

Is morphology supporting a monophyletic *Proustia* Lag., (Nassauvieae, Asteraceae)?

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Abstract *Proustia* is an Andean genus traditionally considered to have three species and ten infraspecific taxa, which has often been placed in tribes other than Nassauvieae mainly because of its distinctive style features. Currently, each of the three species of *Proustia* is included in its own section denoting a consistent morphological variability within the genus. The heterogeneity among *Proustia* species mainly relies on habit, spiny structures arrangement, capitula arrangement, and pappus features. On the contrary, the forms or varieties within each species are apparently more homogeneous. The phylogenetic analysis performed here is based on morphological features and includes all the species, and all but two varieties and forms of *Proustia*. We test the boundaries of *Proustia* and the hypothesis that morphological discontinuities in the genus are phylogenetically uninformative. A total of 26 taxa and 29 morphological, anatomical, and palynological characters were studied. A maximum parsimony analysis yield six most parsimonious trees that showed almost identical topologies. Our results do not support the current generic concept of *Proustia*. Independently, each species of *Proustia* was monophyletic when taxa at sub-specific level were considered. *Proustia pyrifolia* was retrieved sister to the genus *Berylsimpsonia* although this clade did not obtain significant support. The spiny structures usually referred to as diagnostic for *Proustia* are not homologous for the genus. Characteristics of habit, spiny structures, secondary inflorescences and pappus support clades representing each species of *Proustia*, which may in turn, represent different genera.

Keywords Spines · Homology · Compositae · Morphology · Mutisioideae · Phylogeny

Introduction

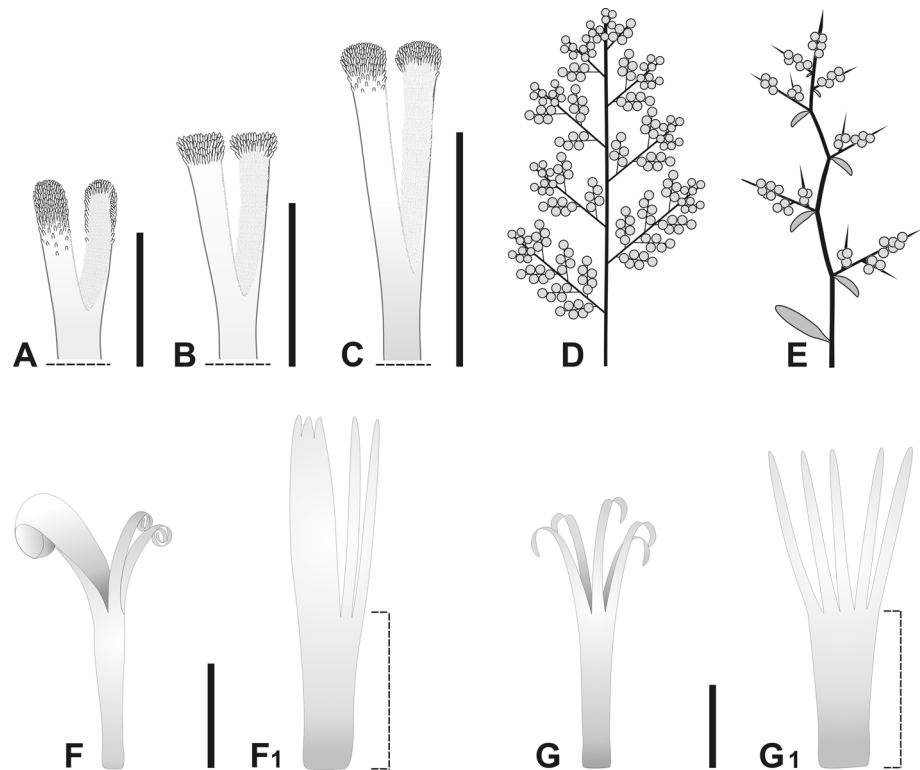
The tribe Nassauvieae (Cassini 1819) constitutes one of the most interesting groups within the basal clades of the phylogenetic tree of Asteraceae because of its well-defined morphology and restricted geographical distribution. Nowadays, Nassauvieae is recognized as one of the tribes of the subfamily Mutisioideae. Different treatments (Cabrera 1977; Crisci 1974, 1980; Katinas et al. 2008a), including those based on molecular evidence (Panero and Funk 2002, 2008), showed Nassauvieae consistently as a “natural” or monophyletic group. While authors have mostly agreed with the overall circumscription of Nassauvieae, significant discrepancy was observed when some individual genera were considered. This was the case of *Proustia* Lag., an Andean genus traditionally considered to have three species, which together with a few genera (e.g., *Lophopappus* Rusby and *Macrachaenium* Hook. f.), has often been placed in tribes other than Nassauvieae (Hoffmann 1893; Cabrera 1961). Specifically, *Proustia* differs from the core of Nassauvieae by its apically rounded style branches (Fig. 1a) with dorsal apical papillae spread on the branch (vs. usually apically truncate style branches with papillae in an apical tuft in most Nassauvieae; Fig. 1b). However, *Proustia* is best placed in Nassauvieae (e.g., Crisci 1974; Cabrera, 1977; Tellería et al. 2003; Katinas et al. 2008a, b) by its predominantly bilabiate corollas, tailed anthers and pollen type of exine stratification.

Proustia has been related alternatively to *Brachyclados* D. Don, *Dinoseris* Griseb., *Hyaloseris* Griseb., and *Lophopappus* on the basis of morphological similarity (Fabris

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Fig. 1 Key morphological characters of *Proustia* I. Style.

a *Proustia cuneifolia* f. *cuneifolia*; drawn from *Punge* 2447, LP. **b** *Perezia pungens*, *López* 605, LP. **c** *Berylsimpsonia vanillosma*, *Ekman* 3034, LP. Scheme of capitula arrangement. **d** Paniculate, *Proustia ilicifolia*; from *Ricardi* 5553, LP. **e** Spikes or glomerules in racemes, from *Proustia cuneifolia* f. *cuneifolia*; *Cabrera* 9008, LP. Corollas. **f** Bilabiate, **f**₁ open corolla, *Proustia pyrifolia*; *Fiedrich* s.n., LP 71038. **g** Deeply 5-lobed, **g**₁ open corolla, *Proustia cuneifolia* f. *cuneifolia*; *Ferreya* 13939, LP. Dashed lines indicate the area where the corolla was open. Scale bars **a** 1 mm, **b** 1.2 mm, **c** 1.8 mm, **f**, **g** 3 mm



1968), to *Acourtia* D. Don, *Burkartia* Crisci, and *Lophopappus* on the basis of numerical and morphological cladistic analyses (Crisci 1974, 1980) and variously to *Trixis* P. Browne and *Lophopappus* based on molecular characters (Hershkovitz et al. 2006; Panero and Funk 2008; Luebert et al. 2009). Most of these molecular studies sampled only one species of *Proustia* and the results vary depending on the marker used in such analyses (e.g., Luebert et al. 2009).

The most consistently related genus to *Proustia* apparently is *Lophopappus*, another small Andean genus (five species; Katinas et al. 2013), the relationships of which were supported by morphology as well as by molecular evidence. Indeed, some authors have merged *Proustia* and *Lophopappus* in one single genus (e.g., Ferreyra 1995). Crisci (1974) pointed out that *Proustia* and *Lophopappus* were very closely related and together with *Acourtia*, but in a different line of evolution, they had affinities with members of the tribe Mutisieae. In fact, *Proustia* and *Lophopappus* were sometimes recovered as basal lineages of Nassauvieae (Panero and Funk 2008; Simpson et al. 2009; Katinas et al. 2008b). *Proustia* occurs in the Andes of South America in Argentina, Bolivia, Chile and Peru and has been revised by Fabris (1968). In his treatment, Fabris included four species: *P. pyrifolia* (the type species), *P. cuneifolia*, *P. ilicifolia* and *P. vanillosma* with two to six varieties or forms each (Table 1). The author

accommodated the four species in three sections following the classifications of Don (1830) and de Candolle (1838) who apparently early noticed the strong morphological differences among the species of this genus. All of the species recognized by Fabris are distributed in the Andes, except by one of them, *P. vanillosma* inhabiting the West Indies. The geographical distribution of *P. vanillosma* was not its unique distinctive feature, as recognized by latter authors. Crisci (1974) excluded *P. vanillosma* from *Proustia* and placed it in *Acourtia* (Crisci 1974) mainly because of style features (style relatively deeply lobed, apically rounded and slightly expanded style branches with dorsal papillae distally arranged; Fig. 1c). Turner (1993) found that peculiarities of *P. vanillosma* were strong enough to consider this species as a monospecific genus, which he called *Berylsimpsonia*. Turner based his decision on the climbing habit, yellow corollas and fusiform, 5-9-ribbed cypselae (vs. mostly shrubby habit, white to pinkish corollas and obpyramidal ribless cypselae in *Proustia*). Differences in pollen exine of *Proustia* and *Berylsimpsonia* pointed out by some authors (Crisci 1974; Turner 1993) were later re-evaluated and found to be not very significant (Tellería et al. 2003). After the establishment of *Berylsimpsonia*, the genus *Proustia* was constituted by only three species.

The morphological discontinuities formerly established in *Proustia*, its unresolved generic relationships, together

Table 1 *Proustia* sections, species and forms (according to Fabris 1968, and Cabrera 1977), diagnostic characters of sections and distribution of the species

Section	Diagnostic characters	Species	Intraspecific taxa	Distribution
<i>Baccharoides</i> DC	Erect shrubs. Branches unarmed (without thorns or infrapetiolar spines), leaf margin spiny. Capitula arranged in loose panicles	<i>Proustia ilicifolia</i> Hook. and Arn.	f. <i>baccharoides</i> (D. Don) Fabris	N and central Chile
			f. <i>ilicifolia</i>	N and central Chile
<i>Harmodia</i> D. Don	Erect shrubs. Inflorescence axes distally spiny (thorns). Capitula arranged in spikes or glomerules in racemes	<i>Proustia cuneifolia</i> D. Don	f. <i>angustifolia</i> (Wedd.) Fabris	Bolivia
			f. <i>cinerea</i> (Phil.) Fabris	Central Chile
			f. <i>cuneifolia</i>	NW Argentina, Bolivia, central and S Chile, Peru,
			f. <i>mendocina</i> (Phil.) Fabris var. <i>mollis</i> (Kuntze) Cabrera	NW and central Argentina NW Argentina and S Bolivia
			f. <i>oblongifolia</i> (Wedd.) Fabris	Bolivia and Peru
<i>Proustia</i>	Scandent shrubs. Branches with infrapetiolar spines. Capitula arranged in glomerulose panicles	<i>Proustia vanillosma</i> C. Wright <i>Proustia pyrifolia</i> DC	f. <i>tipia</i> (Phil.) Fabris	N Chile
			f. <i>glandulosa</i> (DC.) Fabris	Cuba, Santo Domingo, Puerto Rico
			f. <i>pyrifolia</i>	S Chile Central and S Chile

Proustia vanillosma is currently a species of the genus *Berylsimpsonia* B. L. Turner

with the absence of a comprehensive phylogenetic analysis involving all its species, cast doubts about the identity of this genus. In this paper, we propose to investigate some key morphological features and to carry out a complete approach to the phylogeny of *Proustia* for the first time. The present analysis that includes all its species and varieties aims to identify the boundaries of *Proustia* obtained from morphological evidence in the frame of the Nassauvieae. We test the hypothesis that morphological discontinuities in *Proustia* are phylogenetically uninformative.

Materials and methods

Taxon sampling

The selection of genera was based on previous taxonomic treatments of the tribe Nassauvieae (e.g., Crisci 1974; Cabrera 1977; Katinas et al. 2008a). All the species of *Proustia* and nearly all their forms were sampled in the analysis except by two forms. These forms, *P. cuneifolia* f. *cinerea* and *P. pyrifolia* f. *glandulosa* (the latter regarded by Fabris, 1968, as probably a mere ecological variant of the typical form), could not be sampled because we lacked enough material to study their reproductive characters. For the purpose of this phylogenetic analysis, we followed

Fabris (1968) and Cabrera (1978) in the taxonomic ranks assigned to the infraspecific entities of *Proustia* (i.e., variety or form). To investigate the generic relationship of *Proustia*, we included closely related genera according to Hershkovits et al. (2006), Panero and Funk (2008) and Luebert et al. (2009). Because *Lophopappus* was consistently regarded as closely related to *Proustia* by most authors (e.g., Fabris 1968; Crisci 1974, 1980; Panero and Funk 2008; Luebert et al. 2009), its entire species were included in the analysis. *Chuquiraga* Juss., in the Barnadesioideae, was selected as outgroup based on molecular studies that resolved this subfamily as sister group to the rest of Asteraceae (e.g., Panero and Funk 2008).

Morphological data set

Morphological characters (Appendix 1) were scored from the specimens deposited in CONC, F, GH, HUT, LP, NY, US (Holmgren et al. 1990) (Appendix 2) and pertinent literature (Katinas et al. 2008a, 2013). A total of 26 species and 29 morphological, anatomical, and palynological characters obtained from floral and vegetative parts of the plant were studied. Missing characters represented 2.51 % of the total characters. For polymorphic characters, all the alternative states were codified. For light microscopic examination, rehydrated leaves were isolated and transversely free hand cut. Floral and vegetative parts were

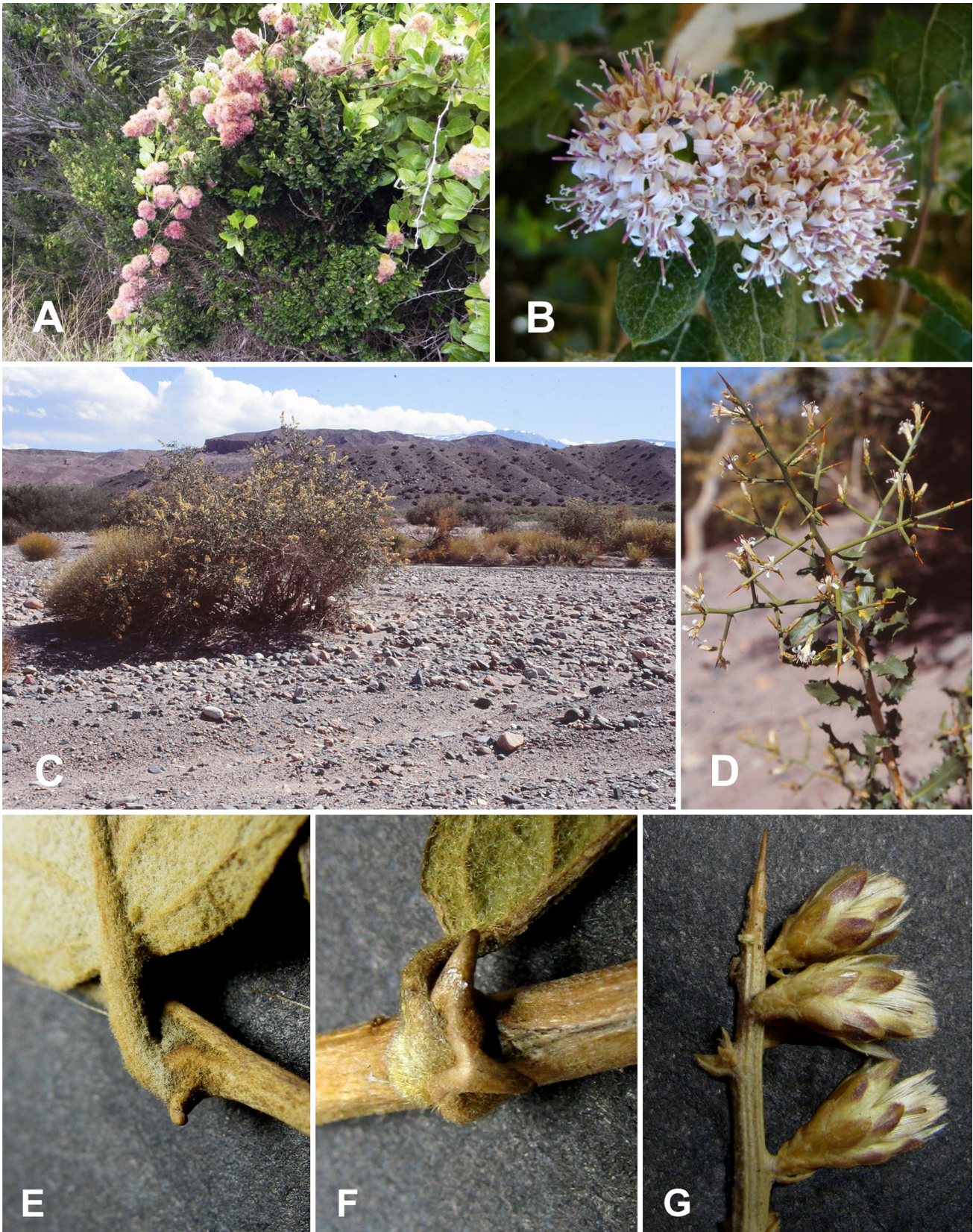


Fig. 2 Key morphological characters of *Proustia* II. *P. pyrifolia* **a** Scandent habit. **b** Glomerulose panicle. *P. cuneifolia* f. *mendocina*. **c** Shrubby habit. **d** Spikes in racemes showing thorns and spiny leaf margins. Infrapetiolar spines. **e** *Proustia pyrifolia*; Lourteig 2514, LP. **f** *Berylsimpsonia vanillosma*; Ekman 4306, LP. **g** Thorns, *Proustia cuneifolia* f. *cuneifolia*; Punge 2447, LP (Photographs **a** and **b** from Chilebosque.cl/2013; **c** and **d** by L. Katinas; **e–g** by G. Sancho)

rehydrated and stained in 2 % safranin. Drawings were made by the authors using a Nikon SMZ1000 stereomicroscope and a Nikon Eclipse E200 Lux microscope with camera lucida. General terminology follows Harris and Wolf Harris (1994). Style and pollen terminology follows Crisci (1974) and Tellería et al. (2003), respectively. Morphological variation for selected characters is illustrated in Figs. 1 and 2. Morphological data matrix for the 26 species is presented in Appendix 3.

Phylogenetic analysis

The maximum parsimony phylogeny was reconstructed with TNT v.1.1 (Goloboff et al. 2008). All characters were treated as equally weighted and unordered. Gaps were regarded as missing data. The heuristic searches used 1,000 random stepwise taxon additions to obtain starting trees and the tree bisection–reconnection (TBR) branch swapping option. Relative support for the clades was calculated using standard bootstrap analyses (BS; with TBR branch swapping and 2000 bootstrap replicates) absolute (AB) and GC (Group present/Contradicted) frequencies, and Jackknife (JK; with a probability removal of 0.36 and 1,000 replicates).

Results

Morphological heterogeneity within *Proustia*

A comparative analysis of the three species of *Proustia* shows a consistent morphological variability that mainly relies on habit, spiny structures arrangement, capitula arrangement, and less so in pappus features. On the contrary, the forms or varieties within each species are apparently more homogeneous. They vary mostly in leaf shape, pubescence degree, and margin type. Though, the morphological discontinuities among the forms of each species were scarce and the specimens showed commonly intermediate states. This was especially evident in *P. cuneifolia* which forms *angustifolia*, *cuneifolia* and *oblongifolia* showed a considerable overlapping in, for instance, blade shape.

Proustia pyrifolia is a scandent shrub (Fig. 2a) whereas the other two species have a typical shrubby habit

(Fig. 2c). The scandent habit of *P. pyrifolia* is also present in the excluded *Berylsimpsonia vanillosma*.

Transversal section of leaves of *Proustia* shows quite similar anatomical structure. All species have a developed cuticle, stomata on both faces or only in the abaxial face, dorsiventral mesophyll and sclerenchyma that embrace the vascular strand; the species show different degree of sclerenchyma development. Below the middle vein, a tissue with an apparently secretory function was observed, which shows inflated cells and a dense and refractive content. Only *Proustia cuneifolia* var. *mendocina* showed an isolar lateral mesophyll with sclerenchyma very strongly developed.

One of the most distinctive features of species of *Proustia* is its spiny structures. The spiny structures could be foliar or cauline according to their position in the plant. The foliar structures are represented by leaf spiny margins in *P. cuneifolia* f. *mendocina*, *P. cuneifolia* f. *tipia*, *P. ilicifolia* and, in less degree, in *P. pyrifolia*. There are two different types of cauline spiny structures that vary in position and shape: 1. Infrapetiolar spines: a short, persistent, stiff sharp pointed structure below the petiole; they are present in *P. pyrifolia* (Fig. 2e). Similar spines are found in *Berylsimpsonia vanillosma* (Fig. 2f) although in this species they are bifurcates. 2. Thorns: a stiff woody modified stem apex with a sharp point; they are present in all the taxonomic forms of *P. cuneifolia* (Fig. 2d, g), except some specimens of *P. cuneifolia* var. *mollis* which directly lacks thorns or they are small and sub-apical. The thorns are restricted to the end of the secondary inflorescence axes.

Regarding the capitula arrangement, *Proustia ilicifolia* and *P. pyrifolia* have loose (Fig. 1d) or glomerulose panicles (Fig. 2a, b) respectively, whereas in *P. cuneifolia* the capitula are arranged as spikes or glomerules in racemes (Figs. 1e, 2d).

Proustia has all bilabiate corollas (Fig. 1f). However, the sporadic occurrence of some deeply 5-lobed corollas in *Proustia cuneifolia* (our observations; Fig. 1g) and in *P. pyrifolia* (Crisci 1974; our own observations) has intrigued the authors who have taken into consideration this character and others to relate *Proustia* with *Lophopappus* (Fabris 1968), two genera where transitional types of corollas, from bilabiate to tubular, are common.

The pappus of *P. pyrifolia* is usually pinkish (Fig. 2b), in *P. cuneifolia* pale yellow (Fig. 2g) and in *P. ilicifolia* persistently white.

Phylogenetic analysis

The maximum parsimony analysis yield six most parsimonious trees, each 96 steps long (consistence index CI = 0.43; retention index RI = 0.74). One of the trees is shown in Fig. 3a. Twenty-nine characters were included in

Fig. 3 **a** One of the six cladograms obtained from the analysis of the morphological data set. *Black circles* indicate synapomorphies, *white circles* indicate homoplastic characters. *Gray surface* includes current *Proustia* species. **b** Reduced strict consensus of six equally most parsimonious trees resulting from morphological data set. *Numbers* above branches are bootstrap values (Absolute, AB/Group present/contradicted, GC); numbers below branches are Jackknifing values (bootstrap values below 50 % not shown). *Asterisk* indicates the type species of *Proustia*



the analysis and all were parsimony informative. The six cladograms varied in two clades, the *Proustia cuneifolia* clade and the *Calopappus-Triptilion-Perezia* clade, which showed different internal arrangements of their lineages. Apart from these two clades, the other relationships recovered by the six trees were identical. Only selected clades, however, obtained support values ≥ 50 . The strict consensus of the six trees (Fig. 3b) retrieved *Proustia* polyphyletic. Independently, each species of *Proustia* was

monophyletic when taxa at infraspecific level were considered. For instance, the two forms of *P. ilicifolia* were monophyletic (BS_{AB} = 65; BS_{GC} = 64; JK = 60) and sister to *Lophopappus* and other members of Nassauvieae (clade including *Acourtia* and *Nassauvia*). The *Proustia ilicifolia* clade was supported by spiny leaf margin (character 7[1]). In addition, all the six forms of *P. cuneifolia* were recovered in a clade (BS_{AB} = 54; BS_{GC} = 50; JK = 55) sister to the monophyletic group including, for

instance, *Proustia ilicifolia*, *Lophopappus* and *Acourtia*. The characters inflorescence axes with thorns (3 [1]), presence of brachyblasts (5 [1]) and spikes or glomerules in racemes (29 [1]) supported the relationships among the forms of *P. cuneifolia*. Apart from the *P. cuneifolia* clade and the *P. ilicifolia* clade, only the *Lophopappus* clade obtained support values ≥ 50 ($BS_{AB} = 58$; $BS_{GC} = 59$; $JK = 61$). Finally, *Proustia pyrifolia* was retrieved sister to *Berylsimpsonia* although this clade did not obtain significant support.

Discussion

The present phylogenetic analysis provides new insights into *Proustia* delimitation by showing this genus as non-monophyletic, although the obtained clades were weakly supported. Our results based on morphological data would not support the current generic concept of *Proustia* which could be better understood if its species are regarded as three independent entities. To some extent, these results agree with the idea of previous authors (Don 1830; de Candolle 1838; Fabris 1968) who recognized three sections within this genus with only three species (see Table 1) denoting a morphologically heterogeneous *Proustia*.

Within Nassauvieae, *Proustia* as well as *Lophopappus* was regarded as distinctive by their apically rounded style branches with dorsal papillae (Crisci 1974). According to our results, this character apparently evolved in parallel along with the derived *Macrachaenium-Adenocaulon* clade. For some authors, characteristics of styles of *Proustia* would approach this genus to others in the Mutisieae. Our analysis, however, shows that this character has a complex history within Nassauvieae. Undoubtedly, for a complete understanding of the evolution of this character in the frame of the tribe, a more extensive sampling of Nassauvieae species should be undertaken, also aiming to obtain a better support for the relationships. To add complexity to the understanding of character evolution within the tribe scale, recent molecular studies on Nassauvieae have yielded variable generic relationships (Hershkovitz et al. 2006; Katinas et al. 2008b; Simpson et al. 2009).

Previous distance-based and morphological phylogenetic studies (Crisci 1974, 1980) and the few molecular studies that included both *Proustia* and *Lophopappus* (Panero and Funk 2008; Luebert et al. 2009) obtained these genera as sister. Our results based on morphology did not show these tight relationships as expected. However, these results could vary with the addition of new molecular evidence in a complete analysis involving all the species of both genera (in progress).

According to our studies, *Berylsimpsonia vanillosma* was sister to *Proustia pyrifolia*. This relationship, however, was weakly supported. With the current evidence, and also taking into consideration their different geographic distributions, *Berylsimpsonia* is regarded as distinct from *Proustia* in agreement with Crisci (1974) and Turner (1993).

Specifically for *Proustia*, this study proved to be useful in showing the strengths of morphological discontinuities in this genus which was phylogenetically informative. Each species is confirmed as monophyletic (although with a weak support) by recovering their taxonomic forms together in the same clade. These forms, however, need to be reassessed in light of the scarce differentiation evidenced during the morphological study, together with future molecular evidence. The species of *Proustia* share key characters of styles, corollas and pollen features that are distinct within Nassauvieae. However, some of these characters could be considered parallelisms since they are also variously present in other genera, such as *Lophopappus* and *Adenocaulon* among others. This, together with the presence of morphological discontinuities makes it difficult to define *Proustia* in its wide sense. The spiny structures usually referred to as diagnostic for *Proustia* (e.g., Turner 1993) were shown here to be not homologous for the genus. This is in agreement with our morphological studies that pointed out differences in the morphology and position for these structures. Also, the spiny structures of *Proustia* species could be the result of different ecological strategies. In the case of *P. pyrifolia*, the spines would enhance the climbing capability by attaching the specimens to the supporting plants (Fig. 2a, e). Thorns of *P. cuneifolia* and spiny leaf margins of *P. ilicifolia*, however, could be better postulated as playing a defensive role (Fig. 2d). These differences in ecological function could be linked also to environmental conditions that differ in the species. Whereas *P. pyrifolia* has been indicated as a characteristic local element of sclerophyll forests in Chile (Luebert and Pliscoff 2006) (Fig. 2a), *P. cuneifolia* and *P. ilicifolia* inhabit more open and exposed environments where spiny and desert scrubs (Fig. 2c) in Argentina and Chile dominate. Spiny structures have been indicated in other Asteraceae of Argentina (Ezcurra et al. 1997) as having a defensive role against mammals in dry, open and exposed environments like those inhabited by *Proustia cuneifolia*.

Together, the spiny structure type, the habit characteristic, type of secondary inflorescences, and pappus features support individual clades of each species of *Proustia*.

In light of our results, one possible scenario would consider each species within a different genus. Monospecific genera are relatively common in Nassauvieae (see Crisci 1974; Katinas et al. 2008a for an account of genera)

which would give to the new entities raised from *Proustia* s.l. an appropriated context. However, more evidence is needed to make such a decision. The inclusion of molecular data will help in establishing the *Proustia* boundaries and the definite value of morphological characters. In the meantime, this analysis provides a preliminary conclusion that *Proustia* would not be monophyletic as currently circumscribed. Also, it has evaluated the non-homologous status of the spines considered a key feature of the genus. These results may be better expressed through the visionary sentence of de Candolle (1838), who in his *Prodromus*, after the genus *Proustia* description, indicated: “an genus dividendum?”

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Appendix 1

Morphological characters and character scores used in the phylogenetic analyses of *Proustia*. 1. Habit: Shrubs (0); subshrubs (1); herbs (2). 2. Stem position: Erect (0); scandent (1). 3. Inflorescence axes distally spiny (thorns): absent (0); present (1). 4. Infrapetiolar spines: absent (0); present (1). 5. Brachyblasts: absent (0); present (1). 6. Leaves disposition: sparce (0); clustered at the base (1). 7. Leaf margin spiny: absent (0); present (1). 8. Leaf consistency: coriaceous to sub-coriaceous (0); herbaceous (1). 9. Leaf glandular trichomes: absent (0); present (1). 10. Leaf glandular trichomes: 1-seriate (1); 2-seriate (2); multiseriate (3). 11. Leaf structure: isolateral (0); dorsiventral (1); undifferentiated (2). 12. Number of capitula per capitulescence: few (2-8) (0); solitary (1); numerous (more than 15) (2). 13. Receptacle: pubescent (0); glabrous (1). 14. Capitulum sexuality: homogamous (0); heterogamous (female florets in the margin, bisexual in the center) (1). 15. Corolla morphology in homogamous capitula: all tubular (0); all bilabiate (1). 16. Corolla color: yellow (0); white (1); pink to purple (2). 17. Corolla vestiture: pubescent (0); glabrous or with apical papillae (1). 18. Style branches (according to Crisci, 1974): type 1 (1); type 2 (2); type 3 (3). 19. Style base widened: absent (0); present (1). 20. Cypsela apex: truncate (0); constricted to attenuate (1). 21. Carpodium: absent (0); present (1). 22. Cypsela vestiture: pubescent (0); glabrous (1). 23. Cypsela type of trichomes: non-glandular (0); glandular (1). 24. Cypsela

type of non-glandular hair: barnadesioid (0); 1-seriate (1); 2-seriate (twin hairs) (2). 25. Pappus bristle apex: plumose (0); scabrous or barbelate (1). 26. Pappus bristle body: plumose (0); scabrous or barbelate (1). 27. Pappus bristles color: tawny to pinkish (0); white (1). 28. Pollen exine type (Crisci, 1974; Zhao et al., 2000; Tellería et al., 2003): *Chuquiraga* type (0); *Trixis* type (1); *Proustia* type (2); *Oxyphyllum* type (3) *Mutisia* type (4). 29. Capitula arrangement: glomerules or solitary (0); spikes or glomerules in racemes (1); panicles (2).

Appendix 2

List of selected specimens examined for the morphological analysis and voucher data. Abbreviations for herbaria follow Holmgren et al. (1990). For analyzed specimens of *Lophopappus* see Katinas et al. (2013) ***Acourtia parryi* (A. Gray) Reveal & R.M. King:** *I. M. Johnston* 7370-Mexico, Zacatecas (2 Mar 1938), (LP!). ***Adenocaulon chilense* Less.:** *A. L. Cabrera & M. M. Job* 136-Argentina, Rio Negro, Cerro Otto (Jul 1935), (LP!); *J. C. Montiel* 205-Argentina, Rio Negro, Puerto Blest (1 Feb 1946), (LP!); *M. J. Bonifacino, D. Gutiérrez & P. Simón* 248-Argentina, Rio Negro, Cerro López (19 Jan 2000), (LP!). ***Berylsimpsonia vanillosma* (C. Wright) B. L. Turner:** *E. L. Ekman* 3034-Haiti, Port au Prince (without date), (LP!); *E. L. Ekman* 4306-Haiti, Ile La Tortue (14 Jun 1925), (LP!); *J. I. Otero* 391-Puerto Rico, Bayamon, Aibonito (19 Dec 1937), (GH!); *A. A. Heller* 6263 *PIO4306*-Puerto Rico, along Bucana river east of Ponce (11 Dec 1902), (GH!); *E. C. Leonard* 7445-Haiti, vicinity of St. Michael de l' Atalaye (26 Nov 1925), (F!); *N. L. Britton & E. G. Britton* 9143-Puerto Rico, between Coano and Aibonito (11 Jan 1929), (F!). ***Calopappus acerosus* Meyen:** *O. Zöllner* 1406-Chile, Aconcagua, Los Andes (24 Mar 1967), (LP!); *M. Ricardi* 3226-Chile, Colchagua, San Fernando, Vegas del Flaco (10 Feb 1955), (CONC!); *F. Schegel* 2492-Chile, Santiago, Cerro Pirámide (5 Apr 1959), (CONC!); *Ricardi* 2971-Chile, Aconcagua, Portillo (11 Mar 1954), (CONC!). ***Chuquiraga avellanadae* Lorentz:** *A. L. Cabrera, S. Botta, C. Ezcurra, R. Kiesling* 33197-Argentina, Chubut, Sarmiento (14 Dec 1981), (LP!); *A. L. Cabrera, A. Giaotti, R. Kiesling, M. Ronco, E. Zardini, F. O. Zuloaga* 23245-Argentina, Chubut, Sarmiento (25 Jan 1973), (LP!); *M. Gentili* 524-Argentina, Neuquén, Cerro El Marucho (4 Jan 1973), (LP!). ***Jungia polita* Griseb.:** *A. L. Cabrera* 3740-Argentina, Salta, Guachipas (12 Aug 1936), (LP!); *A. L. Cabrera* 20777-Argentina, Jujuy, Capital, Cuesta de Las Lajitas (28 Aug 1970), (LP!); *S. Venturi* 9674-Argentina, Jujuy, sierra de Santa Bárbara, (8 Oct 1929), (LP!); *J. B. Sotelo* 10051-Argentina, Jujuy, Capital, Yala, (9 Jun 1948), (LP!) *H. Fabris* 4695-Argentina, Jujuy, Capital,

- alrededores de San Salvador de Jujuy (20 Oct 1963), (LP!); *A. L. Cabrera & H. Fabris* 15991-Argentina, Jujuy, Ledesma, entrada al camino a Valle Grande (15 Oct 1964), (LP!). ***Leucheria achillaeifolia* Hook. et Arn.:** *J. J. Neumeyer* 407-Argentina, Chubut, Cushamen, Lago Puelo (10 Dec 1940), (LP!); *G. Covas* 428-Argentina, Mendoza, Malargüe, cerros al norte de Calmuco (16 Feb 1942), (LP!); *A. L. Cabrera* 11161-Argentina, Neuquén, Minas, Andacollo (9 Dec 1952), (LP!); *R. Hauthal* s.n.-Argentina, Santa Cruz, Lago Argentino, (Jan 1902), (LP!); *A. Soriano* 3783-Argentina, Chubut, Futaleufú, Esquel, (10 Nov 1949), (LP!). ***Macrachaenium gracile* Hook. f.:** *E. Pisano* 3081-Chile, Magallanes, Fiordo Parry (21 Feb 1971), (LP!); *E. Pisano* 2876-Chile, Magallanes, Fiordo Parry (13 Dec 70), (LP!). ***Nassauvia cumingii* Hook. & Arn.:** *A. Ruíz Leal* 61-Argentina, Mendoza, La Cuevas (without date), (LP!); *F. Pastore* 121-Argentina, Neuquén, Arroyo Mamanque (18 Apr 1912), (LP!); *A. Ruíz Leal* 16786-Argentina, Mendoza, San Rafael (6-7 Feb 1955), (LP!). ***Proustia cuneifolia* f. *angustifolia* (Wedd.) Fabris:** *A. Jiménez* 39-Bolivia, Cochabamba, Angostura (3 Apr 1955), (LP!); *T. Herzog* 2021-Bolivia (Apr 1911), (LP); *S. Venturi* 8297-Argentina, Jujuy, Humahuaca, Sierra del Zenta (27 Feb 1929), (US!, GH!); *J. R. I. Wood* 8313-Bolivia, Chuquisaca, on the escarpment between Zudanez and Tarabuco (11 Apr 1994), (US!); *E. Asplund* 4182-Bolivia, Cochabamba, Capinata (11 Jun 1921), (GH!). ***Proustia cuneifolia* f. *cuneifolia* D. Don:** *F. Vervoort* 8638-Argentina, Catamarca, Andalgalá, Cuesta de la Chilca, (10 Jan 1973), (US!); *S. Venturi* 6634-Argentina, Catamarca, Santa María (1 Feb 1925), (US!); *A. Bridarolli* 1067-Argentina, Córdoba, San Javier (13 Jan 1940), (LP!); *T. Meyer, R. Cuezco & R. Legname* 21083-Argentina, Jujuy, Humahuaca (8 Mar 1960), (LP!); *S. Venturi* 4878-Argentina, Jujuy, Tilcara (8 Feb 1927), (US!, F!, GH!); *A. Bohi & D. Liesner* 4-Argentina, Jujuy, Yavi (11 Jan 1967), (LP!); *T. Meyer* 3933-Argentina, La Rioja, Capital (30 Dec 1941), (US!); *Rodríguez* 1435 (LIL 27912)-Argentina, Salta, Cafayate (6 Apr 1914), (GH!); *A.L. Cabrera* 9008-Argentina, Salta, Rosario de Lerma (9 Feb 1946), (LP!); *R. F. Steinbach* 186-Bolivia, Cochabamba, pie de colina San Pedro (11 May 1966), (F!); *S. G. Beck* 8473-Bolivia, La Paz, Loayza (27 Jun 1983), (US!); *C. Grünge* 3162-Chile, Biobío, Los Ángeles (29 Jan 1961), (US!); *G. Montero* O. 755-Chile, Calchagua, San Fernando (24 Feb 1928), (F!, GH!); *C. Punge* 2447-Chile, Biobío, Antuco (19 Jan 1941), (LP!); *R. Ferreyra* 13939-Perú, Arequipa, Carevalí (19 Dec 1959), (LP!); *H. Fabris & J. V. Crisci* 6986-Argentina, Jujuy, Valle Grande, Caspalá (12 Mar 1967), (HUT!, LP!). ***Proustia cuneifolia* f. *mendocina* (Phil.) Fabris:** *A. L. Cabrera* 1179-Argentina, Catamarca, Belén (5 Mar 1929), (LP!); *M. Layaga* 2269-Argentina, Catamarca, La Ciénaga (Jan 1956), (LP!); *R. Schreiter* 10588 (LIL 58106)-Argentina, Catamarca, Las Mansas (Mar 1938), (GH!); *J. H. Hunziker* 1821-Argentina, La Rioja, Famatina (12 Jan 1947), (LP!); *R. Falcone & J. Castellanos* 3643-Argentina, La Rioja, General Belgrano (12 Mar 1957), (LP!); *A. T. Hunziker, A. E. Cocucci & R. Subils* 15866-Argentina, La Rioja, Independencia (3 Feb 1961), (NY!); *M. I. H. Scott de Birabén & M. Birabén* 997-Argentina, La Rioja, Tinogasta (23 Nov 1939), (LP!); *D. O. King* 1926-Argentina, Mendoza, Las Heras (30 Oct 1936), (LP!); *E. M. García* 509-Argentina, Mendoza, Luján (6 Jan 1948), (GH!); *L. Serra* s.n. (LP 900747)-Argentina, Mendoza, Luján de Cuyo (26 Jan 1952), (LP!); *O. Boelcke, N. M. Bacigalupo & M. N. Correa* 10415-Argentina, Mendoza, Malargüe (31 Jan 1963), (LP!); *A. Burkart, N. S. Troncoso & E. G. Nicora* 14362-Argentina, Mendoza, San Carlos (10 Feb 1942), (LP!); *O. Boelcke* 4196-Argentina, Mendoza, San Rafael (6 Feb 1950), (LP!); *A. Ruiz Leal* 1099-Argentina, Mendoza, Tunuyán (19 Feb 1933), (LP!); *A. L. Cabrera, D. Añon Suarez, M. A. Torres, J. Crisci & N. Tur* 18008-Argentina, San Juan, Iglesia, Pismanta (26 Feb 1967), (LP!); *T. M. Pedersen* 15228-Argentina, San Juan, Ullún (13 Mar 1989), (F!, NY!). ***Proustia cuneifolia* var. *mollis* Cabrera:** *A. L. Cabrera & H. A. Fabris* 21042-Argentina, Jujuy, Santa Bárbara (21 Nov 1970), (LP!); *A. Burkart* 13287-Argentina, Salta, Coronel Moldes (14 Nov 1942), (LP!); *A. L. Cabrera, J. Frangi, A. M. de Frangi, R. Kiesling & E. M. Zardini* 22074-Argentina, Salta, Rosario de Lerma (12 Feb 1972), (LP!); *C. Spegazzini* s.n. (LPS 1873)-Argentina, Salta, Pampa Grande (Jan 1897), (LP!). ***Proustia cuneifolia* f. *oblongifolia* (Wedd.) Fabris:** *R. S. Shepard* 172-Bolivia, La Paz, Cañon La Paz River (6 Aug 1920), (GH!); *A. Gentry, M. Dillon, P. Berry & J. Aronson* 23340-Perú, Apurímac, río Chalhuanca (24 Jun 1978), (F!); *A. Weberbauer* 5762-Perú, Ayacucho, Tal v. Huacata (1909-1914), (F!). ***Proustia cuneifolia* f. *tipia* (Phil.) Fabris:** *M. O. Dillon, D. Dillon, V. Asencio & M. Villarroel* 5735-Chile, Antofagasta (23 Oct 1988), (F!); *A. Borchers* s.n.-Chile, Atacama (1887), (LP!); *H. Niemeyer* s.n. (F 2065915)-Chile, II Región, Comuna Taltal (Apr 1985), (F!). ***Proustia ilicifolia* f. *baccharoides* (D. Don) Fabris:** *E. M. L. Kausel* 5150-Chile, Atacama, zona interior, Panamericana (20 Sep 1966), (LP!); *F. Ruiz* s.n. (LP 071041)-Chile, Coquimbo, Illapel (Feb 1931), (LP!); *E. Barros* 2369-Chile, Coquimbo, Ovalle (15 Jan 1942), (LP!); *F. Claude Joseph* 4054-Chile, Río Blanco (Nov 1925), (US!); *A. Garaventa Limache* 332-Chile, Cerro de la Virgen, 6 Mar 1928), (LP!). ***Proustia ilicifolia* f. *ilicifolia* Hook. & Arn.:** *E. Werdermann* 423-Chile, Atacama, Copiapó (Sep 1924), (GH!, F!); *M. Ricardi* 3751-Chile, Atacama, Estancia Manflas (2 Nov 1956), (LP!); *M. Ricardi & C. Marticorena* 4888 (CONC 25683)-Chile, Atacama, Cachiyuyo (10 Oct 195), (LP!); *M. Ricardi* 3667-Chile,

Atacama, La Puerta (28 Oct 1956), (LP!); *M. Ricardi* 3851-Chile, Atacama, San Félix (10 Nov 1956), (LP!); *I. M. Johnston* 6267-Chile, Coquimbo, Elqui (18-19 Jan 1926), (GH!); *M. Ricardi* 5553 (CONC 37022)-Chile, Coquimbo, La Serena (16 Feb 1963), (LP!); *C. Jiles* 1256-Chile, Coquimbo, Ovalle (17 Jan 1949), (LP!); *C. Jiles* 1074-Chile, Coquimbo, Ovalle (10 Oct 1948), (LP!); *G. Montero* O. 2845-Chile, Coquimbo, Rivadavia (17 Sep 1936), (GH!); *J. P. Simón* 257-Chile, Coquimbo, Road Punitaqui to Combarbalá (24 Oct 1970), (US!); without collector s.n. (LP s.n.)-Chile, Coquimbo, Paihuano (5 Feb 1883), (LP!); *G. T. Hastings* 618 (US 580477)-Chile, Santiago, San Cristóbal (Dec 1901), (US!); without collector s.n. (LP s.n.)-Chile, Santiago, San Cristóbal (1881), (LP!). ***Proustia pyrifolia* DC.:** *C. Jiles* 2329-Chile, Aconcagua, Petorca (16 Nov 1952), (LP!); *O. Boelcke* 3991-Chile, Aconcagua (5 Jan 1949), (LP!); *J. Acuña* s.n. (CONC 9638)-Chile, Cautín, Villarrica (23 Feb 1950), (LP!); *M. Ricardi* s.n. (CONC 10027)-Chile, Colchagua, San Fernando (3 Jan 1951), (LP!); *H. Rizzo* 12888-Chile, Concepción (1-4 Mar 1925), (GH!); *A. Lourteig* 2514-Chile, Concepción, Hualpén (3 Jan 1971), (LP!). *H. A. Fabris & J. Crisci* 7549-Chile, Concepción, Rocoto (Jan 1969), (LP!); *A. L. Cabrera* 19661-Chile, Concepción, Rocoto (19 Jan 1969), (LP!); *Mertens* s.n.-Chile, Concepción, Camarico (without data), (GH!); *Y. Mexia* 7857-Chile, Curicó (13 Feb 1936), (F!); *F. Fredrich* s.n. (LP 071038)-Chile, río Tolten cerca de Villarica, Cautín (Mar 1935), (LP!); *A. Lourteig* 2514-Chile, Concepción, Huelpén (3 Jan 1971), (LP!); *E. Werdermann* 569-Chile, Curicó, Hacienda Monte Grande (Dec 1924), (F!); *P. Germain* s.n. (F 1013019)-Chile, Guillota, Colchagua (without date), (F!); *M. H. de Looser* 5176-Chile, Maule,

Constitución (Jan 1946), (GH!); *E. M. L. Kausel* 4347-Chile, Santiago, San Antonio (Feb 1958), (F!); *A. Caldeleugh* s.n. (F 1013154)-Chile, Santiago, Colchagua (without date), (F!); *L. Moreira* s.n.-Chile, Talca, Camarico (Feb 1926), (GH!); *A. Hollermayer* 86-Chile, Valdivia (4 Mar 1943), (LP!); *F. Schlegel* 579 (CONC 40338)-Chile, Valparaíso (17 Jan 1955), (F!); *C. L. G. Bertero* 1263-Chile, Valparaíso (1829), (GH!, F!); *J. West* 5197-Chile, Valparaíso, Cajón de San Pedro, (19 Jan 1936), (GH!). ***Perezia pungens* (Bonpl.) Less.:** *I. Sánchez Vega & W. M. Ruíz Vigo* 468-Peru, Cajamarca, Challuayaco (4 May 1970), (LP!); *A. López* 605-Peru, La Libertad, Otuzco (1 Jun 1951), (LP!). ***Triptilion achilleae* DC.:** *A. Soriano* 2454-Argentina, Chubut, Futaleufú, Estancia Pampa Chica (22 Jan 1947), (LP!); *A. L. Cabrera* 11286-Argentina, Neuquén, Huiliches (17 Dec 1952), (LP!); *A. L. Cabrera & Job* 357-Argentina, Río Negro, Bariloche, Nahuel Huapi (16 Jan 1935), (LP!); *A. Burkart* 9602-Chile, Malleco, Liucura, (4 Mar 1939), (LP!); *A. Ruiz Leal* 26763-Argentina, Neuquén, Aluminé, camino Aluminé-Las Coloradas, (6 Jan 1970), (LP!). ***Trixis lessingii* DC.:** *A. Macêdo* 2852-Brazil, Minas Gerais, Ouro Preto, Andorinha (5 Jan 1951), (LP!); *A. P. Duarte* 2116-Brazil, Serra do Cipó (6 Dec 1948), (LP!); *G. Hatschbach* 17851-Brazil, Paraná, Campina Grande Sul (15 Nov 1967), (LP!); *M. Magalhaes* 5393-Brazil, Minas Gerais, Rawcharia, (30 Jan 1948), (LP!); *R. Klein* 3569-Brazil, Santa Catarina, Matos Costa (8 Mar 1962), (LP!).

Appendix 3

See Table 2.

Table 2 Data matrix of morphological characters used in the phylogenetic analysis of *Proustia* and allied genera

	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	
<i>Acourtia parryi</i>	2	0	0	0	0	1	0	0	1	1	2	1	1	0	1	2	1	3	1	1	1	0	0	0	2	1	1	1	1	0
<i>Adenocaulon chilense</i>	2	0	0	0	0	1	0	1	0	?	1	0	1	1	0	1	1	2	0	0	0	0	1	?	?	?	?	4	1	
<i>Berylsimpsonia vanillosma</i>	0	1	0	1	0	0	0	0	1	1	1	2	0	0	1	0	0	3	1	0	0	0	(01)	1	1	1	0	1	2	
<i>Catopappus aceroseus</i>	0	0	0	0	0	?	(01)	0	1	2	1	1	1	0	1	1	1	1	1	1	0	1	?	?	1	1	1	5	0	
<i>Chuiriraga avellanadae</i>	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0	
<i>Jungia polita</i>	(12)	0	0	0	0	0	0	0	(01)	1	1	2	0	0	1	1	1	1	1	1	0	0	1	?	0	0	1	1	2	
<i>Leucheria achillaeifolia</i>	2	0	0	0	0	(01)	0	1	(01)	1	2	2	1	0	1	1	1	1	0	1	0	0	1	?	0	0	1	3	?	
<i>Lophopappus berberidifolius</i>	0	0	0	0	1	0	0	0	1	3	1	(01)	1	0	(01)	(01)	1	2	1	1	1	1	0	(01)	2	0	1	0	1	0
<i>Lophopappus blakei</i>	0	0	0	0	1	0	0	0	1	3	1	0	1	0	1	(01)	1	2	1	1	1	1	0	(01)	2	0	1	0	2	0
<i>Lophopappus cuneatus</i>	0	0	0	0	1	0	0	0	1	3	1	1	1	0	1	1	1	2	1	1	1	1	0	(01)	2	0	1	0	2	0
<i>Lophopappus foliosus</i>	0	0	0	0	1	0	0	0	1	3	1	1	0	0	1	1	1	2	1	1	1	1	0	(01)	2	0	0	0	2	0
<i>Lophopappus peruvianus</i>	0	0	0	0	1	0	0	0	1	3	1	1	1	0	0	1	1	2	1	1	1	0	(01)	2	0	1	0	(12)	0	
<i>Macrachaenium gracile</i>	2	0	0	0	1	0	1	0	?	?	1	1	1	0	1	1	1	2	0	1	0	1	?	?	0	0	1	1	0	
<i>Nassauvia cunningii</i>	2	0	0	0	0	0	0	0	?	?	1	2	1	0	1	1	1	1	1	0	1	1	?	?	0	0	1	3	0	
<i>Perezia pungens</i>	2	0	0	0	1	0	0	1	2	1	(01)	0	0	1	2	1	1	1	0	0	1	(01)	(01)	(12)	1	1	0	3	0	
<i>Proustia cuneifolia</i> f. <i>angustifolia</i>	0	0	1	0	1	0	0	0	1	2	1	2	0	0	1	1	1	2	1	0	0	0	(01)	2	0	1	0	1	1	
<i>Proustia cuneifolia</i> f. <i>cuneifolia</i>	0	0	1	0	1	0	0	0	1	2	1	2	0	0	(01)	1	1	2	1	0	0	0	(01)	2	0	1	0	1	1	
<i>Proustia cuneifolia</i> f. <i>mendocina</i>	0	0	1	0	1	0	1	0	1	2	0	2	0	0	1	1	1	2	1	0	0	0	(01)	2	0	1	0	1	1	
<i>Proustia cuneifolia</i> var. <i>mollis</i>	0	0	1	0	1	0	0	0	1	1	1	2	0	0	1	1	0	2	1	0	0	0	0	0	2	0	1	0	1	1
<i>Proustia cuneifolia</i> f. <i>oblongifolia</i>	0	0	1	0	1	0	0	0	1	1	1	2	0	0	1	1	1	2	1	0	0	0	(01)	2	0	1	0	1	1	
<i>Proustia cuneifolia</i> f. <i>tipia</i>	0	0	1	0	1	0	1	0	1	(12)	1	2	0	0	1	1	1	2	1	0	0	0	(01)	2	0	1	0	1	1	
<i>Proustia ilicifolia</i> f. <i>baccharoides</i>	0	0	0	0	0	0	1	0	1	1	1	2	0	0	1	1	1	2	1	0	1	0	0	0	2	0	1	1	2	
<i>Proustia ilicifolia</i> f. <i>ilicifolia</i>	0	0	0	0	0	0	1	0	1	1	1	2	0	0	1	1	1	2	1	0	1	0	(01)	2	0	1	1	(12)	2	
<i>Proustia pyriformis</i> f. <i>pyriformis</i>	0	1	0	1	0	0	(01)	0	1	(23)	1	2	0	0	1	2	1	2	1	0	0	0	1	?	0	1	0	1	2	
<i>Triptilion achilleae</i>	2	0	0	0	0	1	0	1	1	2	1	0	1	0	1	1	1	1	1	0	0	1	0	1	0	1	1	3	1	
<i>Trixis lessingii</i>	2	0	0	0	0	1	0	1	1	1	1	0	0	0	1	0	0	1	0	1	0	0	(01)	2	1	1	0	1	2	

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