

# *Shangwua* (Compositae), a new genus from the Qinghai-Tibetan Plateau and Himalayas

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**Abstract** A new genus of Compositae, *Shangwua*, is described to accommodate all species formerly placed in *Saussurea* sect. *Jacea*. This genus is distinct from the other genera of tribe *Cardueae* in its unique combination of states of characters including involucral bracts, receptacle, paleae, anther, style, achene and pappus. Phylogenetic analyses based on molecular data suggest that this new genus belongs to the *Xeranthemum* group, a lineage of the Carduinae that diversified early, with only distant relationships to *Saussurea* and related genera. The genus *Shangwua* consists of three species occurring in the Qinghai-Tibetan Plateau and Himalayas.

**Keywords** Compositae; Himalayas; molecular phylogenetics; new genus; taxonomic revision; *Saussurea*; *Shangwua*

**Supplementary Material** The Electronic Supplement (Appendix S1: Taxonomic revision under the genus *Shangwua*; Figs. S1–S5) and the alignment files are available in the Supplementary Data section of the online version of this article (<http://www.ingentaconnect.com/content/iapt/tax>).

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## ■ INTRODUCTION

*Cardueae* was one of the first tribes to be recognised in Compositae (Cassini, 1819). Its members share a thickened hairy node below the style branches, and they occur mainly in temperate regions of Eurasia (Dittrich, 1977; Häffner, 2000). The most recent revisions of the tribe (Susanna & Garcia-Jacas, 2007, 2009) recognised around 2500 species in 73 genera. Four of the genera (*Centaurea* L., *Cirsium* Mill., *Cousinia* Cass., *Saussurea* DC.) are extremely species-rich (Bremer, 1994; Susanna & Garcia-Jacas, 2007, 2009). Substantial progress towards understanding the evolutionary relationships of the tribe has been made recently using molecular data (e.g., Raab-Straube, 2003; Kita & al., 2004; Martins, 2006; Susanna & al., 2006; Barres & al., 2013). However, generic delimitations and phylogenetic relationships remain unresolved for some groups, notably the *Carduus-Cirsium* group and, in particular, the *Saussurea* group.

First established by Candolle (1810a, b), *Saussurea* was initially described as having a pappus composed of an outer row of short, discrete and scabrid bristles, and an inner layer of long, basally connate and plumose bristles. Candolle later found that certain species assigned to *Saussurea* lacked an outer row of pappus bristles, although they resembled *Saussurea* in other

characters. He thus established a new genus, *Aplotaxis* DC., to accommodate these species (Candolle, 1833). However, an outer row of pappus bristles was observed for some *Aplotaxis* species by Schultz (1846), having merely been overlooked by Candolle. Schultz therefore returned *Aplotaxis* to synonymy with *Saussurea*, and this treatment was followed by Clarke (1876), Hooker (1881) and many others. This broad generic circumscription was also adopted by Lipschitz (1979) in his monographic revision of *Saussurea*, which recognised a total of 390 species and established an infrageneric system of six subgenera and twenty sections. Subsequent floristic works largely followed this system (Chen, 1985; Liu, 1996, 2004; Shi & Jin, 1999; Saklani & Rao, 2000), and recently described species have been assigned to these subgenera and sections (Wang & al., 2005; Fujikawa & Ohba, 2007; Raab-Straube, 2009, 2011; Liu & Ho, 2010; Chen, 2010, 2011; Chen & Gan, 2011). However, the status of *Saussurea* subg. *Jurinocera* (Baill.) Lipsch. and *S.* subg. *Frolovia* (DC.) Lipsch. and that of *S.* sect. *Elatae* Hook. f. within *S.* subg. *Saussurea* is controversial, with some authors suggesting that each be recognised as an independent genus based on morphological and molecular phylogenetic evidence (Kamelin, 1993; Häffner, 2000; Raab-Straube, 2003; Kita & al., 2004; Shi & Raab-Straube, 2011). Others have suggested transferring these three groups into the genera *Jurinea* Cass.

or *Dolomiaeae* DC. (Susanna & al., 2006; Wang & al., 2007). In the latest taxonomic treatment for China (Shi & Raab-Straube, 2011), *Saussurea* sect. *Elatae*, *S.* sect. *Frolovia* (DC.) Kitam. and *S.* sect. *Aucklandia* (Falc.) O. Hoffm. were treated under the genera *Himalaiella* Raab-Straube, *Frolovia* (DC.) Lipsch. and *Aucklandia* Falc., respectively. The number of remaining *Saussurea* subgenera and sections in China was reduced to four and eight respectively, including *Saussurea* sect. *Jacea* Lipsch., and 289 species of *Saussurea* were recognised (Shi & Raab-Straube, 2011).

Previous molecular analyses (Raab-Straube, 2003; Wang & al., 2009), examined 56 *Saussurea* species, covering four subgenera and seven of the sections recognised by Shi & Raab-Straube (2011), or all six subgenera and 19 out of 20 sections recognised by Lipschitz (1979). Those analyses confirmed the exclusion of some sections from *Saussurea* and resulted in the recognition of *Saussurea* s.str. as a monophyletic lineage (Wang & al., 2009). In particular, *Saussurea forrestii* Diels (= *Saussurea denticulata* (DC.) Wall. ex C.B. Clarke 1876, non Lebed. 1829, nom. illeg.), up to now placed in *Saussurea* (subg. *Saussurea*) sect. *Jacea*, was found to occupy a relatively basal position in Cardueae, making it only distantly related to *Saussurea* and its segregates (Wang & al., 2009). However, the exact systematic position of this species remained uncertain because of the limited number of Cardueae genera sampled in that study. This rather surprising result prompted closer examination of the morphology of the six species (*Saussurea fastuosa* (Decne.) Sch. Bip., *S. forrestii* Diels, *S. glabrata* (DC.) C. Shih, *S. jacea* (Klotzsch) C.B. Clarke, *S. masarica* Lipsky, *S. tadshikorum* Iljin & Gontsch.) of *S.* sect. *Jacea*. These species share the following characteristic features: dark-rimmed involucral bracts, elongated receptacular paleae, and a uniseriate or subuniseriate pappus with plumose bristles (Lipschitz, 1979; Shi & Jin, 1999). These species were diagnosed mainly by the shape and the indumentum of the leaves and some other quantitative characters with continuous variations, which caused delimitations of some species to be extremely difficult (Lipschitz, 1979; Liu, 2004).

Here we present the results of molecular phylogenetic and morphological analyses of these species, designed to determine their true position within tribe Cardueae. Based on these data, a new genus is erected and a taxonomic revision of the group is presented (for the complete taxonomic treatment, see Electr. Suppl.: Appendix S1).

## ■ MATERIALS AND METHODS

**Plant material and sampling.**— Only two species of *Saussurea* sect. *Jacea* were included for molecular phylogenetic study. The examined material of these two species comprised one accession of *Saussurea jacea* C.B. Clarke from the western Himalayas, and eight accessions of *S. forrestii* from the central Himalayas and the Qinghai-Tibetan Plateau (Appendix 1). The third species (*S. masarica*) with a distinct morphology was not analyzed because it is difficult to collect fresh material of this species in the field and we also failed to amplify the DNA fragments used in this study from the poor DNAs extracted

from the specimens kept in herbaria. For the morphological comparison of the species of the new genus with *Saussurea* and with possibly related genera identified in previous phylogenetic analyses (Wang & al., 2009; Barres & al., 2013; *Amphoricarpos* Vis., *Berardia* Vill., *Chardinia* Desf., *Siebera* J. Gay, *Staelhelina* L., *Xeranthemum* L.), selected herbarium specimens were examined (Appendix 2). Additional morphological data were taken from the literature (Bremer, 1994; Dittrich, 1996; Susanna & Garcia-Jacas, 2007; Shi & Raab-Straube, 2011). According to our previous and initial phylogenetic examination of all genera of Cardueae (Susanna & Garcia-Jacas, 2007; Wang & al., 2009; Shi & Raab-Straube, 2011; Barres & al., 2013), the selected genera should comprise all those potentially related to *Saussurea* sect. *Jacea* based on both morphological and molecular evidence.

**DNA amplification.**— Total DNA was extracted from *Saussurea forrestii* and *S. jacea* samples using Qiagen DNeasy Kits, following the manufacturer's instructions. Five DNA fragments (*rbcL*, *ndhF*, *matK*, *trnL-F*, ITS) were amplified and sequenced, following the protocol used in our previous studies (Wang & al., 2009; Zhang & al., 2009). All five fragments from *S. forrestii* were successfully sequenced, but only the ITS, *trnL-F* and partial *matK* fragments were obtained from *S. jacea*. These fragments, also obtained from five selected species of *Saussurea* and other related genera, were amplified and sequenced. After validation by visual inspection of chromatograms employing Mega v.4.0 (Tamura & al., 2007) and further confirmation of the nuclear ITS sequences by forward and backward sequencing, a total of 23 newly obtained sequences were deposited in GenBank (Appendix 1). In addition, sequences representing all known lineages of Cardueae, mainly following Barres & al. (2013) (Appendix 1), were downloaded.

**Phylogenetic analyses.**— Two datasets were constructed. The first dataset was composed of nuclear ITS and *trnL-F* and *matK* sequences of *Saussurea forrestii*, *S. jacea* and 24 species representing all major subtribes of Cardueae to test whether the two species of *Saussurea* sect. *Jacea* form a monophyletic clade and to determine their probable positions in the tribe (Susanna & al., 2006). The second dataset comprised data from nuclear ITS and *trnL-F*, *matK*, *ndhF* and *rbcL* for a total of 105 taxa of Cardueae (based on Barres & al., 2013) including *S. forrestii*, in order to further determine the systematic position of *S. sect. Jacea*. *Oldenburgia* Less. was used as outgroup for the phylogenetic analyses of the first dataset, and additionally *Brachylaena* R. Br. and *Tarchonanthus* L. from other tribes of subfamily Carduoideae (Barres & al., 2013) for the second dataset. The incongruence length difference (ILD) test (Farris & al., 1995) was used to detect potential conflicts between different DNA fragments, using the partition homogeneity test implemented in PAUP\* v.4.0b10 (Swofford, 2003), with 1000 replicates, and the heuristic search option, with 100 random taxon addition and TBR branch swapping.

Mega v.4.0 (Tamura & al., 2007) was used to calculate genetic distances under the Kimura two-parameter (K2P) model, and to count singleton sites of *Saussurea forrestii* and *S. jacea*. Bayesian inference (BI) methods were used to do phylogenetic analyses for all datasets using MrBayes v.2.1 (Ronquist

& Huelsenbeck, 2001). The GTR+G model, for which the parameters were initially considered to be unknown and estimated during the course of the run, was employed for the following analyses. Four chains, each with a different starting seed, were run for two million generations, and the temperature was set to the default value of 0.2. The trees were sampled every 100 generations, and Tracer v.1.5 (<http://tree.bio.ed.ac.uk/software/tracer/>) was used to choose a suitable burn-in. Finally, PAUP\* v.4.0b10 (Swofford, 2003) was used to calculate a consensus tree and posterior probabilities (PP) from the sampled trees after the burn-in period were then calculated.

## ■ RESULTS

**Phylogenetic analyses.** — Among the eight individuals examined of *Saussurea forrestii*, no variation was detected for any of the chloroplast loci, but up to four polymorphic sites were detected in their ITS sequences. Since these eight individuals formed a monophyletic lineage, only one sequence was chosen for further analyses. The ILD test revealed the absence of strong conflicts between the chloroplast and nuclear partitions included in the first dataset ( $P = 0.213$ ). From a total of 1604 bp, following alignment, 200 singleton and 255 parsimony-informative sites were recovered when the gaps were treated as missing data. The genetic distance between *S. forrestii* and *S. jacea* was found to be 1.98%, far less than the distances between them and the other *Saussurea* species (4.93%–5.43%) or between any other pair of genera (3.33%–8.18%). *Saussurea forrestii* and *S. jacea* formed a highly supported monophyletic clade when the first dataset was examined (PP = 100%; Electr. Suppl.: Fig. S1). This clade was only distantly related to the other three selected *Saussurea* species, and fell outside of a clade comprising these and related genera from in and around the Qinghai-Tibetan Plateau, such as *Dolomiaeae* and *Himalaiella*.

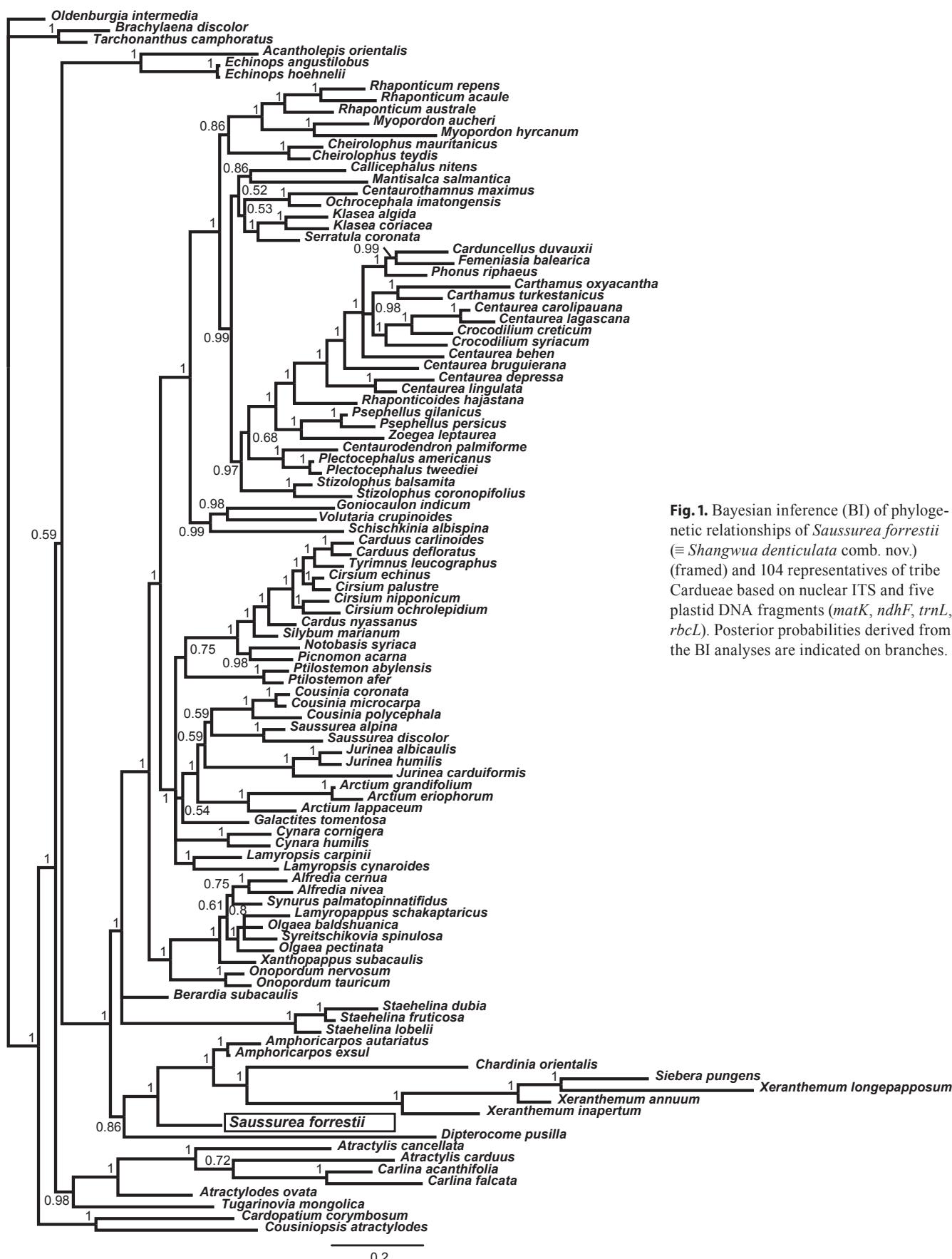
The ILD test also revealed the absence of strong conflicts between cpDNA fragments included in the second dataset. The aligned fragments comprised a total of 4728 bp, with 601 parsimony-informative sites when gaps were treated as missing data. Phylogenetic analysis of this dataset placed *Saussurea* in a derived position within a strongly supported (PP = 100%; Fig. 1) subclade comprising most species of Cardinae but not *S. forrestii*. Instead, *S. forrestii* was revealed to be sister to the *Xeranthemum* group (*Amphoricarpos*, *Chardinia*, *Siebera* and *Xeranthemum*; PP = 100%; Fig. 1), which is one of the basal lineages of Cardinae.

**Morphological differences.** — All species of *Saussurea* sect. *Jacea* share certain characters with other *Saussurea* species. They all have multiple rows of imbricate involucral bracts, discoid, homogamous capitula and a plumose, basally connate pappus (Lipschitz, 1979; Bremer, 1994; Susanna & Garcia-Jacas, 2007; Shi & Raab-Straube, 2011). However, they show marked differences to *Saussurea* in a number of characters, as described below (Figs. 2, 3, 4A–L) and in Table 1.

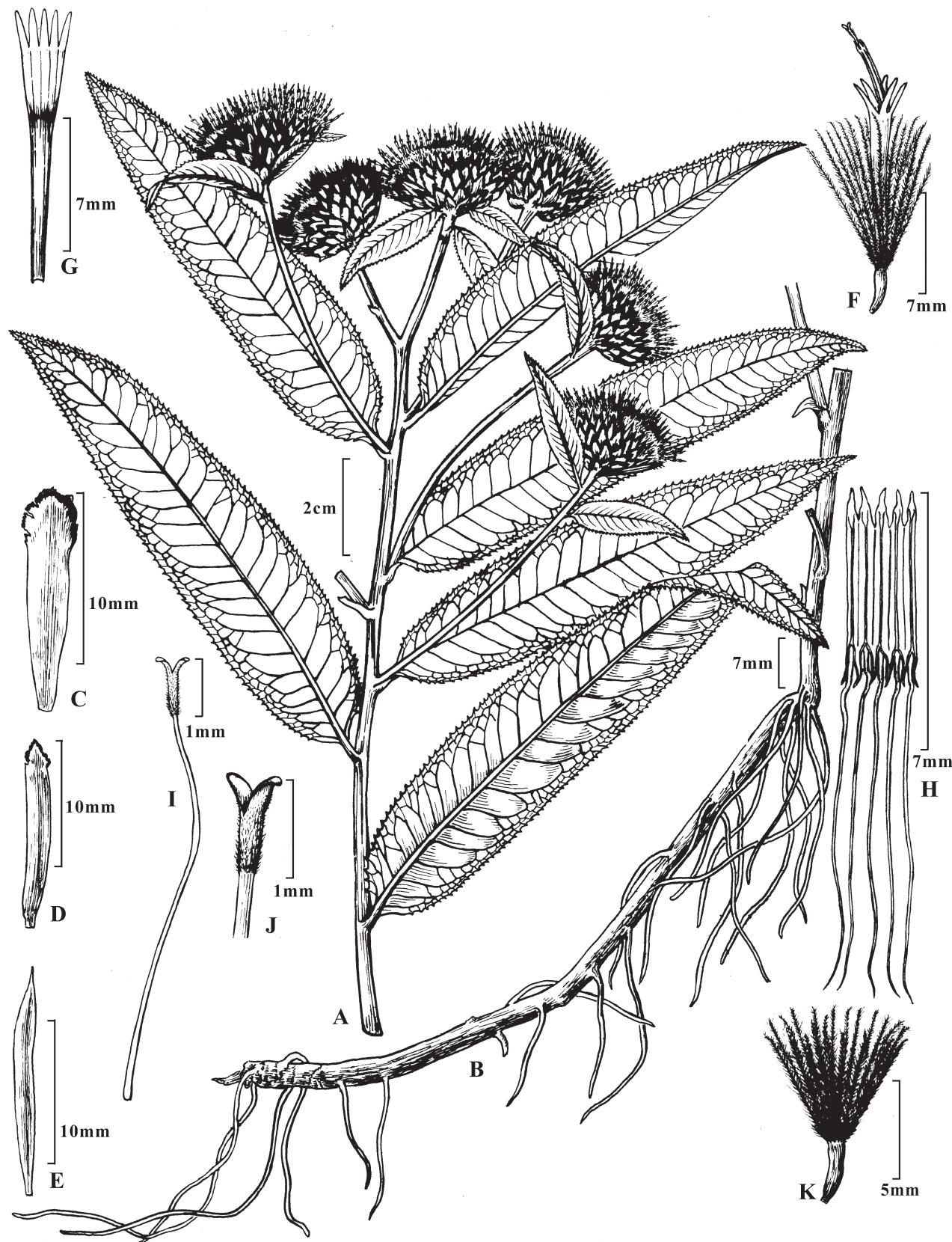
The roots of *S. sect. Jacea* are lignified, and field observations suggest that this species is capable of clonal reproduction

(Figs. 2B, 3F). Both these features have rarely been reported for other *Saussurea* species (Lipschitz, 1979; Shi & Raab-Straube, 2011). The receptacle is alveolate and almost flat (Fig. 4D, J), whereas in most *Saussurea* species the margin of the alveolae is elongated, forming many subulate, acute bristles. Conversely, in the remaining *Saussurea* sections true paleae are lacking, whereas in *S. sect. Jacea*, 1–2 cm long paleae (one per floret) are present. Involucral bracts in *S. sect. Jacea* have dark, lacerate and membranous margins (Figs. 2C, 3E, 4A, G). Anther tails of *S. sect. Jacea* species are short and undivided (Figs. 2H, 4C, I), while those of most remaining *Saussurea* species are deeply lacerate or woolly. Both genera have thickened hairy nodes below the style branches, but in *S. sect. Jacea* (Figs. 2I, J, 4B, H) these are at least three times longer than those of the remaining *Saussurea* species and other genera of Cardinae examined. The character of short and acute style branches is shared between *S. sect. Jacea* (Figs. 2I, 4B, H), genera of subtribe Carlininae, and the *Xeranthemum* group of Cardinae (Susanna & Garcia-Jacas, 2007). Style branches of most *Saussurea* species, however, are linear, apically obtuse to sub-obtuse, and at least twice as long as broad (Lipschitz, 1979; Bremer, 1994; Shi & Raab-Straube, 2011). The pappus of *S. sect. Jacea* is homomorphic, consisting of a single row of connate, plumose pappus bristles that form a basal ring (Fig. 4E, F, K, L). It therefore lacks the outer layer of distinct, scabrous pappus bristles that are diagnostic for *Saussurea*. In this respect, *S. sect. Jacea* resembles *Carlinea* L. (Susanna & Garcia-Jacas, 2007). Occasionally, some of these bristles are shorter and bent outwards, so they can easily be mistaken for a second row of bristles. However, *Saussurea* species always have an inner row of plumose bristles that are connate at the base, and nearly always an outer row of scabrid bristles, which are free from each other, deciduous and much shorter than the inner ones. In contrast to the other *Saussurea* species, the pappus of *S. sect. Jacea* is directly and firmly attached to the pericarp wall and not surrounded by an apical rim (Fig. 4F, L). This character is also common in the Carlininae, in *Berardia* and *Staelhelina*, and in the *Xeranthemum* group (Dittrich, 1996; Susanna & Garcia-Jacas, 2007).

*Saussurea* sect. *Jacea* differs from *Berardia*, *Staelhelina* and the *Xeranthemum* group in having a pappus of plumose bristles instead of smooth to scabrid or barbellate bristles or scarious scales (Table 1). The paleae (one per floret) are coriaceous, subulate, apically bent or hooked, and always longer than the florets (Fig. 4D, J), whereas the paleae or bristles in the other genera are scarious, straight and usually shorter than the florets. *Saussurea* sect. *Jacea* is also unique among the basal genera of Cardinae in having coriaceous or herbaceous involucral bracts with a broad, scarious, blackish and often lacerate margin (Fig. 4A, G). Involucral bracts in the *Xeranthemum* group, for example, are scarious and often coloured. *Saussurea* sect. *Jacea* has homogamous capitula and achenes that are glabrous and smooth (Fig. 4E, K), whereas all other genera of the *Xeranthemum* group have heterogamous capitula and achenes that are sericeous and often sulcate. It also differs from these in its perennial habit; the genera *Chardinia*, *Siebera* and *Xeranthemum* are all annual.



**Fig. 1.** Bayesian inference (BI) of phylogenetic relationships of *Saussurea forrestii* ( $\equiv$  *Shangwua denticulata* comb. nov.) (framed) and 104 representatives of tribe Cardueae based on nuclear ITS and five plastid DNA fragments (*matK*, *ndhF*, *trnL*, *rbcL*). Posterior probabilities derived from the BI analyses are indicated on branches.



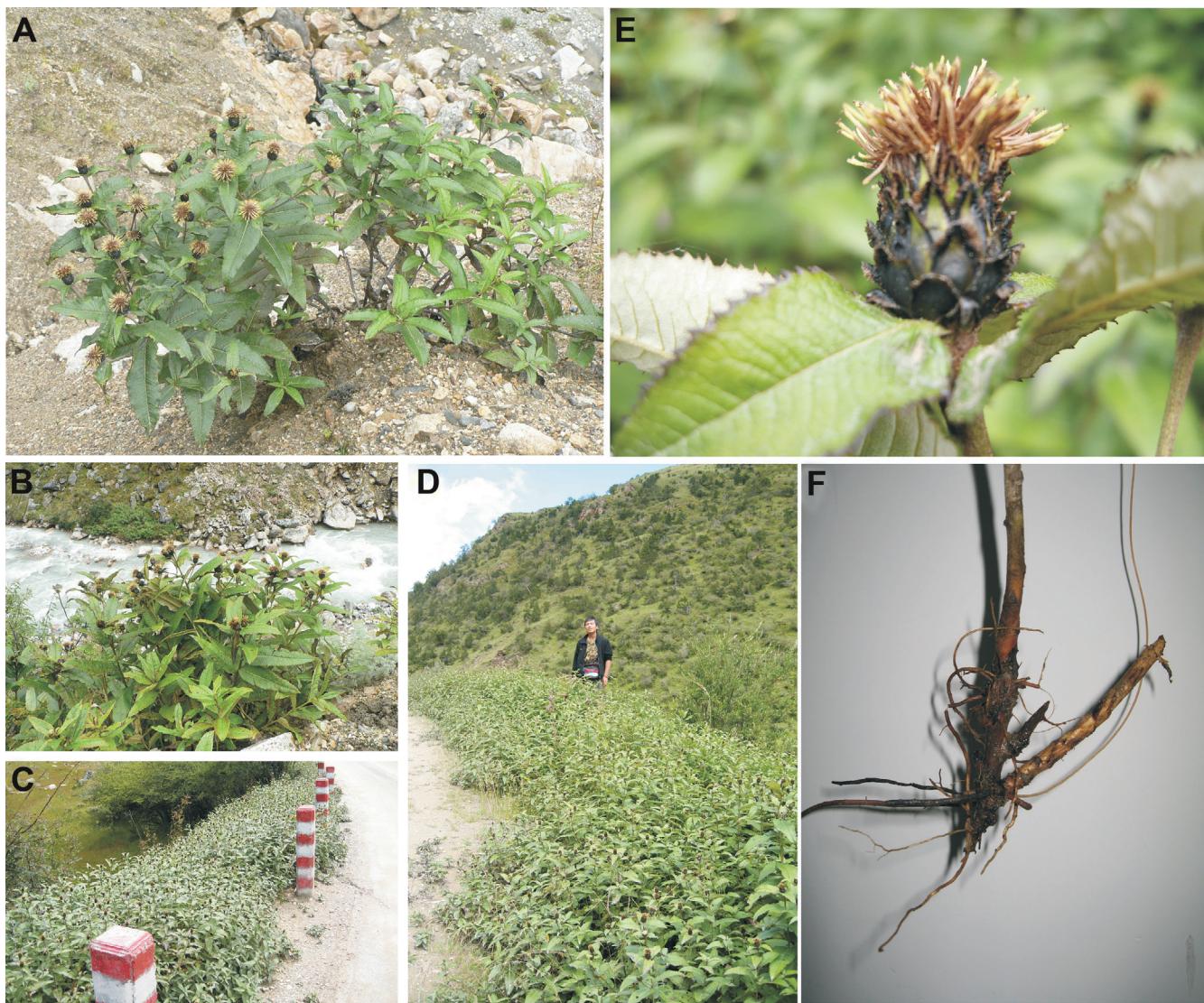
**Fig. 2.** *Shangwua denticulata* comb. nov. (from J.Q. Liu 07150, Lzu). **A**, habit; **B**, rootstock; **C–E**, involucral bracts from outer to inner row; **F**, floret; **G**, corolla; **H**, stamens; **I**, style; **J**, upper part of style with short branches and thickened hairy node; **K**, achene with pappus. — Drawn by Han-Ping Yu.

## ■ DISCUSSION

The pappus structure is the main diagnostic character used to delimit *Saussurea* (Candolle, 1810a, b, 1833; Schultz, 1846; Lipschitz, 1979; Shi & Raab-Straube, 2011). *Himalaiella* and *Frolovia* both comprise species that were previously included in *Saussurea* (Raab-Straube, 2003) but differ in having only one homomorphic row of pappus bristles, rather than the two heteromorphic rows found in most *Saussurea* species. While the status of these segregates is still a matter of debate, they are unambiguously only distantly related to *Saussurea*, and closer to *Jurinea* (Susanna & al., 2006). In *S.* sect. *Jacea*, the pappus also consists of a single row of basally connate, plumose bristles. Some of these bristles can be markedly shorter than the others and more strongly bent outwards, resembling an outer row. Moreover, the pappus of *S.* sect. *Jacea* is inserted on

top of the achene, a character shared with Carlininae and the *Xeranthemum* group; in other members of Carduinae including *Saussurea*, *Himalaiella* and *Frolovia*, the pappus is surrounded by the apical rim of the achene (Häffner, 2000).

Our molecular phylogenetic analyses suggest that the two species of *S.* sect. *Jacea* examined (*S. forrestii*, *S. jacea*) are closely related to each other, comprising a monophyletic clade among the genera of Cardueae (Electr. Suppl.: Fig. S1). However, this clade is not closely related to *Saussurea*, nor to any of the genera closely allied to it (Fig. 1). Instead, our phylogenetic analyses confirm that *S.* sect. *Jacea* occupies a rather isolated position within the *Xeranthemum* group, a lineage of subtribe Carduinae that apparently diversified early. The reconstructed phylogenetic relationships, together with its unique combination of morphological characters, strongly support the recognition of *S.* sect. *Jacea* as a new genus.



**Fig. 3.** Photographs of *Shangwua denticulata* comb. nov. **A**, habit; **B–D**, habitat; **E**, capitulum with subtending leaves; **F**, rootstock with adventive shoots. — A–B, China, Xizang, Jilong (J.Q. Liu Liujq-09xz-lzt-073, LZU); C–F, China, Xizang, Nielamu (J.Q. Liu 07150, LZU).



**Fig. 4.** Morphological details of two species of *Shangwua* gen. nov. **A–F**, *Sh. jacea* (A–C from D.J. Broadhead 119, E; D–F from Koelz 2617, L0833898); **G–L**, *Sh. denticulata* (G–I from J.Q. Liu 07150, LZU; J–L from Dhewoj 256, E00451529). **A, G**, involucral bracts (from outer to inner rows); **B, H**, style branches; **C, I**, anther tails; **D, J**, fruiting capitulum with involucral bracts partly removed, receptacle with paleae (p); **E, K**, achene with pappus; **F, L**, insertion of pappus on achene. — Scale bars: A, G = 1 cm; B, C, F, H, I = 1 mm; D, E, J, K = 5 mm; L = 0.5 mm.

Our morphological examinations show that all species of *S.* sect. *Jacea* share a number of distinctive morphological characters such as involucral bracts, receptacular paleae, shape of anther tails, style branches, achenes and pappus structure and insertion. This combination of characters clearly distinguishes

the new genus from both *Saussurea* and all other genera of Cardueae (Table 1). However, these characters provide no clear clues to the relationship of this new genus to other basal genera of subtribe Carduinae, e.g., *Xeranthemum*, *Staelhelina* and *Berardia*. In some respects, species of the new genus are

**Table 1.** Diagnostic features of *Shangwua* (≡ *Saussurea* sect. *Jacea*), *Saussurea* (the remaining sections) and basal genera of tribe Cardueae.

Character	<i>Shangwua</i>	<i>Saussurea</i>	<i>Berardia</i>	<i>Staelhelina</i>	<i>Amphoricarpos</i>	<i>Xeranthemum</i>	<i>Siebera</i>	<i>Chardinia</i>
Life form	perennial herbs or subshrubs	biennial or perennial herbs, rarely subshrubs	perennial rosulate herbs	shrubs or subshrubs	perennial herbs or subshrubs	annual herbs	annual herbs	annual herbs
Capitula	homogamous	homogamous	homogamous	homogamous	heterogamous (outer florets female)	heterogamous (outer florets sterile)	heterogamous (outer florets sterile)	heterogamous (outer florets female)
Involucral bracts	ovate with scarious, lacerate dark rim	variable, but without lacerate dark rim	subulate, woolly	ovate-lanceolate, without lacerate dark rim	scarious, ovate-lanceolate to obovate and mucronate	scarious, inner ones elongate and coloured	scarious, inner ones coloured and pungent	scarious, obovate to lanceolate
Receptacle	with 1.3–1.5 cm long, subulate, apically hooked paleae, longer than florets	mostly with numerous alveolate subulate bristles, shorter than florets, or alveolate	alveolate, without bristles	with scarious, silvery subulate scales, shorter than florets	with scarious, apically lacerate silvery scales, shorter than florets	with scarious, linear-lanceolate scales, longer than florets	with scarious scales	with scarious, lanceolate to subulate scales
Anther tails	short, undivided	mostly woolly or strongly lacerate	short, lacinate to entire	strongly lacerate	short, lacinate to entire			
Style branches	short, divergent, apex acute	long, strongly divergent, apex obtuse	short, coherent, apex obtuse	very short, coherent, apex obtuse	short, divergent, apex acute	very short, divergent, apex obtuse	very short, coherent, apex obtuse	very short, divergent, apex obtuse
Achenes	glabrous, without corona	mostly glabrous, with distinct apical rim or crown	glabrous, slightly sulcate	glabrous or sericeous, with a minute corona	sericeous	sericeous	sericeous, sulcate	dimorphic, glabrous or partly sericeous
Pappus structure	homomorphic, uniseriate, plumose bristles	heteromorphic, biserrate bristles; outer ones mostly scabrid, inner ones longer and always plumose	homomorphic, multiseriate bristles, basally smooth, apically scabrid	homomorphic, uniseriate bristles, basally smooth, apically scabrid	homomorphic, uniseriate, scarious scales, basally smooth, apically scabrid	homomorphic, uniseriate, scarious scales, basally smooth, apically scabrid	homomorphic, uniseriate, scarious scales, basally smooth, apically scabrid	homomorphic, uniseriate, scarious scales, basally smooth, apically scabrid
Pappus insertion	directly attached on upper edge of achene	attached within apical rim of achene	directly attached on upper edge of achene	directly attached on upper edge of achene	directly attached on upper edge of achene	directly attached on upper edge of achene	directly attached on upper edge of achene	directly attached on upper edge of achene

morphologically intermediate between the *Xeranthemum* group and subtribe Carlininae, especially in terms of pappus characters (Dittrich, 1996).

*Saussurea* sect. *Jacea* currently comprises three morphologically recognisable and geographically separate species in the western and central Himalayas and the Qinghai-Tibetan Plateau, indicating that it diversified within this region. Two of its species were first described under *Aplotaxis* (or *Haplotaxis*, a mere orthographic variant). However, the name *Aplotaxis* is typified by a species that belongs to *Saussurea* (Raab-Straube, 2003), so it cannot be used for this genus (Art. 10.2, *Melbourne Code*, McNeill & al., 2012). Therefore, the new genus name *Shangwua* is proposed here, to accommodate the accepted species formerly placed in *Saussurea* sect. *Jacea*.

## ■ TAXONOMIC TREATMENT

***Shangwua*** Yu J. Wang, Raab-Straube, Susanna & J. Quan Liu, gen. nov. ≡ *Saussurea* sect. *Jacea* Lipsch. in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.R. 16: 441. 1954 – Type: *Shangwua jacea* (Klotzsch) Yu J. Wang & Raab-Straube.

**Description.** – Perennial herbs with woody rootstock. Stems solitary, erect, usually much-branched, densely leafy. Leaves alternate, shortly petiolate or sessile, undivided, largest at middle of stem, the lower and upper ones smaller, glabrous or abaxially densely tomentose and with sessile glands. Capitula numerous or few, usually solitary and terminal on stem and branches, homogamous, discoid. Involucral bracts in several rows, imbricate, leathery, straw-coloured with brown or black membranous margin. Receptacle flat, alveolate, without numerous alveolar bristles, but paleate with one palea per floret; paleae 1.2–2 cm, usually longer than inner phyllaries. Florets all fertile, hermaphroditic. Corolla tubular, glabrous,

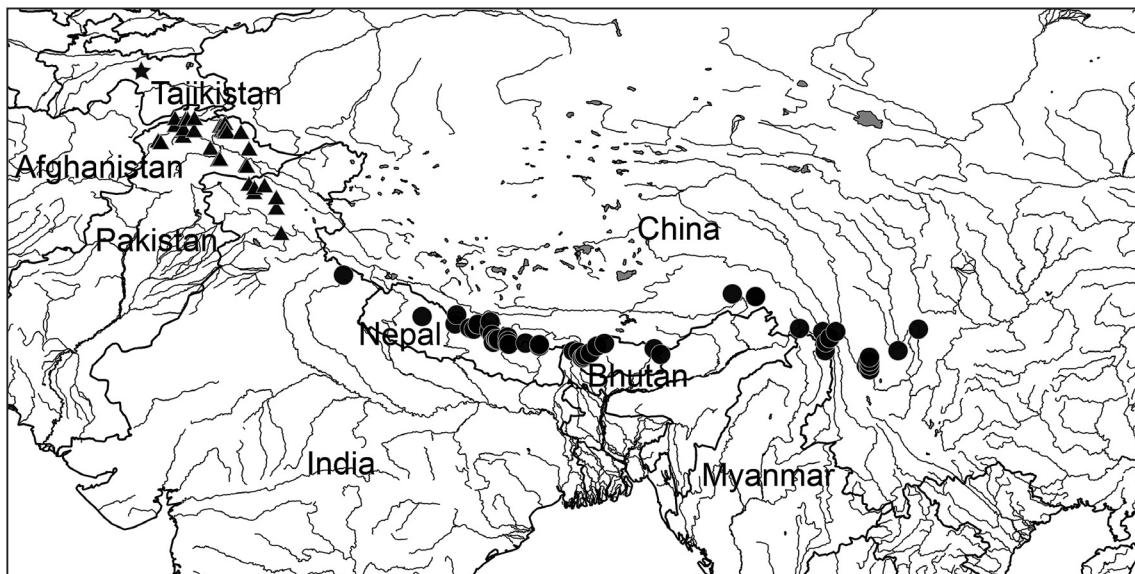
actinomorphic, limb ± as long as tube, throat 2–3 times longer than lobes. Filaments glabrous. Anther tube with short, undivided basal appendages. Style with thickened, 1.5–2 mm long hairy node below branches; style branches flat, acute or subacute, very short (less than 1 mm), diverging. Achenes glabrous, cylindrical, longitudinally ribbed, with basal attachment scar; apex truncate, without conspicuous rim. Pappus homomorphic, bristles straw-coloured to brownish, arranged in a single row, plumose, unequal in length, connate at base and fused with achene, persistent.

**Etymology.** – The name *Shangwua* is proposed here after the given name of Prof. Shangwu Liu, a taxonomist who has made major contributions to our understanding of the Compositae of the Qinghai-Tibetan Plateau.

**Taxonomy and distribution.** – After a complete revision, three species are recognised under the genus *Shangwua* (see below; for details see Electr. Suppl.: Appendix S1). All of them are distributed in high mountains of Asia. Two of them occur in Pamir, Hindukush and Karakorum, whereas the third has a wider distribution on the southern edge of the Qinghai-Tibetan Plateau from the western Himalaya in India to the Hengduan mountains in Yunnan and Sichuan (Fig. 5).

### Key to three species recognised in *Shangwua*

1. Middle stem leaves lanceolate, more than 6 cm long, margin serrulate or denticulate ... 1. *Shangwua denticulata*
1. Middle stem leaves ovate to elliptic, less than 6 cm long, margin entire or minutely denticulate ..... 2
2. Middle stem leaves ovate or elliptic, more than 2 cm wide, abaxially usually green, glabrous, but densely glandular, margin entire ..... 2. *Shangwua jacea*
2. Middle stem leaves ovate, less than 2 cm wide, abaxially usually whitish, densely arachnoid-tomentose, margin minutely denticulate ..... 3. *Shangwua masarica*



**Fig. 5.** Distribution of *Shangwua masarica* (star), *Sh. jacea* (triangles) and *Sh. denticulata* (circles).

1. *Shangwua denticulata* (DC.) Raab-Straube & Yu J. Wang, **comb. nov.** ≡ *Aplotaxis denticulata* DC., Prodr. 6: 539. 1838 ≡ *Aplotaxis denticulata* var. *glabrata* DC., Prodr. 6: 540. 1838 ≡ *Saussurea wallichii* Sch. Bip. in Linnaea 19: 330. 1846 ≡ *S. denticulata* (DC.) Wall. ex C.B. Clarke, Compos. Ind.: 234. 1876, non Lebed. 1829 ≡ *S. glabrata* (DC.) C. Shih in Chen & Shi, Fl. Reipubl. Popularis Sin. 78(2): 84. 1999 – **Lectotype (designated here)** of *Aplotaxis denticulata* and holotype of *Aplotaxis denticulata* var. *glabrata*: “27, *Saussurea* (*Serratula*) *denticulata* Wall., Kamaon [= Kumaon], R. Blinkw., Comp. angl. des Indes 1830”, *Blinkworth s.n. in herb. Wallich 2917/27* (G-DC No. G00137866!); isolectotype: K-W No. 2917!. — Figures 2, 3, 4G–L; Electr. Suppl.: Fig. S2.
- = *Saussurea forrestii* Diels in Notes Roy. Bot. Gard. Edinburgh 5: 198. 1912 – Holotype: “China, NW Yunnan, in pine forest on the eastern flank of the Lichiang range, 10000–11000 ft.”, Sep. 1906, G. Forrest 2940 (E No. E00383921!).

**Lectotypification.** – When Candolle described *Aplotaxis denticulata*, he recognized two varieties in the material collected by Robert Blinkworth in Kumaon and distributed by Nathaniel Wallich under the herbarium number 2917/C27. The two sheets in the herbarium of Candolle’s *Prodromus* correspond to those two varieties: var. *glabrata* and var. *hypoleuca* (Electr. Suppl.: Figs. S2, S3). The specimen which morphologically clearly corresponds to the former variety has a more complete label with indications of collector and locality (Electr. Suppl.: Fig. S2), and is thus chosen as the lectotype for *Aplotaxis denticulata* ≡ *Shangwua denticulata*.

#### Key to varieties of *Shangwua denticulata*

1. Leaves abaxially light green, tomentose to glabrescent; veins clearly visible .....  
..... 1a. *Shangwua denticulata* var. *denticulata*
1. Leaves abaxially whitish, densely tomentose; veins obscured by indumentum .....  
..... 1b. *Shangwua denticulata* var. *hypoleuca*

1a. *Shangwua denticulata* (DC.) Raab-Straube & Yu J. Wang var. *denticulata*.

1b. *Shangwua denticulata* var. *hypoleuca* (DC.) Raab-Straube & Yu J. Wang, **comb. nov.** ≡ *Aplotaxis denticulata* var. *hypoleuca* DC., Prodr. 6: 540. 1838 – Holotype: “C 27, *Saussurea denticulata*”, *Blinkworth s.n. in herb. Wallich 2917/27* (G-DC No. G00137917!). — Electr. Suppl.: Fig. S3.

= *Aplotaxis fastuosa* Decne. in Jacquemont, Voy. Inde 4: 97. 1844 ≡ *Saussurea fastuosa* (Decne.) Sch. Bip. in Linnaea 19: 331. 1846 – Holotype: [INDIA]. “Buspa valley”, *Jacquemont 1150* (P No. P00603697!).

2. *Shangwua jacea* (Klotzsch) Yu J. Wang & Raab-Straube, **comb. nov.** ≡ *Aplotaxis jacea* Klotzsch in Klotzsch & Garcke, Bot. Ergebni. Reise Waldemar: 79. 1862 (“*Haplo-*

- taxis*”) ≡ *Saussurea jacea* (Klotzsch) Clarke, Compos. Ind.: 233. 1876 – Type: “Himalaya, Dr. Hoffmeister” (B, amissus est). **Lectotype (designated here):** Illustration in Klotzsch & Garcke, Bot. Ergebni. Reise Waldemar: t. 79. 1862. — Figure 4A–F; Electr. Suppl.: Fig. S4.
- = *Saussurea jacea* var. *tomentosa* Lipsch. in Novosti Sist. Vyssh. Rast. 1964: 328. 1964 – Holotype: “Kashmir, distr. Baltistan, Drás valley, 10–11000 ft.”, 22 Aug 1893, J.F. Duthie 13701 (LE; isotype: E No. E00451552!).
- = *Codonocephalum serratuloides* Gilli in Oesterr. Bot. Z. 104: 311. 1957 ≡ *Inula serratuloides* (Gilli) Grierson in Notes Roy. Bot. Gard. Edinburgh 33: 250. 1974 – Holotype: [PA-KISTAN, GILGIT-BALTISTAN]. Karakorum, between Gasherbrum and Shigar; between Bardumal and Askole”, 3500 m, 3 Aug 1956, G. Weiler (W!).

**Lectotypification.** – The original type specimen collected by W. Hoffmeister was almost certainly housed in the herbarium of Klotzsch (Berlin), which was almost entirely destroyed during the Second World War. The only extant original material is the plate from the protologue (Klotzsch & Garcke, 1862: t. 79), designated as the lectotype (Fig. S4). It shows some important diagnostic features of the genus in detail, such as the undivided, short, basal anther tails (Fig. 4C), the short, diverging style arms and the long, thickened, hairy zone below the bifurcation (Fig. 4B), the uniserrate pappus (Fig. 4E, F), and a dissected receptacle with few, long paleae (Fig. 4D) instead of the many bristles characteristic of most *Cardueae*.

3. *Shangwua masarica* (Lipsky) Yu J. Wang & Raab-Straube, **comb. nov.** ≡ *Saussurea masarica* Lipsky in Trudy Imp. S.-Peterburgsk. Bot. Sada 18: 81. 1900 – Lectotype (designated by Lipschitz, 1979: 103): [TAJIKISTAN]. “Bukhara, Darvaz, Mazarskij khrebet, lednik Badgut, 9000”, 21 Jul 1899, V.I. Lipsky 286 (LE!). — Electr. Suppl.: Fig. S5.
- = *Saussurea tadzhikorum* Iljin & Gontsch. in Izvest. Tadzhik. Baz. Akad. Nauk SSSR, Bot. 1(1): 67. 1933, **syn. nov.** – Holotype: “Tajikistan, Wakhshki khrebet”, 13 July 1932, N. Gontsharov, G. Grigoriev & V. Nikitin 639 (LE!).

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**Appendix 1.** List of taxa, geographic origin, voucher and GenBank accession numbers (ITS, *trnL-F*, *matK*, *ndhF*, *rbcL*). Detailed location is only given for newly extracted material. GenBank accession numbers marked with superindex were already published (<sup>1</sup>Susanna & al., 2006; <sup>2</sup>Susanna & al., 2011; <sup>3</sup>Anderberg & al., 2007; <sup>4</sup>Sánchez-Jiménez & al., 2010; <sup>5</sup>Hidalgo & al., 2006; <sup>6</sup>Vilatersana & al., 2010; <sup>7</sup>Barres & al., 2013).

- Alfredia cernua** (L.) Cass.; Denmark, Copenhagen Botanical Garden (BC); AY826225<sup>1</sup>; AY772269<sup>1</sup>; AY013519<sup>1</sup>; KC589912<sup>7</sup>; KC589785<sup>7</sup>. **Alfredia nivea** Kar. & Kir.; Kazakhstan; AY826226<sup>1</sup>; AY772270<sup>1</sup>; AY785087<sup>1</sup>; KC589913<sup>7</sup>; KC589786<sup>7</sup>. **Amphoricarpos autariatus** Blecie & Mayer; Serbia and Montenegro; AY826227<sup>1</sup>; AY772271<sup>1</sup>; AY785088<sup>1</sup>; KC589914<sup>7</sup>; KC589787<sup>7</sup>. **Amphoricarpos exsul** O. Schwarz; Turkey; AY826228<sup>1</sup>; AY772272<sup>1</sup>; AY785089<sup>1</sup>; KC589915<sup>7</sup>; KC589788<sup>7</sup>. **Arctium eriophorum** (Regel & Schmalh.) Kuntze; Kazakhstan; AY826326<sup>1</sup>; AY772361<sup>1</sup>; AY373681<sup>1</sup>; KC589917<sup>7</sup>; KC589790<sup>7</sup>. **Arctium grandifolium** (Kult.) S. López, Romaschenko, Susanna & N. Garcia; Kazakhstan; AY826268<sup>1</sup>; AY772310<sup>1</sup>; AY373679<sup>1</sup>; KC589918<sup>7</sup>; KC589791<sup>7</sup>. **Arctium lappa** (Schrenk) Kuntze; Kazakhstan; AY826269<sup>1</sup>; AY772311<sup>1</sup>; AY373677<sup>1</sup>; KC589919<sup>7</sup>; KC589792<sup>7</sup>. **Atractylis cancellata** L.; Spain; AY826231<sup>1</sup>; AY772275<sup>1</sup>; AY013522<sup>1</sup>; KC589924<sup>7</sup>; KC589797<sup>7</sup>. **Atractylis carduus** (Forssk.) Christ.; Egypt; AY826232<sup>1</sup>; AY772276<sup>1</sup>; AY013523<sup>1</sup>; KC589925<sup>7</sup>; KC589798<sup>7</sup>. **Atractyloides japonica** Koidz. ex Kitam.; Japan, Tokyo Botanical Garden (BC); AY826233<sup>1</sup>; AY772277<sup>1</sup>; AY013524<sup>1</sup>; KC589926<sup>7</sup>; KC589799<sup>7</sup>. **Berardia subacaulis** Vill.; France; AY826234<sup>1</sup>; AY772278<sup>1</sup>; AY013525<sup>1</sup>; KC589927<sup>7</sup>; KC589800<sup>7</sup>. **Brachylaena discolor** DC.; South Africa; AY826236<sup>1</sup>; AY772280<sup>1</sup>; AY785090<sup>1</sup>; KC589928<sup>7</sup>; KC589801<sup>7</sup>. **Callicephalus nitens** (M. Bieb. ex Willd.) C.A. Mey.; Armenia; AY826237<sup>1</sup>; AY772281<sup>1</sup>; AY013492<sup>1</sup>; JF75483<sup>7</sup>; KC589802<sup>7</sup>. **Cardopodium corymbosum** (L.) Pers.; Greece; AY826238<sup>1</sup>; AY772282<sup>1</sup>; AY013526<sup>1</sup>; KC589929<sup>7</sup>; KC589803<sup>7</sup>. **Carduncellus duvauxii** Batt. & Trab.; Morocco; AY826239<sup>1</sup>; AY772283<sup>1</sup>; AY013493<sup>1</sup>; KC589930<sup>7</sup>; KC589804<sup>7</sup>. **Carduus carlinoides** Gouan; Spain; AY826240<sup>1</sup>; AY772284<sup>1</sup>; AY013527<sup>1</sup>; KC589931<sup>7</sup>; KC589805<sup>7</sup>. **Carduus defloratus** L.; Spain; AY826241<sup>1</sup>; AY772285<sup>1</sup>; AY785091<sup>1</sup>; KC589932<sup>7</sup>; KC589806<sup>7</sup>. **Carduus nyassanus** R.E. Fr.; Tanzania, Olmoti crater, *Galbany s.n.* & Arrabal (BC); KC590041<sup>7</sup>; KC590048<sup>7</sup>; KC590014<sup>7</sup>; KC589934<sup>7</sup>; KC589808<sup>7</sup>. **Carlina acanthifolia** All.; Spain; AY826242<sup>1</sup>; AY772286<sup>1</sup>; AY013529<sup>1</sup>; KC589935<sup>7</sup>; KC589809<sup>7</sup>. **Carlina falcata** Svent.; Spain; AY826243<sup>1</sup>; AY772287<sup>1</sup>; AY013530<sup>1</sup>; KC589936<sup>7</sup>; KC589810<sup>7</sup>. **Carthamus oxyacantha** M. Bieb.; Iran; AY826248<sup>1</sup>; AY772292<sup>1</sup>; AY013494<sup>1</sup>; KC589940<sup>7</sup>; KC589814<sup>7</sup>. **Carthamus turkestanicus** Popov.; Armenia; AY826249<sup>1</sup>; AY772293<sup>1</sup>; AY785093<sup>1</sup>; KC589941<sup>7</sup>; KC589815<sup>7</sup>. **Centauraea behen** L.; Armenia; AY826250<sup>1</sup>; AY772294<sup>1</sup>; AY013496<sup>1</sup>; KC589942<sup>7</sup>; KC589816<sup>7</sup>. **Centauraea bruguierana** (DC.) Hand.-Mazz.; Armenia; AY826251<sup>1</sup>; AY772295<sup>1</sup>; AY013497<sup>1</sup>; KC589943<sup>7</sup>; KC589817<sup>7</sup>. **Centaura caroli-papuana** Fern. Casas & Susanna; Morocco; AY826253<sup>1</sup>; AY772296<sup>1</sup>; AY013498<sup>1</sup>; KC589944<sup>7</sup>; KC589818<sup>7</sup>. **Centaura depressa** M. Bieb.; Turkey; AY826255<sup>1</sup>; AY772297<sup>1</sup>; AY013499<sup>1</sup>; KC589945<sup>7</sup>; KC589819<sup>7</sup>. **Centaura lagascana** Graells; Spain; AY826257<sup>1</sup>; AY772299<sup>1</sup>; AY013504<sup>1</sup>; KC589947<sup>7</sup>; KC589821<sup>7</sup>. **Centaura lingulata** Lag.; Spain; AY826258<sup>1</sup>; AY772300<sup>1</sup>; AY013505<sup>1</sup>; KC589948<sup>7</sup>; KC589822<sup>7</sup>. **Centaudron palmiforme** Skottsb.; Chile; JF754806<sup>2</sup>; JF754757<sup>2</sup>; KC590015<sup>7</sup>; JF754836<sup>2</sup>; KC589823<sup>7</sup>. **Centaurothamnus maximus** Wagenitz & Dittrich; Yemen; AY826259<sup>1</sup>; AY772301<sup>1</sup>; AY013506<sup>1</sup>; JF754837<sup>2</sup>; KC589824<sup>7</sup>. **Chardinia orientalis** (L.) O. Kuntze; Iran; AY826260<sup>1</sup>; AY772302<sup>1</sup>; AY013534<sup>1</sup>; KC589949<sup>7</sup>; KC589825<sup>7</sup>. **Cheirolophus mauritanicus** (Font Quer) Susanna; Morocco; AY826261<sup>1</sup>; AY772303<sup>1</sup>; AY013507<sup>1</sup>; JF754838<sup>7</sup>; KC589826<sup>7</sup>. **Cheirolophus teydis** (C. Smith) G. López; Spain; AY826262<sup>1</sup>; AY772304<sup>1</sup>; AY785094<sup>1</sup>; JF754839<sup>7</sup>; KC589827<sup>7</sup>. **Cirsium echinum** (M. Bieb.) Hand.-Mazz.; Iran; AY826263<sup>1</sup>; AY772305<sup>1</sup>; AY013535<sup>1</sup>; KC589950<sup>7</sup>; KC589828<sup>7</sup>. **Cirsium nipponicum** Makino; Japan, Tokyo Metropolitan Medicinal Plant Garden (BC); KC590042<sup>7</sup>; KC590049<sup>7</sup>; KC590016<sup>7</sup>; KC589951<sup>7</sup>; KC589829<sup>7</sup>. **Cirsium ochrolepidum** Juz.; Uzbekistan; AY826264<sup>1</sup>; AY772306<sup>1</sup>; AY785095<sup>1</sup>; KC589952<sup>7</sup>; KC589830<sup>7</sup>. **Cirsium palustre** (L.) Scop.; Spain; AY826265<sup>1</sup>; AY772307<sup>1</sup>; AY013536<sup>1</sup>; KC589953<sup>7</sup>; KC589831<sup>7</sup>. **Cousinia coronata** Franch.; Uzbekistan; AY826267<sup>1</sup>; AY772309<sup>1</sup>; AY736621<sup>1</sup>; KC589957<sup>7</sup>; KC589835<sup>7</sup>. **Cousinia microcarpa** Boiss.; Kazakhstan; AY826270<sup>1</sup>; AY772312<sup>1</sup>; AY736671<sup>1</sup>; JF754840<sup>7</sup>; KC589836<sup>7</sup>. **Cousiniopsis atracyloides** (C. Winkl.) Nevska; Uzbekistan; AF319071<sup>1</sup>/AF319125<sup>1</sup>; AY772317<sup>1</sup>; AY785097<sup>1</sup>; KC589959<sup>7</sup>; KC589838<sup>7</sup>. **Crocodilium creticum** (Boiss. & Heldr.) N. Garcia & Susanna; Greece; AY826278<sup>1</sup>; AY772318<sup>1</sup>; AY013490<sup>1</sup>; KC589960<sup>7</sup>; KC589839<sup>7</sup>. **Crocodilium syriacum** Cass.; Egypt; AY826279<sup>1</sup>; AY772319<sup>1</sup>; AY785098<sup>1</sup>; KC589961<sup>7</sup>; KC589840<sup>7</sup>. **Cynara cornigera** Lind.; Egypt; AY826281<sup>1</sup>; AY772321<sup>1</sup>; AY013538<sup>1</sup>; KC589962<sup>7</sup>; KC589841<sup>7</sup>. **Cynara humilis** L.; Portugal; AY826282<sup>1</sup>; AY772322<sup>1</sup>; AY785099<sup>1</sup>; KC589963<sup>7</sup>; KC589842<sup>7</sup>. **Dipterome pusilla** Fisch. & C.A. Mey.; Voucher 1: Iran; FJ813487<sup>3</sup>; –; FJ813488<sup>3</sup>; –. Voucher 2: Iran, Joharchi & Zangoori 19925 (S); –; KC590053<sup>7</sup>; KC590020<sup>7</sup>; –; KC589843<sup>7</sup>. **Dolomiaeae souliei** (Franch.) C. Shih; China, Sichuan, Daocheng, *WYJ20090914* (LZU); JQ303104; JQ303108; JQ303113; –; **Echinops acantholepis** Jaub. & Spach; Uzbekistan; AY826222<sup>1</sup>; AY772267<sup>1</sup>; AY785086<sup>1</sup>; KC589964<sup>7</sup>; KC589844<sup>7</sup>. **Echinops angustilobus** S. Moore; Tanzania; GU116505<sup>4</sup>; GU134531<sup>4</sup>; KC590021<sup>7</sup>; KC589965<sup>7</sup>; KC589845<sup>7</sup>. **Echinops hoehnelii** Schweinf.; Kenya; GU116506<sup>4</sup>; GU134565<sup>4</sup>; KC590022<sup>7</sup>; KC589966<sup>7</sup>; KC589846<sup>7</sup>. **Femeniasia balearica** (J.J. Rodr.) Susanna; Spain; AY826284<sup>1</sup>; AY772327<sup>1</sup>; AY013509<sup>1</sup>; KC589971<sup>7</sup>; KC589851<sup>7</sup>. **Frolovia frolowii** (Ledeb.) Raab-Straube; China, Xinjiang, Altai, *Liu 200014* (LZU); AY914822; AY914862; JQ303114; –; **Galactites tomentosa** Moench; Spain; AY826285<sup>1</sup>; AY772328<sup>1</sup>; AY013541<sup>1</sup>; KC589972<sup>7</sup>; KC589852<sup>7</sup>. **Goniocaulon indicum** C.B. Clarke; Ethiopia; *Friis s.n. & al.* (K); JF775393<sup>7</sup>; JF775385<sup>7</sup>; KC590023<sup>7</sup>; JF775397<sup>7</sup>; KC589853<sup>7</sup>. **Jurinea albicalyx** Bunge; Greece; AY826287<sup>1</sup>; AY772330<sup>1</sup>; AY373684<sup>1</sup>; KC589973<sup>7</sup>; KC589854<sup>7</sup>. **Jurinea carduiformis** Boiss.; Iran; AY826289<sup>1</sup>; AY772332<sup>1</sup>; AY785103<sup>1</sup>; KC589974<sup>7</sup>; KC589855<sup>7</sup>. **Jurinea humilis** DC.; Spain; L35868<sup>1</sup>; KC590054<sup>7</sup>; KC590024<sup>7</sup>; KC589975<sup>7</sup>; KC589856<sup>7</sup>. **Jurinea robusta** Schrenk; AY826291<sup>1</sup>; AY772333<sup>1</sup>; AY373685<sup>1</sup>; –; **Klasea algida** (Iljin) Hidalgo; Armenia; DQ310926<sup>5</sup>; DQ310892<sup>5</sup>; KC590025<sup>7</sup>; KC589976<sup>7</sup>; KC589857<sup>7</sup>. **Klasea coriacea** (Fisch. & C.A. Mey. ex DC.) Holub; Armenia; DQ310926<sup>5</sup>; DQ310892<sup>5</sup>; KC590026<sup>7</sup>; JF754843<sup>7</sup>; KC589858<sup>7</sup>. **Lamyropappus schacaparicus** (B. Fedtsch.) Knorr. & Tamamsch.; Kyrgyzstan; AY826296<sup>1</sup>; AY772335<sup>1</sup>; AY785104<sup>1</sup>; KC589977<sup>7</sup>; KC589860<sup>7</sup>. **Lamyropsis carpini** Greuter; Greece; GU907724<sup>6</sup>; KC590055<sup>7</sup>; KC590027<sup>7</sup>; KC589978<sup>7</sup>; KC589861<sup>7</sup>. **Lamyropsis cynaroidea** (Lam.) Dittrich; Turkey; AY826297<sup>1</sup>; AY772336<sup>1</sup>; AY785105<sup>1</sup>; KC589979<sup>7</sup>; KC589862<sup>7</sup>. **Mantisalca**

**Appendix 1.** Continued.

*salmantica* (L.) Briq. & Cavill.; Spain; AY012292<sup>1</sup>/AY012328<sup>1</sup>; JF754765<sup>2</sup>; KC590028<sup>1</sup>; JF754846<sup>2</sup>; KC589863<sup>2</sup>. *Myopordon aucheri* Boiss.; Iran; AY826299<sup>1</sup>; AY772338<sup>1</sup>; KC590029<sup>2</sup>; JF754847<sup>2</sup>; KC589864<sup>2</sup>. *Myopordon hyrcanum* (Bornm.) Wagenitz; Iran; AY826300<sup>1</sup>; AY772339<sup>1</sup>; KC589980<sup>2</sup>; KC589865<sup>2</sup>. *Notebasis syriaca* (L.) Cass.; Egypt; AY826302<sup>1</sup>; AY772340<sup>1</sup>; AY013545<sup>1</sup>; KC589981<sup>2</sup>; KC589866<sup>2</sup>. *Ochrocephala imatongensis* (Philipson) Dittrich; Ethiopia; DQ310931<sup>5</sup>; DQ310897<sup>5</sup>; KC590030<sup>7</sup>; KC589982<sup>7</sup>; KC589867<sup>7</sup>. *Oldenburgia intermedia* Bond.; South Africa; AY826303<sup>1</sup>; AY772341<sup>1</sup>; AY785106<sup>1</sup>; KC589983<sup>7</sup>; KC589868<sup>7</sup>. *Olgaea baldshuanica* (C. Winkl.) Iljin; Tadzhikistan; AY826304<sup>1</sup>; AY772342<sup>1</sup>; AY785107<sup>1</sup>; KC589984<sup>2</sup>; KC589869<sup>2</sup>. *Olgaea pectinata* Iljin; Kazakhstan; AY826305<sup>1</sup>; AY772343<sup>1</sup>; AY785108<sup>1</sup>; KC589985<sup>2</sup>; KC589870<sup>2</sup>. *Onopordum nervosum* Boiss.; France, Dijon Botanical Garden (BC); AY826308<sup>1</sup>; AY772346<sup>1</sup>; AY785109<sup>1</sup>; KC589986<sup>7</sup>; KC589871<sup>7</sup>. *Onopordum tauricum* Willd.; Germany, Berlin Botanical Garden (BC); AY826309<sup>1</sup>; AY772347<sup>1</sup>; AY785110<sup>1</sup>; KC589987<sup>7</sup>; KC589872<sup>7</sup>. *Phonus rhiphaeus* (Font Quer & Pau) G. López; Morocco; AY826310<sup>1</sup>; AY772348<sup>1</sup>; AY013512<sup>1</sup>; KC589988<sup>7</sup>; KC589873<sup>7</sup>. *Picnomon acarna* (L.) Cass.; Iran; AY826311<sup>1</sup>; AY772349<sup>1</sup>; AY013549<sup>1</sup>; KC589989<sup>7</sup>; KC589874<sup>7</sup>. *Plectocephalus americanus* D. Don; USA; JF754817<sup>2</sup>; JF754769<sup>2</sup>; KC590031<sup>7</sup>; JF754853<sup>2</sup>; KC589875<sup>7</sup>. *Plectocephalus tweediei* (Hook. & Arn.) N. Garcia & Susanna; Argentina; JF775392<sup>2</sup>; JF775384<sup>2</sup>; KC590033<sup>7</sup>; JF775396<sup>2</sup>; KC589877<sup>7</sup>. *Psephellus gilanicus* (Bornm.) Wagenitz; Iran; AY826315<sup>1</sup>; AY772351<sup>1</sup>; AY013501<sup>1</sup>; KC589990<sup>7</sup>; KC589879<sup>7</sup>. *Psephellus persicus* (DC.) Wagenitz; Iran; AY826316<sup>1</sup>; AY772352<sup>1</sup>; AY013500<sup>1</sup>; JF754852<sup>2</sup>; KC589880<sup>7</sup>. *Ptilostemon abyensis* (Maire) Greuter; Morocco; GU907726<sup>6</sup>; KC590056<sup>7</sup>; KC590035<sup>7</sup>; KC589991<sup>7</sup>; KC589882<sup>7</sup>. *Ptilostemon afer* (Jacq.) Greuter; Germany, Freiburg Botanical Garden (BC); AY826318<sup>1</sup>; AY772354<sup>1</sup>; AY785111<sup>1</sup>; KC589992<sup>7</sup>; KC589883<sup>7</sup>. *Rhaponticoidea hajastana* (Tzvel.) M.V. Agab. & Greuter; Armenia; AY826325<sup>1</sup>; AY772279<sup>1</sup>; AY013502<sup>1</sup>; JF754857<sup>2</sup>; KC589886<sup>7</sup>. *Rhaponticum acaule* DC.; Algeria; AY826334<sup>1</sup>; AY772369<sup>1</sup>; AY013515<sup>1</sup>; JF754859<sup>2</sup>; KC589887<sup>7</sup>. *Rhaponticum australe* (Gaud.) Soskov; Australia; AY826335<sup>1</sup>; AY772370<sup>1</sup>; AY785120<sup>1</sup>; KC589995<sup>7</sup>; KC589888<sup>7</sup>. *Rhaponticum repens* (L.) Hidalgo; Uzbekistan; AY826223<sup>1</sup>; AY772268<sup>1</sup>; AY013489<sup>1</sup>; JF754831<sup>2</sup>; KC589889<sup>7</sup>. *Saussurea alpina* (L.) DC.; Italy, Cogne Botanical Garden (BC); AF319091<sup>1</sup>/AF319145<sup>1</sup>; KC590058<sup>7</sup>; KC590037<sup>7</sup>; KC589996<sup>7</sup>; KC589890<sup>7</sup>. *Saussurea discolor* (Willd.) DC.; Switzerland, Meyrin Botanical Garden (BC); AF319092<sup>1</sup>/AF319146<sup>1</sup>; KC590059<sup>7</sup>; KC590038<sup>7</sup>; KC589997<sup>7</sup>; KC589891<sup>7</sup>. *Saussurea gnaphalodes* (Royle) Sch. Bip.; China, Qinghai, Chenduo, *J.Q. Liu* 839 (LZU); AY366324; AY328106; AB118147; –. *Saussurea involucrata* (Kar. & Kir.) Sch. Bip.; China, Xinjiang (LZU); AY366335; AY328115; AB118148; –. *Saussurea leontodontoides* (DC.) Sch. Bip.; China, Qinghai, Maqing, *C.Q. Ao* 49 (LZU); JQ303105; JQ303115; –. *Schischkinia albispina* (Bunge) Iljin; Turkmenistan; AY826325<sup>1</sup>; AY772360<sup>1</sup>; AY785113<sup>1</sup>; JF754862<sup>2</sup>; KC589892<sup>7</sup>. *Serratula coronata* L.; Austria, Vienna Botanical Garden (BC); AY826327<sup>1</sup>; AY772362<sup>2</sup>; AY785114<sup>1</sup>; JF754863<sup>2</sup>; KC589893<sup>7</sup>. *Shangwua denticulata* (DC.) Raab-Straube & Yu J. Wang; China, Xizang, Nielamu, *J.Q. Liu* 07150 (LZU); JQ303106; JQ303110; JQ303116; JQ303118; JQ303120. *Shangwua jacea* (DC.) Yu J. Wang & Raab-Straube; Pakistan, *O.J. Broadhead* 119 (E); JQ303107; JQ303111; JQ303112; –. *Siebera pungens* (Lam.) DC.; Turkey; AY826328<sup>1</sup>; AY772363<sup>1</sup>; AY785115<sup>1</sup>; KC589998<sup>7</sup>; KC589894<sup>7</sup>. *Silybum marianum* (L.) Gaertner; Spain; AY826329<sup>1</sup>; AY772364<sup>1</sup>; AY013551<sup>1</sup>; KC589999<sup>7</sup>; KC589895<sup>7</sup>. *Staehelina dubia* L.; France; AY826330<sup>1</sup>; AY772365<sup>1</sup>; AY785116<sup>1</sup>; KC590000<sup>7</sup>; KC589896<sup>7</sup>. *Staehelina fruticosa* L.; Greece; AY826331<sup>1</sup>; AY772366<sup>1</sup>; AY785117<sup>1</sup>; KC590001<sup>7</sup>; KC589897<sup>7</sup>. *Staehelina lobeliae* DC.; Turkey; AY826332<sup>1</sup>; AY772367<sup>1</sup>; AY785118<sup>1</sup>; KC590002<sup>7</sup>; KC589898<sup>7</sup>. *Stizolophus balsamita* (Lam.) Cass. ex Takht.; Armenia; AY826336<sup>1</sup>; AY772371<sup>1</sup>; AY785121<sup>1</sup>; JF754864<sup>7</sup>; KC589899<sup>7</sup>. *Stizolophus coronopifolius* Cass.; Turkey; AY826337<sup>1</sup>; AY772372<sup>1</sup>; AY013516<sup>1</sup>; JF754865<sup>7</sup>; KC589900<sup>7</sup>. *Synurus palmatopinnatifidus* (Makino) Kitam.; Japan, the Nippon Shinyaku Institute for Botanical Research (BC); AY826338<sup>1</sup>; AY772373<sup>1</sup>; AY013552<sup>1</sup>; KC590003<sup>7</sup>; KC589901<sup>7</sup>. *Syreitschikovia spinulosa* (Franch.) Pavlov; Kazakhstan; AY826339<sup>1</sup>; AY772374<sup>1</sup>; AY785122<sup>1</sup>; KC590004<sup>7</sup>; KC589902<sup>7</sup>. *Tarchonanthus camphoratus* L.; South Africa; AY826340<sup>1</sup>; AY772375<sup>1</sup>; AY785123<sup>1</sup>; KC590005<sup>7</sup>; KC589903<sup>7</sup>. *Tugarinovia mongolica* Iljin; Mongolia; AY826342<sup>1</sup>; AY772377<sup>1</sup>; AY785124<sup>1</sup>; KC590006<sup>7</sup>; KC589904<sup>7</sup>. *Tyrimnus leucographus* (L.) Cass.; Spain; AY826343<sup>1</sup>; AY772378<sup>1</sup>; AY013554<sup>1</sup>; KC590007<sup>7</sup>; KC589905<sup>7</sup>. *Voluntaria crupinoides* (Desf.) Maire; Morocco; AY826344<sup>1</sup>; AY772379<sup>1</sup>; AY785125<sup>1</sup>; JF754867<sup>2</sup>; KC589906<sup>7</sup>. *Xanthopappus subacaulis* C. Winkl.; China, Qinghai, *Liu* 50 (PE); KC590046<sup>7</sup>; KC590060<sup>7</sup>; KC590039<sup>7</sup>; KC590008<sup>7</sup>; KC589907<sup>7</sup>. *Xeranthemum annuum* L.; Turkey; AY826345<sup>1</sup>; AY772380<sup>1</sup>; AY785126<sup>1</sup>; KC590009<sup>7</sup>; KC589908<sup>7</sup>. *Xeranthemum inapertum* (L.) Miller; Spain; AY826347<sup>1</sup>; AY772381<sup>1</sup>; AY013555<sup>1</sup>; KC590010<sup>7</sup>; KC589909<sup>7</sup>. *Xeranthemum longepapposum* Fisch. & C.A. Mey; Kazakhstan; AY826348<sup>1</sup>; AY772382<sup>1</sup>; AY785127<sup>1</sup>; KC590011<sup>7</sup>; KC589910<sup>7</sup>. *Zoegea leptarea* L.; Iran; AY826349<sup>1</sup>; AY772383<sup>1</sup>; AY0135172; JF754868<sup>7</sup>; KC589911<sup>7</sup>.

**Appendix 2.** Voucher specimens of taxa used for morphological examinations in this study.

*Amphoricarpos neumayerianus* (Vis.) Greuter; Bosnia-Hercegovina; 9.8.1908, K. *Maly* s.n. (B). *Berardia subacaulis* Vill.; Italy, 17.7.2009, M. *Ristow* 783/09, D. Lauterbach & B. Gemeinholzer (B100355114). *Chardinia orientalis* (L.) Kuntze; Uzbekistan; AY826339<sup>1</sup>; AY772374<sup>1</sup>; AY785122<sup>1</sup>; KC590004<sup>7</sup>; KC589902<sup>7</sup>. *Saussurea leontodontoides* (DC.) Sch. Bip.; China, Qinghai, Maqing, *C.Q. Ao* 49 (LZU). *Shangwua denticulata* (DC.) Raab-Straube & Yu J. Wang; Nepal, 1929, *L. Dhevoj* 256 (E00451529); China, Xizang, Nielamu, *J.Q. Liu* 07150 (LZU); China, Xizang, Jilong, *J.Q. Liu* Liujq-09xz-lzt-073 (LZU). *Shangwua jacea* (Klotzsch) Yu J. Wang & Raab-Straube; Pakistan, *O.J. Broadhead* 119 (E); India, Ladak, 17.8.1931, W. *Koelz* 2617 (L0833898). *Siebera pungens* (Lam.) J. Gay; Turkey, 24.8.1999, F. *Schuhwerk* 99/299 (B100021017). *Staehelina dubia* L.; Spain, 2.7.1995, B. *Catón* & P.M. *Uribe-Echebarria* IAN 790 (B); *Xeranthemum annuum* L.; Greece, 13.7.1998, R. *Eisenblätter* & E. *Willing* 66918 (B).