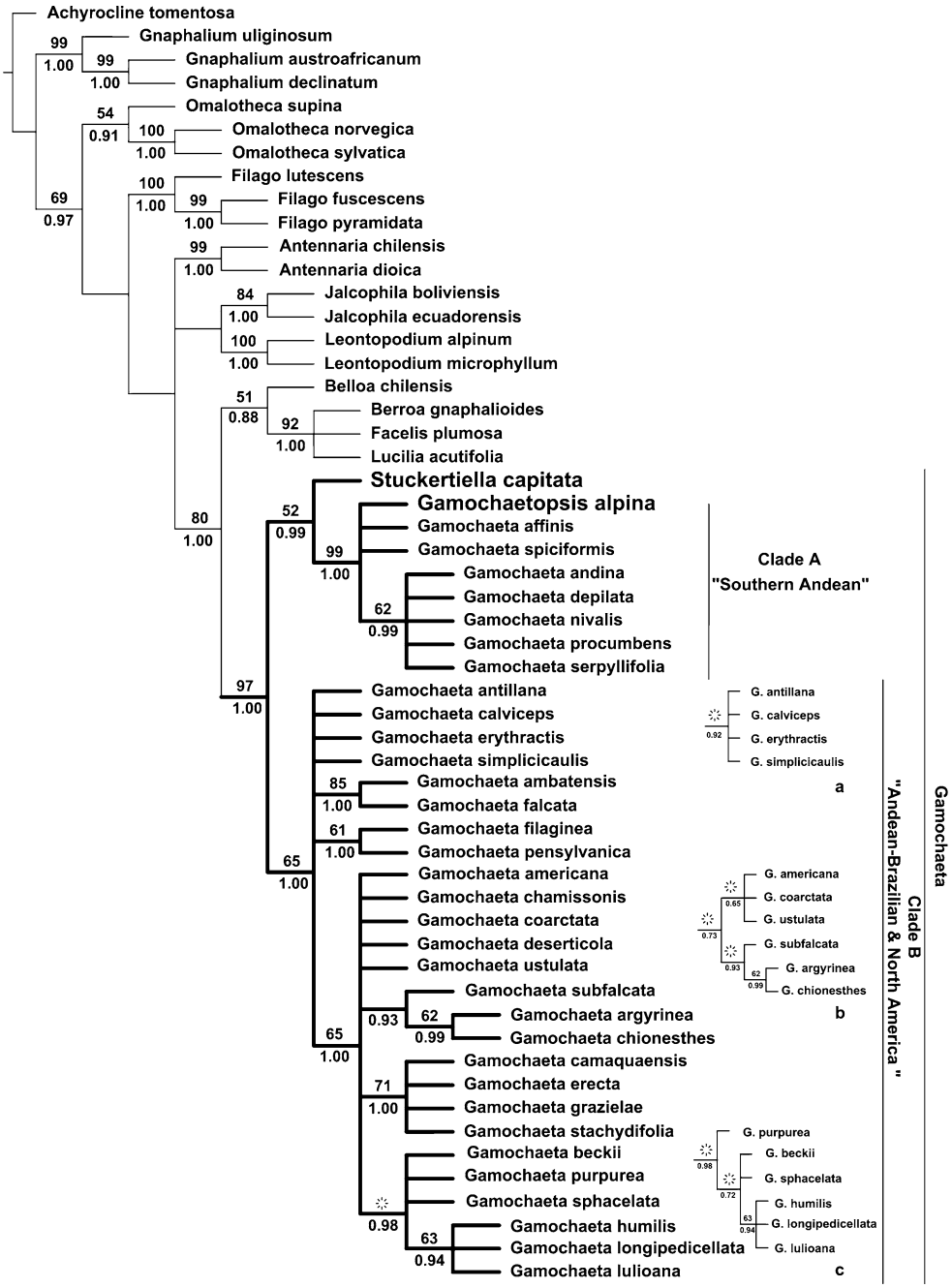

Fig. 3 Strict consensuses tree from combined molecular (ETS + ITS +*trn*L-F) data. *Numbers above* branches are JK values from the parsimony analysis, and *numbers below* branches Bayesian posterior probabilities (PP, *asterisk* indicates lack support). **a**–**c** Bayesian topologies. *Bold lines* indicate *Gamochaeta* and related genera

with Bayesian posterior probabilities and jackknife of 98 and 97, respectively (Figs. 2 and 3).

Discussion

The analyses affirm that *Gamochaeta* as currently circumscribed is paraphyletic, indicating the need of a revised circumscription at the generic level in the group.

Taxonomic position of *Stuckertiella* and *Gamochaetopsis* (Figs. 2, 3, 6)

Stuckertiella was described by Beauverd (1913) with two species: *Stuckertiella capitata* transferred from *Gamochaeta* and *S. peregrina*. The monotypic genus *Gamochaetopsis* was established by Anderberg and Freire (1991) to include *Gamochaetopsis alpina* from southern Chile and Argentina, which was principally diagnosed by

its achenes with short clavate twin hairs and capitula arranged in head-like clusters. The position of *Stuckertiella* and *Gamochaetopsis* in our analyses is congruent with morphological evidence. All the morphological characters that define *Stuckertiella* and *Gamochaetopsis* are also found in species of *Gamochaeta* (Table 1) with the exception of the autoapomorphy in *Stuckertiella* of the presence of functionally male central florets with four anthers (three with a small obtuse apical appendage and one with a long, acute apical appendage). The close similarity between *Gamochaetopsis* and *Gamochaeta*, and between *Stuckertiella* and *Gamochaeta* had previously been noted by Cabrera (1971) and Anderberg (1991), respectively. Furthermore, *Stuckertiella* shares with *Gamochaetopsis* clade its capitula arranged in head-like clusters, and with the remaining species of *Gamochaeta* its capitula with many florets (Table 1).

Unfortunately, we were unable to obtain living material of *Stuckertiella peregrina,* and herbarium specimens were not of sufficient quality for DNA extractions. However, we predict that this species will also group with *Gamochaeta,* given that it has character states like *Stuckertiella capitata* that unite this group with *Gamochaeta*.

Redefinition of *Gamochaeta* boundaries

(Figs. 2, 3, 4, 5, 6)

Gamochaeta is taxonomically difficult due to the fact that most species exhibit considerable morphological and ecological variability (Table 2). In this work, we included a broad geographical-taxonomic sampling, including species that grow at middle elevation (less than 3000 m), especially in dry hills, grasslands, sand hills, and disturbed habitats characterized by having ascending or erect stems, or more rarely, cespitose habit (e.g., *G. alpina*, *G. depilata, G. nivalis, G. procumbens*, *G. serpyllifolia,* and *G. spiciformis*). A small number of species (e.g., *G. deserticola, G. erythractis, G. meridensis, G. meridensis, G. paramora*) grow at high altitudes (3000–4000 m) in paramo, jalca and puna; and a few prostrate and acaulescent species (e.g., *G. cabrerae, G. humilis, G. longipedicellata, G. lulioana*) are adapted to life at even higher elevations between 3500–4500 m.

In order to have *Gamochaeta* monophyletic, we propose that the two species of *Stuckertiella* and the single species of *Gamochaetopsis* are transferred to *Gamochaeta* (Table 3). Synapomorphies for this large clade include the following: multistemmed perennial herbs, oblanceolate leaves, small capitula arranged in spikes or head-like clusters, marginal female florets outnumbering the hermaphroditic central florets, style branches truncate and penicillate, short-pilose achenes with globose twin hairs, and pappus bristles basally connate.

The low sequence divergence and lack of resolution within the *Gamochaeta* clade is probably due to a rapid and recent diversification in the Andes, as was postulated by Hughes and Eastwood (2006). In this way, two centers of diversity in the Andes could be suggested, one in the southern portion of South America and the second one mainly in the Andean-Brazilian region, with few species reaching North America.

Omalotheca (Figs. 2, 3)

Cassini published *Omalotheca* in Cuvieŕs Dictionnaire des Sciences Naturelles in 1828 to include the Eurasian *Gnaphalium supinum* L. and distinguished it from *Gnaphalium* based on a uniseriate pappus and obovoid, compressed achenes. Drury (1970) also distinguished *Omalotheca* from *Gnaphalium* and *Gamochaeta* based on terminal inflorescences in a leafy spikes and elongate twin hairs not emitting mucilage in water.

The molecular phylogeny we present here shows *Omalotheca supina, O. norvegica* and *O. sylvatica* forming a monophyletic group (Figs. 2, 3) distantly related to *Gamochaeta* and to *Gnaphalium uliginosum* (which is the generic type of *Gnaphalium*). This was pointed out by Galbany-Casals et al. (2010), who showed that *Gnaphalium supinum* was neither closely related to *Gnaphalium* s.str. nor to *Gamochaeta*. Similarly, Blöch et al. (2010) indicated that *Omalotheca* (sub *Gnaphalium*) was distantly related to *Gamochaeta*. The diagnostic characters for *Omalotheca* are the presence of connate pappus bristles (vs. free in *Gnaphalium*), lack of myxogenic twin hairs on the fruits (vs. usually myxogenic in *Gamochaeta*), spiciform capitulescence (vs. corymbs in *Gnaphalium*) and pistillate flowers with corollas filiform-tubular (vs. filiform in *Gamochaeta* and *Gnaphalium*). Further, as was pointed out by Nesom (1990b), *Gamochaeta* is strictly a New World genus.

Gamochaeta nanchuanensis (Y.Ling & Y.Q.Tseng) Y.S.Chen & R.J.Bayer was not included in our present analyses, so its phylogenetic position remains untested, although the original description of *Gnaphalium nanchuanense* Y.Ling & Y.Q.Tseng (Ling and Tseng 1978) states that it is very similar to *G. sylvaticum*, thus indicating that it, too, likely belongs in *Omalotheca*.

Taxonomic treatment

Gamochaeta Wedd., Chlor. And. 1(4–6): 151. 1856. *Gnaphalium* L. subgen. *Gamochaeta* (Wedd.) Gren., Fl. Jurass. 2: 427. 1869. ≡ *Gnaphalium* L. sect. *Gamochaeta* (Wedd.) Benth. & Hook. f., Gen. Pl. 2(1): 306. 1873. ≡ *Gnaphalium* L. sect. *Gamochaeta* (Wedd.) O.Hoffm., Nat.

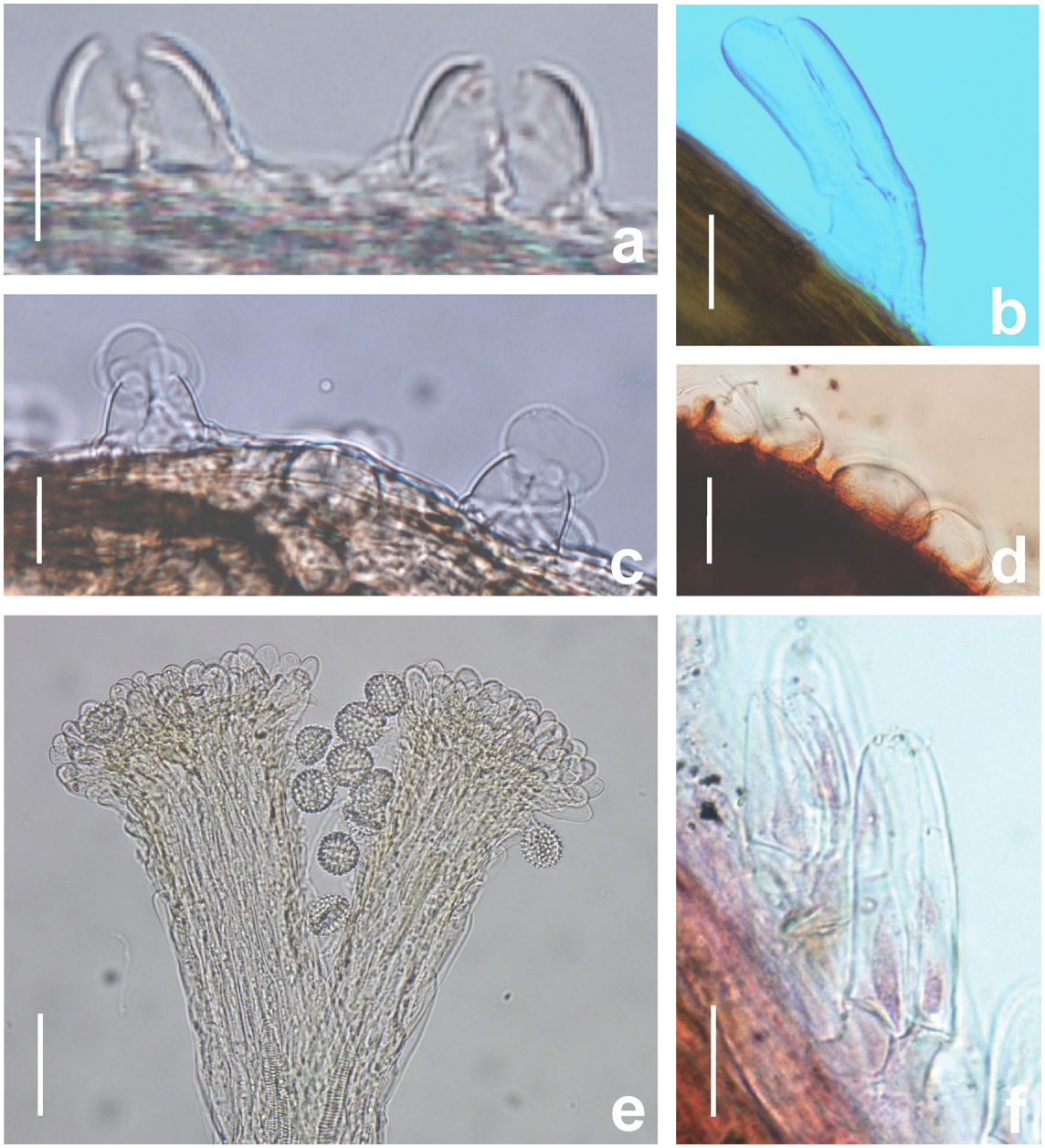

Fig. 4 Achenial hairs in *Gamochaeta*. **a** globose achenial hairs (*G. peregrina, Cabrera 8009*, SI), **b** clavate achenial hairs (*G. hiemalis, Deble* and *Deble 11875*, SI), **c** globose myxogenic achenial hairs (*G. americana, Urtubey 187*, SI), **d** globose achenial hairs (*G. girardiana, Deble* and *Deble 4501*, SI), **e** style branches with pollen of disk floret (*G. americana*, *Urtubey 187*, SI), **f** clavate achenial hairs (*G. alpina, Cabrera 5902*, LP). *Scale bars* **a** 20 µm, **b** 20 µm, **c** 20 µm, **d** 40 µm, **e** 40 µm, **f** 20 µm

Pflanzenfam. 4(5): 188. 1894, **comb. illeg.** (Art. 53)—LECTOTYPE (designated by Cabrera 1961: 362): *G. americana* (Mill.) Wedd.

= *Stuckertiella* Beauverd, **syn. nov.** Bull. Soc. Bot. Genève sér. 2, 5: 205. 1913. —LECTOTYPE (designated by Cabrera, 1978: 128): *S. capitata* (Wedd.) Beauverd.

= *Gamochaetopsis* Anderb. & S.E.Freire, **syn. nov.** Bot. J. Linn. Soc. 106(2): 186. 1991—TYPE: *G. alpina* (Poepp.) Anderb. & S.E.Freire.

Sixty-one species distributed from the USA to Argentina: *G. affinis* Cabrera [*Gnaphalium affine* d'Urv., **nom. illeg.** (Art. 53); *G.malvinense* H.Koyama, **nom. illeg.** (Art. 52); *Gamochaeta malvinensis* (H.Koyama) T.R.Dudley, **comb.**

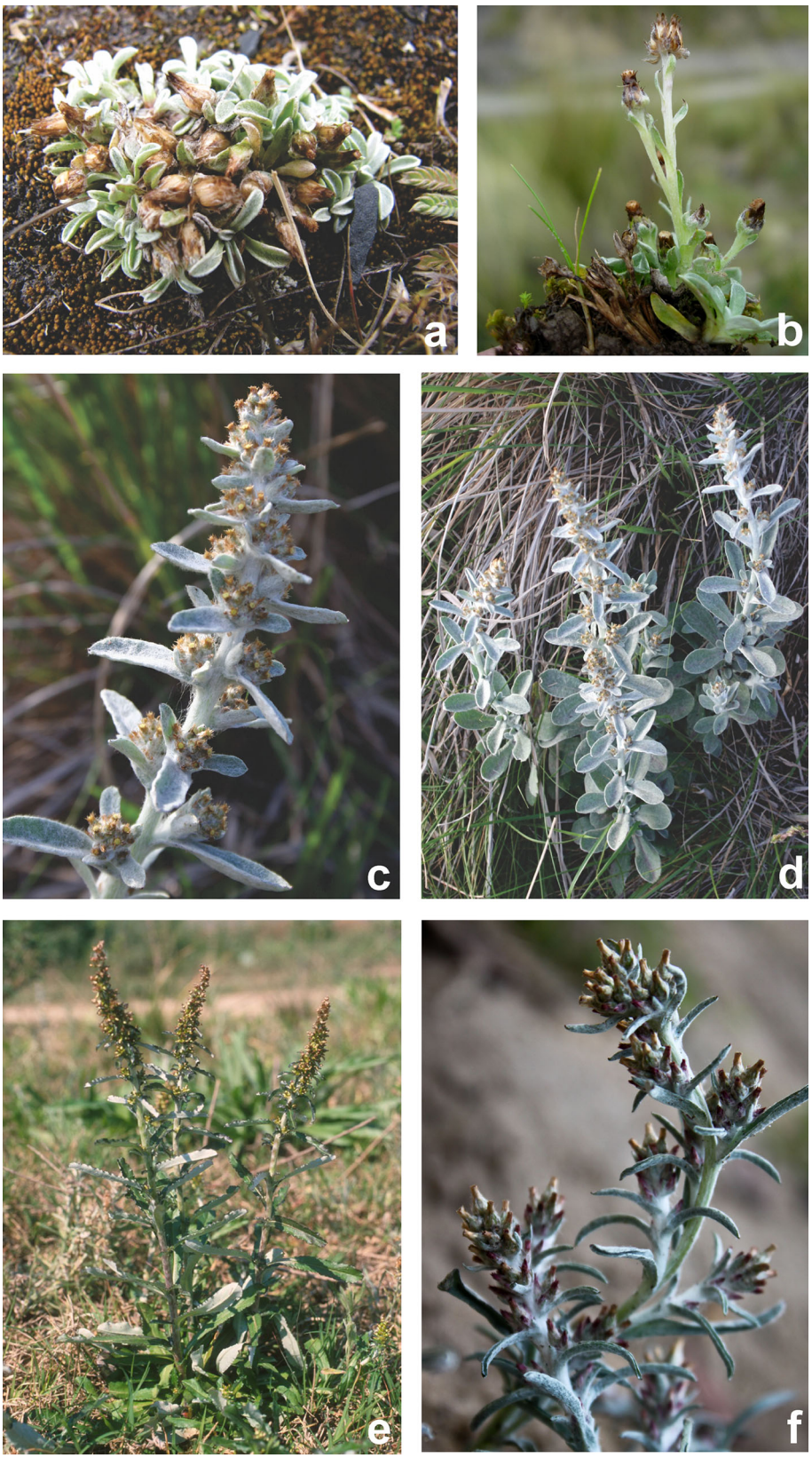

Fig. 5 Morphological diversity in *Gamochaeta* and allied genera: **a** *G. lulioana*, capitula solitary (photo S. Beck), **b** *G. longipedicellata*, capitula solitary (photo E. Urtubey), **c** *G. stachydifolia*, capitula arranged in spikes (photo F.O. Zuloaga), **d** Spike basally discontinuous of *G. stachydifolia* (photo F.O. Zuloaga), **e** *G. coarctata*, capitula arranged in spikes (photo Pensiero), **f** *G. filaginea*, capitula arranged in spikes (photo F.O. Zuloaga)

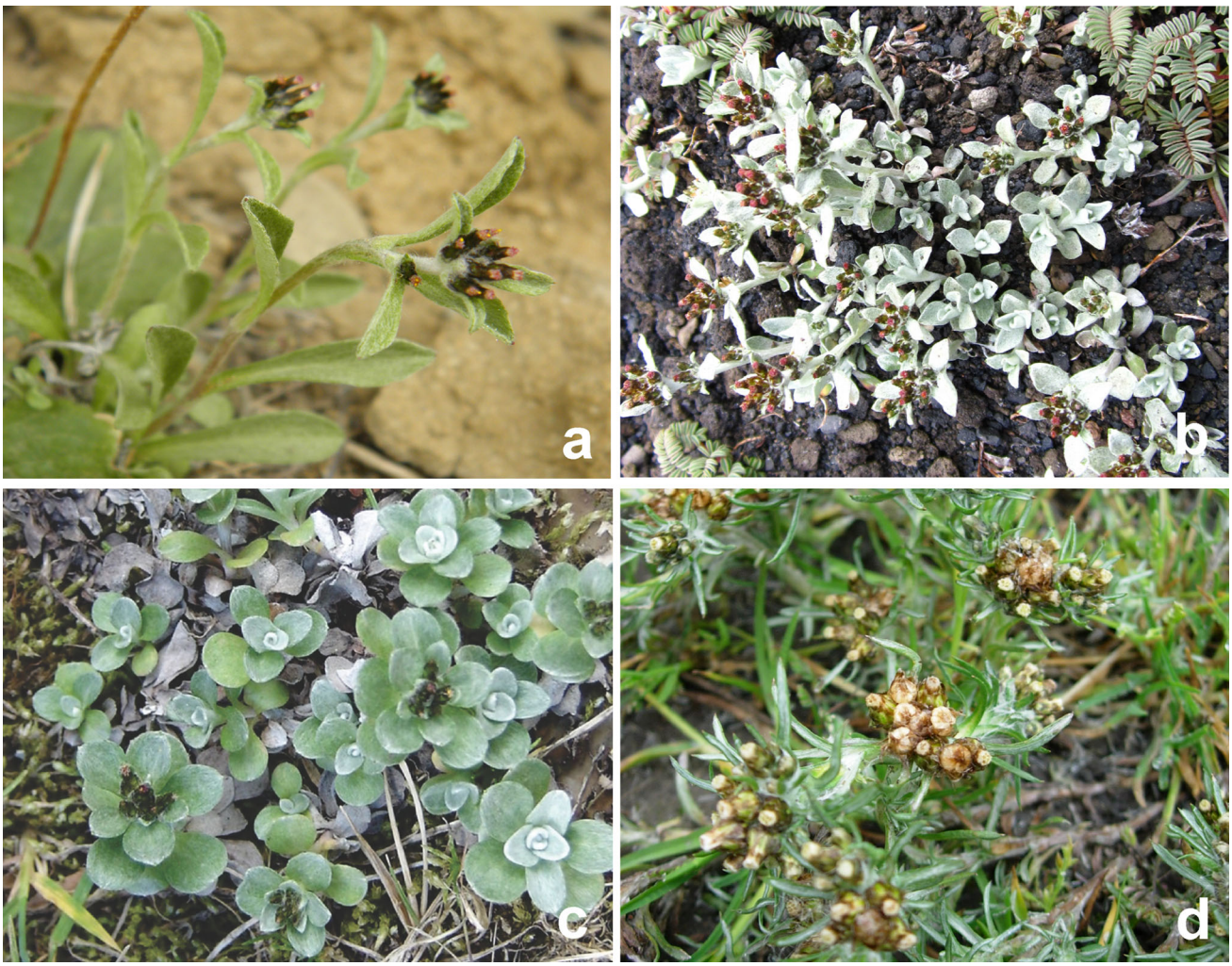

Fig. 6 Capitula arranged in head-like clusters **a** *Gamochaeta spiciformis* (photo L. Zavala), **b** *Gamochaeta nivalis* (photo M.C. Baeza), **c** *Gamochaeta alpina* (photo N. Bayón), **d** *Gamochaeta capitata* (photo E. Urtubey)

illeg. (Art. 53)]; *G. aliena* (Hook. & Arn.) Cabrera (*Gnaphalium alienum* Hook. & Arn.); ***Gamochaeta alpina*** (Poepp.) S.E.Freire & Anderb., **comb. nov.** ≡ *Laennecia alpina* Poepp., Nov. Gen. Sp. Pl. 3: 56, tab. 262. 1845 [= *Lucilia alpina* (Poepp.) Cabrera, *Gamochaetopsis alpina* (Poepp.) Anderb. & S.E.Freire]; *G. ambatensis* Ariza; *G. americana* (Mill.) Wedd. [*Gnaphalium americanum* Mill.; *G. purpureum* L. var. *americanum* (Mill.) Klatt; *G. consanguineum* Gaudich.; *G. guatemalense* Gand.; *Gamochaeta guatemalensis* (Gand.) Cabrera]; *G. andina* (Phil.) Cabrera (*Gnaphalium andinum* Phil.); *G. antarctica* (Hook.f.) Cabrera (*Gnaphalium antarcticum* Hook.f.); *G. antillana* (Urb.) Anderb. (*Gnaphalium antillanum* Urb.); *G. argentina* Cabrera; *G. argyrinea* G.L.Nesom; *G. axillaris* (J.Rémy) Cabrera (*Gnaphalium axillaris* J.Rémy); *G. badillana* (Aristeg.) Anderb. (*Gnaphalium badillanum* Aristeg.); *G. beckii* Urtubey & S.E.Freire; *G. berteroana* (DC.) Cabrera [*Gnaphalium berteroanum* DC.; *G. stachydifolium* Lam. var. *berteroanum* (DC.) DC.]; *G. cabrerae* Anderb. [*Gamochaeta monticola* M.O.Dillon & Sagástegui, **nom. illeg.** (Art. 53); *G. oreophila* M.O.Dillon & Sagástegui, **nom. illeg.** (Art. 53)]; *G. calviceps* (Fernald) Cabrera (*Gnaphalium calviceps* Fernald); *G. camaquaensis* Deble; *Gamochaeta capitata* Wedd., Chlor. And. 1: 153. 1855 [= *Stuckertiella capitata* (Wedd.) Beauverd, *Gnaphalium capitatum* (Wedd.) Griseb., **comb. illeg.** (Art. 53), non Lamarck, 1786, nec Thunberg, 1799, *Gnaphalium weddellianum* Rusby, *Gamochaeta weddelliana* (Rusby) Anderb., **nom. illeg.** (Art. 52)]; *G. chamissonis* (DC.) Cabrera [*Gnaphalium chamissonis* DC.; *G. fernandezianum* Phil.; *G. julietii* Phil.; *G. polybotryum* Phil.; *G. purpureum* L. var. *julietii* (Phil.) Reiche; *G. serranoi* Phil.; *Gamochaeta. fernandeziana* (Phil.) Anderb.; *G. julietii* (Phil.) Anderb.; *G. polybotrya* (Phil.) Cabrera; *G. serranoi* (Phil.) Cabrera]; *G. chionesthes* G.L.Nesom; *G. coarctata* (Willd.) Kerguélen [*Gnaphalium coarctatum* Willd.; *G. purpureum* L. var. *spicatum* Klatt; *G. spicatum* Lam., **nom. illeg.** (Art. 53); *Gamochaeta spicata* Cabrera]; *G. depilata* (Phil.) Cabrera

(*Gnaphalium depilatum* Phil.; *G. obscurum* Phil.); *G. deserticola* Cabrera; *G. diffusa* Deble & Marchiori; *G. erecta* Deble; *G. erythractis* (Wedd.) Cabrera [*Merope erythractis* Wedd.; *Belloa erythractis* (Wedd.) Cabrera); *Gnaphalium erythractis* (Wedd.) Griseb.]; *G. falcata* (Lam.) Cabrera [*Gnaphalium falcatum* Lam., *G. purpureum* L. var. *falcatum* (Lam.) Torr. & A.Gray; *G. stachydifolium* Lam. var. *falcatum* (Lam.) Klatt]; *G. filaginea* (DC.) Cabrera (*Gnaphalium filagineum* DC.); *G. foliosa* (Phil.) Anderb. [*Gnaphalium foliosum* Phil.; *Gamomochaeta chilensis* Deble, **nom. illeg.** (Art. 53)]; *G. girardiana* Deble & A.S.Oliveira; *G. grazielae* (Rizzini) Deble (*Gnaphalium grazielae* Rizzini); *G. hiemalis* Cabrera [*Gnaphalium hiemale* Rizzini, **nom. illeg.** (Art. 53); *Gamochaeta brasiliana* Deble]; *G. humilis* Wedd.; *G. irazuensis* G.L.Nesom; *G. longipedicellata* Cabrera; *G. lulioana* S.E.Freire & Iharl.; *G. meridensis* V.M.Badillo; *G. monticola* (Phil. ex Reiche) Cabrera (*Gnaphalium monticola* Phil. ex Reiche); *G. neuquensis* Cabrera; G. *nigrevestis* Deble & Marchiori; *G. nivalis* Cabrera [*Gnaphalium affine* d'Urv. var. *pusillum* Speg.; *G. nivale* Phil., **nom. illeg.** (Art. 53); *Gamochaeta spiciformis* (Sch.Bip.) Cabrera var. *subaffinis* Cabrera]; *G. oligantha* (Phil.) L.E.Navas (*Gnaphalium oliganthum* Phil.); *G. paramora* (S.F.Blake) Anderb. [*Gnaphalium paramorum* S.F.Blake; *Lucilia paramora* (S.F.Blake) V.M.Badillo]; *G. pensylvanica* (Willd.) Cabrera [*Gnaphalium pensylvanicum* Willd.; *G. peregrinum* Fernald; *G. purpureum* L. subsp. *pensylvanica* (Willd.) O.Bolòs & Vigo; *G. purpureum* L. var. *spathulatum* Baker; *G. spathulatum* Lam., **nom. illeg.** (Art. 53); *G. platense* Cabrera; *Gamochaeta platensis* (Cabrera) Cabrera]; ***Gamochaeta peregrina*** (Beauverd) S.E.Freire & Anderb., **comb. nov.** = *Stuckertiella peregrina* Beauverd, Bull. Soc. Bot. Genève sér. 2, 5: 208. 1913. [= *Stuckertiella peregrina* Beauverd var. *fusca* Beauverd, *Stuckertiella peregrina* Beauverd var. *albida* Beauverd]; *G. procumbens* (Phil.) Cabrera (*Gnaphalium procumbens* Phil.); *G. purpurea* (L.) Cabrera [*Gnaphalium purpureum* L.; *G. rosaceum* I.M. Johnst.; *Gamochaeta rosacea* (I.M.Johnst.) Anderb.]; *G. rizzini* Cabrera; *G. serpyllifolia* Wedd. [*Gnaphalium serpyllifolium* J.Rémy, **nom. illeg.** (Art. 53); *Gamochaeta munnozii* Cabrera, **nom. illeg.** (Art. 52)]; *G. simplicicaulis* (Willd. ex Spreng.) Cabrera [*Gnaphalium simplicicaule* Willd. ex Spreng.; *G. purpureum* L. var. *simplicicaule* (Willd. ex Spreng.) Klatt]; *G. sphacelata* (Kunth) Cabrera [*Gnaphalium sphacelatum* Kunth; *G. purpureum* L. var. *sphacelatum* (Kunth) Speg.]; *G. spiciformis* (Sch.Bip.) Cabrera [*Gnaphalium spiciforme* Sch.Bip.; *G. affine* dUrv. var. *medium* Speg.; *G. mucronatum* Phil.; *G. peteroanum* Phil.; *Gamochaeta peteroana* (Phil) Anderb.]; *G. stachydifolia* (Lam.) Cabrera [*Gnaphalium stachydifolium* Lam.; *G. purpureum* L. var. *stachydifolium* (Lam.) Baker]; *G. stagnalis* (I.M.Johnst.) Anderb. (*G. stagnale* I.M.Johnst.); *G. standleyi* (Steyerm.) G.L.Nesom (*Gnaphalium standleyi* Steyerm.); *G. subfalcata* (Cabrera) Cabrera (*Gnaphalium subfalcatum* Cabrera); *G. suffruticosa* (Phil.) Anderb. (*Gnaphalium suffruticosum* Phil.); *G. thouarsii* (Spreng.) Anderb. (*Gnaphalium thouarsii* Spreng.); *G. ustulata* (Nutt.) Holub [*Gnaphalium ustulatum* Nutt.; *G. pannosum* Gand.; *G. purpureum* L. var. *ustulatum* (Nutt.) B.Boivin; *Gamochaeta ustulata* (Nutt.) G.L.Nesom]; *G. valparadisea* (Phil.) Anderb. (*Gnaphalium valparadiseum* Phil.); *G. villarroelii* (Phil.) Cabrera (*Gnaphalium villarroelii* Phil.).

Concluding remarks

Our study, using a plastid marker (*trn*L-F) and two nuclear markers (ETS and ITS), suggested that the genus *Gamochaeta* is paraphyletic and that *Stuckertiella* and the monotypic genus *Gamochaetopsis* should be included for the establishment of the monophyly in the genus. This American genus *Gamochaeta* is diagnosed by having slender pappus bristles that are basally connate, central florets hermaphroditic (rarely functionally male), capitula arranged in terminal head-like clusters or more usually crowed into spiciform inflorescences, and achenes pilose (occasionally glabrous), with short globose or sometimes clavate, duplex hairs. Two new combinations are proposed under *Gamochaeta*: *Gamochaeta alpina* (Poepp.) S.E.Freire & Anderb. and *Gamochaeta peregrina* (Beauverd) S.E.Freire & Anderb., and *Gamochaeta capitata* Wedd. is resurrected from synonymy of *Stuckertiella capitata* (Wedd.) Beauverd.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Appendix

Species used in the molecular studies with voucher information and GenBank accession numbers (ETS, ITS and *trn*L-F). Accession number in bold indicates data obtained

from GenBank. * indicates sequence not obtained for that marker.

Achyrocline tomentosa. **KM091358**, **KM091389**, **KM091420**. ***Antennaria chilensis*** var. ***magellanica***. **KM091373**, **KM091395,** *. ***Antennaria dioica***. **FN645610, FJ639964, FN645790**. ***Belloa chilensis*** **KM091349, KM091388, KM091430**. ***Berroa gnaphalioides***. **KM091355**, **KM091386**, **KM091418.** ***Facelis plumosa***. **KM091372**, **KM091394**, **KM091428**. ***Filago fuscescens***. **FN645579**, **FN645846**, **FN645764**. ***Filago lutescens***. **FN645596**, **FN645883**, **FN645779**. ***Filago pyramidata***. **FN645589**, **FN645872**, **HM364535**. ***Gamochaeta affinis***. Argentina. Tierra del Fuego: Ushuaia, Bahía Valentín, 16 Oct 1971, *Dudley* et al. *303* (MO). KX078016, *, *. ***Gamochaeta alpina***. (under ***Gamochaetopsis alpina***). **KM091356**, **KM091390**, **KM091417**. ***Gamochaeta ambatensis***. Argentina. Jujuy: Valle Grande, de San Francisco a Alto de Calilegua, 21 Feb 2008, *Zuloaga* et al. *10324* (SI). KX078017, *, KX078049. ***Gamochaeta americana***. **KM091382**, **KM091411**, **KM091437**. ***Gamochaeta andina***. Chile. Maule: Maule, *Lueberg* and *Teiller* 2290 (CONC). KX078018, KX077990, KX078050. ***Gamochaeta antillana***. USA. Mississippi: Lamar County, *Alford 3892* (USMS). KX078019, KX077991, KX078051. ***Gamochaeta argyrinea***. USA. *Nesom WMGT8* (LP). KX078020, *, *. ***Gamochaeta beckii***. Bolivia. La Paz: Nor Yungas, camino a Coroico, entrada del camino viejo hacia la Mina Lourdes, 30 Mar 2010, *Urtubey* et al. *508* (SI). KX078021, KX077992, KX078052. ***Gamochaeta calviceps***. Argentina. Entre Ríos: Colón, camino al arroyo El Palmar, 51 m a. s. l., 7 Dec 2008, *Urtubey* and *Baztarrica 384* (SI). KX078022, *, *. ***Gamochaeta camaquaensis***. Brasil. Rio Grande do Sul: Cacapava do Sul, 30 Sep 2009, *Deble* and *Deble 11879* (SI). KX078023, KX077993, KX078053. ***Gamochaeta capitata*** (under ***Stuckertiella capitata***) **KM091369**, **KM091398**, **KM091412.** ***Gamochaeta chamissonis***. Chile. Metropolitana: El Yeso, 1283 m a. s. l., 26 Jan 2012, *Urtubey* and *Freire 713* (SI). KX078024, KX077994, KX078054. ***Gamochaeta chionesthes***. USA. Giorgia: 15 Apr 2001, *Nesom GASC04-26* (LP). KX078025, KX077995, KX078055. ***Gamochaeta coarctata***. Argentina. Neuquén: Minas, de Chos Malal a Andacollo, ca. 40 km junto al arroyo El Manzanito, 1443 m a. s. l., 12 Jan 2009, *Urtubey* et al. 409 (SI). KX078026, KX077996, KX078056. ***Gamochaeta depilata***. Chile. Biobío: *Mihoc* et al. 4092 (CONC). KX078027, KX077997, KX078057. ***Gamochaeta deserticola***. Bolivia. La Paz: Murillo, 4100 m a. s. l., 4.8 km al NE del autopista por el camino subiendo el Valle del Río Kaluyo 28 Feb 1987, *Solomon 16209* (LPB). KX078028, *, KX0780580. ***Gamochaeta erecta***. Brasil. Rio Grande do Sul: Cacapava do Sul, 28 Oct 2009, *Deble* and *Deble 11874* (SI). KX078029, KX077998, KX078060. ***Gamochaeta erythractis***. Argentina. Jujuy: Humahuaca, camino a la Mina Aguilar, 3940 m a. s. l., 23 Mar 2009, *Urtubey* and *Freire* 442 (SI). KX078030, KX077999, KX078061. ***Gamochaeta falcata***. Argentina. Córdoba: Calamuchita, desde Yacanto de Calamuchita al Champaquí, ca. 2100 m a. s. l., 18 Jan 2006, *Urtubey* and *Baztarrica 197* (SI). *, KX078000, *. Uruguay. Colonia: Conchillares, playa, 18 Nov 2010, *Urtubey 520* (SI). KX0780310, *, *. ***Gamochaeta filaginea***. Argentina. Buenos Aires: Isla Martín García, 24 Sep 2000, *Hurrell 4363* (LP). KX078032, *, *. ***Gamochaeta grazielae***. Brasil. Río de Janeiro: Nov 2006, *Deble* and *Deble 6018* (SI). KX078033, KX078001, KX078062. ***Gamochaeta humilis*** Bolivia. La Paz: Nor Yungas, camino a Coroico, bajando de la ruta en la entrada del camino viejo hacia la Mina Lourdes, 3919 m a. s. l., 30 Mar 2010, *Urtubey* et al. *506* (SI). KX078034, KX078002, KX078059. ***Gamochaeta longipedicellata***. Bolivia. La Paz: Murillo, 24 Mar 2010, *Urtubey* et al. *473* (SI). **KM091381**, **KM091410**, KX078063. ***Gamochaeta lulioana***. Bolivia. La Paz: Murillo, en el borde de bofedal, 4661 m a. s. l., 24 Mar 2010, *Urtubey* et al. *480* (SI). KX078035, KX078003, KX078064. ***Gamochaeta nivalis***. Argentina. Río Negro: Bariloche, Cerro Catedral, 16 Jan 2009, *Urtubey* et al. *415* (SI). KX078036, *, KX078065. ***Gamochaeta pensylvanica***. Argentina. Buenos Aires: La Plata, ciudad Vieja, 6 Oct 2012, *Urtubey 755* (SI). *, *, KX078066. USA. Mississippi: Lamar County, *Alford 4156* (USMS). KX078037, KX078004, *. ***Gamochaeta procumbens***. Argentina. Tierra del Fuego: Rio Grande, Estancia Cullén, 6 Jan 1971, *Goodall 3118* (Herb. Goodall). KX078038, KX078005, *. ***Gamochaeta purpurea***. USA, *Nesom WMGT13* (LP) KX078039, KX078006, KX078067. ***Gamochaeta serpyllifolia*** Chile. Los Ríos: Valdivia, Comuna de Panguipulli, faldeos Volcán Chosuenco, 39°55'/71°59', 1558 m a. s. l., 5 Feb 2012*, Baeza 4357* (CONC). **KM091380**, KX078010, KX078068. ***Gamochaeta simplicicaulis***. Argentina. Jujuy: Tilcara, camino de Molulo a Huairahuasi, 3100 m a. s. l., 11 Feb 2010, *Zuloaga* et al. *11702* (SI). KX078040, KX078007, KX078069. ***Gamochaeta sphacelata***. Argentina. Salta: Santa Victoria, Nazareno, 3308 m a. s. l., *Adler 4* (MNCS 1665). KX078041, *, KX078070. ***Gamochaeta spiciformis***. Chile. Magallanes: *Domínguez 984* (CONC). *, KX078011, KX078071. Argentina. Tierra del Fuego: Ushuaia, Brown Sawmill, *Goodall 286* (LP). KX078042, *, *. ***Gamochaeta stachydifolia***. Argentina. 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County, *Shannon Straub 201* (USMS). KX078045, KX078012, KX078074. ***Gnaphalium austroafricanum*. FN645630**, **FN645830**, **FN645756**. ***Gnaphalium declinatum* FR821617**, *, **FR822634**. ***Gnaphalium uliginosum*** Austria. Upper Austria: Innviertel, Reichersberg am Inn, Hübing, 22 Aug 2010, *Pflugbeil 936* (SZU). KX078048, KX078015, KX07807077. ***Jalcophila boliviensis*. KM091370**, **KM091402, KM091429. *Jalcophila ecuadorensis*. KM091383***,*. ***Leontopodium alpinum* FM173135**, **GU943413**, **AF141821 + AF141733**. ***Leontopodium microphyllum*. FJ640015**, **FJ639947**, **FJ640047 + FJ639977**. ***Lucilia acutifolia*. KM091374**, **KM091396**, **KM091432. *Omalotheca norvegica*** (Gunnerus) Sch.-Bip. & F.W.Schultz. Russia. Republic Altai: surroundings of Zeminsky (Zeminskij) pass to area NE of the pass, ca. 105 km S Gorno Altaysk (Altajsk), subalpine Siberian pine forest, 1700-1730 m a. s. l., 11 Aug 2003, *Tribsch* and *Essl 10383* (W). KX078047, KX078013, KX078075. ***Omalotheca supina* FN645558**, **AY445230**, **FN645789**. ***Omalotheca sylvatica***. Austria. Carinthia: Lavanttal, Koralpe, Hartelsberg SE Wolfsberg, 1345 m a. s. l., *Riegler-Hager 921* (W). KX078046, KX078014, KX078076.

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