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Androsace komovensis sp. nov., a long mistaken local endemic from the southern Balkan Peninsula with biogeographic links to the Eastern Alps

Peter Schönswetter & Gerald M. Schneeweiss

Department of Biogeography and Botanical Garden, University of Vienna, 1030 Vienna, Austria. peter.schoenswetter@univie.ac.at (author for correspondence)

In the course of molecular phylogeographical investigations in *Androsace* sect. *Aretia* a previously unrecognised entity from Crna Gora/Montenegro was identified as a genetically and morphologically clearly separated lineage and is described here as a new species, *Androsace komovensis* Schönswetter & Schneew. It is restricted to a single high-alpine rock-cliff in the Komovi mountain range in Montenegro. The new species morphologically resembles *A. mathildae* Levier from the Abruzzo mountains (Italy), but differs in the persistent, dense and regular indumentum of the leaf margin. Molecular phylogenetic data indicate that *A. komovensis* Schönswetter & Schneew. is not closely related to *A. mathildae* Levier, but instead is sister species to the Eastern Alpine endemic *A. hausmanni* Leyb.

KEYWORDS: *Androsace komovensis*, Crna Gora/Montenegro, Primulaceae, species nova

INTRODUCTION

The genus *Androsace* L. (Primulaceae) comprises ca. 150 species mainly distributed in extra-tropical mountain ranges of the Northern Hemisphere (Mabberley, 2008). A phylogeny based on nuclear ribosomal ITS and chloroplast *trnLF* data (Schneeweiss & al., 2004) strongly suggested the monophyly of the clade /*Aretia* (for details on the clade names, designated with / as a clademark, see Schneeweiss & al., 2004). The latter mainly comprises *A.* sect. *Aretia* (L.) W.D.J. Koch endemic to Europe, but also includes *A. vitaliana* Lapeyr., which is often treated as segregate genus *Vitaliana* Sesl., the high Arctic Asian *A. triflora* Adans., and an amphi-Beringian to western North American group of species often treated as separate genus *Douglasia* Lindl. (Schneeweiss & al., 2004, and references therein). /*Aretia* falls into two groups roughly corresponding to previously recognised subsections within *A.* sect. *Aretia* (L.) W.D.J. Koch. Members of /*Eu-Aretia* (including *A. vitaliana* Lapeyr.) usually have single axillary flowers, often grow in dense cushions and mostly have a chromosome base number of $x = 20$, while those of /*Dicranothrix* (including *A. triflora* Adans. and the *Douglasia* Lindl. species) usually have long stalked inflorescences, often grow in loose mats and have a chromosome base number of $x = 19$ (Schneeweiss & al., 2004, and references therein). In Europe, /*Aretia* is most diverse in the Alps (thirteen to fifteen species) followed by the Pyrenees with nine species. In contrast, the diversity in other European mountain ranges is considerably lower, with four species in the Cordillera Cantábrica, three species in the Balkan Peninsula and the Apennines, two species each in the Sierra Nevada (Spain), the central Spanish mountains and the Carpathians, and one species in the French Massif Central.

In the course of molecular phylogeographical investigations covering the European members of /*Aretia* (e.g., Dixon & al., 2007, 2008), we investigated the single Balkan population of *A. mathildae* Levier. Among the few members of *A.* sect. *Aretia* (L.) W.D.J. Koch on the Balkan Peninsula, it is by far the rarest. This species was reported from the southern flank of Kom Kučki in the Komovi mountain range in Crna Gora/Montenegro for the first time by Baldacci (1892), but due to the wrong determination ("? *A. carnea* L." in Baldacci, 1893) it remained forgotten (T. Wraber, Ljubljana, pers. comm.). Baldacci's specimen (in FI) was revised by I.K. Ferguson in 1968 and determined as *A. mathildae*, but under the assumption that this species is endemic to the central Apennines he noted the following on the revision label: "It seems to me that the label and specimen may not belong together." The species (and probably the same population) was rediscovered in the Komovi mountains by Wraber (1983), confirmed as *A. mathildae* Levier and consequently considered an addition to the list of species showing an amphi-Adriatic distribution. Initial analysis of Amplified Fragment Length Polymorphism (AFLP) markers revealed an unexpectedly strong genetic divergence between the Italian and the Montenegrin populations (P. Schönswetter, unpub. data), which turned out to coincide with morphological differences in the leaf indumentum. Therefore, we included the Balkan population of *A. mathildae* Levier in our extensive dataset of nuclear ITS and plastid *trnLF* sequences of European *Androsace* L. in order to assess its phylogenetic position and relationships, specifically, whether it is closely related to the Apennine plants. As the plants from the Komovi mountains constitute the southeastern-most occurrence of /*Eu-Aretia*, we use the phylogenetic framework to reveal the biogeographic links of the Balkan population, specifically we test the hypothesis of an amphi-Adriatic disjunction, as suggested by current taxonomy.

MATERIALS AND METHODS

We extended our previous sampling (Schneeweiss & al., 2004) to include at least one accession of every currently recognised species and subspecies of European /*Aretia* plus most members of the amphi-Beringian group (*A. triflora* Adans., *Douglasia* Lindl.), using members of /*Elongata* and /*Septentrionalis* as outgroup taxa (Appendix). DNA extraction was done as described in Schneeweiss & al. (2004). The PCR reaction mix of 25 µL contained 8 µL PCR ReadyMix (Sigma-Aldrich, Vienna, Austria), 0.83 µM of each primer (17SE and 26SE of Sun & al., 1994, for nuclear ITS; c and f of Taberlet & al., 1991, for plastid *trnLF*) and 2 µL of diluted DNA extract of unknown concentration. PCR conditions for ITS were 4 min at 94°C followed by 35 cycles of 1 min at 95°C, 1 min at 56°C, 70 s at 72°C, followed by a final 10 min extension period at 72°C; those for *trnLF* were 4 min at 94°C followed by 35 cycles of 30 s at 94°C, 30 s at 51°C, 90 s at 68°C, followed by a final 10 min extension period at 72°C. The PCR products were cleaned with Exonuclease I and Calf Intestine Alkaline Phosphatase (CIAP; both MBI Fermentas, St.-Leon-Rot, Germany) according to the manufacturer's instructions. Cycle sequencing used Big-Dye Terminator chemistry (Applied Biosystems, Foster City, California, U.S.A.), according to the manufacturer's instructions, after which electrophoresis was carried out with an ABI 3100 capillary sequencer (Applied Biosystems). Sequences were edited with SeqMan™ II v. 5.05 (DNAStar Inc. Madison, Wisconsin, U.S.A.) and aligned by eye using BioEdit 7.0.4.1 (Hall, 1999).

The newly obtained sequences (20 for ITS, 19 for *trnLF*) were added to the alignment from Schneeweiss & al. (2004), totalling in 74 accessions sequenced for both regions. As outgroups for /*Aretia*, we used only members of /*Septentrionalis* and /*Elongata* (Schneeweiss & al., 2004), and resulting all-gapped regions were removed from the alignment. Based on our previous results, sequences were a priori concatenated. Maximum parsimony analysis was conducted using PAUP* 4.0b10 (Swofford, 2001) using a heuristic search with 1,000 random sequence addition replicates saving no more than 200 trees per replicate, TBR branch swapping, MulTrees on, steepest descent option not in effect, swap on best trees only, and collapse branches if minimum length is zero. Characters were treated as unordered and of equal weight, and gaps were treated as missing data. Clade support was assessed using bootstrap (BS) with 1,000 replicates with heuristic search options as above.

The best-fit substitution models for each data partition were determined using the Akaike Information Criterion as implemented in Modeltest 3.7 (Posada & Crandall, 1998). While for ITS, General Time Reversible models (GTR) with gamma distribution accounting for rate heterogeneity (Γ) without or with a proportion of invariable sites (I) already had a cumulative Akaike weight >0.99, model uncertainty for the *trnLF* partition was much higher, the best model having only a weight of 0.20 and ten models being included until the cumulative Akaike weight exceeded 0.95. Since all models had more than two substitution rates and the most complex model GTR + Γ + I was included in the set of models, we used the GTR + Γ for both data partitions, subsuming the proportion of invariable sites under the gamma distribution accounting for rate heterogeneity (Yang, 1993; Dixon & al., 2007). A mixed model Bayesian inference was conducted in MrBayes 3.2 (Ronquist & Huelsenbeck, 2003) run on the Bioportal computer cluster at the University of Oslo (http://www.bioportal.uio.no/) using GTR + Γ models for both partitions with parameter values being estimated separately for each partition during the analyses. The settings for the Metropolis-coupled Markov chain Monte Carlo (MC^3) process were: four runs with four chains each (one cold, three heated chains using incremental heating with heating parameter of 0.1 to enable better mixing among chains) were run simultaneously for 10^7 generations each with trees being sampled every 1,000th generation using the default priors (flat Dirichlet priors for the substitution matrix and state frequencies; uniform prior [0.05, 50] for the shape parameter of the gamma distribution; uniform prior [0, 1] for the proportion of invariable sites; all topologies equally probable; exponential prior [10] for the branch lengths). Convergence of the independent runs was considered reached when all parameters had reached stationarity and split frequencies were <0.015. The posterior probability of the phylogeny and its branches was determined for two sets of two runs each (see Results and Discussion) from the combined set of trees discarding the first 1,000 trees of each run as burn-in. Due to the reported over-confidence of posterior clade probabilities, especially for short internodes (reviewed in Wróbel, 2008), we conservatively consider only nodes with PP > 0.99 as statistically significantly supported.

RESULTS AND DISCUSSION

The final alignment included 1,658 characters (641 from ITS, 1,017 from *trnLF*, 6.7% of cells with missing data due to gaps), of which 308 and 250 are variable and parsimony-informative, respectively. Maximum parsimony analysis resulted in 2,744 equally most parsimonious trees (tree length 521, consistency index 0.7486, retention index 0.9162). The Bayesian analysis with four simultaneous runs resulted in two runs each sampling in two distinct regions of the likelihood surface with different values for the rate parameters, the base frequencies and especially the shape parameters of the gamma distribution causing significantly different marginal likelihoods (harmonic means –ln 5,796.30 versus –ln 5,842.32). Since both sets of runs resulted in similar topologies with nearly identical posterior clade probabilities (the few notable exceptions do not affect our conclusions), we only show and discuss results from the set of runs with the higher marginal likelihood. The majority rule consensus tree from the Bayesian analysis is topologically very similar to the maximum parsimony strict consensus tree, discrepancies concerning only nodes with insufficient support, and only the maximum parsimony strict consensus tree is shown (Fig. 1).

The relationships among /*Septentrionalis*, /*Elongata*, and /*Aretia* have already been discussed elsewhere (Schneeweiss & al., 2004). Compared to our previous study, the circumscription of /*Septentrionalis* and /*Elongata* is extended. /*Septentrionalis* also includes *A. albana* Steven, a biennial mountain plant from SW Asia, and the North American *A. septentrionalis* L. subsp. *subulifera* (A. Gray) G.T. Robbins. The latter is genetically clearly distinct from subsp. *septentrionalis* suggesting that the current wide circumscription of *A. septentrionalis* L. does not adequately reflect the species' diversity. Similarly, current taxonomy underestimates the diversity within *A. elongata* L. of /*Elongata*, because *A. elongata* L. subsp. *breistrofferi* (Charpin & Greuter) Molero & J.M. Monts. appears to be as distinct from subsp. *elongata* as the latter is from the North American *A. occidentalis* Pursh. (Fig. 1).

Relationships within the two subclades of /*Aretia*, /*Dicranothrix* and /*Eu-Aretia*, the latter only weakly supported, are similar to those presented previously (Schneeweiss & al., 2004), exceptions concerning insufficiently supported clades. For instance, a sister relationship of *A. rioxana* and *A. chaixi* of /*Dicranothrix*, as suggested by Schneeweiss & al. (2004), finds no support here. Although not the main focus of this study, two points concerning /*Dicranothrix* are worth mentioning. *Androsace halleri* L. from the eastern Pyrenees appears to be more

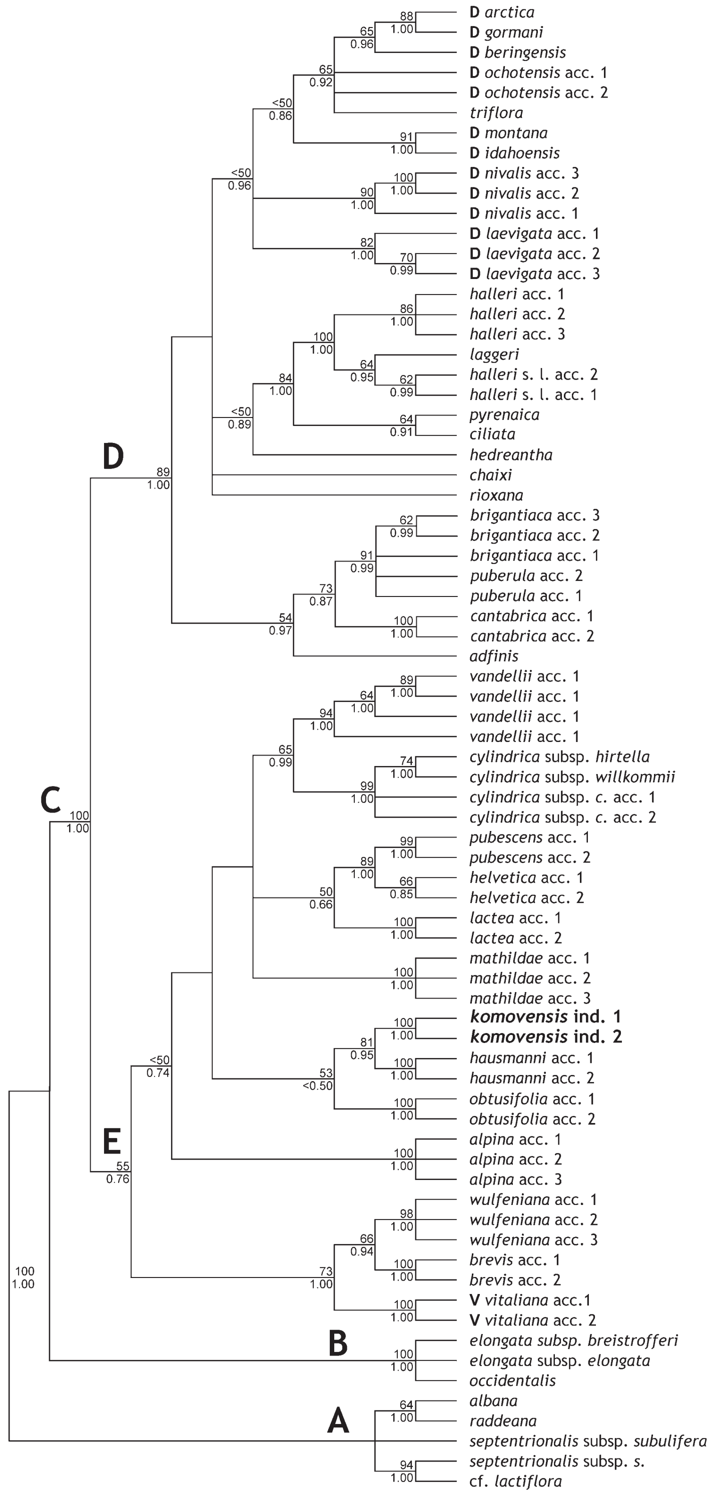

Fig. 1. Phylogenetic relationships of *Androsace* inferred from maximum parsimony analysis (strict consensus tree) of the combined nuclear ITS region and the plastid *trnLF* region. Major clades are indicated: A, /*Septentrionalis*; B, /*Elongata*; C, /*Aretia*; D, /*Dicranothrix*; E, /*Eu-Aretia*. Members of the segregate genera *Douglasia* and *Vitaliana* are highlighted by a prefix D and V, respectively. Number above branches are maximum parsimony bootstrap values, those below branches are posterior probabilities.

closely related to *A. laggeri* Huet than to *A. halleri* L. elsewhere (Fig. 1), in agreement with its distinctness inferred from AFLP data (Dixon & al., 2007) and in line with the hypothesis of a hybridogenic influence of *A. laggeri* Huet on the east Pyrenean *A. halleri* L. (Kress, 1991). Only recently, *A. cantabrica* (Losa & P. Monts.) Kress from the Cordillera Cantábrica has been shown to be sister to the *A. adfinis*-group (*A. adfinis* Biroli, *A. brigantiaca* Jord. & Fourr., *A. puberula* Jord. & Fourr.) from the south-western Alps (Dixon & al., 2008). The present data not only corroborate this, but actually suggest that *A. cantabrica* (Losa & P. Monts.) Kress might even be nested within the *A. adfinis*-group (Fig. 1).

As expected, *A. mathildae* Levier from the Balkan Peninsula is a member of /*Eu-Aretia*. However, instead of being closely related to *A. mathildae* Levier from the Apennines, it appears as moderately supported sister taxon of *A. hausmanni* Leyb. from the Eastern Alps (BS 81, PP 0.95; Fig. 1). The alternative hypothesis of a monophyletic *A. mathildae* Levier is marginally significantly rejected in a parsimony framework (Kishino-Hasegawa test $P = 0.0522$; Wilcoxon rank sum test $P = 0.0522$; both conducted in PAUP) and outright rejected in a Bayesian framework (PP = 0). Therefore, and based on the differences in leaf indumentum between *A. mathildae* Levier from the Apennines, with leaves being totally glabrous (except for a few hairs at the leaf tips; Fig. 2E), and *A. mathildae* Levier from the Balkans, with leaves being persistently ciliate (Figs. 2B, 3), it is necessary to describe the Balkan plants as a new species *A. komovensis* sp. nov. (for details see "Taxonomic treatment"). From *A. hausmanni* Leyb., the new species can be easily distinguished by the glabrous leaf surfaces (except for the leaf tips) and the less-branched and longer hairs.

Fig. 3. Habit of *Androsace komovensis* (photo: K. Bardy, 26 July 2007).

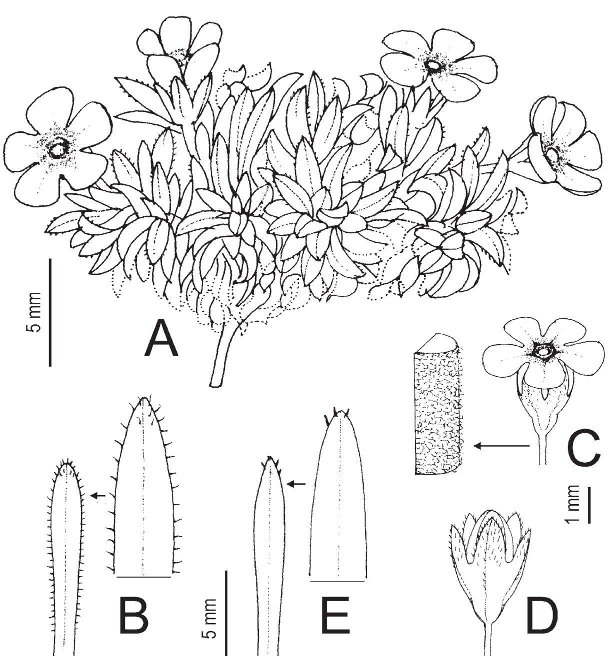

Fig. 2. *Androsace komovensis* (*Wraber s.n.*, LJU 122565) and *A. mathildae* (*Hörandl 6220*, WU). A–D, *A. komovensis*. A, habit; B, leaf: entire leaf and leaf tip; C, flower: entire flower, indumentum of pedicel and calyx; D, young fruit enclosed by calyx. E, *A. mathildae,* entire leaf and leaf tip. Drawing by Arndt Kästner.

Instead of being an example for an amphi-Adriatic distribution, as asserted previously (Wraber, 1983) and seen in, for instance, *Aurinia rupestris* (Ten.) Cullen & T.R. Dudley (Brassicaceae) and *Saxifraga glabella* Bertol. (Saxifragaceae), *A. komovensis* Schönswetter & Schneew. shows a biogeographic link to the Eastern Alps. Examples for a disjunction between the Eastern Alps and the southern Balkan include *Alyssum ovirense* A. Kern. (Brassicaeae), *Viola zoysii* Wulf. (Violaceae), and *Wulfenia carinthiaca* Jacq. (Plantaginaceae), although in the absence of independent corroboration from molecular data floristic links need to be interpreted with the appropriate caution. The close relationship between *A. komovensis* Schönswetter & Schneew. and *A. hausmanni* Leyb. suggests independent range expansion of /*Eu-Aretia* from the centre of diversity in the European Alps into the Balkan Peninsula and the central Apennines and rejects the hypothesis of a trans-Adriatic connection.

TAXONOMIC TREATMENT

Androsace komovensis Schönswetter & Schneew., **sp. nov.** – Type: Crna Gora (Montenegro), in summis cacuminis M. Kom Kučki. 2,448 m. 8. August 1891. *A. Baldacci, Flora Exsiccata Crnaegorae 153* (holotype: FI).

= *A. mathildae* auct. non Levier

Etymology. – Named after the mountain range Komovi in Montenegro, close to the Albanian border.

Latin diagnosis. – *Androsace mathildae* similis sed ciliis foliorum persistentibus non solum apice sed fere ad basim ± aequaliter distributis.

Species description. – Perennial cushion plant, up to 3 cm high, rosettes 0.8–1.3(3.0) cm diameter, single or forming a cushion of 3–5 cm diameter (Figs. 2A, 3). Leafs basal, lanceolate, 5–8(18) × 1–2 mm, glabrous except for the margins. Leaf margin entire, densely and regularly hairy (Fig. 2B). Hairs persistent, usually simple, straight or slightly recurved, sometimes with a short, subordinate branch, 0.1–0.2 mm long, composed of 3–4 cells. Flowers axillary, single. Pedicel ebracteate, stellate pubescent (Fig. 2C), 4–5 mm long, elongated to 16 mm and often recurved when fruiting. Calyx green, stellate pubescent, 2.5–3.0 mm long, elongated to 6 mm in fruit, divided up to 45%–55% (Fig. 2D). Corolla diameter ca. 7 mm, petals white. Capsule ovoid, 4.5–5.0 × 2.0–3.0 mm. Chromosome number unknown. Flowering time July.

Additional Specimens Examined. – Crna Gora (Montenegro): Montes Komovi: In rupium fissuris cacuminis meridionalis montis Kom Kučki. Solo calcareo. 2,400 m s. m. 17. July 1980. *T. Wraber s.n.* (LJU 122565). Crna Gora (Montenegro): Komovi Mts., Kom Kučki, southern rock face of the summit ca. 2,400 m, 19°38′30″ E, 42°40′50″ N, limestone cliffs. 23. August 2006, *B. Frajman & P. Schönswetter 11750* (WU).

Distribution and Ecology. – Androsace komovensis Schönswetter & Schneew. is only known from the type locality on the southern slope of Mt. Kom Kučki, where it grows in crevices and scree in a south-facing limestone rock face.

Conservation. – The single known population of *A. komovensis* Schönswetter & Schneew. comprises an extremely low number of individuals (ca. 10). As large parts of the summit area of Mt. Kom Kučki are inaccessible, but likely harbour further (sub)populations, the actual population size may be significantly larger. Nevertheless, the species meets the criteria for being ranked as Critically Endangered (CE; IUCN Red List of Threatened Species v.3.1, available at http://www.iucnredlist.org/info/categories_criteria2001). Any further collecting activities must be avoided and ex situ cultivation measures should urgently be taken.

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Appendix. Taxa sampled, voucher information and GenBank accession numbers of *Androsace* species analysed here. Asterisks indicate sequences published previously in Schneeweiss & al. (2004).

Species; origin; collector, collection number and herbarium; ITS GenBank number; *trnLF* GenBank number

/Septentrionalis

albana Steven; Georgia, mountain range Trialeti, village Azavreti; *P. Schönswetter & A. Tribsch 8176* (WU); EU655562; EU655583. cf. ***lactiflora*** Fisch.; Russia: Altai; *M. Staudinger 5726* (WU); AY275076*; EU655582. ***raddeana*** Somm. & Levier; Georgia: Great Caucasus, Kazbeg; *P. Schönswetter & A. Tribsch s.n. (It-Nr. 48)* (WU); AY275073*; AY274960*. ***septentrionalis*** L. subsp. ***septentrionalis***; Austria: Wienerwald; *P. Schönswetter & A. Tribsch 4544* (WU); AY275074*; AY274959*. ***septentrionalis*** L. subsp. ***subulifera*** (A. Gray) G.T. Robbins; U.S.A.: Colorado, Rio Blanco Co.; Nelson 18870 (COCO); EU655561; EU655581.

/Elongata

elongata L. subsp. ***elongata***; Austria: Leithagebirge; *P. Schönswetter & A. Tribsch 4547* (WU); AY275072*; AY275014*. ***elongata*** L. subsp. ***breistrofferi*** (Charpin & Greuter) Molero & J.M. Monts.; France: Drôme, Grignan; *P. Schönswetter & A. Tribsch 8761* (WU); EU655564; EU655585. ***occidentalis*** Pursh; U.S.A.: Colorado, Rabbit Mtn.; *P. Schönswetter & A. Tribsch 12196* (WU); EU655563; EU655584.

/Aretia

/Eu-Aretia

alpina Lam. acc. 1; Austria: Silvretta; *P. Schönswetter & A. Tribsch* 5201 (WU); AY275054*; AY274973*. ***alpina*** Lam. acc. 2; France: Alpes Graies; *P. Schönswetter & A. Tribsch 5141* (WU); AY275052*; AY274974*. ***alpina*** Lam. acc. 3; Italy: Dolomiti; *P. Schönswetter & A. Tribsch 3641* (WU); AY275053*; AY274975*. ***brevis*** (Hegetschw.) Ces. acc. 1; Italy: Alpi Orobie, Mte. Legnone; *P. Schönswetter & A. Tribsch 4961* (WU); AY275049*; AY274963*. ***brevis*** (Hegetschw.) Ces. acc. 2; Italy: Alpi Orobie, Mte Rotondo; *P. Schönswetter & A. Tribsch 5004* (WU); EU655573; AY274964*. ***cylindrica*** DC. subsp. ***cylindrica*** acc. 1; Spain: Pyrenees, Ordesa; *P. Schönswetter & A. Tribsch 6487* (WU); AY275068*; AY274988*. ***cylindrica*** DC. subsp. ***cylindrica*** acc. 2; Spain: Pyrenees, Sierra Sardanera; *P. Schönswetter & A. Tribsch 8869* (WU); EU655576; EU655595. ***cylindrica*** DC. subsp. ***hirtella*** (Dufour) Greuter & Burdet; Spain: Pyrenees, Punta d'a Ralla; *P. Schönswetter & A. Tribsch 8882* (WU); EU655575; EU655594. ***cylindrica*** DC. subsp. ***willkommii*** P. Monts.; Spain: Pyrenees, Oroel; *P. Schönswetter & A. Tribsch 6430* (WU); AY275067*; AY274987*. ***hausmanni*** Leyb. acc. 1; Austria: Totes Gebirge; *E. Hörandl 5467* (Herb. E. Hörandl); AY275056*; AY274983*. ***hausmanni*** Leyb. acc. 2; Austria: Lienzer Dolomiten; *P. Schönswetter & A. Tribsch 7083* (WU); AY275055*; AY274984*. ***helvetica*** All. acc. 1; Switzerland: Glarner Alpen; *P. Schönswetter & A. Tribsch 4855* (WU); AY275065*; AY274980*. ***helvetica*** All. acc. 2; Switzerland/Italy: Ortler Alpen; *P. Schönswetter & A. Tribsch 5079* (WU); AY275066*; AY274981*. ***komovensis*** Schönswetter & Schneew.; Crna Gora/Montenegro: Komovi Mtns.; *B. Frajman & P. Schönswetter 11750* (WU); EU655577 & EU655578; EU655596 & EU655597. ***lactea*** L. acc. 1; Austria: Grünauer Berge; *W. Gutermann 26171* (Herb. Gutermann); AY275069*; AY274985*. ***lactea*** L. acc. 2; Slovacia: Nizké Tatry; *W. Gutermann 36691* (Herb. Gutermann); AY275070*; AY274986*. ***mathildae*** Levier acc. 1; cultivated in Jardin Botanique Alpin du Lautaret (France); no voucher; AY275071*; AY274976*. ***mathildae*** Levier acc. 2; Italy: Abruzzo, Gran Sasso, Mte. Camicia; *P. Schönswetter & A. Tribsch 8919* (WU); EU655579; EU655598. ***mathildae*** Levier acc. 3; Italy: Abruzzo, Majella, Mte. Amaro; *P. Schönswetter & A. Tribsch 8930* (WU); EU655580; EU655599. ***obtusifolia*** All. acc. 1; Italy: Alpi Carnie; *P. Schönswetter & A. Tribsch 4582* (WU); EU655574; AY274971*. ***obtusifolia*** All. acc. 2; France: Alpes Graies; *P. Schönswetter & A. Tribsch 4746* (WU); AY275057*; AY274972*. ***pubescens*** DC. acc. 1; Italy/France: Alpi Cozie; *P. Schönswetter & A. Tribsch 4719* (WU); AY275064*; AY274979*. ***pubescens*** DC. acc. 2; France: Alpes Cottiennes; *P. Schönswetter & A. Tribsch 4750* (WU); AY275062*; AY274978*. ***vandellii*** Chiov. acc. 1; France: Eastern Pyrenees; *P. Schönswetter & A. Tribsch 6390* (WU); AY275058*; AY274968*. ***vandellii*** Chiov. acc. 2; Italy: Bernina; *P. Schönswetter & A. Tribsch 5439* (WU); AY275059*; AY274969*. ***vandellii*** Chiov. acc. 3; Italy: Dolomiti; *P. Schönswetter & A. Tribsch 4663* (WU); AY275060*; AY274970*. ***vandellii*** Chiov. acc. 4; Spain: Sierra Nevada; *P. Schönswetter & A. Tribsch 6560* (WU); AY275061*; AY274967*. ***vitaliana*** Lapeyr. s.l. acc. 1; France: Alpes Maritimes; *P. Schönswetter & A. Tribsch 4700* (WU); AY275050*; AY274966*. ***vitaliana*** Lapeyr. s.l. acc. 2; Italy: Alpi Graie; *P. Schönswetter & A. Tribsch 5125* (WU); AY275051*; AY274965*. ***wulfeniana*** Sieber ex Koch acc. 1; Italy: Dolomiti; *P. Schönswetter & A. Tribsch 4657* (WU); AY275047*; AY274961*. ***wulfeniana*** Sieber ex Koch acc. 2; Austria: Rottenmanner Tauern; *P. Schönswetter & A. Tribsch 5213* (WU); AY275048*; AY274962*. ***wulfeniana*** Sieber ex Koch acc. 3; Italy, Dolomiti, Lagorai; *P. Schönswetter & A. Tribsch 6330* (WU); EU655572; EU655593.

/Dicranothrix

adfinis Biroli; Italy: Alpi Cozie; *P. Schönswetter & A. Tribsch 5617* (WU); EU655571; AY275008*. ***arctica*** Cham. & Schltdl.; U.S.A.: Alaska, Eagle Quad; *Lipkin & Cook 93/04* (COCO); AY275016*; AY274998*. ***beringensis*** (S. Kelso, Jurtzev & D.F. Murray) Cubey; U.S.A.: Alaska, Nulato Hills; *Parkert & al. 8017* (COCO); AY275018*; AY274999*. ***brigantiaca*** Jord. & Fourr. acc. 1; France: Dauphiné; *P. Schönswetter & A. Tribsch 5135* (WU); AY275043*; AY275005*. ***brigantiaca*** Jord. & Fourr. acc. 2; France: Alpes Cottiennes; *P. Schönswetter & A. Tribsch 9218* (WU); EU655570; EU655591. ***brigantiaca*** Jord. & Fourr. acc. 3; France: Alpes Cottiennes; *P. Schönswetter & A. Tribsch 6343* (WU); AY275041*; EU655592. ***chaixi*** Gren. & Godr.; France: Hautes Alpes, W of Gap; *P. Schönswetter & A. Tribsch 8780* (WU); AY275044*; AY275003*. ***cantabrica*** (Losa & P. Monts.) Kress acc. 1; Spain: Cordillera Cantabrica; *A. Kress s.n.* (Herb. A. Kress); AY275038*; AY275009*. ***cantabrica*** (Losa & P. Monts.) Kress acc. 2; Spain: Cordillera Cantabrica; *D. Mowle s.n.* (E: cultivated plants); AY275039*; AY275011*. ***ciliata*** DC.; Spain: Pyrenees, Ordizeta; *P. Schönswetter & A. Tribsch 6495* (WU); AY275034*; AY274982*. ***gormani*** Greene; U.S.A.: Alaska, Charley River; *Parkert & Hasslbach 4268* (COCO); AY275017*; AY275000*. ***halleri*** L. acc. 1; France: Vosges (cultivated in Conservatoire Botanique de la Ville de Mulhouse); EU655566; EU655587. ***halleri*** L. acc. 2; France: Massif Central, Mont Dore; *P. Schönswetter & G.M. Schneeweiss 8812* (WU); EU655565; EU655586. ***halleri*** L. acc. 3; Spain: Cordillera Cantábrica; *P. Schönswetter & G.M. Schneeweiss 8899* (WU); EU655567; EU655588. ***halleri*** L. s.l. acc. 1; France: Pyrenees, Canigou; *P. Schönswetter & A. Tribsch 6416* (WU); AY275037*; AY275013*. ***halleri*** L. s.l. acc. 2; Spain: Pyrenees, Puigmal d'Err; *P. Schönswetter & G.M. Schneeweiss 8836* (WU); EU655568; EU655589. ***hedreantha*** Griseb.; Bulgaria: Stara Planina; *P. Schönswetter & A. Tribsch 7174* (WU); AY275046*; AY275010*. ***idahoensis*** (Douglass M. Hend.) Cubey; U.S.A.: Idaho, Idaho Co., Gospel Peak; *Henderson & al. 3403* (COCO); AY275025*; AY275001*. ***laevigata*** (A. Gray) Wendelbo acc. 1; U.S.A.: Oregon, Cone Peak; *Kelso & Levin 00-200* (COCO); AY275029*; AY274995*. ***laevigata*** (A. Gray) Wendelbo acc. 2; U.S.A.: Washington, S Mt. Rainier; *D. Mowle s.n.* (E: cultivated plants); AY275032*; AY274993*. ***laevigata*** (A. Gray) Wendelbo acc. 3; U.S.A.: Washington, Olympic Mts.; *D. Mowle s.n.* (E: cultivated plants); AY275033*; AY274994*. ***laggeri*** Huet; Spain: Pyrenees, Vall de Cardós; *P. Schönswetter & G.M. Schneeweiss 8907* (WU); EU655569; EU655590. ***montana*** (A. Gray) Wendelbo; U.S.A.: Montana; *D. Mowle s.n.* (E: cultivated plants); AY275023*; AY275002*. ***nivalis*** (Lindl.) Wendelbo acc. 1; U.S.A.: Washington, Entiat Mts.; *R. Ratco NNS 97-79* (E: cultivated plants); AY275028*; AY274990*. ***nivalis*** (Lindl.) Wendelbo acc. 2; U.S.A.: Washington, Kittitas Co.; *Sondenna 336* (COCO); AY275027*; AY274991*. ***nivalis*** (Lindl.) Wendelbo acc. 3; U.S.A.: Washington, Kittitas Co.; *Olmstead 2001-77* (WTU); AY275026*; AY274989*. ***ochotensis*** Willd. ex Roem. & Schult. acc. 1; U.S.A.: Alaska, Delang Mts.; *Parkert & Meyers 10676* (COCO); AY275019*; AY274997*. ***ochotensis*** Willd. ex Roem. & Schult. acc. 2; U.S.A.: Alaska, Hawand Pass; *Parker & Meyers 7574* (COCO); AY275022*; AY274996*. ***puberula*** Jord. & Fourr. acc. 1; Italy: Alpi Ligurie; *P. Schönswetter & A. Tribsch 6366* (WU); AY275040*; AY275007*. ***puberula*** Jord. & Fourr. acc. 2; Italy: Alpi Graie; *P. Schönswetter & A. Tribsch 4766* (WU); AY275042*; AY275006*. ***pyrenaica*** Lam.; Spain: Pyrenees, Ordizeta; *P. Schönswetter & A. Tribsch 6493* (WU); AY275035*; AY274977*. ***rioxana*** Segura Zubizarreta; Spain: Sierra de la Demanda; *A. Kress s.n.* (Herb. A. Kress); AY275045*; AY275004*. ***triflora*** Adans.; Russia: Franz Joseph Land; *H. Pauli v-73* (WU); AY275020*; AY274992*.