

Generic boundaries in subtribe Saussureinae (Compositae: Cardueae): Insights from Hyb-Seq data

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Abstract The subtribe Saussureinae is a highly speciose group with more than 600 species distributed in the Northern Hemisphere and is particularly species-rich at the high mountains of central and eastern Asia. *Saussurea* and *Jurinea* are the two main genera described within the subtribe. However, up to 15 satellite genera are recognized in some recent taxonomic treatments with an analytical viewpoint. For the first time, we carried out a complete sampling to clarify generic boundaries based on a well-resolved phylogeny of Saussureinae. We employed a Hyb-Seq technique that targets 1061 nuclear conserved ortholog loci designed for Compositae. After a filtering of potential paralogs, 588 loci were retained to infer phylogenetic trees under concatenation and coalescence approaches. High branch support resolution was recovered at the generic level, but a non-monophyletic pattern was detected for most of the genera as they are currently circumscribed. Accordingly, we propose a new generic delimitation based on the three main clades recovered in the backbone tree, which are also in agreement with morphological evidence: *Dolomiaea*, *Saussurea*, and *Jurinea*. Following this classification into three genera, 18 new combinations are proposed. This new genus delineation will be used as a basis for future evolutionary studies in the Saussureinae.

Keywords Asteraceae; *Dolomiaea*; *Jurinea*; phylogenomics; *Saussurea*; taxonomy

Supporting information may be found online in the Supporting Information section at the end of the article.

INTRODUCTION

Saussureinae are one of the subtribes recently described in tribe Cardueae (Compositae or Asteraceae family; [Herrando-Moraira & al., 2019](#)). It is a highly speciose group comprising around 600 species, with two of the largest genera of the Cardueae: *Saussurea* DC., with ca. 400 species, and *Jurinea* Cass., with over 200 ([Lipschitz, 1979](#); [Susanna & Garcia-Jacas, 2007, 2009](#); [Shi & Raab-Straube, 2011](#); [Y.-S. Chen, 2015](#); [Raab-Straube, 2017](#)). Saussureinae comprises unarmed perennial herbs or subshrubs with leaves silver white below and glabrous above. The capitula are cylindrical or globose, often paniculate, homogamous, with achenes with an inner pappus of very long, showy, plumose bristles, basally connate in a ring ([Susanna & Garcia-Jacas, 2007](#)). On morphological basis, the group is well-defined, and it has been traditionally accepted as a natural one ([Susanna & al., 2006](#); [Susanna & Garcia-Jacas, 2007, 2009](#); [Shi & Raab-Straube, 2011](#)). However, molecular confirmation has been long delayed by the difficulties in analyzing the terminal branches of the former subtribe Carduinae, but recent advances in phylogenetics using nuclear data from high-throughput sequencing (HTS) have verified the monophyly of the subtribe ([Herrando-Moraira & al., 2018, 2019](#)).

As a general geographic distribution, Saussureinae are located in the Northern Hemisphere. It is particularly species-rich in the high mountains (>1000 m above sea level) of central and eastern Asia. *Saussurea* and *Jurinea*, the main genera, represent excellent models to explore mountain radiations across the Northern Hemisphere regions ([Wen & al., 2014](#); [Xu & al., 2019](#)). *Saussurea* has spectacularly radiated in the Himalayas, the Qinghai-Tibetan Plateau and particularly in the adjacent Hengduan mountains. *Jurinea* has radiated in the Middle Asia mountains, the Tian Shan and the Pamir-Alai.

A clarification of the generic limits is a mandatory first step to obtain independent phylogenies for the two main genera. The problem arises from the high number of small genera segregated from *Saussurea* and *Jurinea*. These are *Aegopordon* Boiss., *Anacantha* (Iljin) Soják, *Aplotaxis* DC., *Aucklandia* Falc., *Boloecephalus* Hand.-Mazz., *Diplazoptilon* Y.Ling, *Dolomiaea* DC., *Frolovia* (DC.) Lipsch., *Hemisteptia* Fisch. & C.A.Mey., *Himalaiella* Raab-Straube, *Hyalochaete* Dittrich & Rech.f., *Jurinella* Jaub. & Spach, *Lagurostemon* Cass., *Lipschitzella* Kamelin, *Mazzettia* Iljin, *Modestia* Kharadze & Tamamsch., *Outreya* Jaub. & Spach, *Perplexia* Iljin, *Pilostemon* Iljin, *Polytaxis* Bunge, *Theodorea* Cass., and *Vladimiria* Iljin. Differences in recent treatments are striking ([Table 1](#)) and include from a wide concept of *Saussurea* and *Jurinea* ([Susanna & Garcia-Jacas, 2009](#)) to the extreme analytical view of [Shi & Raab-Straube \(2011\)](#). Traditional syntheses of Compositae ([Bentham, 1873](#); [Hoffmann, 1894](#); [Dittrich, 1977](#); [Bremer, 1994](#)) also differ significantly and without agreement in the classification. Some of the described genera are no longer accepted in major Floras or taxonomic treatments ([Table 1](#)), and they are synonymized under *Saussurea* (*Aplotaxis*, *Lagurostemon*, *Theodorea*), under *Jurinea* (*Perplexia*), or under *Dolomiaea* (*Mazzettia*, *Vladimiria*). To delineate an updated generic classification, the affinities of the rest of genera should be examined.

One of the main reasons for this proliferation of segregates is that almost all the morphological comparisons were made to *Saussurea*, not to *Dolomiaea* or *Jurinea*, and most of them were based on achene characters. The smooth achenes of *Saussurea* s.str. are quite uniform, but the achenes of *Dolomiaea* and *Jurinea* are highly variable: they are usually wrinkled, sulcate, pitted or diversely ridged, and prone to develop protrusions, horns or coronules (see especially [Häffner, 2000](#)) that have been overinterpreted. An example of this is the traditional but polyphyletic circumscription of *Saussurea* by [Lipschitz \(1954, 1979\)](#), the source of a considerable part of segregate genera (e.g., from *S.* subg. *Jurinocera* to *Lipschitzella* [[Kamelin, 1993](#)], from *S.* sect. *Frolovia* to *Frolovia* [[Lipschitz, 1954](#)], or *S.* sect. *Elatae* to *Himalaiella* [[Raab-Straube, 2003](#)]).

Another challenge within the study of Saussureinae's systematics is that most of the species are adapted to the extreme environments like those found at higher elevations (even beyond 5000 m) or dry habitats ([Shi & Raab-Straube, 2011](#); [Raab-Straube, 2017](#); [Szukala & al., 2019](#)). As a consequence, taxonomists could have interpreted as synapomorphies some traits resulting from convergent/parallel evolution (homoplastic characters) that have emerged multiple times across the subtribe. [Wang & al. \(2009\)](#) already pointed out that the special "glasshouse" habit of some species of *Saussurea* appeared several times in different sections of the genus. Certainly, molecular characters and phylogenetic evidence would aid to discard misclassifications based on morphological adaptations ([Huang & al., 2015](#)).

Under a phylogenetic approach, some attempts have been made, but the phylogenetic studies with a wider taxon sampling were generally focused only on *Saussurea* ([Raab-Straube, 2003](#); [Kita & al., 2004](#); [Wang & al., 2009](#); [Xu & al., 2019](#)) or only on *Jurinea* ([Szukala & al., 2019](#)). At the moment, none of the 12 existing phylogenetic studies has reunited a comprehensive sampling of the segregate genera (see [suppl. Table S1](#) for a summary of phylogenetic studies performed and genus sampling). The most complete ones gathered a generic coverage of 71% in [Susanna & al. \(2006\)](#) and 65% in [Szukala & al. \(2019\)](#) (see

suppl. Table S1) The monophyly of the non-monotypic segregate genera (>1 sp.) has not been evaluated because published studies only included one species (for *Diplazoptilon*, *Modestia*, and *Pilostemon*). When several species have been included, most genera were paraphyletic or polyphyletic (*Aegopordon*, *Dolomiaea*, *Frolovia*, *Himalaiella*, *Jurinella*, *Lipschitzella*). One notable exception is *Polytaxis*, from which the two sampled species formed a strongly supported monophyletic group (Susanna & al., 2006; Yuan & al., 2015).

Despite these limitations, several clades have been recovered by molecular data (see an overview in Fig. 1): (1) the “Saussurea clade”: it includes *Hemisteptia* and *Polytaxis*, which are clustered as sister to the Saussurea s.str. clade, in which is deeply anchored *Diplazoptilon picridifolium* (Hand.-Mazz.) Y.Ling; (2) the “Dolomiaea clade”: it includes *Dolomiaea*, *Aucklandia*, *Boloecephalus*, and *Frolovia*; (3) the “Himalaiella clade”: it includes *Himalaiella*, *Lipschitzella*, *Pilostemon*, and *Diplazoptilon cooperi* (J.Anthony) C.Shih; and (4) the “Jurinea clade”: it includes *Aegopordon*, *Hyalochaete*, *Jurinella*, *Modestia*, and *Outreya*, which are closely related to, or nested in, the *Jurinea* s.str. clade. Among these four clades, the only supported sister relationship was found between *Himalaiella* (clade 3) and *Jurinea* (clade 4). The relationships of this group (clades 3+4) with *Dolomiaea* (clade 2) and *Saussurea* (clade 1) remain unresolved (Fig. 1), although as a general trend *Saussurea* (clade 1) is recovered sister to the others (clades 2+3+4).

The exploration of Saussureinae phylogeny has also been difficult due to the lack of informative phylogenetic signal provided by traditional Sanger sequence markers (see references in suppl. Table S1). Previous studies failed to recover a supported dichotomous bifurcating pattern, and most of the species analyzed were anchored into large polytomies especially on trees performed with plastid datasets (Kita & al., 2004; Wang & al., 2009). Rapid species diversification has been proposed as the most plausible reason for the resulting unresolved trees. However, the emergence of HTS techniques represents a promising tool for the clarification of Saussureinae radiation (Herrando-Moraira & al., 2018; Xu & al., 2019; Zhang & al., 2019). As an example, in a comparison of two *Saussurea*-focused studies, the phylogenetic informative sites vary from 2%, in that performed with *trnL-F* and *psbA-trnH* markers (Wang & al., 2009), to 38%, in that including whole chloroplast genomes (Xu & al., 2019).

Here, in view of the well-resolved phylogenies obtained in preliminary works on tribe Cardueae (Herrando-Moraira & al., 2018, 2019), we used the same Hyb-Seq HTS approach based on a probe set of 1061 nuclear conserved ortholog loci (hereafter COS, for Conserved Ortholog Set; Mandel & al., 2014) with the following goals: (1) to obtain a well-resolved phylogeny of subtribe Saussureinae with a complete genus sampling; and (2) to test the validity of the genera described or accepted in recent taxonomic treatments based on phylogenetic evidence.

MATERIALS AND METHODS

Taxon sampling. — Our sampling comprised for the first time a full generic representation of Saussureinae, including all the genera currently accepted in the analytical treatments (Häffner, 2000; Raab-Straube, 2003; Shi & Raab-Straube, 2011). We analyzed in total 17 genera, represented by 112 different species and 138 individuals (indiv.; note that more than one specimen per species was included when possible): *Aegopordon* (2 sp., 3 indiv.), *Aucklandia* (1 sp.), *Boloecephalus* (1 sp.), *Diplazoptilon* (2 sp.), *Dolomiaea* (9 sp., 15 indiv.), *Frolovia* (5 sp.), *Hemisteptia* (1 sp., 2 indiv.), *Hyalochaete* (1 sp.), *Himalaiella* (11 sp., 19 indiv.), *Jurinea* (31 sp., 32 indiv.), *Jurinella* (4 sp., 10 indiv.), *Lipschitzella* (2 sp., 3 indiv.), *Modestia* (= *Anacantha*, 1 sp.), *Outreya* (1 sp.), *Pilostemon* (1 sp.), *Polytaxis* (2 sp.), and *Saussurea* (36 sp., 39 indiv.). Two species of *Jurinea* (*J. cartilaginea* Mozaff., *J. gedrosiaca* Bornm.) that have been moved to genera *Karvandarina* Rech.f. and *Tricholepis* DC., respectively from Centaureinae (Mirtadzadini & al., 2018, 2019; Szukala & al., 2019) were included to confirm their new generic identity. Based on Herrando-Moraira & al. (2018, 2019), we included 13 representatives of the genera *Arctium* L. and *Cousinia* Cass. from the sister subtribe Arctiinae. We also added 6 members of Centaureinae, 4 of Carduinae, 2 of Onopordiinae, and 2 of Staehelininae. Vouchers and accession numbers are detailed in Appendix 1. From the total sampling (167), 97 individuals were newly sequenced in this study, and the remaining 70 were obtained from raw reads sequenced on previous studies (Mandel & al., 2014, 2019; Herrando-Moraira & al., 2018, 2019; Jones & al., 2019) (see suppl. Table S2).

DNA extraction, library preparation, sequence capture, and sequencing. — Total genomic DNA was obtained from dried leaf material from herbarium collections for most of the species (Appendix 1). From the leaves, around 10–30 mg per sample were selected and homogenized with a Mixer Mill MM 301 (Retsch, Haan, Germany). Then, the E.N.Z.A SP Plant

DNA Mini Kit (Omega Bio-Tek, Norcross, Georgia, U.S.A.) was used to extract the DNA following manufacturer's specifications. The quantity of the extracted DNA was measured with the Qubit 3.0 Fluorometer (Thermo Scientific, Waltham, Massachusetts, U.S.A.), which was used to standardize the amount of DNA in all the samples (1 µg in 70 µl). The DNA was fragmented in microTUBEs using a Covaris S2 Biodisruptor from the Genomics Unit of the Centre for Genomic Regulation (CRG, Barcelona, Spain). For the shearing step, a target size of 400 bp on average was selected. The libraries were constructed using the NEBNext Ultra II DNA Library Prep kit for Illumina (New England Biolabs, Ipswich, Massachusetts, U.S.A.), which then were pooled in groups of 4 samples and the target COS loci enriched with MyBaits COS 1Kv1 (MYcroarray, Ann Arbor, Michigan, U.S.A.). For protocol details of library and capture preparation see [Herrando-Moraira & al. \(2018\)](#). Before sequencing, we additionally conducted a spiking procedure combining 40% of pre-capture libraries with 60% of post-capture library solution. The final spiked samples were sequenced in the DNA Sequencing Core CGRC/ICBR of the University of Florida using one lane of an Illumina HiSeq 3000 with a 100 bp paired-end format.

Extraction of target-enriched sequences. — The quality control evaluation of raw reads was performed with FastQC v.0.10.1 (<https://www.bioinformatics.babraham.ac.uk/projects/fastqc/>). Then, we used the software Trimmomatic v.0.36 ([Bolger & al., 2014](#)) to obtain a cleaned read set: trimming the Illumina adapters, removing reads that did not pass the defined quality threshold (sliding-window set to 5:20), and finally discarding short cleaned reads (<36 bp length) or with a missing forward or reverse pair.

The extraction of the 1061 target COS loci was conducted with the easy-to-use workflow of HybPiper pipeline v.1.1 ([Johnson & al., 2016](#)). With this method, a first mapping step of cleaned reads to targets is conducted with BWA mapper ([Li & Durbin, 2009](#)). Secondly, the assembler SPAdes ([Bankevich & al., 2012](#)) was used to obtain the contigs, performing a *de novo* assembly of the reads previously mapped to targets. In the case of several coexisting contigs for a same target locus (potential paralogs), HybPiper is designed to finally retain only one contig through a series of hierarchical decisions (for details see [Johnson & al., 2016](#)), but flagging these loci as potential paralogs. To prevent the problems of inclusion of loci potentially affected by paralogy, we did not include them in downstream analyses.

The individual multi-fasta files obtained for each COS locus were aligned using the *auto* setting mode of MAFFT v.7.266 ([Katoh & Standley, 2013](#)). To remove the ambiguously aligned regions from the aligned sequence files, we applied the *automated1* flag of trimAl v.1.4 ([Capella-Gutiérrez & al., 2009](#)). A short length locus (6 bp) that was recovered after the alignment trimming and two loci recovered for less than three species were not included in the final used matrices. In order to conduct two different phylogenetic inference methods (see below), we created two sequence datasets. One consisted in the separate trimmed alignments for each locus, and the other consisted in a single supermatrix file obtained from the concatenation of all trimmed aligned loci with FASconCAT-G v.1.02 ([Kück & Longo, 2014](#)). For the supermatrix, a set of summary statistics were calculated using AMAS ([Borowiec, 2016](#)).

Phylogenetic inference analyses. — To reconstruct the phylogeny of Saussureinae, two complementary approaches were employed: the concatenation approach (using the supermatrix dataset as input) and the coalescence approach (using the separate matrices of each locus).

For the concatenation approach, the sequence data were analyzed under maximum likelihood (ML) assumptions using RAxML v.8.2.9 ([Stamatakis, 2014](#)). The method selected was a simultaneous rapid bootstrapping of 1000 replicates to assess branch support, and best ML tree search with 10 randomized maximum parsimony starting trees. The branches with bootstrap support (BS) >70% were considered statistically well supported ([Hillis & Bull, 1993](#)). As partition scheme, each locus was treated as a unit evolving under the model GTRGAMMA following the recommendations of [Stamatakis \(2006\)](#). The ML analysis was conducted on XSEDE in the CIPRES Science Gateway v.3.1 ([Miller & al., 2010](#)).

For the coalescence approach, we first estimated the individual gene trees for each locus using RAxML under the same conditions as specified above, but this time with a bootstrap resampling of 200 replicates. Second, a summary statistic method as implemented in ASTRAL-III v.5.5.3 ([Zhang & al., 2018](#)) was used to estimate the species tree from the previous set of gene trees. Default parameters were selected for the ASTRAL running. Branch support values were calculated using local posterior probabilities (LPP; [Sayyari & Mirarab, 2016](#)), and values of LPP > 0.95 were considered as branches strongly supported. Resulting trees from both methods were visualized in FigTree v.1.4.3 ([Rambaut, 2016](#)). Alignments and tree files for each dataset are deposited in Mendeley Data repository (<https://doi.org/10.17632/hrmyfhpb5c.2>) with initial-tested and definitive-proposed final taxon names.

RESULTS

Sequencing efficiency and target loci recovery. — On average 6,450,918 (SD = $\pm 4,420,030$) of raw sequence reads were sequenced per species (see details in [suppl. Table S2](#)). The sequence efficiency was notably different among some species (e.g., the ones with lowest and highest number of raw reads were *Cynara cardunculus* L. with 454,885 and *Dolomiaea baltalensis* Dar & Naqshi with 42,600,816, respectively). From the total 1061 target COS loci, we were able to recover 1054, which represents 99.3% of targets ([Table 2](#)).

After a step of loci filtering (by potential paralogy, short length, and poor species recovery; see Methods for details), 588 loci were retained in our final dataset, representing approximately half of the targets (55.4%; [Table 2](#)). From these loci finally used, 86.6% were captured in $\geq 90\%$ of species and were on average 336 bp of alignment length ([Table 2](#)). The concatenation of the 588 loci resulted in a supermatrix of 197,784 bp with 46.7% of variable sites, 31.3% of parsimony-informative sites, and 12.6% of missing data ([Table 2](#)). Raw sequence data are deposited at the National Center for Biotechnology Information (NCBI) Sequence Read Archive (see [suppl. Table S2](#) for BioProjects codes for each species).

Phylogenetic analyses. — The two species recently excluded from Saussureinae, *Jurinea cartilaginea* and *J. gedrosiaca*, and currently considered as *Karvandarina cartilaginea* (Mozaff.) Parishani & al. and *Tricholepis edmondsonii* Rech.f., respectively, were placed with high confidence within Centaureinae ([Figs. 2, 3](#)). Considering this exclusion, Saussureinae formed a highly supported and monophyletic group itself (BS = 100 and LPP = 1), which was recovered as sister to Arctiinae.

Deep tree branches of Saussureinae phylogenies resulted in highly supported topologies ([Figs. 2, 3](#)). Otherwise, branch support resolution decreased gradually in internal nodes closer to the tips, especially at close species relationships. All genera with more than three species (*Dolomiaea*, *Frolovia*, *Himalaiella*, *Jurinea*, *Jurinella*, *Saussurea*) were recovered as non-monophyletic assemblies ([Figs. 2, 3](#)) as currently circumscribed ([Table 1](#)). Some of the genera with less than four species (*Aegopordon*, *Aucklandia*, *Bolocephalus*, *Diplazoptilon*, *Modestia*, *Outreya*, *Pilostemon*) appeared nested within one of the large genera mentioned above, while the others emerged as separate distant lineages sister to more speciose clades (*Hemisteptia*, *Hyalochaete*, *Lipschitzella*, *Polytaxis*; [Figs. 2, 3](#)).

Comparing the trees inferred with the two approaches (concatenation and coalescence), we found that both showed almost identical topologies under a generic-level focus ([Figs. 2, 3](#)). Exceptions regarding the positions of *Lipschitzella*, *Hemisteptia*, and *Polytaxis* were detected. *Lipschitzella* was recovered as sister to a diverse clade composed mainly of *Himalaiella* under the concatenation approach ([Fig. 2](#)), while under coalescence it was embedded in that clade but not statistically supported as sister to all other members ([Fig. 3](#)). *Hemisteptia* was resolved as sister to the *Polytaxis*+*Saussurea* clade under concatenation ([Fig. 2](#)), and conversely, *Polytaxis* was sister to *Hemisteptia*+*Saussurea* under coalescence but without support (LPP = 0.46; [Fig. 3](#)). In general, the tree inferred under the coalescence approach ([Fig. 3](#)) resulted in lower resolution and support than the one obtained under the concatenation approach ([Fig. 2](#)), particularly for shallow nodes close to the tree tips.

Overall, three main lineages were recovered at the backbone of the trees with maximum statistical support (BS = 100 and LPP = 1; [Figs. 2, 3](#)): (1) the *Dolomiaea* clade, composed of *Dolomiaea* and some segregates, namely *Aucklandia*, *Bolocephalus*, and most *Frolovia*; (2) the *Saussurea* clade, including the bulk of *Saussurea*, *Diplazoptilon*, *Polytaxis*, and *Hemisteptia*; and (3) the *Jurinea* clade, comprising *Jurinea*, *Aegopordon*, some *Frolovia*, *Himalaiella*, *Hyalochaete*, *Jurinella*, *Lipschitzella*, *Modestia*, *Outreya*, *Pilostemon*, and some species of *Saussurea*. The first diverging lineage within the subtribe was the *Dolomiaea* clade that emerged as sister to the remainder. The next two diverging lineages were the *Saussurea* clade and the *Jurinea* clade that formed a sister-group relationship.

Within the *Dolomiaea* clade, two highly supported groups were found. One was primarily composed of *Dolomiaea* species and *Bolocephalus* (BS = 100 and LPP = 1), and the other by two *Dolomiaea* species, *Frolovia*, and *Aucklandia* (BS = 100 and LPP = 0.97; [Figs. 2 and 3](#)). *Frolovia* appeared in three separate clades, highly supported themselves ([Figs. 2, 3](#)): (1) three species of *Frolovia* were clustered with two of *Dolomiaea* (BS = 100 and LPP = 1); (2) *Frolovia frolovii* (Ledeb.) Raab-Straube was clustered with *Aucklandia* (BS = 100 and LPP = 1); and (3) *Frolovia gilesii* (Hemsl.) B.A.Sharipova was placed within the *Jurinea* clade with *J. chondrilloides* (C.Winkl.) O.Fedtsch., *J. karategina* (Lipsky) O.Fedtsch. [*Pilostemon*], and *Saussurea leptophylla* Hemsl. [*Jurinea ancistrophylla* Boiss.] (BS = 94 and PP = 0.86).

Regarding the *Saussurea* clade, we found that *Diplazoptilon* (*D. picridifolium*) was completely embedded within the *Saussurea* genus ([Figs. 2, 3](#)). Conversely, *Polytaxis* was placed as sister to *Saussurea*, and *Hemisteptia* as sister to *Polytaxis*+*Saussurea*. The two species of *Polytaxis* were clustered together with the maximum support (BS = 100 and LPP =

1; Figs. 2, 3), as well as the two individuals of *Saussurea lyrata* (Bunge) Sch.Bip [*Hemisteptia*].

The *Jurinea* clade presented two main highly supported groups (BS = 100 and LPP = 1; Figs. 2, 3), a first one including *Jurinea* s.str., *Aegopordon*, *Hyalochaete*, *Jurinella*, *Modestia*, and *Outreya*; and the second one including *Himalaiella*, *Lipschitzia*, *Pilostemon*, and *Frolovia*, in addition to *Jurinea chondrilloides* and *Diplazoptilon cooperi* (outlined as *Saussurea yakla* C.B.Clarke on the Figures). Within the first group, *Hyalochaete* was recovered as the sister lineage. *Aegopordon* was placed at the core of *Jurinea* species, specifically *A. berardioides* Boiss. nested with *J. carduiformis* (Jaub. & Spach) Boiss. [*Outreya*] (BS = 100 and LPP = 1) and *A. fontqueri* (Cuatrec.) Tscherneva with *J. pinnata* (Pers.) DC. (BS = 100 and LPP = 1). *Modestia* (= *Anacantha*) was also deeply embedded within the *Jurinea* s.str. clade. *Jurinella* was recovered in two well-defined and separate clades with a clear polyphyletic pattern. Within the second group of the *Jurinea* clade, *Himalaiella* also resulted as a polyphyletic assembly, occurring in several supported clades. *Pilostemon* appeared highly related to *Jurinea chondrilloides* (BS = 100 and LPP = 1). Under the coalescence approach, we did not obtain enough branch support resolution at the internal nodes of this group, the included species emerging in a considerable polytomy with some supported small groups of species (Fig. 3).

DISCUSSION

Applicability of Hyb-Seq on Saussureinae phylogeny. — The present study includes for the first time a complete genus-level sampling of Saussureinae in a phylogenetic framework (suppl. Table S1). This sampling improvement was increased using herbarium material, in which the DNA is usually highly degraded and sometimes can be difficult to amplify with Sanger sequencing technologies. With the second generation of sequencing methods, the efficiency of target loci capture is remarkably high even with old herbarium samples. For example, here we recovered in total 99.3% of the initial target set, and 91.2% from a sample from 1899 (*Saussurea lyrata* [*Hemisteptia*] individual 2). Therefore, as also pointed out by other Hyb-Seq studies (Hart & al., 2016; Villaverde & al., 2018; Brewer & al., 2019; Viruel & al., 2019), the use of herbarium material represents a step forward to sort out plant systematics on groups highly speciose, distributed on remote or politically unstable regions, such as Saussureinae.

In recent years, most phylogenomic studies conducted on Compositae have successfully employed the Hyb-Seq technique based on 1061 COS loci, at family (Mandel & al., 2014, 2015, 2017, 2019; Jones & al., 2019), tribe (Herrando-Moraira & al., 2019; Siniscalchi & al., 2019), and genus level (Herrando-Moraira & al., 2018; Thapa & al., 2019). For Saussureinae, this method also allowed to recover a well-supported phylogeny. Sequencing of whole plastid genomes is becoming another widely used method within HTS techniques. However, we detected considerable differences in generic placements between the present study and another performed with plastid genomes by Xu & al. (2019). The plastid phylogeny recovered *Himalaiella* as a part of the *Dolomiaea-Aucklandia-Bolocephalus* clade. This grouping has never been found previously (see Fig. 1), not even in Sanger plastid phylogenies (e.g., Wang & al., 2007). Moreover, in Xu & al. (2019) and also in a study with 20 whole plastomes of *Saussurea* (Zhang & al., 2019), the three main clades recovered showed incongruent topologies when the whole plastid genome and the protein-coding regions from the chloroplast were analyzed separately. Although these results could be due to a poor taxon sampling effect, plastid HTS datasets could tend to produce phylogenetic misplacements but with maximum support values in rapidly radiated lineages like Saussureinae species (e.g., *Oxalis* L., Schmickl & al., 2016). Actually, Herrando-Moraira & al. (2019) already detected incongruence between nuclear and plastid Cardueae phylogenies and discussed the possible causes, which could be added to the differences in taxon sampling between the present work and that of Xu & al. (2019): (1) phylogenetic informativeness much higher in nuclear than in plastid phylogenies; (2) incomplete lineage sorting; and (3) past or current hybridization events. Further studies are needed to explore these differences on nuclear/plastid HTS phylogenies and under concatenation/coalescence approaches.

Generic limits delineation. — Our results call for a reclassification of Saussureinae genera. Taxonomic entities should be ideally based on monophyletic clades. Considering an extremely analytical circumscription that splits the subtribe in 17 genera, we did not find monophyly for almost any of them (see Fig. 4, tree on the left). Along the tree backbone (Figs. 2, 3), three major fully supported lineages emerged that have also been already retrieved in previous studies (Fig. 1): *Dolomiaea*, *Saussurea*, and *Jurinea*. A new generic delimitation based on these three lineages is proposed here under a synthetic point of view (Fig. 4). This treatment seems well-justified according to both molecular and morphological characters, as discussed below. In general terms, the diagnostic morphological characters of segregate genera fall into the broad variability of the three

large lineages *Dolomiaea*, *Saussurea*, or *Jurinea* as previously pointed out by [Susanna & Garcia-Jacas \(2007\)](#). A question that our work leaves open is the subgeneric and sectional classification of the three resulting genera. This classification is especially needed for the two largest ones, *Jurinea* and *Saussurea*. However, this is an extremely complicated issue (see [Y.-S. Chen, 2015](#) and [Szukala & al., 2019](#) for the artificial classification of *Saussurea* and *Jurinea*, respectively) that further work will try to resolve.

Dolomiaea clade. — Besides *Dolomiaea*, three other genera fall deeply nested within this clade: *Aucklandia*, *Bolocephalus*, and *Frolovia* (Figs. 2, 3). All published phylogenies including these genera have found the same grouping pattern (see references and trees in Fig. 1). Within this clade, two highly supported groups emerged, one composed of *Dolomiaea* and *Bolocephalus* and the other of *Dolomiaea*, *Frolovia* and *Aucklandia* (Figs. 2, 3), which included two clades: some *Dolomiaea* + some *Frolovia* and one *Frolovia* + *Aucklandia* (Figs. 2, 3). This points out that both *Dolomiaea* and *Frolovia* as currently described are polyphyletic. In addition, one member of *Frolovia* (*F. gilesii*), which was sequenced for the first time, was placed in the distant *Jurinea* clade (Figs. 2, 3; see more discussion in the *Jurinea* clade section). Undoubtedly, the description of *Frolovia* and *Aucklandia* as sections within *Saussurea* (*S. sect. Frolovia* and *S. sect. Aucklandia*, respectively) reflects that they do not fit into *Saussurea* s.str. ([Lipschitz, 1954, 1961, 1962, 1979](#); [Kamelin, 1993](#); [Kamelin & Kovalevskaja, 1993](#)). *Frolovia* has also been compared to *Jurinea*, but [Raab-Straube \(2003\)](#) claimed that differences in pappus structure prevented its inclusion in this genus. *Aucklandia* has experienced multiple taxonomic changes, being combined as *Aplotaxis*, *Saussurea*, and *Theodorea* ([Kasana & al., 2018](#)). However, from the initial phylogenetic trees (Fig. 1) to the current phylogenomic ones (Figs. 2, 3), both genera are nested within *Dolomiaea*. Accordingly, [Susanna & al. \(2006\)](#) and [Wang & al. \(2007\)](#) already called for a broad redefinition of *Dolomiaea* including *Frolovia*, but without making the formal changes. In our attempt to define monophyletic groups and considering molecular evidence, we also propose that *Frolovia* and *Aucklandia* should be synonymized under *Dolomiaea*. The monotypic *Bolocephalus* was already formally transferred to *Dolomiaea* by [Y.-L. Chen & Shih \(1981\)](#), and also marked as doubtful genus by [Shi & Raab-Straube \(2011\)](#). Our molecular data and the plastid phylogeny reported in [Xu & al. \(2019\)](#) confirm its inclusion within the *Dolomiaea* clade.

Saussurea clade. — The second clade recovered is mainly composed of *Saussurea* s.str. together with the genera *Diplazoptilon*, *Hemisteptia*, and *Polytaxis* (BS = 100 and LPP = 1; Figs. 2, 3). All previous phylogenies have unanimously identified this generic grouping (Fig. 1). *Diplazoptilon* was already transferred back to *Saussurea* by [Yuan & al. \(2015\)](#), and we will comment only the cases of *Hemisteptia* and *Polytaxis*. Both genera have always emerged as a sister group to *Saussurea* s.str. (Figs. 1–3). However, which genus is sister to *Saussurea* remains an open question since the tree topology differed between both inference approaches.

Hemisteptia has been merged into *Saussurea* several times ([Susanna & Garcia-Jacas, 2007, 2009](#)). On the contrary, *Polytaxis* has never been transferred to any other genus since its description. Among the three genera, micromorphological differences in pappus and achene structure have been proposed as diagnostic traits ([Häffner, 2000](#)). Additionally, the life-history trait has been assigned as another distinctive character, *Hemisteptia* and *Polytaxis* being annual plants and *Saussurea* mainly perennials. Despite this, phylogenies of other groups within tribe Cardueae also found that annual species are often resolved as sister to the remaining perennial ones (in *Cousinia* in [López-Vinyallonga & al., 2009](#); in *Echinops* L. in [Garnatje & al., 2005](#)). To what extent the inclusion of annual/perennial species in a single phylogeny would bias tree topologies due in part to generation time effect of neutral molecular markers is still open to discussion and requires further methodological exploration ([Andreasen & Baldwin, 2001](#); [Yue & al., 2010](#); [Gaut & al., 2011](#)). Furthermore, at least one species of *Saussurea* (*S. kingii* J.R.Drumm. ex C.E.C.Fisch.) is an annual herb ([Shi & Raab-Straube, 2011](#); [Y.-S. Chen, 2015](#)), and in a recent plastid phylogenomic study it appeared as sister to the species of the informal “Clade 3” defined by [Xu & al. \(2019\)](#). These facts point out that life form alone would not be a useful diagnostic character to segregate *Hemisteptia*-*Polytaxis* from *Saussurea*.

The only other character alleged by [Shi & Raab-Straube \(2011\)](#) for segregating *Hemisteptia* from *Saussurea* is the pappus structure: double with an incomplete outer row of very short scales and an inner row of plumose bristles in *Hemisteptia*; double with an outer row of long, scabrid bristles and plumose inner bristles in *Saussurea*. However, some species of *Saussurea* have a very reduced or even missing outer pappus and, according to the key of the genera by [Shi & Raab-Straube \(2011\)](#), all species of *Saussurea* have an inner pappus of plumose bristles, as pointed out repeatedly by [Häffner \(2000\)](#) and [Susanna & Garcia-Jacas \(2007\)](#). Moreover, [Kita & al. \(2004\)](#) made an extensive revision of the achenes of *Saussurea* and *Hemisteptia* and did not find any character separating both genera. In the case of *Polytaxis*, the genus shows two autoapomorphic characters not found elsewhere in the whole Cardueae: presence in the pericarp of resin-ducts and long,

slender hairs according to Häffner (2000), who very accurately pointed out: “The possibility of *Polytaxis* being an advanced and morphologically strongly deviant representative of e.g. the *Jurinea* or *Saussurea* group can not be excluded.” The deviating achene of *Polytaxis*, when compared to the typical one of *Saussurea*, is the same case as in the purported genera *Cnicus* L. or *Stephanochilus* Coss. & Durieu ex Benth. & Hook.f., described on the basis of very peculiar achenes and now merged into *Centaurea* L. (Font & al., 2002; Garcia-Jacas & al., 2006). In summary, considering phylogenetic evidence and the morphological characters shared by the three genera (floral morphology and pappus structure), we favor the inclusion of *Hemisteptia* and *Polytaxis* in *Saussurea*, which remains a monophyletic and well-defined genus.

Jurinea clade. — Firstly, our results confirm the exclusion of *Jurinea cartilaginea* (currently classified as *Karvandarina cartilaginea*) and *Jurinea gedrosiaca* (considered a synonym of *Tricholepis edmondsonii*) from *Jurinea* and even from *Saussureinae*. We shall now review the fate of the genera that appear nested in the *Jurinea* clade. Some of them (*Aegopordon*, *Anacantha*, *Hyalochaete*, *Jurinella*, *Outreya*, *Pilostemon*) were already shown to be part of *Jurinea* s.str. (Susanna & al., 2006), and we will focus on the most disputed ones, i.e., *Himalaiella* and *Lipschitziella*.

When examining the resurrection of both genera by Raab-Straube (2003), we can see that all the comparisons were made to *Saussurea*, and not to *Jurinea*. Species of *Himalaiella* and *Lipschitziella* would be aberrant in *Saussurea* because their achenes are very different from *Saussurea* (for a detailed and well-illustrated description, see Häffner, 2000). However, the achenes of *Himalaiella* or *Lipschitziella* would not be so discording in *Jurinea* as already pointed out as early as 1873 (!) by Benth (1873: 474), who suggested that *Saussurea ceratocarpa* Decne. (*Lipschitziella ceratocarpa* (Decne.) Kamelin in Raab-Straube, 2003) should be included in *Jurinea*. We have confirmed this suggestion, because *L. ceratocarpa* was nested in *Jurinea* in Herrando-Moraira & al. (2018), and our current results also support it. As for the very characteristic habit of *Himalaiella*, described as having “large, nodding capitula” (Raab-Straube, 2003), this is obviously a case of convergent evolution, an adaptation to mountain conditions that has appeared several times in the Cardueae and in other tribes of Compositae. Species of the unrelated genera *Alfredia* Cass. and *Synurus* Iljin (Onopordinae) and some species of *Cirsium* Mill. (Carduinae) show this habit, as well as *Saussurea qinghaiensis* S.W.Liu & T.N.Ho (Y.-S. Chen, 2015). Subalpine species with large, nodding heads appear in *Lasiocephalus* of tribe Senecioneae (Silva-Moure & al., 2013). In fact, *Himalaiella* is not monophyletic (Fig. 2) because species of the genus are scattered in two different clades. In one of the clades, *Himalaiella albescens* (DC.) Raab-Straube, *H. chenopodiifolia* (Klatt) Raab-Straube and *H. chitralica* (Duthie) Raab-Straube are grouped with species that share the typical morphology of *Jurinea* s.str., like *J. chondrilloides*, *J. karategina*, and *Saussurea leptophylla* [*Jurinea ancystrophylla*], and even with *Saussurea gilesii* Hemsl., a species wrongly included in *Frolovia* (Fig. 2). It was already suggested that *Saussurea gilesii* is closer to *Jurinea*: a note by Rechinger points out that *Jurinea kerstanii* Bornm. is the same as *Saussurea gilesii* (K.H. Rechinger in schedis, herbarium W). The rest of species of *Himalaiella*, including the type, *H. heteromalla* (D.Don) Raab-Straube, form a robust clade. However, segregating *Himalaiella* would leave *Jurinea* paraphyletic and, in view of the adaptive character of habit and the remarkably close similarities of the achenes to those of *Jurinea*, we strongly favor keeping it in a broadly defined *Jurinea*.

TAXONOMIC IMPLICATIONS

Subtr. **Saussureinae** N.Garcia & Susanna in Molec. Phylogen. Evol. 137: 329. 2019

Unarmed perennial herbs or subshrubs, very rarely annual herbs. Leaves entire or pinnatisect, often silver-white below and glabrous above, sometimes hirsute-scabrid. Capitula cylindrical or globose, often paniculate, homogamous, discoid. Involucral bracts with short appendages, unarmed. Receptacle densely setose or rarely naked. Anther filaments glabrous, rarely papillose. Styles long, with reflexed lobes. Achenes cylindrical, slightly obconical or obpyramidal, indistinctly ribbed to costate, surface smooth or transversally rugose, very rarely with spines or scales, with or without a crown; apical plate with a persisting style base, without caruncle. Pappus of very long (overtopping involucral bracts), showy, scabrid or plumose bristles in one or more usually several rows, often dimorphic; inner bristles basally connate in a ring, persistent or detachable as a single piece, outer ones shorter, bristle-like or scaly, rarely missing, freely deciduous. Genera included in the subtribe: *Dolomiaea*, *Jurinea* and *Saussurea*.

Dolomiaea DC. in Arch. Bot. (Paris) 2: 330. 1833 – Type: *Dolomiaea macrocephala* DC.

= *Aucklandia* Falc. in Ann. Mag. Nat. Hist. 6: 475. 1841 – Type: *Dolomiaea costus* (Falc.) Kasana & A.K.Pandey.

- = *Aplotaxis* [unranked] *Frolovia* DC., Prodr. 6: 538. 1868 ≡ *Frolovia* (DC.) Lipsch. in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 16: 461. 1954, **syn. nov.** – Type: *Dolomiaea frolovii* (Ledeb.) Kasana & A.K.Pandey.
- = *Bolocephalus* Hand.-Mazz. in J. Bot. 76: 291. 1938 – Type: *Dolomiaea saussureoides* (Hand.-Mazz.) Y.L.Chen & C.Shih.
- = *Vladimiria* Iljin in Sovetsk. Bot. 1939(8): 55. 1939 ≡ *Mazzettia* Iljin in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 17: 443. 1955 – Type: *Dolomiaea salwinensis* (Hand.-Mazz.) C.Shih.

Perennial herbs, often rosulate and acaulescent or shortly caulescent and subscapose, very rarely long-stemmed to 0.6–1(2) m. Leaves usually dentate or lobed, rarely entire, hirsute-spinulose above, often densely wooly below. Capitula solitary clustered in the center of a rosette or rarely terminal and then often nodding, large, 2–6(8) cm wide, homogamous. Involucre broadly campanulate, rarely almost sphaeric. Phyllaries in several rows, usually coriaceous, very often broadly triangular with narrow, undulate, black margin, rarely scarioso or herbaceous. Receptacle usually naked and pitted, rarely setose. Florets purple or purple-bluish. Achenes obpyramidal or broadly obconic, 4–6-ribbed, rarely cylindric, usually rugulose-squamulose, straw-colored often with black wavy fringes, with a narrow apical rim. Pappus in one or several rows, subequal or outer row shorter; all bristles from scabrid to shortly plumose, basally connate into a ring, detachable as a single piece.

- Jurinea*** Cass. in Bull. Sci. Soc. Philom. Paris 1821: 140. 1821 – Type: *Jurinea alata* Cass.
- = *Outreya* Jaub. & Spach, Ill. Pl. Orient. 1: 131 [= ad t. 68]. 1843 – Type: *Jurinea carduiiformis* (Jaub. & Spach) Boiss.
- = *Aegopordon* Boiss., Diagn. Pl. Orient. ser. 1, 6: 112. 1846 – Type: *Jurinea berardioides* (Boiss.) Diels.
- = *Jurinella* Jaub. & Spach, Ill. Pl. Orient. 2: 101 [= ad t. 183]. 1847 – **Type (designated here):** *Jurinella aucheri* Jaub. & Spach (= *Jurinea moschus* (Hablitz) Bobrov).
- = *Cirsium* sect. *Anacantha* Iljin in Bot. Mat. Gerb. Glavn. Bot. Sada 3: 57. 1922 ≡ *Modestia* Kharadze & Tamamsch. in Zametki Sist. Geogr. Rast. 19: 40. 1956, nom. illeg. (non *Modesta* Raf. 1838) ≡ *Anacantha* (Iljin) Soják in Sborn. Nár. Muz. Praze, Řada B, Přír. Vědy 1982: 108. 1982 – Type: *Cnicus darwasicus* C.Winkl. (≡ *Jurinea darwasica* (C.Winkl.) Sennikov).
- = *Pilostemon* Iljin in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 21: 391. 1961 – Type: *Jurinea karategina* (Lipsky) O.Fedtsch.
- = *Hyalochaete* Dittrich & Rech.f. in Rechinger, Fl. Iranica 139a: 215. 1979 – Type: *Jurinea modesta* Boiss.
- = *Lipschitzella* Kamelin in Kamelin, Opred. Rast. Sred. Azii 10: 632. 1993 – Type: *Jurinea carducephala* Iljin.
- = *Himalaiella* Raab-Straube in Willdenowia 33(2): 290. 2003, **syn. nov.** – Type: *Jurinea heteromalla* (D.Don) N.Garcia, Herrando & Susanna.
- “*Perplexia* Iljin” in Komarov, Fl. U.S.S.R. 27: 727. 1962, not validly published (Art. 40.1).

Unarmed dwarf shrubs, shrublets or perennial herbs, sometimes acaulescent, exceptionally annual herbs. Leaves dentate to pinnatifid, less often entire, usually white-woolly beneath. Capitula on subscapose leafless pedicels or sessile in the center of a rosette, homogamous, rarely outer florets bent outwards mimicking rays. Involucral bracts narrowly triangular, usually herbaceous and unarmed, very rarely rigid and spiny, without distinct appendages. Florets pink or purple, rarely whitish. Achenes obpyramidal, tetragonal and 4-ribbed; pericarp squamulose, verrucate, tuberculate, ridged or pitted, especially on the upper part. Apical rim usually present, patent, often crenate, rarely horned or toothed, or absent. Pappus of scabrid, barbellate or plumose bristles, pluriseriate, rarely uniseriate; inner row usually longer, basally enlarged and broader, rarely similar to the outer ones, usually attached to a hemisphaeric cupula, deciduous as a single piece with the cupula or persistent.

- Saussurea*** DC. in Ann. Mus. Natl. Hist. Nat. 16: 156. 1810, nom. cons. – Type: *Saussurea alpina* (L.) DC.
- = *Saussurea* subg. *Theodorea* Cass. in Bull. Sci. Soc. Philom. Paris 1818: 168. 1818 ≡ *Theodorea* (Cass.) Cass. in Cuvier, Dict. Sci. Nat. 35: 13. 1819 – Type: *Saussurea amara* (L.) DC.
- = *Heterotrichum* M.Bieb., Fl. Taur.-Caucas. 3: 551. 1819 – Type: *Saussurea salsa* (Pall.) Spreng.
- = *Lagurostemon* Cass. in Cuvier, Dict. Sci. Nat. 53: 466. 1828 – Type: *Saussurea pygmaea* (Jacq.) Spreng.
- = *Eriostemon* Less., Syn. Gen. Compos.: 12. 1832, nom. illeg., non Sm. 1798 ≡ *Aplotaxis* DC. in Arch. Bot. (Paris) 2: 330. 1833 – Type: *Centaurea taraxacifolia* D.Don = *Saussurea eriostemon* Wall. ex C.B.Clarke.
- = *Cyathidium* Lindl. ex Royle, Ill. Bot. Himal. Mts. 7: t. 56, fig. 2. 1835 – Type: *Saussurea taraxacifolia* (Lindl. ex Royle) Wall. ex DC.
- = *Hemisteptia* Bunge ex Fisch. & C.A.Mey., Index Sem. Hort. Petrop. 2: 38. 1836 – Type: *Saussurea lyrata* (Bunge) Sch.Bip.
- = *Polytaxis* Bunge in Bot. Zeitung (Berlin) 1: 256. 14 Apr 1843 [Bunge, Del. Sem. Hort. Dorpat.: VIII. 30 Nov 1843, isonym],

syn. nov. – Type: *Saussurea lehmannii* (Bunge) N.Garcia, Herrando & Susanna.

= *Diplazoptilon* Y.Ling in Acta Phytotax. Sin. 10(1): 85. 1965 – Type: *Saussurea picridifolia* (Hand.-Mazz.) Y.S.Chen & Qian Yuan.

Unarmed perennial herbs, rarely subshrubby, exceptionally annuals, caulescent or acaulescent. Leaves entire to pinnatisect, sometimes decurrent. Capitula solitary, corymbose or paniculate, homogamous, sometimes enclosed into colored and foliaceous or translucent and scariosse bracts, or intermixed with very dense woolly tomentum. Involucral bracts in several rows, entire, from lanceolate to ovate, apically triangular-subulate, not spiny, middle ones sometimes with an appendage. Receptacle with large scales apically divided into very narrow, twisted bristles, sometimes squamulose, rarely naked. Florets purple or pink, sometimes blue-tinged, rarely white. Achenes narrowly obconic, laterally or rarely dorsiventrally compressed, faintly 4- or 6-ridged, exceptionally with six broad longitudinal ribs, rarely smooth, less often glandulose, papillose or hairy, usually with a small apical rim. Pappus biseriate; outer row of short, scabrid, free, easily deciduous bristles, exceptionally of a few flattened scales at the abaxial side of the achene, rarely absent; inner row of much longer, plumose, laterally connate (up to 5 mm) bristles, persistent or deciduous.

Key to the genera

1. Pappus in one row 2
1. Pappus in two or more rows 3
2. Achenes with an indistinct, crenate to minutely denticulate apical rim *Dolomiaea* [*Aucklandia* + *Frolovia*]
2. Achenes with a distinct, prominently dentate apical rim *Jurinea* [*Himalaiella*]
3. Pappus very distinctly dimorphic, in two prominently unequal rows; inner pappus long, with plumose bristles laterally connate at the base (sometimes for up to 5 mm); outer pappus much shorter, with scabrid, fragile scales 4
3. Pappus monomorphic or only undistinctly dimorphic, in several (often more than two) equal or slightly unequal rows; outer bristles not fragile 5
4. Achenes narrowly oblanceolate, usually striate or smooth, seldom rugulose, without a dentate apical rim *Saussurea*
4. Achenes obconical, apically aculeate, with an apical rim of four prominent teeth *Jurinea* [*Lipschitzella*]
5. Pappus bristles inserted on a conic cupule, dimorphic (innermost row with 2–5 longer and broader bristles) or monomorphic, scabrid or plumose *Jurinea*
5. Pappus bristles not inserted on a conic cupule, monomorphic, plumose *Dolomiaea*

New combinations in *Dolomiaea*

The following species from *Frolovia* and *Aucklandia* are newly transferred here.

Dolomiaea asbukinii (Iljin) N.Garcia, Herrando & Susanna, **comb. nov.** ≡ *Saussurea asbukini* Iljin in Bot. Zhurn. S.S.S.R. 27(6): 144. 1942 ≡ *Frolovia asbukinii* (Iljin) Lipsch. in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 16: 462. 1954.

Dolomiaea gorbunovae (Kamelin) N.Garcia, Herrando & Susanna, **comb. nov.** ≡ *Saussurea gorbunovae* Kamelin in Turczaninowia 2(4): 25. 1999 ≡ *Frolovia gorbunovae* (Kamelin) Raab-Straube in Willdenowia 33: 392. 2003.

Dolomiaea sulcata (Iljin) N.Garcia, Herrando & Susanna, **comb. nov.** ≡ *Saussurea sulcata* Iljin in Bot. Mater. Gerb. Glavn. Bot. Sada R.S.F.S.R. 3: 101. 1922 ≡ *Frolovia sulcata* (Iljin) Lipsch. in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 16: 462. 1954.

New combinations and correct names in *Saussurea*

Two new transfers are required to accommodate the species of *Polytaxis*, newly synonymised with *Saussurea* here.

Saussurea lehmannii (Bunge) N.Garcia, Herrando & Susanna, **comb. nov.** ≡ *Polytaxis lehmannii* Bunge, Del. Sem. Hort. Dorpat.: VIII. 1843.

Saussurea winkleri (Iljin) N.Garcia, Herrando & Susanna, **comb. nov.** ≡ *Polytaxis winkleri* Iljin in Bot. Mater. Gerb. Bot.

New combinations in *Jurinea*

The synonymization of *Himalaiella* and *Modestia* to *Jurinea* requires several new species transfers effected here.

Jurinea albescens (DC.) N.Garcia, Herrando & Susanna, **comb. nov.** ≡ *Aplotaxis albescens* DC., Prodr. 6: 540. 1838 ≡ *Saussurea albescens* (DC.) Sch.Bip. in Linnaea 19: 330. 1846 [(DC.) Hook.f. & Thomson ex C.B.Clarke, Compos. Ind. 233. 1876, isonym] ≡ *Theodorea albescens* (DC.) Kuntze, Revis. Gen. Pl. 1: 367. 1891 ≡ *Himalaiella albescens* (DC.) Raab-Straube in Willdenowia 33: 390. 2003.

Jurinea auriculata (DC.) N.Garcia, Herrando & Susanna, **comb. nov.** ≡ *Aplotaxis auriculata* DC., Prodr. 6: 541. 1838 ≡ *Saussurea auriculata* (DC.) Sch.Bip. in Linnaea 19: 331. 1846 ≡ *Theodorea auriculata* (DC.) Kuntze, Revis. Gen. Pl. 1: 367. 1891 ≡ *Himalaiella auriculata* (DC.) Raab-Straube in Willdenowia 33: 390. 2003.

Jurinea chenopodiifolia (Klatt) N.Garcia, Herrando & Susanna, **comb. nov.** ≡ *Saussurea chenopodiifolia* Klatt in Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 8: 92. 1878 ≡ *Himalaiella chenopodiifolia* (Klatt) Raab-Straube in Willdenowia 33: 390. 2003.

Jurinea chitralica (Duthie) N.Garcia, Herrando & Susanna, **comb. nov.** ≡ *Saussurea chitralica* Duthie in Ann. Roy. Bot. Gard., Calcutta 9: 45, t. 57. 1901 ≡ *Himalaiella chitralica* (Duthie) Raab-Straube in Willdenowia 33: 390. 2003.

Jurinea crispa (Vaniot) N.Garcia, Herrando & Susanna, **comb. nov.** ≡ *Saussurea crispa* Vaniot in Bull. Acad. Int. Géogr. Bot., sér. 3, 12: 21. 1902.

≡ *Aplotaxis nivea* DC., Prodr. 6: 541. 1838, non *Jurinea nivea* C.Winkl. 1890 ≡ *Saussurea nivea* (DC.) Sch.Bip. in Linnaea 19: 331. 1846, nom. illeg., non Turcz. 1837 ≡ *Himalaiella nivea* (DC.) Raab-Straube in Willdenowia 33: 391. 2003.

Jurinea deltoidea (DC.) N.Garcia, Herrando & Susanna, **comb. nov.** ≡ *Aplotaxis deltoidea* DC., Prodr. 6: 541. 1838 ≡ *Saussurea deltoidea* (DC.) Sch.Bip. in Linnaea 19: 331. 1846 ≡ *Theodorea deltoidea* (C.B.Clarke) Kuntze, Revis. Gen. Pl. 1: 367. 1891 ≡ *Himalaiella deltoidea* (DC.) Raab-Straube in Willdenowia 33: 391. 2003.

Jurinea gilesii (Hemsl.) N.Garcia, Herrando & Susanna, **comb. nov.** ≡ *Saussurea gilesii* Hemsl. in Hooker's Icon. Pl. 18: t. 1736. 1888 ≡ *Frolovia gilesii* (Hemsl.) B.A.Sharipova in Rasulova, Fl. Tadjikskoï SSR 10: 161. 1991.

Jurinea heteromalla (D.Don) N.Garcia, Herrando & Susanna, **comb. nov.** ≡ *Cnicus heteromallus* D.Don, Prodr. Fl. Nepal.: 166. 1825 ≡ *Theodorea heteromalla* (D.Don) Kuntze, Revis. Gen. Pl. 1: 367. 1891 ≡ *Saussurea heteromalla* (D.Don) Hand.-Mazz., Symb. Sin. 7: 1152. 1936 ≡ *Himalaiella heteromalla* (D.Don) Raab-Straube in Willdenowia 33: 391. 2003.

Jurinea jucunda (C.Winkl.) Sennikov, **comb. nov.** ≡ *Cnicus jucundus* C.Winkl. in Trudy Imp. S.-Peterburgsk. Bot. Sada 9: 427. 1886 ≡ *Saussurea jucunda* (C.Winkl.) O.Fedtsch. & B.Fedtsch. in Izv. Turkestansk. Otd. Imp. Russk. Geogr. Obshch. 6(Suppl. 4): 234. 1911 ≡ *Modestia jucunda* (C.Winkl.) Kharadze & Tamamsch. in Zametki Sist. Geogr. Rast. 19: 42. 1956 ≡ *Anacantha jucunda* (C.Winkl.) Soják in Sborn. Nár. Muz. Praze, Řada B, Přír. Vědy 1982: 108. 1982.

Jurinea leptophylla (Hemsl.) N.Garcia, Herrando & Susanna, **comb. nov.** ≡ *Saussurea leptophylla* Hemsl. in Hooker's Icon. Pl. 18: t. 1734. Mar 1888.

≡ *Jurinea ancistrophylla* Boiss., Fl. Orient. Suppl.: 310. Oct 1888.

Jurinea natmataungensis (Fujikawa) Fujikawa, **comb. nov.** ≡ *Himalaiella natmataungensis* Fujikawa in Makinoa, n.s., 10: 168. 2012.

Jurinea peguensis (C.B.Clarke) N.Garcia, Herrando & Susanna, **comb. nov.** $\equiv$ *Saussurea peguensis* C.B.Clarke, Compos. Ind.: 235. 1876 $\equiv$ *Himalaiella peguensis* (C.B.Clarke) Raab-Straube in Willdenowia 33: 391. 2003.

Jurinea yakla (C.B.Clarke) N.Garcia, Herrando & Susanna, **comb. nov.** $\equiv$ *Saussurea yakla* C.B.Clarke, Compos. Ind.: 227. 1876 $\equiv$ *Himalaiella yakla* (C.B.Clarke) Fujikawa & H.Ohba in J. Jap. Bot. 82(3): 133. 2007.

NOTE ADDED IN PROOF

With this paper closed, Kasana & al. (2020) have published a phylogeny of the subtribe. They agree with us in merging *Aucklandia* and *Frolovia* into *Dolomiaea*. They propose, however, to combine *Himalaiella* and *Lipschitzziella* under a widely defined *Lipschitzziella*. The study is flawed by an insufficient sampling of *Jurinea* and this solution cannot be accepted by two reasons: Firstly, both genera are compared to *Saussurea* and not to *Jurinea*, and achene morphology of the redefined *Lipschitzziella* is compatible with *Jurinea*. Secondly, the presence of species that belong unambiguously to *Jurinea* nested in the *Lipschitzziella/Himalaiella* clade show that the morphological characters alleged for sustaining a different genus are inadequate.

AUTHOR CONTRIBUTIONS

AS, SHM, NGJ, and MGC designed and outlined the study, with contributions from LSX and YSC. JRM provided sequences from previous works and supervised the methods and the analyses together with JAC and CR. ANS reviewed and rewrote part of the nomenclature section. ANS, AS, MGC, NGJ, and SHM interpreted the results and outlined the new taxonomic layout. KF critically read the manuscript and suggested nomenclatural changes. SCK, JQL, JLA, JLP, RV, and IM provided materials and critically read the manuscript and contributed to the discussion. The submitted draft has been reviewed and accepted by all the authors. — SHM, <http://orcid.org/0000-0002-0488-5112>; JAC, <http://orcid.org/0000-0002-6586-0939>; MGC, <https://orcid.org/0000-0002-7267-3330>; NGJ, <https://orcid.org/0000-0003-1893-5122>; JLA, <https://orcid.org/0000-0003-0568-4125>; JLP, <https://orcid.org/0000-0002-2091-6222>; JRM, <https://orcid.org/0000-0003-3539-2991>; IM, <https://orcid.org/0000-0002-5108-2558>; CR, <https://orcid.org/0000-0001-8748-3743>; ANS, <https://orcid.org/0000-0001-6664-7657>; AS, <https://orcid.org/0000-0003-4717-9063>; RV, <https://orcid.org/0000-0002-5106-8764>

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Appendix 1. Voucher information of the studied material and GenBank (NCBI) accession numbers of raw sequence reads. New sequences generated in this study are indicated with an asterisk (*) after GenBank number. Taxon names follow the final proposed taxonomic treatment presented in the study. Notes: ¹ In Herrando-Moraira & al. (2018) appears as *Arctium eriophorum*; ² In Herrando-Moraira & al. (2018) it appears as *Cousinia ninae*; ³ In Herrando-Moraira & al. (2018) it appears as *Jurinea abramowii*; ⁴ In Herrando-Moraira & al. (2018) it appears as *Jurinea bucarica*; ⁵ In Herrando-Moraira & al. (2019) it appears as *Rhaponticum acaule*; ⁶ In Herrando-Moraira & al. (2018) it appears as *Saussurea davurica*; ⁷ In Herrando-Moraira & al. (2018) it appears as *Saussurea jadrinzevii*.

Arctium fedtschenkoanum (Bornm.) S.López & al., Tajikistan, Romaschenko 632 & Susanna (BC), SAMN11585472; *Arctium grandifolium* (Kult.) S.López & al., Kazakhstan, Zambyl'skaya oblast, Talaski Alatau, 6 km W from Il Tai, Susanna 2181 & al. (BC), SAMN15064103*; *Arctium karatavicum* (Regel & Schmalh.) Kuntze, Tadjikistan, s. loc., Romanshenko 607 & Susanna (BC), SAMN15064104*; *Arctium minus* (Hill) Bernh., Spain, Barcelona, Vilatersana 1100 & López-Vinyallonga (BC), SAMN15064105*; *Arctium nidulans*¹ (Regel) Sennikov, Kazakhstan, Almatinskaya oblast, Alatau mt., above Almaty, Susanna 2088 & al. (BC), SAMN15064106*; *Arctium umbrosum* (Bunge) Kuntze, Kazakhstan, Almatinskaya oblast, Alatau mt. above Almaty, Susanna 2100 & al. (BC), SAMN15064107*; *Carduus nutans* L., Tajikistan, Vorzov, Susanna 2481 & al. (BC), SAMN15064108*; *Centaurea aspera* L., cultivated at the Barcelona Botanical Garden, SAMN15064109*; *Cirsium sairamense* (C.Winkl.) O.Fedtsch. & B.Fedtsch., Tadjikistan, Maijora, Susanna 2468 & al. (BC), SAMN11585477; *Cousinia arachnoidea*² Fisch. & C.A.Mey. ex DC., Kyrgyzstan, 20–22 km E of Shakaftar, Sultanova & al. s.n. (FRU, LE), SAMN15064110*; *Cousinia knorringiae* Bornm., Kyrgyzstan, Bozbu-Too, 21 May 1970, Sudnitsyna s.n. (FRU, LE), SAMN15064111*; *Cousinia onopordioides* Ledeb., Iran, Tehran, between Firuzkuh and Semnan, Susanna 1637 & al. (BC), SAMN15064112*; *Cousinia polytimetica* Tscherneva, Uzbekistan, Bukharskaya reg., Zeravshan river, to SE from Uzliskent vil., Kryakin s.n. (LE), SAMN15064113*; *Cousinia pungens* Juz., Iran, Khorasan, Rechinger 51337 (W0007098), SAMN15064114*; *Cousinia splendida* C.Winkl., Tadjikistan, Fan mountains, road above Iskandar-Kul, Susanna 2507 & al. (BC), SAMN15064115*; *Cousinia spryginii* Kult., Uzbekistan, Kashkadarskaya reg., low mountains to SE of vil. Dekhanabad, Botschantzev 46 (LE), SAMN10983402; *Cynara cardunculus* L., U.S.A., UW Medicinal Plant Garden., Mandel s.n. (GA 135), SAMN11585480; *Dolomiaea asbukinii* (Iljin) N.Garcia & al., Tajikistan, Sogdiiskai Oblast, Ashtskii District, Kuraminskii Ridge, the Pangaza River Valley, Suje-kuh city, 25 Jul 1943, Kamelin s.n. (LE), SAMN15064116*; *Dolomiaea baltalensis* Dar & Naqshi, India, Kangi, Ladak, Kashmir, ca. 3950 m, Walter Koelz 2823 (E00469695), SAMN15064117*; *Dolomiaea berardioidea* (Franch.) C.Shih 1, China, Yulong Shan, Gang Ho Ba valley, 3350 m, Chungtien-Lijiang-Dali Expedition no. 717 (E00469654), SAMN15064118*; *Dolomiaea berardioidea* 2, China, Yunnan bor.-occid., Prope urbem Lidjiang, 2950–3100 m, Handel-Mazzetti 662 (WU), SAMN15064119*; *Dolomiaea costus* (Falc.) Kasana & A.K.Pandey, China, Yunnan, Lijiang Prefecture, Xin Zhu forest, between Judian and Litiping Plateau, 2690 m, B. Aldén & al. 1756 (E00003397), SAMN15064120*; *Dolomiaea edulis* (Franch.) C.Shih, China, Yangbi Xian, W side of Diancang Shan mountain range, Sino-Amer. Bot. Exped. No. 534 (E00469665), SAMN15064121*; *Dolomiaea forrestii* (Diels) C.Shih 1, China, Yunnan bord.-occid., prope urbem Lidjiang, Handel-Mazzetti 661 (W0004887), SAMN15064122*; *Dolomiaea forrestii* 2, China, Yunnan, Dêqên Zang Aut., Dêqên, E flank of Bei Ma Xue Shan, 4140 m, 17 Sep 1995, s. col. (E00051554), SAMN15064123*; *Dolomiaea forrestii* 3, China, Yunnan bor.-occid., prope urbem Lidjiang 06–09.1914, 1915, 1916, Handel-Mazzetti 3672 (WU), SAMN15064124*; *Dolomiaea frolowii* (Ledeb.) Kasana & A.K.Pandey, Russia, Altai, Kosh-Agachsky, Kuraiskiy Ridge, the Ortol'yk River, 2249 m, A. Pyak & E. Pyak 11012 (TK a-034-2016), SAMN15064125*; *Dolomiaea georgii* (Anth.) C.Shih 1, China, Yunnan, Yangtze watershed, Likang, J.F. Rock 6138 (E00469683), SAMN15064126*; *Dolomiaea georgii* 2, China, Yunnan, Yangtze watershed, J.F. Rock 6138 (E00469683), SAMN15064127*; *Dolomiaea gorbunovae* (Kamelin) N.Garcia & al., Kyrgyzstan, Kurama Range easternmost side, right side of Kasansay River, Sennikov 461 (H), SAMN15064128*; *Dolomiaea macrocephala* Royle, Pakistan, Khaibar, upper Hunza, 3820 m, G.S. Miede 2627 (W0001920), SAMN15064129*; *Dolomiaea platylepis* (Hand.-Mazz.) C.Shih, China, Muli, SW Szechuan, between Muli Gomba and Baurong and Wa-Erh-Dje, 3700 m, Jul 1928, J.F. Rock s.n. (E00469687), SAMN15064130*; *Dolomiaea salwinensis* (Hand.-Mazz.) C.Shih 1, China, Yunnan, bor.-occid., prope fines Tibeto-Birmanicas inter fluvios Lu-djiang (Salween) et Djiou-djiang (Irrawadi or sup.), ca. 3825 m, Handel-Mazzetti 1853 (WU0061241), SAMN15064131*; *Dolomiaea salwinensis* 2, China, Mekhong, Salween divide Yunnan, ca. 3950 m, George Forrest 14350 (E00469690), SAMN15064132*; *Dolomiaea salwinensis* 3, China, Yunnan, Mekong-Salween divide, ca. 3950 m, Aug 1917, s. col. (W0013379), SAMN15064133*; *Dolomiaea saussureoides* (Hand.-Mazz.) Y.L.Chen & C.Shih, China, SE Tibet, Kongbo Province, Tse La, Langong, ca. 4260–4570 m, F. Ludlow & al. 5620 (E00469649),

SAMN15064134*; *Dolomiaea souliei* (Franch.) C. Shih, China, Sikang, Kangting (Tachienlu) Distr., Chungo valley, Hsintientzü, ca. 3800 m, *Harry Smith 11630* (W0012531), SAMN15064135*; *Dolomiaea sulcata* (Iljin) N. Garcia & al., Kyrgyzstan, Jalal-Abad Region, Aksy District, Ferganskii Ridge, between Maili-sai and Jedde-sai cities, 3000–3200 m, 3 May 1952, *Popova & al. s.n.* (LE), SAMN15064136*; *Galactites tomentosa* Moench, Spain, Barcelona, 8 Jun 2017, *Susanna s.n.* (BC), SAMN15064137*; *Jurinea abramovič*³ Regel & Herder, Tadjikistan, Hissar Mt., *Smirnova 224 & al.* (DUSH), SAMN15064138*; *Jurinea alata* Cass., cultivated at the Barcelona Botanical Garden, SAMN1585483; *Jurinea albescens* (DC.) N. Garcia & al. **1**, India, Kashmir, Dras, 10,000 ft, *Stainton 7175* (E00466963), SAMN15064139*; *Jurinea albescens* **2**, India, Kashmir, Srinagar, in monte Shankaracharya, 1770–2000 m, *K.H. Rechinger 62135* (W0003315), SAMN15064140*; *Jurinea algida* Iljin, Kyrgyzstan, Kok-Suu River, 16 Aug 2006, *Lazkov s.n.* (FRU), SAMN15064141*; *Jurinea atropurpurea* C. Winkl., Tadjikistan, s. loc., *Kotehkariova & Zhogolieva 16094* (DUSH), SAMN11585484; *Jurinea auriculata* (DC.) N. Garcia & al. **1**, Nepal, Taplejung Dist., Mane Bhanjyang–Jalale Polhari, *Y. Omori & al. 9920052* (MBK0254878), SAMN15064142*; *Jurinea auriculata* **2**, cultivated plant in Royal Botanic Garden Edinburgh, *S. Sikkim McPherson s.n.* (E00469273), SAMN15064143*; *Jurinea baldschuanica* C. Winkl., Tadjikistan, mountains above Kara-Chuiráá, *Susanna 2561 & al.* (BC), SAMN15064144*; *Jurinea berardioides* (Boiss.) O. Hoffm. **1**, Pakistan, Kalat, Kolpur to Mach, *Rechinger 28456* (W), SAMN15064145*; *Jurinea berardioides* **2**, Iran, Kazerun, Kotal Dahli, *Stapf 1284* (WU), SAMN15064146*; *Jurinea bucharica*⁴ C. Winkl., s. loc., 22 Apr 1975, s. col. *10387* (DUSH), SAMN15064147*; *Jurinea bungei* Boiss., Iran, Persia, S Fars, 20 km S Abadeh, *F. Kasy 426* (W0016436), SAMN15064148*; *Jurinea caespitans* Iljin, Kyrgyzstan, north of Kara-Jygach village, 9 Jul 2016, *Sennikov s.n.* (H), SAMN15064149*; *Jurinea capusii* Franch., Kyrgyzstan, Chapchyma-Say, 14 Jul 2016, *Sennikov s.n.* (H), SAMN15064153*; *Jurinea carducephala* Iljin, Tajikistan, Gorno-Badakhshan, Shughnon, Shughnonskii Ridge, *Semakov & Dengubenko s.n.* (LE 8428), SAMN15064154*; *Jurinea carduiformis* (Jaub. & Spach) Boiss., Iran, Tehran, near Sorkhehesar, *Susanna 1631 & al.* (BC), SAMN15064155*; *Jurinea ceratocarpa* (Decne.) Benth. ex C.B. Clarke **1**, India, Garhwal, *Polunin 14941* (E00714512), SAMN15064156*; *Jurinea ceratocarpa* **2**, India, Himachal Pradesh, 11,600 ft, *J.D.A. Stainton s.n.* (E00158889), SAMN15064157*; *Jurinea chenopodiifolia* (Klatt) N. Garcia & al., Afghanistan, Parwan, Salang Tal, quelliger Hang bei der Brücke oberhalb km 85, 1800 m, *O. Anders 3800* (W0006559), SAMN15064158*; *Jurinea chitralica* (Duthie) N. Garcia & al. **1**, Afghanistan, Nuristan, Pashki, 2300 m, *Rechinger 1117* (W0000344), SAMN15064159*; *Jurinea chitralica* **2**, Pakistan, Chitral, Zirratt, lowarai pass, 7000 ft, *D.A. Stainton 2546* (E00160033), SAMN15064160*; *Jurinea chondrilloides* (C. Winkl.) O. Fedtsch. **1**, Afghanistan, Ghorat, in faucibus septentriones versus spectantibus Mollah Allah, SW Taiwara, ca. 2200–2300 m, *K.H. Rechinger 18978* (W0006534), SAMN15064161*; *Jurinea chondrilloides* **2**, Afghanistan, Ghorat, in faucibus septentriones versus spectantibus Mollah Allah, SW Taiwara, ca. 2200–2300 m, *K.H. Rechinger 18978* (E00466342), SAMN15064162*; *Jurinea crispa* (Vaniot) N. Garcia & al. **1**, Thailand, Chiang Mai, western flank of Doi Inthanond, Mae Pau, c. 2250 m, *Expedition of the Rijksherbarium, Leiden, Netherlands, and the Forest Herbarium, Bangkok, Thailand 2388* (E00469242), SAMN15064163*; *Jurinea crispa* **2**, China, Gongshan Zizhixian, Dulongjiang Xiang, *Gaoligong Shan Biodiversity Survey 21197* (E00270054), SAMN15064164*; *Jurinea crispa* **3**, China, Yunnan, Mekong, 2100–2500 m, *Handel-Mazzetti 1486* (W0013329), SAMN15064198*; *Jurinea deltoidea* (DC.) N. Garcia & al. **1**, China, Himachal Pradesh, Wegvon Phakding–Namche Bazar, Solo Khumbu, 3100 m, *M. Staudinger N8/22* (W0001056), SAMN15064165*; *Jurinea deltoidea* **2**, India, Distr. Darjeelin, “Tigerhill”, ca. 2500 m, *Ern 3428* (E00466988), SAMN15064166*; *Jurinea ferganica* (Iljin) Iljin, Kyrgyzstan, near Kadamzhay village, 18 Jul 2016, *Sennikov s.n.* (H), SAMN15064167*; *Jurinea filicifolia* Boiss., Georgia, Zazbeg, Bergkamm K’vena mt’a (Kvena mta), 1.7–3.8 km W ober der Kirche Tsminda Sameba (Cminda Sameba), 2450–2940 m, 21 Aug 1997, *M. Staudinger s.n.* (W0014044), SAMN15064168*; *Jurinea fontqueri* Cuatr., Spain, Jaén, cerro Cárcelos, Mágina, *Martinez Lirola s.n.* (GDA 44615), SAMN15064169*; *Jurinea frigida* Boiss. **1**, Iran, Persia borealis, in excelsis alpinum Totschal, 3800 m s.m., *J. et A. Bornmüller 7309* (WU), SAMN15064170*; *Jurinea frigida* **2**, Iran, Tehran, Tuchal Mts., 3700 m, *J. Noroozi 2478* (W0011550), SAMN15064171*; *Jurinea frigida* **3**, Iran, Damavand, 4000 m, *Susanna 2625 & al.* (BC), SAMN15064172*; *Jurinea gilesii* (Hemsl.) N. Garcia & al., Tajikistan, East Pamir, Kara-Djilga, *Kochkariev 17* (TAD), SAMN15064173*; *Jurinea heteromalla* (D. Don) N. Garcia & al. **1**, India, Mussoorie, *Wavra 1498* (W0075519), SAMN15064150*; *Jurinea heteromalla* **2**, India, Utar Pradesh, Kumaon, Supra Katghodam versus Bhimtal, 700–1000 m, *K.H. Rechinger 6242* (W0003374), SAMN15064151*; *Jurinea heteromalla* **3**, Pakistan, Murree, 7800 ft, *Duthie 14606* (WU), SAMN15064152*; *Jurinea heteromalla* **4**, Pakistan, Baluchistan, Quetta, Coralai to Harnai, Tokhan Pass., 900–1400 m, *Jennifer Lamond 1251* (E00469094), SAMN15064174*; *Jurinea jucunda* (C. Winkl.) Sennikov, Kyrgyzstan, 20 km NW of Samarkandyk, Kyzyl-Suu, 10 May 1978, *Aidarova & Ubukeeva s.n.* (FRU), SAMN15064175*; *Jurinea karategina*

(Lipsky) O.Fedtsch., Tajikistan, Surjov, *Susanna* 2542 & al. (BC), SAMN15064176*; *Jurinea kokanica* Iljin, Kyrgyzstan, 15 km E of Kosh-Bulak village, 9 May 2007, *Ganybaeva s.n.* (FRU), SAMN15064177*; *Jurinea kyzylkyrensis* Kamelin & Tscherneva, Kyrgyzstan, left side of Naryn River, Kyzyl-Kyr, 12 Aug 1979, *Botschantzev & al. s.n.* (FRU), SAMN15064178*; *Jurinea lanipes* Rupr., Kyrgyzstan, Boom ravine, *Sennikov 428a* (H), SAMN15064179*; *Jurinea leptoloba* DC., Iran, 30 km N from Tabriz, *Susanna* 1654 & al. (BC), SAMN15064180*; *Jurinea leptophylla* (Hemsl.) N.Garcia & al., Afghanistan, Kapisa, *Podlech 12500* (W), SAMN15064181*; *Jurinea macrocephala* DC., Iran, 20 Km N of Qarabchaman, *Susanna* 1650 & al. (BC), SAMN15064182*; *Jurinea microcephala* Boiss., Iran, Shahrud-Bustam, in declivibus australibus montium Shahvar in saxasis calc., 3500–3900 m, *K.H. et F. Rechinger 5975* (W0003394), SAMN15064183*; *Jurinea modesta* Boiss., Afghanistan, Nangarhar, Torkham, stony slopes, c. 700 m, 30 Apr 1969, *I. Hedge & al. s.n.* (E00467348), SAMN15064184*; *Jurinea moschus* Fisch. & C.A.Mey. 1, Georgia, Mtskheta-Mtianeti, Great Caucasus, from church Tsminda Sameba in direction of Mt. Kasbek, 2650–3160 m, *G.M. Schneeweiss & al. 8684* (W0013182), SAMN15064185*; *Jurinea moschus* 2, Georgia, Pirikiti Khevsureti District. Dusheti District (21), gorge of Arguni river, ca. 2764 m, *Shamil Shetekauri 1073* (W0018609), SAMN15064186*; *Jurinea moschus* 3, Georgia, Mtskheta-Mtianeti, Great Caucasus, from church Tsminda Sameba in direction of Mt. Kasbek, 2650–3160 m, *G.M. Schneeweiss & al. 8684* (WU), SAMN15064187*; *Jurinea moschus* 4, Turkey, Kastamonu, Ilgaz Daglari, *Buchner B83-80-11* (W0010480), SAMN15064188*; *Jurinea narynensis* Kamelin & Tscherneva, Kyrgyzstan, 8 km from Tash-Kumyr to Jangi-Jol, *Lazkov & Omuralieva s.n.* (FRU), SAMN15064189*; *Jurinea natmataungensis* (Fujikawa) Fujikawa, Myanmar, Chin State, Natma Taung National Park, *K. Fujikawa & al. 086717* (MBK0239428), SAMN15064190*; *Jurinea olgae* Regel & Schmalh., Tadjikistan, slopes over kishlag Voru, *Susanna* 2517 & al. (BC), SAMN15064191*; *Jurinea orientalis* (Iljin) Iljin, Kyrgyzstan, near Shekofar village, 13 Jul 2016, *Sennikov s.n.* (H), SAMN15064192*; *Jurinea peguensis* (C.B.Clarke) N. Garcia & al. 1, China, Yunnan, 1916, *Cavalerie s.n.* (W0012455), SAMN15064193*; *Jurinea peguensis* 2, Thailand, Mae hong Son Prov., Maung Dist., *N. Tanaka & al. HN8512* (MBK0202098), SAMN15064194*; *Jurinea pinnata* (Lag. ex Pers.) DC., Morocco, Meknès-Tafilalt, Middle-Atlas, from Midelt to Timahdite, col du Zad, *Calleja & Hipold 20103091* (BC), SAMN15064195*; *Jurinea popovii* Iljin, Tadjikistan, s. loc., *Chukavina & al. 163(86)* (DUSH), SAMN15064196*; *Jurinea pulchella* DC., Iran, Azerbaidjan, Khoi to Schapour, *Belboudi 5462E* (W0015068), SAMN15064197*; *Jurinea schachimardanica* Iljin, Kyrgyzstan, W of Shahimardan, *Sennikov 472* (H), SAMN15064199*; *Jurinea squarrosa* Fisch. & C.A.Mey. 1, Armenian SSR, Gugark region, Gamzachiman, Bazum Ridge, Chingiliyurt mountain, 2100 m, 19 Jun 1968, *A. Pogosyan s.n.* (WU), SAMN15064200*; *Jurinea squarrosa* 2, Armenia, Shirak range, left slope of the remarkable gorge NE of Krashen, 2076 m.s.m., *Ernst Vitek 04-1513 & al.* (W004012), SAMN15064201*; *Jurinea stenophylla* Iljin, Kyrgyzstan, Kasan-Say River near Terek-Say village, 14 Jun 1996, *Pimenov & al. s.n.* (FRU), SAMN15064202*; *Jurinea stoechadifolia* DC., Ukraine, Crimea, *Romo 10321 & al.* (BC), SAMN15064203*; *Jurinea suffruticosa* Regel, Kyrgyzstan, Kasan-Say River, 14 Jul 2016, *Sennikov s.n.* (H), SAMN15064204*; *Jurinea thianschanica* Regel & Schmalh., Kyrgyzstan, between Kochkor and Ottuk, near Orto-Tokoy village, 3 Jul 2016, *Sennikov s.n.* (H), SAMN15064205*; *Jurinea trautvetteriana* Regel & Schmalh., Tadjikistan, s. loc., *Ovczinnikov 16305 & Zaprjagaeva* (DUSH), SAMN15064206*; *Jurinea winkleri* Iljin, Kyrgyzstan, east of Uch-Korgon village, 16 Jul 2016, *Sennikov s.n.* (H), SAMN15064207*; *Jurinea xeranthemoides* Iljin, Kyrgyzstan, near Uch-Korgon village, 16 Jul 2016, *Sennikov s.n.* (H), SAMN15064208*; *Jurinea yakla* (C.B.Clarke) N.Garcia & al., Nepal, Sagarmatha Zone, Solukhumbu Distr., Mosom Kharka, 3600 m, *M. Wakabayashi & al. 97-30345* (E00232078), SAMN15064209*; *Karvandarina cartilaginea* (Mozaff.) Parishani & al., Iran, Khuzistan, between Behbahan and Dehdasht, Tang-e Takab, 500 m, *Mozaffarian 58838* (TARI), SAMN15064210*; *Klasea coriacea* (DC.) Holub, Armenia, Ararat, *Susanna* 1530 & al. (BC), SAMN15064211*; *Leuzea acaulis*⁵ (L.) Holub, cultivated at the Barcelona Botanical Garden, SAMN15064212*; *Olgaea petriprini* B.A.Sharipova, Tajikistan, Selandi, *Susanna* 2539 & al. (BC), SAMN15064213*; *Onopordum nervosum* Boiss., cultivated at the Dijon Botanical Garden, SAMN15064214*; *Plectocephalus cachinalensis* (Phil.) N.Garcia & Susanna, cultivated at the Barcelona Botanical Garden, SAMN15064215*; *Psephellus mucroniferus* (DC.) Wagenitz, Turkey, Niğde, *Susanna* 2300 & al. (BC), SAMN15064216*; *Saussurea andryaloides* (DC.) Sch.Bip. 1, India, Himachal Pradesh, Jalore Pass, [unread.] (WU), SAMN15064217*; *Saussurea andryaloides* 2, India, between Da and Hanle, Rupshu, Kashmir, 15,000 ft., *Walter Koelz 2280* (E00160052), SAMN15064218*; *Saussurea bella* Y.Ling, China, Qinghai 3660 m, 15 Aug 2002, *Liu LJQ852*, SAMN15064219*; *Saussurea candolleana* (DC.) Wall. ex Sch.Bip. 1, India, Kashmir, Jilai, 9000 ft, *Duthie 13966* (WU), SAMN15064220*; *Saussurea candolleana* 2, Nepal, east of Chalike Pahar, in guilles among Bush vegetation, Stainton, *Sykes & Williams 3758* (E00469165), SAMN15064221*; *Saussurea controversa* DC., Russia, Krasnoyarsk Krai, Sharypovsky, village Bolshoe

ozero, *Cazzolla Gatti 10005* & al. (TK t-01-2016), SAMN15064222*; *Saussurea daurica*⁶ Adams, Russia, Altai, Kosh-Agachsky, Kuraiskiy Ridge, village Chagan-Usun, *A. Pyak & E. Pyak 11049* (TK a-067-2016), SAMN15064223*; *Saussurea discolor* (Willd.) DC., Austria, Steiermark, 2130 m, 3 Jul 1997, *Schneeweiss s.n.* (WU), SAMN15064224*; *Saussurea elegans* Ledeb., Tajikistan, Iskandar valley, Fan mountains, *Susanna 2505* & al. (BC), SAMN15064225*; *Saussurea foliosa* Ledeb., Russia, Khakassia, Tashtypsky, Sayanskii Mountain Pass, *Cazzolla Gatti 10025* & al. (TK t-30-2016), SAMN15064226*; *Saussurea glacialis* Herder, Russia, Altai, Kosh-Agachsky, Kuraiskiy Ridge, *A. Pyak & E. Pyak 11021* (TK a-043-2016), SAMN15064227*; *Saussurea gnaphalodes* (Royle ex DC.) Sch. Bip., China, Sichuan Prov., Khangding Xian, *D.E. Boufford 34778* & al. (MBK0147538), SAMN15064228*; *Saussurea gossipiphora* D.Don, Nepal, Sankhuwasabha Dist., Bandhuke, *Y. Otori & al. 9920067* (TI), SAMN15064229*; *Saussurea jadrincevi*⁷ Kryl., Russia, Altai, Ongudaysky, the Mount Belyy Bom, *A. Pyak & E. Pyak 11005* (TK a-023-2016), SAMN15064230*; *Saussurea krylovii* Schischk. & Serg., Russia, Altai, Kosh-Agachsky, Juzhno-Chuysky Ridge, the Jazator River Valley, *A. Pyak & E. Pyak 11079* (TK a-108-2016), SAMN15064231*; *Saussurea larionowii* C.Winkl., Kyrgyzstan, s. loc., *Ovczinnikov 16* (DUSH), SAMN15064232*; *Saussurea latifolia* Ledeb., Russia, Krasnoyarsk Krai, Yermakovskiy, Ergaki Ridge, *A. Pyak & E. Pyak 10009* (TK t-02-2016), SAMN15064233*; *Saussurea lehmannii* (Bunge) N.Garcia & al., Tajikistan, Khatlonskaja Oblast, Shahritusskii District, *Kamelin s.n.* (LE), SAMN15064234*; *Saussurea leontodontoides* (DC.) Sch.Bip., Nepal, between Ghunsa and Tamola, 3960 m, *Kew-Edinburgh Kathmandu expedition to NE Nepal 1989 KEKE 659* (E00466866), SAMN15064235*; *Saussurea leucophylla* Schrenk, Russia, Altai, Kosh-Agachsky, northern spurs of the Mount Tjeplyi Kljuch, *A. Pyak & E. Pyak 11073* (TK a-102-2016), SAMN15064236*; *Saussurea lyrata* (Bunge) Sch.Bip. 1, Republic of Korea, Jeollabuk-do, Jeonji-citu, Geonji-hill, *G.S. Kim & C.H. Oho 116* (WU021661), SAMN15064237*; *Saussurea lyrata* 2, China, Chao-Chow-Fu, a city on the Han river, twenty-four miles north of Swatow, May 1899, *J.M. Dalziel s.n.* (E00467504), SAMN15064238*; *Saussurea manshurica* Kom., Russia, Amur province, 2 Aug 1979, *Boyko & Starchenko s.n.* (LE), SAMN15064239*; *Saussurea nivea* Turcz., China, Tsobili [?], 10 Aug 1930, *E. Licent s.n.* (W0075522), SAMN15064240*; *Saussurea obvallata* (DC.) Sch.Bip., China, Yunnan, 3320–4320 m, *Liu LJQ2621*, SAMN15064241*; *Saussurea orgadayi* Khanm. & Krasnob., Russia, Altai, Kosh-Agachsky, Kuraiskiy Ridge, the Kokorja River Valley, *A. Pyak & E. Pyak 11083* (TK a-119-2016), SAMN15064242*; *Saussurea picridifolia* (Hand.-Mazz.) Y.S.Chen & Qian Yuan, China, Yunnan bor.-occid., in regione frigide temperata jugi Si-la inter fluvios Landsang-djiang (Mekong) et Lu-djiang (Salween), ca. 3800 m, *Handel-Mazzetti 9964* (W0002048), SAMN15064243*; *Saussurea pseudoalpina* N.D.Simpson, Russia, Altai, Kosh-Agachsky, Kuraiskiy Ridge, the Ortolyk River, *A. Pyak & E. Pyak 11032* (TK a-048-2016), SAMN15064244*; *Saussurea pulchella* (Fisch.) Colla 1, Republic of Korea, Gangwon Province, Mt. Hambaek, *Yun 130926024* (SKK), SAMN15064245*; *Saussurea pulchella* 2, Japan, Honshu Yamanashi Pref., Okishinhata, Yamanakakomura, Mina-mitsuru-gun, 950 m, *M. Togashi 541* (WU), SAMN15064246*; *Saussurea roylei* (DC.) Sch.Bip., Nepal, Marsiandi Valley, 13,500 ft, *D.G. Lowndes L1179* (E00469184), SAMN15064247*; *Saussurea salicifolia* (L.) DC., Russia, Tyva, Kaa-Khemsky, the Mount Ondum, the Kaa-Khem River, *A. Pyak & E. Pyak 10014* (TK t-12-2016), SAMN15064248*; *Saussurea salsa* (Pall.) Spreng., Russia, Altai, Kosh-Agachsky, Chuya Steppe, village Aktal, *A. Pyak & E. Pyak 11087* (TK a-120-2016), SAMN15064249*; *Saussurea scabrida* Franch., China, Sichuan Province, Xiangcheng Xian, between Xiangcheng and Sandui near the viallge of Riyin, S of Wuming Shan, 3550–4000 m, *D.E. Boufford & al. 28405* (E00280462), SAMN15064249*; *Saussurea scaposa* Franch. & Sav., Japan, Shikoku, Kochi Pref., Nanotani, Yusuhara Town, *S. Kobayashi FOK-074378* (MBK0129268), SAMN15064250*; *Saussurea schanginiana* (Wydler) Fisch. ex Herd., Russia, Khakassia, Tashtypsky, Sayanskii Ridge, Sayanskii Mountain Pass, *A. Pyak & E. Pyak 10057* (TK t-24-2016), SAMN15064251*; *Saussurea simpsoniana* (DC.) Wall. ex Sch.Bip., Nepal, Mustang Dist., around Yak Kharka, *K. Fujikawa 9920116* (MBK0254898), SAMN15064252*; *Saussurea sorocephala* (Schrenk) Schrenk, Pakistan, Ghareda glacier, 16,100 ft, *Polunin 6305* (E00710753), SAMN15064253*; *Saussurea stubendorffii* Herder, Russia, Tyva, Barun-Khemchiksky, Sayanskii Ridge, Ak-sug River Valley, *A. Pyak & E. Pyak 10057* (TK t-24-2016), SAMN15064254*; *Saussurea subacaulis* (Ledeb.) Serg., Russia, Altai, Kosh-Agachsky, Kuraiskiy Ridge, Ortolyk River, *A. Pyak & E. Pyak 11026* (TK a-046-2016), SAMN15064255*; *Saussurea taraxacifolia* (Lindl. ex Royle) Wall. ex DC., China, Yushu Xian, SW of Machang, in a side valley on S side the Baitang He basin, 4000 m, *T.N. Ho & al. 2133* (E00064934), SAMN15064256*; *Saussurea uniflora* (DC.) Wall. ex Sch.Bip., Nepal, Solukhumbu Dist., Tashing Dingma–Thuli Kharka, *M. Wakabayashi & al. 9730355* (MBK0254886), SAMN15064257*; *Saussurea winkleri* (Iljin) N.Garcia & al., Tajikistan, Khatlonskaja Oblast, Shahritusskii District, 600 m, *Botchancev s.n. & al.* (LE), SAMN15064258*; *Staehelina lobelii* DC., Turkey, Antalya, *Susanna 2272* & al. (BC), SAMN15064259*; *Staehelina petiolata* (L.) Hilliard & B.L.Burt, Greece, Crete, *Vitek 081418* (BC),

SAMN15064260*; *Tricholepis edmondsonii* Rech.f., Iran, Hormozgan, 5 km from Bandar-Abbas to Fareghan village, 1100 m, *Mozaffarian 44869* (TARI), SAMN15064261*; *Volutaria canariensis* Wagenitz, Spain, Gran Canaria, *Kunkel 200-2* (BC), SAMN15064262*.

TABLES

Table 1. Recent generic taxonomic treatments for subtribe Saussureinae.

Häffner (2000)	Raab-Straube (2003, 2017), Shi & Raab-Straube (2011), Szukala & al. (2019)	Susanna & Garcia-Jacas (2007)	Susanna & Garcia-Jacas (2009)
<i>Dolomiaea</i>	<i>Dolomiaea</i> <i>Aucklandia</i> <i>Bolocephalus</i> <i>Frolovia</i>	<i>Dolomiaea</i>	<i>Dolomiaea</i>
<i>Jurinea</i> <i>Aegopordon</i> <i>Anacantha</i> * <i>Hyalochaete</i> <i>Jurinella</i> <i>Outreya</i> <i>Pilostemon</i>	<i>Jurinea</i> <i>Himalaiella</i> <i>Lipschitziella</i>	<i>Jurinea</i>	<i>Jurinea</i>
<i>Saussurea</i> <i>Diplazoptilon</i> <i>Hemisteptia</i> <i>Polytaxis</i>	<i>Saussurea</i> <i>Diplazoptilon</i> <i>Hemisteptia</i> <i>Polytaxis</i>	<i>Saussurea</i> <i>Polytaxis</i>	<i>Saussurea</i>

* Note that *Anacantha* is a nomenclatural synonym of *Modestia*.

Table 2. Summary metrics of target recovering performance using HybPiper (Johnson & al., 2016) method.

Parameters	Extraction performance values
1. Number of species included	167
2. Number of recovered loci (% respect COS targets)	1054 (99.3)
3. Number of used loci (% respect COS targets)	588 (55.4)
4. Number of captured loci in $\geq 90\%$ of species (%)	509 (86.6)
5. Average of recovered loci per species (SD; min–max)	550 (13; 457–565)
6. Average of species recovered per loci (SD; min–max)	156 (29; 7–167)
7. Mean alignment length per locus in bp (SD; min–max)	336 (188; 54–1191)
8. Length of concatenated matrix in bp	197,784
9. Number of variable sites in the concatenated matrix (%)	92,301 (46.7)
10. Number of parsimony-informative sites in the concatenated matrix (%)	61,990 (31.3)
11. Proportion (%) of missing data in the concatenated matrix	12.6

Values of parameters were calculated with FASconCAT-G v.1.02 (Kück & Longo, 2014) and AMAS (Borowiec, 2016) programs. Parameters from 4 to 11 are calculated based on dataset “3. N° of used loci”, which includes those loci (1) not detected as potential paralogs; (2) recovered for more than three species; and (3) more than 6 bp length (see text for details). Abbreviations: bp = base pairs; max = maximum; min = minimum; SD = standard deviation.

FIGURE CAPTIONS

Fig. 1. Comparison of previous phylogenies performed on subtribe Saussureinae with considerable generic sampling. The number of species for each genus included in the phylogenies is indicated in brackets. Below the study citation are specified the molecular markers and the phylogenetic inference method used. The branch support values correspond to bootstrap values in case of maximum parsimony (MP) and maximum likelihood (ML) methods, posterior probabilities in Bayesian inference (BI), and local posterior probabilities in coalescence Astral method. A dash (-) indicates a bootstrap support value below 50%. Note that *Diplazoptilon cooperi* is synonymized as *Himalaiella yakla* by Shi & Raab-Straube (2011).

Fig. 2. Phylogenetic reconstruction of subtribe Saussureinae genera inferred with 588 nuclear conserved ortholog loci under the concatenation approach (maximum likelihood analysis performed with RAxML). Branch labels indicate bootstrap support values. Between claudators are specified the segregate genera, when the species have been synonymized as *Jurinea* or *Saussurea*. The new generic delimitation and the species newly combined are shown on the right. **Anacantha* is a synonym of *Modestia*. According to *Flora of China* (Shi & Raab-Straube, 2011), ***Saussurea radiata* is a synonym of *Himalaiella deltoidea* and ****Saussurea yakla* [*Himalaiella*] is a synonym of *Diplazoptilon cooperi*.

Fig. 3. Phylogenetic reconstruction of subtribe Saussureinae genera inferred with 588 nuclear conserved ortholog loci under the coalescence approach (individual gene trees obtained with RAxML and the species tree with Astral). Branch labels indicate support values of local posterior probabilities (LPP). Between claudators are specified the segregate genera, when the species have been synonymized as *Jurinea* or *Saussurea*. The new generic delimitation and the species newly combined are shown on the right. **Anacantha* is a synonym of *Modestia*. According to *Flora of China* (Shi & Raab-Straube, 2011), ***Saussurea radiata* is a synonym of *Himalaiella deltoidea* and ****Saussurea yakla* [*Himalaiella*] is a synonym of *Diplazoptilon cooperi*.

Fig. 4. Schematic representation of the phylogenetic trees inferred in this study under two different treatments (analytic vs. synthetic). The analytic treatment considers the genera currently accepted in most recent analytical classifications (see Table 1). The tree topology of the analytic treatment is outlined following the consensus clades between concatenation and coalescence approaches. Branch labels indicate support values of bootstrap (above branches) and local posterior probabilities (below branches).

SUPPLEMENTARY MATERIAL

Table S1. Overview of previous phylogenetic studies and present study performed on the subtribe Saussureinae with extensive generic sampling.

Genus (no. of species)	Garcia- Jacas & al., 2002	Raab- Straube, 2003	Kita & al., 2004	Susanna & al., 2006	Wang & al., 2007	Wang & al., 2009	Yuan & al., 2015	Fu & al., 2016	Her- rando- Moraira & al., 2018	Her- rando- Moraira & al., 2019	Szukala & al., 2019	Xu & al., 2019	This study
<i>Aegopordon</i> (2)				1					1	1	2		2
<i>Aucklandia</i> (1)					1	1	1	1				1	1
<i>Boloecephalus</i> (1)												1	1
<i>Diplazoptilon</i> (2)*					1	1	1						2
<i>Dolomiaea</i> (17)				1	5	1	1	1			1	1	9
<i>Frolovia</i> (8)		1		2	1	1	1	1			2		5
<i>Hemisteptia</i> (1)			1		1	1	1	1			1	1	1
<i>Hyalochaete</i> (1)	1		1	1									1
<i>Himalaiella</i> (16)		1	4	1	1	1	1				3	1	12
<i>Jurinea</i> (200)	4	3	3	8	1	1	1	3	23	1	80		32
<i>Jurinella</i> (9)	1		1	1							4		4
<i>Lipschitzia</i> (2)		1	1	2	1	1			1	1	1		2
<i>Modestia</i> ** (3)				1					1				1
<i>Outreya</i> (1)	1		1	1					1		1		1
<i>Pilostemon</i> (2)										1			1
<i>Polytaxis</i> (3)				2	1	1	2				1		2
<i>Saussurea</i> (400)	2	42	23	4	1	50	18	5	21	3	4	136	35
Generic coverage (%)	29	29	47	71	59	59	53	35	35	29	65	35	100

* Considering *Diplazoptilon picridifolium* and *D. cooperi*, but *D. cooperi* is considered a synonym of *Himalaiella yakla* (Shi & Raab-Straube, 2011; Yuan & al., 2015).

** Synonymized as *Anacantha* (*Modestia darwasica*, *M. jucunda*, *M. mira*). *Modestia pteroclada* is considered a synonym of *Jurinea jucunda* (Sennikov & Lazkov, 2013).

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Table S2. Species sampled and their corresponding number of raw reads, number of loci extracted with HybPiper (the total were 588), sequencing project, and NCBI accession number. Taxon names follow the final proposed taxonomic treatment presented in the study. New combinations are in bold. Notes: ¹ In Herrando-Moraira & al. (2018) it appears as *Arctium eriophorum*; ² In Herrando-Moraira & al. (2018) it appears as *Cousinia ninae*; ³ In Herrando-Moraira & al. (2018) it appears as *Jurinea abramowii*; ⁴ In Herrando-Moraira & al. (2018) it appears as *Jurinea bucarica*; ⁵ In Herrando-Moraira & al. (2019) it appears as *Rhaponticum acaule*; ⁶ In Herrando-Moraira & al. (2018) it appears as *Saussurea davurica*; ⁷ In Herrando-Moraira & al. (2018) it appears as *Saussurea jadrinzevii*.

Species	N° raw reads	N° loci extracted	Sequencing project	NCBI BioSample accession numbers
<i>Arctium fedtschenkoanum</i>	3,550,984	561	Herrando-Moraira & al. (2018), Mandel & al. (2019)	SAMN11585472
<i>Arctium grandifolium</i>	2,300,488	556	Herrando-Moraira & al. (2018)	SAMN15064103
<i>Arctium karatavicum</i>	2,976,529	561	Herrando-Moraira & al. (2018)	SAMN15064104
<i>Arctium minus</i>	10,007,019	558	Herrando-Moraira & al. (2018)	SAMN15064105
<i>Arctium nidulans</i> ¹	2,984,349	557	Herrando-Moraira & al. (2018)	SAMN15064106
<i>Arctium umbrosum</i>	4,663,613	560	Herrando-Moraira & al. (2018)	SAMN15064107
<i>Carduus nutans</i>	3,891,005	528	Herrando-Moraira & al. (2019)	SAMN15064108
<i>Centaurea aspera</i>	3,215,383	527	Herrando-Moraira & al. (2019)	SAMN15064109
<i>Cirsium sairamense</i>	5,389,901	544	Herrando-Moraira & al. (2018) Mandel & al. (2019)	SAMN11585477
<i>Cousinia arachnoidea</i> ²	3,280,858	552	Herrando-Moraira & al. (2018)	SAMN15064110
<i>Cousinia knorringiae</i>	3,129,866	557	Herrando-Moraira & al. (2018)	SAMN15064111
<i>Cousinia onopordioides</i>	2,369,328	554	Herrando-Moraira & al. (2018)	SAMN15064112
<i>Cousinia polytimetica</i>	2,905,323	556	Herrando-Moraira & al. (2018)	SAMN15064113
<i>Cousinia pungens</i>	13,672,179	560	Present study	SAMN15064114
<i>Cousinia splendida</i>	3,595,227	561	Herrando-Moraira & al. (2018)	SAMN15064115
<i>Cousinia spryginii</i>	3,305,209	557	Herrando-Moraira & al. (2018), Jones & al. (2019)	SAMN10983402
<i>Cynara cardunculus</i>	454,885	457	Mandel & al. (2014, 2019), Herrando-Moraira & al. (2018)	SAMN11585480
<i>Dolomiaea asbukinii</i>	5,880,400	549	Present study	SAMN15064116
<i>Dolomiaea baltalensis</i>	42,600,816	557	Present study	SAMN15064117
<i>Dolomiaea berardioidea</i> 1	6,613,635	555	Present study	SAMN15064118
<i>Dolomiaea berardioidea</i> 2	6,613,635	548	Present study	SAMN15064119
<i>Dolomiaea costus</i>	3,494,166	552	Present study	SAMN15064120
<i>Dolomiaea edulis</i>	6,753,360	559	Present study	SAMN15064121
<i>Dolomiaea forrestii</i> 1	9,965,954	559	Present study	SAMN15064122
<i>Dolomiaea forrestii</i> 2	10,642,455	555	Present study	SAMN15064123
<i>Dolomiaea forrestii</i> 3	7,744,898	557	Present study	SAMN15064124
<i>Dolomiaea frolowii</i>	5,353,925	562	Present study	SAMN15064125
<i>Dolomiaea georgii</i> 1	12,272,881	557	Present study	SAMN15064126
<i>Dolomiaea georgii</i> 2	8,697,941	554	Present study	SAMN15064127
<i>Dolomiaea gorbunovae</i>	3,365,645	540	Present study	SAMN15064128
<i>Dolomiaea macrocephala</i>	13,913,282	554	Present study	SAMN15064129

<i>Dolomiaea platylepis</i>	10,077,877	555	Present study	SAMN15064130
<i>Dolomiaea salwinensis</i> 1	6,830,748	558	Present study	SAMN15064131
<i>Dolomiaea salwinensis</i> 2	10,219,376	562	Present study	SAMN15064132
<i>Dolomiaea salwinensis</i> 3	1,681,110	543	Present study	SAMN15064133
<i>Dolomiaea saussureoides</i>	8,318,886	550	Present study	SAMN15064134
<i>Dolomiaea souliei</i>	6,823,494	559	Present study	SAMN15064135
<i>Dolomiaea sulcata</i>	9,931,761	552	Present study	SAMN15064136
<i>Galactites tomentosa</i>	3,680,490	516	Herrando-Moraira & al. (2019)	SAMN15064137
<i>Jurinea abramovii</i> ³	4,803,672	548	Herrando-Moraira & al. (2018)	SAMN15064138
<i>Jurinea alata</i>	5,069,639	558	Herrando-Moraira & al. (2018), Mandel & al. (2019)	SAMN11585483
<i>Jurinea albescens</i> 1	6,185,365	552	Present study	SAMN15064139
<i>Jurinea albescens</i> 2	11,082,089	552	Present study	SAMN15064140
<i>Jurinea algida</i>	3,743,171	548	Herrando-Moraira & al. (2018)	SAMN15064141
<i>Jurinea atropurpurea</i>	4,316,866	556	Herrando-Moraira & al. (2018), Mandel & al. (2019)	SAMN11585484
<i>Jurinea auriculata</i> 1	6,172,402	549	Present study	SAMN15064142
<i>Jurinea auriculata</i> 2	5,081,700	548	Present study	SAMN15064143
<i>Jurinea baldschuanica</i>	5,113,980	555	Herrando-Moraira & al. (2018)	SAMN15064144
<i>Jurinea berardioides</i> 1	9,192,788	547	Present study	SAMN15064145
<i>Jurinea berardioides</i> 2	5,074,375	543	Present study	SAMN15064146
<i>Jurinea bucharica</i> ⁴	4,255,435	544	Herrando-Moraira & al. (2018)	SAMN15064147
<i>Jurinea bungei</i>	5,593,772	558	Present study	SAMN15064148
<i>Jurinea caespitans</i>	4,407,313	552	Herrando-Moraira & al. (2018)	SAMN15064149
<i>Jurinea capusii</i>	4,726,638	550	Herrando-Moraira & al. (2018)	SAMN15064153
<i>Jurinea carduicephala</i>	7,948,211	565	Present study	SAMN15064154
<i>Jurinea carduiformis</i>	5,200,789	550	Herrando-Moraira & al. (2018)	SAMN15064155
<i>Jurinea ceratocarpa</i> 1	6,897,455	554	Present study	SAMN15064156
<i>Jurinea ceratocarpa</i> 2	5,504,601	555	Present study	SAMN15064157
<i>Jurinea chenopodiifolia</i>	12,228,813	553	Present study	SAMN15064158
<i>Jurinea chitralica</i> 1	3,957,539	491	Present study	SAMN15064159
<i>Jurinea chitralica</i> 2	3,883,146	544	Present study	SAMN15064160
<i>Jurinea chondrilloides</i> 1	3,384,274	545	Present study	SAMN15064161
<i>Jurinea chondrilloides</i> 2	13,741,521	556	Present study	SAMN15064162
<i>Jurinea crispa</i> 1	6,413,883	554	Present study	SAMN15064163
<i>Jurinea crispa</i> 2	5,185,407	545	Present study	SAMN15064164
<i>Jurinea crispa</i> 3	9,236,288	547	Present study	SAMN15064198
<i>Jurinea deltoidea</i> 1	6,719,836	499	Present study	SAMN15064165
<i>Jurinea deltoidea</i> 2	6,854,780	551	Present study	SAMN15064166

<i>Jurinea ferganica</i>	5,170,117	552	Herrando-Moraira & al. (2018)	SAMN15064167
<i>Jurinea filicifolia</i>	7,046,917	556	Present study	SAMN15064168
<i>Jurinea fontqueri</i>	5,240,423	552	Herrando-Moraira & al. (2018)	SAMN15064169
<i>Jurinea frigida</i> 1	17,424,490	563	Present study	SAMN15064170
<i>Jurinea frigida</i> 2	10,174,994	555	Present study	SAMN15064171
<i>Jurinea frigida</i> 3	16,431,602	561	Present study	SAMN15064172
<i>Jurinea gilesii</i>	8,514,559	558	Present study	SAMN15064173
<i>Jurinea heteromalla</i> 1	2,007,573	545	Present study	SAMN15064150
<i>Jurinea heteromalla</i> 2	7,869,423	524	Present study	SAMN15064151
<i>Jurinea heteromalla</i> 3	14,178,130	548	Present study	SAMN15064152
<i>Jurinea heteromalla</i> 4	3,342,983	554	Present study	SAMN15064174
<i>Jurinea jucunda</i>	5,083,617	548	Herrando-Moraira & al. (2018)	SAMN15064175
<i>Jurinea karategina</i>	7,713,700	553	Present study	SAMN15064176
<i>Jurinea kokanica</i>	4,531,178	549	Herrando-Moraira & al. (2018)	SAMN15064177
<i>Jurinea kyzylkyrensis</i>	5,561,006	550	Herrando-Moraira & al. (2018)	SAMN15064178
<i>Jurinea lanipes</i>	4,601,775	548	Herrando-Moraira & al. (2018)	SAMN15064179
<i>Jurinea leptoloba</i>	5,487,798	554	Herrando-Moraira & al. (2018)	SAMN15064180
<i>Jurinea leptophylla</i>	6,055,256	562	Herrando-Moraira & al. (2018)	SAMN15064181
<i>Jurinea macrocephala</i>	4,093,061	542	Herrando-Moraira & al. (2018)	SAMN15064182
<i>Jurinea microcephala</i>	9,602,332	552	Present study	SAMN15064183
<i>Jurinea modesta</i>	7,983,429	552	Present study	SAMN15064184
<i>Jurinea moschus</i> 1	14,116,368	557	Present study	SAMN15064185
<i>Jurinea moschus</i> 2	7,778,198	553	Present study	SAMN15064186
<i>Jurinea moschus</i> 3	12,327,877	564	Present study	SAMN15064187
<i>Jurinea moschus</i> 4	12,414,230	558	Present study	SAMN15064188
<i>Jurinea narynensis</i>	4,564,064	544	Herrando-Moraira & al. (2018)	SAMN15064189
<i>Jurinea natmataungensis</i>	9,238,450	546	Present study	SAMN15064190
<i>Jurinea olgae</i>	4,941,133	549	Herrando-Moraira & al. (2018)	SAMN15064191
<i>Jurinea orientalis</i>	3,155,790	546	Herrando-Moraira & al. (2018)	SAMN15064192
<i>Jurinea peguensis</i> 1	4,024,000	537	Present study	SAMN15064193
<i>Jurinea peguensis</i> 2	4,555,896	544	Present study	SAMN15064194
<i>Jurinea pinnata</i>	2,996,426	553	Herrando-Moraira & al. (2018)	SAMN15064195
<i>Jurinea popovii</i>	3,304,462	554	Herrando-Moraira & al. (2018)	SAMN15064196
<i>Jurinea pulchella</i>	15,259,336	555	Present study	SAMN15064197
<i>Jurinea schachimardanica</i>	3,568,519	550	Herrando-Moraira & al. (2018)	SAMN15064199
<i>Jurinea squarrosa</i> 1	11,922,309	561	Present study	SAMN15064200
<i>Jurinea squarrosa</i> 2	3,734,717	544	Present study	SAMN15064201

<i>Jurinea stenophylla</i>	3,240,161	556	Herrando-Moraira & al. (2018)	SAMN15064202
<i>Jurinea stoechadifolia</i>	4,403,856	560	Herrando-Moraira & al. (2018)	SAMN15064203
<i>Jurinea suffruticosa</i>	2,658,663	554	Herrando-Moraira & al. (2018)	SAMN15064204
<i>Jurinea thianschanica</i>	3,111,323	550	Present study	SAMN15064205
<i>Jurinea trautvetteriana</i>	2,087,532	549	Herrando-Moraira & al. (2018)	SAMN15064206
<i>Jurinea winkleri</i>	2,061,087	543	Present study	SAMN15064207
<i>Jurinea xeranthemoides</i>	2,333,426	549	Present study	SAMN15064208
<i>Jurinea yakla</i>	4,325,189	549	Present study	SAMN15064209
<i>Karvandarina cartilaginea</i>	8,454,714	540	Present study	SAMN15064210
<i>Klasea coriacea</i>	6,205,566	537	Herrando-Moraira & al. (2019)	SAMN15064211
<i>Leuzea acaulis</i> ⁵	4,209,726	548	Herrando-Moraira & al. (2019)	SAMN15064212
<i>Olgaea petriprimi</i>	5,310,933	549	Herrando-Moraira & al. (2018)	SAMN15064213
<i>Onopordum nervosum</i>	2,796,798	544	Herrando-Moraira & al. (2019)	SAMN15064214
<i>Plectocephalus cachinalensis</i>	5,898,634	548	Herrando-Moraira & al. (2019)	SAMN15064215
<i>Psephellus mucroniferus</i>	2,573,295	540	Herrando-Moraira & al. (2019)	SAMN15064216
<i>Saussurea andryaloides</i> 1	3,088,154	497	Present study	SAMN15064217
<i>Saussurea andryaloides</i> 2	2,463,229	547	Present study	SAMN15064218
<i>Saussurea bella</i>	5,899,937	546	Present study	SAMN15064219
<i>Saussurea candolleana</i> 1	4,599,912	547	Present study	SAMN15064220
<i>Saussurea candolleana</i> 2	4,504,851	550	Present study	SAMN15064221
<i>Saussurea controversa</i>	8,091,449	561	Herrando-Moraira & al. (2018)	SAMN15064222
<i>Saussurea daurica</i> ⁶	11,202,023	553	Present study	SAMN15064223
<i>Saussurea discolor</i>	16,539,934	541	Present study	SAMN15064224
<i>Saussurea elegans</i>	2,784,084	553	Present study	SAMN15064225
<i>Saussurea foliosa</i>	4,089,960	560	Herrando-Moraira & al. (2018)	SAMN15064226
<i>Saussurea glacialis</i>	4,072,633	554	Herrando-Moraira & al. (2018)	SAMN15064227
<i>Saussurea gnaphalodes</i>	6,179,290	550	Present study	SAMN15064228
<i>Saussurea gossipiphora</i>	5,563,927	551	Present study	SAMN15064229
<i>Saussurea jadrincevi</i> ⁷	9,091,105	562	Herrando-Moraira & al. (2018)	SAMN15064230
<i>Saussurea krylovii</i>	3,576,809	557	Herrando-Moraira & al. (2018)	SAMN15064231
<i>Saussurea larionowii</i>	4,733,404	554	Herrando-Moraira & al. (2018)	SAMN15064232
<i>Saussurea latifolia</i>	5,065,459	556	Herrando-Moraira & al. (2018)	SAMN15064233
<i>Saussurea lehmannii</i>	7,854,228	541	Present study	SAMN15064234
<i>Saussurea leontodontoides</i>	7,209,427	560	Present study	SAMN15064235
<i>Saussurea leucophylla</i>	5,597,695	562	Herrando-Moraira & al. (2018)	SAMN15064236
<i>Saussurea lyrata</i> 1	7,057,764	545	Present study	SAMN15064237
<i>Saussurea lyrata</i> 2	3,919,740	539	Present study	SAMN15064238

<i>Saussurea manshurica</i>	4,417,126	559	Herrando-Moraira & al. (2018)	SAMN15064239
<i>Saussurea nivea</i>	7,048,980	557	Present study	SAMN15064240
<i>Saussurea obvallata</i>	12,608,195	558	Present study	SAMN15064241
<i>Saussurea orgaadayi</i>	3,578,510	554	Herrando-Moraira & al. (2018)	SAMN15064242
<i>Saussurea picridifolia</i>	8,055,160	558	Present study	SAMN15064243
<i>Saussurea pseudoalpina</i>	3,887,786	559	Herrando-Moraira & al. (2018)	SAMN15064244
<i>Saussurea pulchella</i> 1	11,166,564	542	Present study	SAMN15064245
<i>Saussurea pulchella</i> 2	16,171,554	528	Present study	SAMN15064246
<i>Saussurea roylei</i>	4,576,394	562	Present study	SAMN15064247
<i>Saussurea salicifolia</i>	4,799,838	554	Herrando-Moraira & al. (2018)	SAMN15064248
<i>Saussurea salsa</i>	2,458,299	552	Herrando-Moraira & al. (2018), Mandel & al. (2019)	SAMN11585485
<i>Saussurea scabrida</i>	4,100,343	555	Present study	SAMN15064249
<i>Saussurea scaposa</i>	6,065,931	553	Present study	SAMN15064250
<i>Saussurea schanginiana</i>	4,568,611	559	Herrando-Moraira & al. (2018)	SAMN15064251
<i>Saussurea simpsoniana</i>	5,378,069	548	Present study	SAMN15064252
<i>Saussurea sorocephala</i>	2,834,853	550	Present study	SAMN15064253
<i>Saussurea stubendorffii</i>	5,329,546	559	Herrando-Moraira & al. (2018)	SAMN15064254
<i>Saussurea subacaulis</i>	8,252,488	559	Herrando-Moraira & al. (2018)	SAMN15064255
<i>Saussurea taraxacifolia</i>	2,743,424	554	Present study	SAMN15064256
<i>Saussurea uniflora</i>	4,097,420	544	Present study	SAMN15064257
<i>Saussurea winkleri</i>	5,243,142	540	Present study	SAMN15064258
<i>Staehelina lobelii</i>	6,287,680	550	Herrando-Moraira & al. (2019)	SAMN15064259
<i>Staehelina petiolata</i>	5,695,551	544	Herrando-Moraira & al. (2019)	SAMN15064260
<i>Tricholepis edmondsonii</i>	9,369,430	554	Present study	SAMN15064261
<i>Volutaria canariensis</i>	4,551,867	529	Herrando-Moraira & al. (2019)	SAMN15064262

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