



Phylogenetic position and taxonomy of the enigmatic *Orobanche krylowii* (Orobanchaceae), a predominately Asian species newly found in Albania (SE Europe)

BOŽO FRAJMAN¹, LUIS CARLÓN², PETR KOSACHEV³, ÓSCAR SÁNCHEZ PEDRAJA⁴, GERALD M. SCHNEEWEISS⁵ & PETER SCHÖNSWETTER¹

¹Institute of Botany, University of Innsbruck, Sternwartestraße 15, A-6020 Innsbruck, Austria; bozo.frajman@uibk.ac.at, peter.schoenswetter@uibk.ac.at

²Jardín Botánico Atlántico, Avenida del Jardín Botánico 2230, E-33394 Gijón (Asturias), Spain; lcarlon@hotmail.com

³Altai State University, Barnaul, Lenina 61, Russia; pakosachev@yandex.ru

⁴E-39722 Liérganes (Cantabria), Spain; osanchez@farmaliérganes.com

⁵Department of Systematic and Evolutionary Botany, University of Vienna, Rennweg 14, A-1030 Vienna, Austria; gerald.schneeweiss@univie.ac.at

Abstract

We report on the occurrence of *Orobanche krylowii* in the Alpet Shqiptare (Prokletije, Albanian Alps) mountain range in northern Albania (Balkan Peninsula). The species was previously known only from eastern-most Europe (Volga-Kama River in Russia), more than 2500 km away, and from adjacent Siberia and Central Asia. We used morphological evidence as well as nuclear ribosomal ITS sequences to show that the Albanian population indeed belongs to *O. krylowii* and that its closest relative is the European *O. lycoctoni*, but not *O. elatior* as assumed in the past. Both *Orobanche krylowii* and *O. lycoctoni* parasitize Ranunculaceae (*Thalictrum* spp. and *Aconitum lycoctonum*, respectively). We provide an identification key and a taxonomic treatment for *O. krylowii*, and suggest the IUCN category CE (critically endangered) for the highly disjunct Albanian population.

Key words: *Orobanche*, taxonomy, critically endangered, Albania

Introduction

In spite of the peculiarity of its rich flora and its importance for European phytogeography (Markgraf 1932) Albania is one of the botanically least explored regions of Europe. After the last editions of the national flora (Paparisto *et al.* 1988, Qosja *et al.* 1992, 1996, Vangjeli *et al.* 2000) including 3758 taxa (3250 species) of vascular plants a multitude of species new for Albania were published (e.g., Barina & Pifko 2008, Rakaj 2009, Ball 2011, Barina *et al.* 2011, Meyer 2011, Barina *et al.* 2013). For instance, Meyer (2011), based on his botanical explorations of Albania during four months in 1959–1961, described 37 new taxa for science (28 species and 9 subspecies).

The holoparasitic broomrapes (*Orobanche* L., Orobanchaceae) belong to the taxonomically most difficult non-apomictic genera. This is due to the, compared to other plants, strongly reduced number of potentially useful characters, especially vegetative ones, the high phenotypic variability and the uniform darkening during desiccation resulting in the loss of potentially useful coloration characters in herbarium specimens (Kreutz 1995, Schneeweiss *et al.* 2009). Consequently, our knowledge on taxonomy and distribution of many broomrape species is still insufficient, even in botanically well-explored regions, such as the Iberian Peninsula or Central Europe. New species of *Orobanche* s. str. and *Phelipanche* Pomel (syn. *O.* sect. *Trionychon* Wallr.) have been described (Foley 1998, 2004, Carlón *et al.* 2005, 2008, Pujadas-Salvà & Crespo 2004, Pujadas-

Salvà 2008), previously neglected species resurrected (Zázvorka 2010, Frajman *et al.* 2011), and new localities, sometimes far outside the previously known distribution range, (re)discovered (Pusch 2000, Carlón *et al.* 2005, 2008, Frajman & Schönswetter 2008, Pusch & Günther 2009, Schneeweiss *et al.* 2009, Dakskobler *et al.* 2010, Schaupp 2011, Schönswetter *et al.* 2011, in press, Uhlich 2013).

Application of molecular data greatly advanced our understanding of phylogenetic relationships among major clades of broomrapes (Manen *et al.* 2004, Schneeweiss *et al.* 2004, Park *et al.* 2007, 2008) and of species-level relationships (Carlón *et al.* 2005, 2008). Carlón *et al.* (2005, 2008) successfully combined traditional morphological systematic approaches supplemented by thorough photographic documentation with analyses of nuclear ITS data and allowed recognition of new species and clarification of the taxonomic status of poorly known and often neglected taxa. The ITS sequences were, in a fashion similar to barcoding, also used to confirm the identity of broomrapes parasitizing on *Aconitum lycoctonum* L. in the Alps, namely *O. lycoctoni* Rhiner (Schneeweiss *et al.* 2009).

Orobanche taxa parasitize flowering plants from various families. Whereas some families, such as Asteraceae or Fabaceae, contain host species for numerous broomrape species, other families, such as Ranunculaceae, are only rarely attacked. Three *Orobanche* species are reliably known to parasitize on Ranunculaceae (Carlón *et al.* 2013a), i.e., *O. lycoctoni* exclusively on *Aconitum lycoctonum* (Carlón *et al.* 2008), *O. haenseleri* (= *O. hellebori* Miégev.) mainly on *Helleborus* L. (Beck Mannagetta 1930), and *O. krylowii* exclusively on *Thalictrum* (*minus* L.) (Beck 1881, Uhlich 2013). Whereas *O. haenseleri* and *O. lycoctoni* were shown not to be closely related (Schneeweiss *et al.* 2009), nothing is known about the phylogenetic position of *O. krylowii*.

Orobanche krylowii was described by Beck (1881) based on a specimen collected by Krylov on the banks of Chusovaya River in the Perm Region in the Central Ural Mts. (Kynowski sawod). Beck (1881) considered it most similar to *O. major* L. (syn. *O. elatior* Sutton) and *O. libanotidis* Rupr. (syn. *O. alsatica* var. *libanotidis* (Rupr.) Beck, *O. bartlingii* Griseb.) and later he treated it as form of *O. major* (Beck Mannagetta 1890). Similarly, Nyman (1890) considered it a subspecies of *O. major*. Krylov (1907), based on different indumentum (pubescent vs. glabrous) described two forms, *O. k. f. puberula* Krylov and *O. k. f. glaberrima* Krylov, which were not recognized by Beck Mannagetta (1930). Up to now, *O. krylowii* was only known from Asia (Siberia, Central Asia: Tien Shan, Dzungaria, Tarbagatai, Balkhash, Kashgaria) and eastern-most Europe (Volga-Kama river region) (Novopokrovskii & Tzvelev 1958, Kurbatskij 2007).

Here we report on the occurrence of *Orobanche krylowii* Beck in the Alpet Shqiptare (=Prokletije, “Albanian Alps”) in northern Albania, more than 2500 km away from its currently known distribution area. We use morphological evidence as well as nuclear ribosomal ITS sequences from Albanian as well as northern Central Asian populations to test the taxonomic assignment of the Albanian population to *O. krylowii* and to determine the phylogenetic position of *O. krylowii*. Specifically, we test whether *O. krylowii* is more closely related to *O. elatior* as proposed by previous taxonomic treatments or to any other *Orobanche* species parasitizing Ranunculaceae. We provide a taxonomic treatment of *O. krylowii* including a comprehensive description accompanied by an illustration plate as well as diagnostic characters, along with an identification key to differentiate it from taxa that are closely related, morphologically similar or otherwise have been brought in connection with *O. krylowii*. Finally, we propose an IUCN conservation status.

Material & Methods

Plant material

Plant material of *O. krylowii* from one locality in Northern Albania and from several localities in Russia and Kazakhstan was investigated and is listed in the Appendix. The accessions with GenBank numbers were analyzed molecularly and all (along with the types, cited below) were examined morphologically.

Lab work and phylogenetic analyses

DNA was extracted from herbarium material using the 2 × cetyl trimethyl ammonium bromide (CTAB) method of Doyle & Doyle (1987). Amplification and sequencing of the nuclear ITS region followed methods described in Schneeweiss *et al.* (2004). The newly obtained sequences (GenBank accession numbers KF359499 to KF359504) were manually aligned to the data set of Schneeweiss *et al.* (2009). The determination of the following taxa from Schneeweiss *et al.* (2009) was revised based on the most recent taxonomic and nomenclatural knowledge: *O. crinita* Viv. (AY209244) was revised as *O. sanguinea*, *O. elatior* (EU655618, EU655619) as *O. leptantha* Pomel, *O. ozanonis* F.W. Schultz (AY960723) as *O. serbica* Beck & Petrovic, *O. cf. raddeana* (AY209259) and *O. elatior* (EU655621, EU655622, EU655623) as *O. kochii*, and *O. macrolepis* Coss. (AY209286, AY209287, AY209288) as *Boulardia latisquama* F.W. Schultz. There are different opinions on the circumscription of *O. ritro* Gren. We here follow Zazvorka (2010) in considering *O. loscosii* Carlón, M. Láinz, Moreno Mor. & Ó. Sánchez (EU655617) a separate taxon, while *O. ritro* Gren. should be synonymized with *O. kochii* (but see Pujadas Salvà 2012).

Tree searching and bootstrapping (with 1000 replicates; MLB) relied on maximum likelihood (ML) under the GTRCAT model of substitution, using RAxML 7.2.0 (Stamatakis 2006, Stamatakis *et al.* 2008) on Cipres Portal (Miller *et al.* 2010). Maximum parsimony (MP) and MP bootstrap (MPB) analyses were performed using PAUP 4.0b10 (Swofford 2002). The most parsimonious trees were searched heuristically with 1000 replicates of random sequence addition, TBR swapping, and MulTrees on. The swapping was performed on a maximum of 1000 trees (nchuck=1000). All characters were equally weighted and unordered. The data set was bootstrapped using full heuristics, 1000 replicates, TBR branch swapping, MulTrees option off, and random addition sequence with five replicates. *Diphelypaea tournefortii* (Desf.) Nicolson and *D. coccinea* (M. Bieb.) Nicolson were used as outgroups, based on previous studies (Schneeweiss *et al.* 2004).

Results & Discussion

Taxonomic treatment

Orobanche krylowii Beck in Oesterr. Bot. Z. 31: 309. 1881 ["krylovii" (orthographic variant)] ≡ *O. krylowii* Beck in Krylov, Mater. Fl. Perm. Gouv. 2: 202. 1881, nom. nud. (cf. Beck 1890: 171 "sine descript.") ≡ *O. major* subsp. *krylowii* (Beck) Nyman, Consp. Fl. Eur., Suppl. 2: 243. 1890 ≡ *O. major* f. *krylowii* (Beck) Beck in Biblioth. Bot. 19: 171 t. 3 f. 45(3). 1890.—Type: "514. *Orob. major* L. / f. *O. Krylowi* G. Beck / Leg. Porph. Krylov. / Gubern. Perm.- Kynowski sawod / Beck / 130 [m. Beck]" (holotype, LE!). Iconography: Beck (1890): t. 3. f. 45(3).

= *Orobanche krylowii* f. *puberula* Krylov, Fl. Alt.: 997. 1907 (Krylov 1907).—Type: "Na tayozhnyh lugah, okolo Pesczanogo / ozera, - v Temerchinskoy dache. / 20 ijunja 90 g. Sobr. P. Krylov" [on taiga clearings of the Temerchinski forest around lake Pesczanoe, leg. P. Krylov, 20.6.1890] (TK!), lectotype, designated here. "Okolo Pesczanogo ozera v Temerchinskoy / dache. 23 ijunja 1902 g. Sobr. P. Krylov" [around the lake Pesczanoe in the Temerchinski forest, leg. P. Krylov, 23.6.1902] (syntype, TK!). The locality is in the vicinity of Tomsk, village Golownino (N56.461258, E84.880857).

Note: it is not clear if the second specimen (syntype) actually belongs to *O. krylowii*, as the erect flowers with straight dorsal line and rather long calyx teeth are not typical for *O. krylowii*.

= *Orobanche krylowii* f. *glaberrima* Krylov, Fl. Alt.: 997. 1907 (Krylov 1907).—Type: "Okr. Salairskogo rudn. i dr m. Tomsk. gub. / Sobral F. E. Zass / Posl. B Eks. №2" [vicinity of Salair mines in gubernija Tomsk (N54.286473, E85.928078) / Leg. F. E. Zass / exs. №2 sent to B—probably Beck]—two herbarium sheets (TK!), lectotype, designated here. "Okr. Tomska, blis rechki Maloj Kirgizki, smeschanny les. / 1 avg. 1899 g. Wydrin / Posl. G. Beck'u, №3" [vicinity of Tomsk, near the river Malaja Kirgizka (N56.55778, E85.072231), mixed forest / leg. Wydrin, 1.8.1899 / exs. №2 sent to G. Beck] (syntype, TK!).

– *Orobanche flava* auct. [p.p. min.], non *Orobanche flava* Mart. ex F.W. Schultz., Beitr. Kenntn. Deutsch. Orob.: 9. 1829 (cf. Teryokhin *et al.* 1993, Schlauer *et al.* 2012)

Several authors (e.g., Chater & Webb 1972, Pignatti 1982, Domina & Raab-Straube 2010) reported *O. elatior* Sutton as parasitizing on "*Thalictrum*", which was likely based on the fact that *O. krylowii* was considered conspecific with *O. elatior*.

≠ *Orobanche krylowii* var. *mirabilis* Serg. in Krylov, Fl. Zapadnoi Sibiri 10: 2545. 1939 (Krylov 1939).— Type: "Semipalatinskaja gubernija, Buchtarminskii uesd, okrestnosti Katon-Karagaja, podnozhie Narymskogo chrehta, utschel'e ruczja Sernoj, 49 1/6°N 55 1/10°E, tschebnistye sklony. 22 ijulja 1928. P. Krylow and L. Sergeevskaya" [Republic Kazakhstan, Vostochno-Kazachstanskaya oblast: Semipalatinskaja gubernija, Buchtarminskii region, surroundings of Katon-Karagaja, foot of Mts. Narymskogo, gorge of the stream Sernoj, 49 1/6°N 55 1/10°E, cliffs. Leg. P. Krylow & L. Sergeevskaya, 22.7.1928] (holotype, TK!)

Taxonomic remarks: as forms with (*f. glaberrima*) and without (*f. puberula*) glandular hairs in the inflorescence were only recognized by Krylov (1907) and later neglected, and as all plants seen by us are glandular, we consider the glabrous form an exception known only from its type locality and of no taxonomic value. The current taxonomic status of *O. krylowii* var. *mirabilis*, allegedly parasitic on *Iris ruthenica*, is unclear. As the type specimen of *O. krylowii* var. *mirabilis* has almost glabrous filaments lacking the dense and almost evenly distributed indumentum characteristic for *O. krylowii*, the bracts and scales are shorter and the inflorescence laxer, the corolla has a different, narrowly tubular shape and exhibits strongly irregularly toothed corolla lobes, we believe that it does not belong to *O. krylowii* but likely to the *O. minor* group. It should also be noted that the specimen most likely was not parasitic on *Iris*, as no clear connections between the roots of *Iris* and *Orobanche* are visible.

Description: Plant light yellow or whitish, with an evenly distributed indumentum of short glandular and eglandular hairs; stems slender, up to 45 cm high, less than 7 mm in diameter; scale leaves elongated triangular-lanceolate, more abundant towards the almost unswollen stem base; inflorescence with usually fewer than 20 erecto-patent flowers forming a spike that is not very dense and is limited to the upper third of the stem; bracts narrow lanceolate, approximately equaling the flowers in length, early withering to brown and then vividly contrasting the rest of the plant; calyx about ½ as long as the corolla, segments free, often entire, with one pair of shortly subulated teeth strongly reduced or absent; corolla up to 20 mm long, tubular, strongly constricted below the insertion of the stamens, with short light glandular hairs, its dorsal line regularly curved (but straight near the apex), its tube about 5 mm wide and about 3 times as long as the lips; upper lip slightly emarginate, porrect (continuing the dorsal line of the corolla tube); lower lip 3-lobed, with divergent, spatulate, somewhat concave and finely irregularly denticulate margin; stamens inserted at about ¼ of the total corolla length, the 10 mm long filaments beset with abundant, long, eglandular white hairs almost to the apex and scant short glandular hairs below the anthers; anthers light brown to pinkish-brown, with short hairs along the sutures of thecae; ovary whitish, with a yellow nectary at its base, glabrous or glabrescent with scant hairs at the apex; style whitish, with very sparse (more abundant on the upper part) short glandular hairs; stigma bright yellow, very slightly 2-lobed, with a flat or widely concave distal surface, crowning the style in an almost reniform to disciform funnel-like structure. Iconography and photos of *Orobanche krylowii* from Albania are shown in Figs. 2 and 3.

Host and habitat: Parasitic exclusively on *Thalictrum* L. species [on *Thalictrum minus* L., s.l. (cf. Krylov *et al.* 1939: 2545, Tzvelev 1981: 334)] (Carlón *et al.* 2013b). Forest clearings, sparse mixed and coniferous forests, in Albania also slightly above the timberline.

Distribution: Europe: Alpet Shqiptare in Albania, southern and eastern Volga-Kama (Republic Tatarstan) and Trans-Volga region in Russia. Asia: Western (southern Ob, upper Tobol and Irtysh rivers systems as well as Altai mountains: Altai Krai, Kemerovo Oblast, Tomsk Oblast, Tyumen Oblast) and Eastern Siberia (Krasnoyarsk Krai, Republic of Khakassia, Tyva Republic, Angara-Sayan river system: Buryatia Republic and Irkutsk Oblast) in Russia, Central Asia (Tien Shan, Tarbagatai Mountains) in Kazakhstan, Kyrgyzstan and Mongolia (Novopokrovskii & Tzvelev 1958, Tzvelev 1981, Grubov *et al.* 2006, Kurbatskij 2007, Kosachev 2013). It has also been reported for Dzungaria (Xinjiang) in China, but no material has been found in Chinese herbaria (cf. Zhang & Tzvelev 1998). The distribution map presented in Fig. 4 is based on our own as well as the literature data (see Appendix).

Nature conservation: The species is uncommon in the major part of its distribution area and is included in the red data lists of the Baikal region and Irkutsk (Ivanova 1999, 2010). Any categorization of threat of the Albanian population of *O. krylowii* following the IUCN (2013) categories is strongly dependent on the size of

the species' regional distribution and/or the number of populations. As currently only a single, albeit individual-rich and not endangered population is known, we here provisionally suggest the category CE (critically endangered). Future field research will show if more populations will be found, which should translate into a change of categorization. We have recorded *O. krylowii* on two localities along the path from the village Dragobi to Mt. Maja Hekuraves in the Alpet Shqiptare. These localities are about 500 m apart and it is likely that additional populations thrive in this remote side valley of the Valbona valley.

Identification key

In the following, *O. krylowii* is keyed out against species previously considered conspecific (*O. elatior*) or similar (*O. alsatica*). In addition, we included *O. haenseleri* and *O. lycoctoni* parasitising on Ranunculaceae. We have also included *O. kochii* F.W. Schultz, as it resembles *O. krylowii* (mainly the straight dorsal segment of the corolla), which might explain Beck's (1930) ultimate decision to include *O. krylowii* into *O. major*, which has been convincingly shown to actually correspond to at least two species, *O. elatior* and *O. kochii* (Zázvorka 2010).

- 1 Plant always pale yellow or whitish; stigma flattened, widely concave, reniform to disciform, very shallowly 2-lobed; upper lip porrect (continuing the dorsal line of the corolla tube) 2
- Plant usually strongly pigmented, rarely yellowish; stigma deeply divided into distinct subspherical lobes; upper lip erect or recurved 3
- 2 Stems short and stout, up to 40×1.2 cm; inflorescence usually dense, club-like; flowers patent; calyx-segments usually unequally bidentate; corolla with a regularly and strongly arched-curved dorsal line (straight in the apical third); corolla lips with coarsely eroded-denticulate margin; on *Aconitum* ***O. lycoctoni***
- Stems more slender, up to 45×0.7 cm; inflorescence laxer; flowers erecto-patent; calyx-segments often entire or more unequally bidentate; corolla with an almost regularly curved dorsal line (straight only near the apex); corolla lips with finely eroded-denticulate margin; on *Thalictrum* ***O. krylowii***
- 3 Corolla with distally straight dorsal line, with a distinctly flattened subapical area; lower lip cruciform, with concave, spatulate, very divergent lobes; on *Centaurea* and *Echinops* ***O. kochii***
- Corolla with regularly curved dorsal line; lower lip with less divergent, elliptic or rounded and flat to convex lobes 4
- 4 Apex of the inflorescence acute, due to the appressed bracts with a comose appearance; flowers erecto-patent, tubular-infundibuliform; corolla variably (pink, reddish, yellow), but always vividly pigmented; filaments hairy almost to the apex; on Ranunculaceae (*Helleborus*) and Lamiaceae (*Phlomis*, *Sideritis*) ***O. haenseleri***
- Apex of the inflorescence rounded, with no crown of bracts; flowers patent, tubular to wide-tubular; corolla brownish, purple or reddish to yellowish brown, rarely yellow, but usually feebly pigmented; filaments hairy at most in its lower two thirds 5
- 5 Plants up to 85 cm, tall and stout; inflorescences long, cylindrical, often covering the upper two thirds of the stem; corolla with dorsal line regularly curved, sometimes more or less deflexed at the apex; upper corolla lip shallowly emarginate; mainly on *Centaurea* ***O. elatior* s. str.**
- Plants up to 60 cm, usually shorter and more slender, with relatively narrower stems; oval inflorescences, dense, at most covering the upper half of the stem; corolla with regularly and strongly curved dorsal line, but somewhat straight at the apex; upper corolla lip more deeply and distinctly emarginate; on Apiaceae (mainly on *Peucedanum*) ***O. alsatica***

Both, phylogenetic analyses (Fig. 1) and comparison of morphological characters confirm that the Albanian population indeed belongs to *O. krylowii*. Whereas samples of *O. krylowii* from across most of its Asian distribution had identical ITS sequences, the population from Albania, separated from the main distribution area in easternmost Europe and adjacent Asia (Novopokrovskii & Tzvelev 1958) by more than 2500 km, differs by a single substitution and two polymorphic sites, which may be due to geographic isolation. *Orobanche krylowii* is not the only species in Albania with biogeographic connections to the East. Other well-known examples, albeit on the genus level, include the ornamentals *Forsythia europaea* Degen & Bald. with East Asian relatives and *Aesculus hippocastanum* L., whose congeners are restricted to East Asia and eastern North America (Meusel *et al.* 1965, 1978).

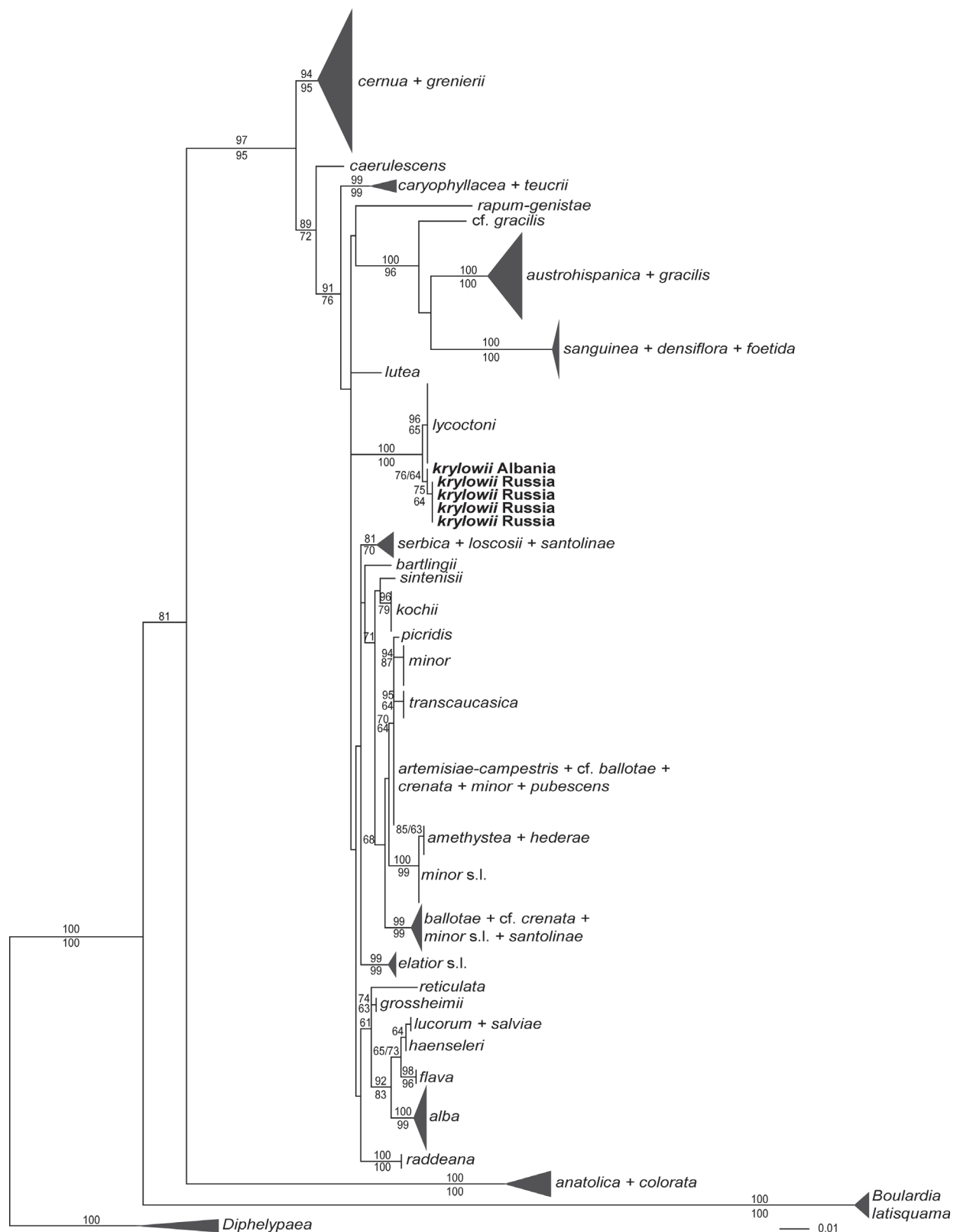


FIGURE 1. Maximum likelihood tree of nuclear ITS sequences of *Orobanche*, using the genus *Diphelypaea* as outgroup. Some clades with more sequences per species and/or several closely related species are collapsed to aid legibility. *Orobanche krylowii* is indicated in bold larger font. Numbers above branches are maximum likelihood, those below maximum parsimony bootstrap support values above 60%.

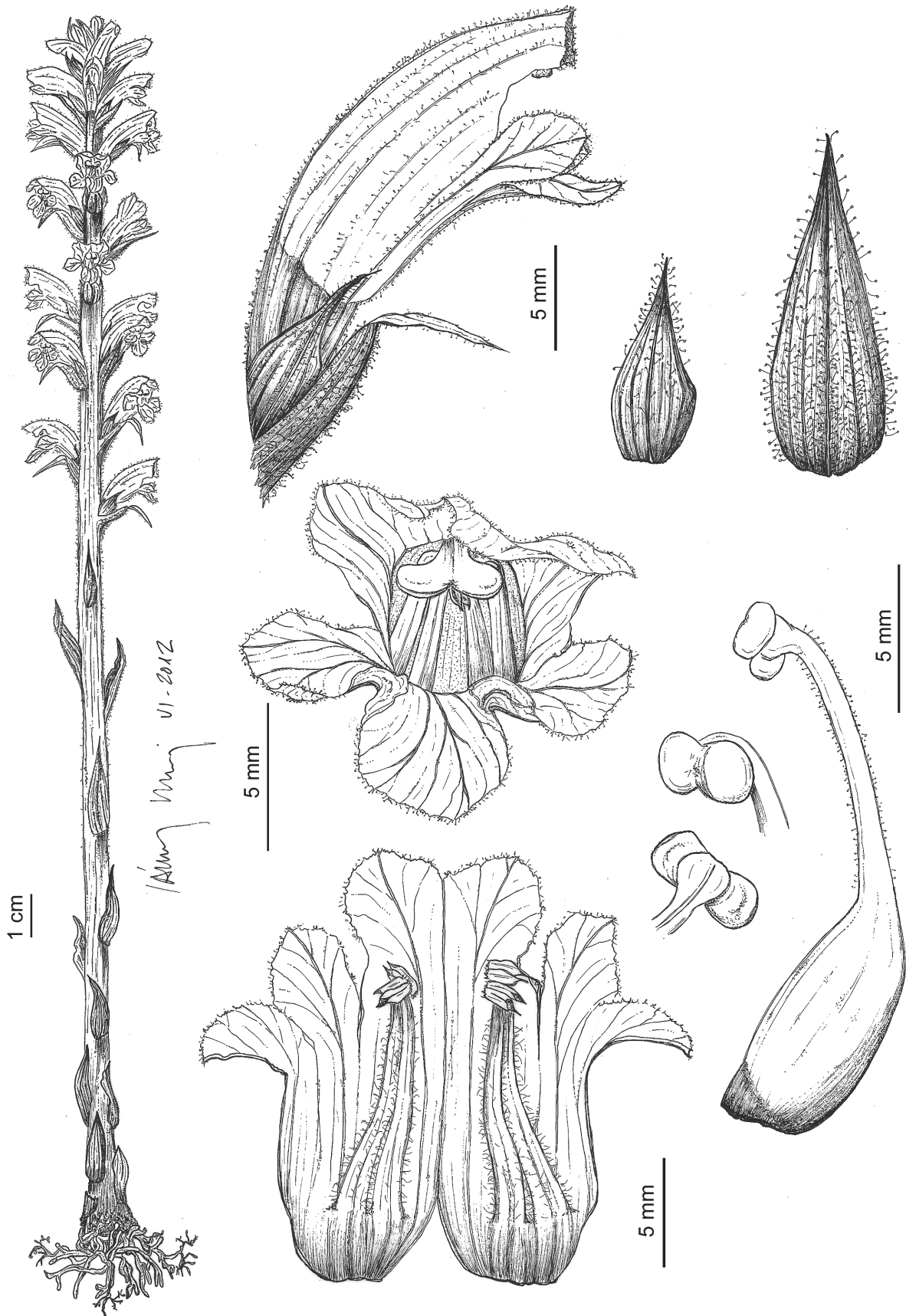


FIGURE 2. Iconography of *Orobanche krylowii* from Albania.

Morphological inspection did not reveal any significant differences between *O. krylowii* from Albania on one hand and the type material (LE) and other inspected specimens from Asia (see Appendix) on the other hand. The Albanian specimens have distinctly woolly bracts, which can, however, also be observed in Asian specimens (e.g., specimen (3) cited in Appendix as well as the type material of f. *puberula* cited below). Moreover, the Albanian population (Figs. 2–3) corresponds perfectly to the descriptions of Russian authors (Novopokrovskii & Tzvelev 1958, Tzvelev 1981, Kubatskij 2007). We therefore refrain from describing it as separate subspecies despite the slightly different ITS sequence and the strongly disjunct occurrence.



FIGURE 3. Photos of *Orobanche krylowii* from Albania with its host *Thalictrum minus*.

The closest relative of *O. krylowii* is the European *O. lycoctoni* (Fig. 1) distributed from the Cantabrian Mountains in northern Spain to the Eastern Alps (Schneeweiss *et al.* 2009). The sister relationship is strongly supported by MLB and MPB (100%), but the relationship of this clade to other *Orobanche* species remains unclear. *Orobanche krylowii* and *O. lycoctoni* are morphologically similar and share, for instance, a uniquely enlarged, flattened yellow stigma. However, *O. lycoctoni* is more robust in all parts, has stouter stems, denser club-shaped inflorescences and patent and widely tubular flowers with a more marked dorsal geniculation (Figs. 2–3). Even if *O. krylowii* and *O. lycoctoni* are morphologically similar, we found no transitional forms in the extensive herbarium material investigated. This together with the consistent genetic differentiation suggests that both entities deserve taxonomic recognition, most conveniently at the specific level. In contrast, *O. krylowii* differs strongly from *O. elatior*, with which it was sometimes considered conspecific (Beck Managetta 1890, Nyman 1890, Chater & Webb 1972), and from *O. alsatica* var. *libanotidis*, which was deemed similar by Beck (1881). Characters that differentiate both *O. krylowii* and *O. lycoctoni* from *O. alsatica* and *O. elatior* are the deeply bilobed stigma with subspherical lobes, the calyx, which is much longer in relation to the corolla, the filaments, which are hairy only in their lower half, and the regularly curved, not geniculate corolla. Many of these characters (e.g., the distinctively flattened stigma) are either not at all or at least not unambiguously detectable on herbarium specimens, and therefore should be recorded on fresh material and photographically documented.

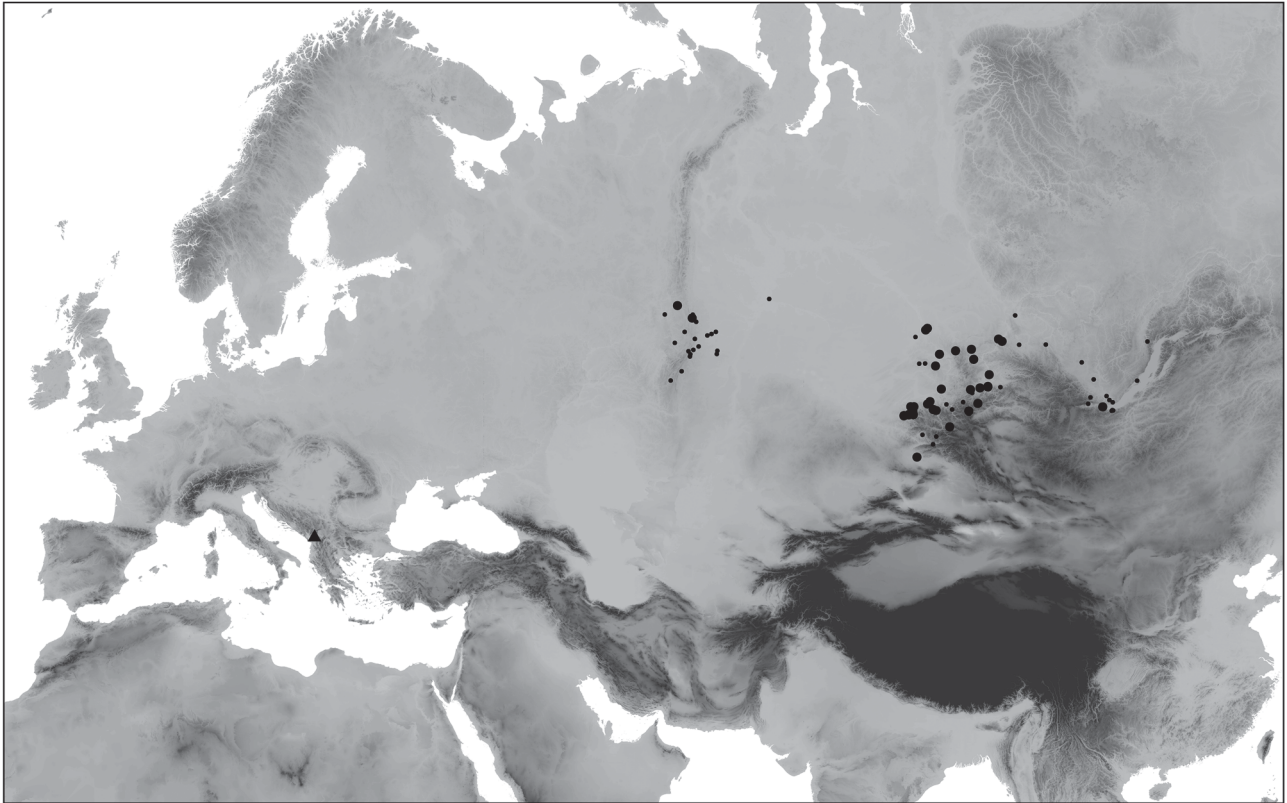


FIGURE 4. Distribution of *Orobanche krylowii* based on the examined herbarium material and photos (big dots) as well as literature data (small dots). The locality in Albania is marked with a triangle.

To our knowledge, *O. krylowii* is restricted to *Thalictrum minus* (Ranunculaceae) as a host, which may serve as an additional diagnostic feature. Its sister species *O. lycoctoni* parasitizes *Aconitum lycoctonum*, suggesting that adaptation to that family already occurred in the ancestor of *O. krylowii* and *O. lycoctoni*.

Our discovery of another species new for the flora of Albania and the Balkan Peninsula adds to the growing body of evidence (e.g., Barina & Pifko 2008, Rakaj 2009, Barina *et al.* 2011, Meyer 2011, Frajman *et al.* submitted) that botanical exploration of this part of Europe is still very rewarding. In the future, floristic mapping activities should accompany molecular phylogenetic studies, thereby enhancing both our knowledge about species diversity as well as of the evolutionary mechanisms and patterns involved in the origin of this high diversity. Hopefully, as was in the case of *O. lycoctoni*, it will stimulate botanists to search for *O. krylowii* also in the areas between the Albanian Alps and the Volga River in Russia.

Acknowledgements

We are grateful to Dr. Jiří Zázvorka for providing the photos of the type material from LE, and Dr. Alexandr Ebel for providing the herbarium material and photos of the types from the herbarium TK. The work was supported by the Austrian Science Fund (FWF, project P19404 to G. M. Schneeweiss).

References

- Alekseev, J.E., Galeeva, A.H., Gubanov, I.A., Gufranova, I.B., Zhirnova, T.V., Knjazev, M.V., Kulagin, J.Z., Kulakovskaja, L.A., Kultiasov, I.M., Kucherov, E.V., Michajlova, T.P., Muldashev, A.A., Skvortzov, A.K., Tichomirov, V.N. & Schurova, E.A. (1989) *Opredelitel' vysshikh rastenii Bashkirskoi ASSR [Identification key to Higher plants of the Bashkir Republic]*. Nauka, Moscow, 375 pp.

- Artemov, I.A. (2012) *Opredelitel' rastenij Katunskogo biosfernogo zapovednika* [The key to the plants of the Katunskiy biosphere reserve]. Pjat'-Pljus, Barnaul, 320 pp.
- Ball, P.W. (2011) *Source of Records for Albania in Flora Europaea, TRTE Herbarium*. University of Toronto, Mississauga. Available from: http://www.erin.utoronto.ca/~trteherb/resources_assets/Albania_V1.pdf (accessed 7 March 2013).
- Barina, Z. & Pifko, D. (2008) Additions and amendments to the flora of Albania. *Willdenowia* 38: 455–464. <http://dx.doi.org/10.3372/wi.38.38206>
- Barina, Z., Pifko, D. & Mesterházy, A. (2011) Contributions to the flora of Albania, 3. *Willdenowia* 41: 329–339. <http://dx.doi.org/10.3372/wi.41.41214>
- Barina, Z., Rakaj, M. & Pifko, D. (2013) Contributions to the flora of Albania, 4. *Willdenowia* 43: 165–184. <http://dx.doi.org/10.3372/wi.43.43119>
- Beck Mannagetta, G. von (1890) Monographie der Gattung *Orobanche*. *Bibliotheca Botanica* 19: 1–275.
- Beck Mannagetta, G. von (1930). *Orobanchaceae*. In: Engler, A. (ed.) *Das Pflanzenreich. Regni vegetabilis conspectus*. W. Engelmann, Leipzig, pp. 1–348.
- Beck, G. (1881) *Plantae novae. Oesterreichische Botanische Zeitschrift* 31: 309–313. <http://dx.doi.org/10.1007/bf01647094>
- Carlón, L., Gómez Casares, G., Láinz, M., Moreno Moral, G., Sánchez Pedraja, Ó. & Schneeweiss, G.M. (2005) Más, a propósito de algunas *Orobanche* L. y *Phelipanche* Pomel (*Orobanchaceae*) del oeste del Paleártico. *Documentos del Jardín Botánico Atlántico (Gijón)* 3: 1–71.
- Carlón, L., Gómez Casares, G., Láinz, M., Moreno Moral, G., Sánchez Pedraja, Ó. & Schneeweiss, G.M. (2008) Más, a propósito de algunas *Phelipanche* Pomel, *Boulardia* F. W. Schultz y *Orobanche* L. (*Orobanchaceae*) del oeste del Paleártico. *Documentos del Jardín Botánico Atlántico (Gijón)* 6: 1–127.
- Carlón, L., Gómez Casares, G., Láinz, M., Moreno Moral, G., Sánchez Pedraja, Ó. & Schneeweiss, G.M. (2013a) *Index of Orobanchaceae*. Liérganes, Cantabria, Spain. Available from: <http://www.farmalierganes.com/Otrospdf/publica/Orobanchaceae%20Index.htm> (accessed: 1 February 2013).
- Carlón, L., Gómez Casares, G., Láinz, M., Moreno Moral, G., Sánchez Pedraja, Ó. & Schneeweiss, G.M. (2013b) *Annotated checklist of host plants of Orobanchaceae*. Liérganes, Cantabria, Spain. Available from: http://www.farmalierganes.com/flora/angiospermae/orobanchaceae/Host_Orobanchaceae_Checklist.htm (accessed: 1 February 2013).
- Chater, A.O. & Webb, D.A. (1972) *Orobanche* L. In: Tutin, T.G., Heywood, V.H., Burges, N.A., Moore, D.M., Valentine, D.H., Walters, S.M. & Webb, D.A. (eds.) *Flora Europaea* 3. CUP, Cambridge, pp. 286–293.
- Dakskobler, I., Vreš, B. & Pusch, J. (2010) *Orobanche panicii* Beck, a new species to the flora of Slovenia. *Hacquetia (Ljubljana)* 9: 171–176. <http://dx.doi.org/10.2478/v10028-010-0008-9>
- Domina, G. & Raab-Straube, E. von (2010) *Orobanchaceae*. In: *Euro+Med Plantbase—the information resource for Euro-Mediterranean plant diversity*. Available from: <http://www.emplantbase.org/home.html> (accessed: 20 March 2013).
- Doyle, J.J. & Doyle, J.L. (1987) A rapid DNA isolation procedure for small amounts of fresh leaf tissue. *Phytochemical Bulletin* 19: 11–15.
- Foley, M.J.Y. (1998) Two new *Orobanche* species from the Arabian Peninsula. *Edinburgh Journal of Botany* 55: 229–234. <http://dx.doi.org/10.1017/s0960428600002158>
- Foley, M.J.Y. (2004) *Orobanchaceae* of the Arabian Peninsula. *Candollea* 59: 231–254.
- Frajman, B. & Schönswetter, P. (2008) Notes on some rare *Orobanche* and *Phelipanche* species (*Orobanchaceae*) in Croatia. *Acta Botanica Croatica* 67: 103–107.
- Frajman, B., Pachschröck, C. & Schönswetter, P. (submitted to Phyton) Contributions to the flora of the Dinarides (Balkan Peninsula).
- Frajman, B., Strgulc Krajšek, S. & Dakskobler, I. (2011) *Orobanche kochii* F. W. Schultz in *Orobanche elatior* Sutton (*Orobanchaceae*)—novi vrsti za floro Slovenije.—*Orobanche kochii* F. W. Schultz and *Orobanche elatior* Sutton (*Orobanchaceae*)—new species for the flora of Slovenia. *Hladnikia (Ljubljana)* 27: 57–65.
- Gorchakovskij, P.L., Schurova, E.A., Knyazev, M.S., Marina, L.V., Morozova, L.M., Nikonova, N.N., Prjamonosova, S.A., Salmina, N.P., Schlykova, N.A., Beljaeva, I.V., Balandin, S.V., Vasfilova, E.S., Famelis, T.V., Trotcenko, G.V., Zueva, V.N. & Meling, E.A. (1994) *Opredelitel' sosudistych rastenij Ccentralnogo Urala* [Key to the vascular plants of the Central Ural]. Nauka, Moscow, 525 pp.
- Grubov, V.I., Borodina-Grabovskaja, A.J., Illarionova, I.D., Krestovskaja, T.V. & Tzvelev, N.N. (2006) *Rastenija Central'noj Azii*, vol. 15. Akad. nauk SSSR, Moskva, 142 pp.
- Ivanova, M.M. (1999) *Orobanche krylovii* G. Beck. In: Hmel'nov, A. (ed.) *Krasnaja kniga rastenij Baikalskogo regiona* [Red List of Plants of the Lake Baikal Region]. Botanic Garden of the Irkutsk State University, Irkutsk. Available

- from: <http://bg.isu.ru/ru/science/kkrbr/> (accessed: 20 March 2013).
- Ivanova, M.M. (2010) *Orobanche krylovii* G. Beck. In: Gajkova, O.J. (ed.) *Krasnaja kniga Irkutskoj oblasti [Red List of Plants of the Irkutsk Region]*. Vremja stranstvija, Irkutsk, p. 168.
- IUCN (2013) *IUCN Red List Categories and Criteria: Version 3.1*, 2nd edition. Gland, Switzerland and Cambridge. Available from: <http://www.iucnredlist.org/> (accessed: 20 March 2013).
- Kosachev, P.A. (2009) Dopolnenije k sem. Scrophulariaceae Juss. s. l. i Orobanchaceae Vent. flory Sibiri i Kazachstana [Addition to the families Scrophulariaceae Juss. s. l. and Orobanchaceae Vent of the flora of Siberia and Kazakhstan]. *Turczaninowia* 12: 40–47.
- Kosachev, P.A. (2013) *Orobanche krylovii*. In: Vaganov, A. (ed.) *Bioraznoobrazie Altae-Sajanskogo Ecoregiona [Biodiversity of Altai-Sayan Ecoregion]*. Available from: <http://bioaltai-sayan.ru> (accessed: 20 March 2013).
- Krasnoborov, I.M. (2000) Orobanchaceae. In: Krasnoborov, I.M., Lomonosova, M.N., Schaulo, D.N., Vibe, E.I., Zhirova, O.S., Koroljuk, E.A., Krasnikov, A.A., Snytko, O.N. & Tupitzyna, N.N. *Opredelitel' rastenii Novosibirskoi oblasti [Key to the plants of Novosibirskaya oblast]*. Nauka, Novosibirsk, p. 492.
- Kreutz, C.A.J. (1995) *Orobanche. Die Sommerwurzarten Europas. Band 1: Mittel- und Nordeuropa*. Sichtung Natuurpublikaties Limburg, Maastricht, 159 pp.
- Krylov, P. (1907) *Flora Altaya i Tomskoi gubernii [Flora of Altai and Tomsk Province]*, vol. 4. Typo-lithography K. Ya. Zelenevskago, Tomsk, pp. 865–1088.
- Krylov, P., Schischkin, B.K., Sergievskaja, L.P. & Steinberg, E.I. (1939) *Flora Zapadnoi Sibiri [Flora of Western Siberia]*, vol. 10. Krasnoe Znamja, Tomsk, pp. 2544–2545.
- Kulikov, P.V. (2005). *Konspekt flory Cheljabinskoi oblasti (sosudistye rastenija) [Check-list of flora of the Chelyabinsk region (vascular plants)]*. Geotur, Yekaterinburg-Miass, 537 pp.
- Kurbatskij V.I. (1979) Orobanchaceae. In: Polozhij, A.V. (ed.) *Flora Krasnojarskogo kraja [Flora of Krasnojarskii kraj]* 9(2). Isdatel'stvo Tomskogo universiteta, Tomsk, p. 38.
- Kurbatskij, V.I. (2007) Orobanchaceae. In: Polozhij, A.V. & Peschkova, G.A. (eds.) *Flora of Siberia*, vol. 12. English translation from Russian, Enfield, USA, 221 pp.
- Malyshev, L.I. & Peschkova, G.A. (1979) *Flora tsentral'noj Sibiri [Flora of the Central Siberia]*. Nauka, Novosibirsk, 1048 pp.
- Chepinoga, V.V., Stepantzova, N.V., Grebenjuk, A.V., Verchosina, A.V., Vin'kovskaja, O.P., Gnutikov, A.A., Dulepova, N.A., Enutschenko, I.V., Zarubin, A.M., Kazanovskij, S.G., Konovalov, A.S., Korobkov, A.A., Luferov, A.N. & Rosbah, S.A. (2008) Orobanchaceae. Vent. In: Malyshev, L.I. (ed.) *Konspekt flory Irkutskoj oblasti (sosudistye rastenija) [Check-list of the vascular flora of the Irkutsk region]*. Isdatel'stvo Irkutskogo universiteta, Irkutsk, 327 pp.
- Manen, J.F., Habashi, C. Jeanmonod, D., Park, J.M. & Schneeweiss, G.M. (2004) Phylogeny and intraspecific variability of holoparasitic *Orobanche* (Orobanchaceae) inferred from plastid *rbcl* sequences. *Molecular Phylogenetics and Evolution* 33: 482–500.
<http://dx.doi.org/10.1016/j.ympev.2004.06.010>
- Markgraf, F. (1932) *Pflanzengeographie von Albanien*. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, 132 pp.
- Meusel, H., Jäger, E. & Weinert, E. (1965) *Vergleichende Chorologie der Zentraleuropäischen Flora*. Gustav Fischer Verlag, Jena, 583 pp.
- Meusel, H., Jäger, E., Rauschert, S. & Weinert, E. (1978) *Vergleichende Chorologie der Zentraleuropäischen Flora*, vol. 2. Gustav Fischer Verlag, Jena, 418 pp.
- Meyer, F.K. (2011) Beiträge zur Flora von Albanien. *Haussknechtia Beiheft* 15: 1–220.
- Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 Nov. 2010, New Orleans, LA, pp. 1–8.
<http://dx.doi.org/10.1109/gce.2010.5676129>
- Naumenko, N.I. (2008) *Flora i rastitelnost' Juzhnogo Urala [Flora and vegetation of Southern Urals]*. Kurgan University, Kurgan, 512 pp.
- Novopokrovskii, I.V. & Tzvelev, N.N. (1958) Orobanchaceae Vent. In: Komarov, V.L. (ed.) *Flora of the USSR*, vol. 23. Akademiia Nauk SSSR, Moskva-Leningrad [translation published by Israel Program for Scientific Translations, Jerusalem], pp. 18–127.
- Nyman, C.F. (1890) *Conspectus florum Europaeae*, Suppl. 2(2). Typis officinae Bohlinianae, Örebro.
<http://dx.doi.org/10.5962/bhl.title.11052>
- Paparisio, K., Demiri, M., Mitrushi, I & Qosja, X.H. (1988) *Flora e Shqiperise*, vol. 1. Akademia e Shkencave e RPS te Shqiperise, Qendra e Kerkimeve Biologjike, Tirana, 457 pp.
- Park, J.M., Manen, J.F. & Schneeweiss, G.M. (2007) Horizontal gene transfer of a plastid gene in the non-photosynthetic flowering plants *Orobanche* and *Phelipanche* (Orobanchaceae). *Molecular Phylogenetics and Evolution* 43: 974–985.
<http://dx.doi.org/10.1016/j.ympev.2006.10.011>

- Park, J.M., Manen, J.F., Colwell, A.E. & Schneeweiss, G.M. (2008) A plastid gene phylogeny of the non-photosynthetic parasitic *Orobanche* (*Orobanchaceae*) and related genera. *Journal of Plant Research* 121: 365–376.
<http://dx.doi.org/10.1007/s10265-008-0169-5>
- Pignatti, S. (1982) *Flora d'Italia*, vol. 2. Edagricole, Bologna, 732 pp.
- Popov, M.G. & Busik, V.V. (1966). *Konspekt flory poberezhij ozera Baikal* [Check-list of the flora of coasts of Lake Baikal]. Nauka, Moskau-Leningrad, 157 pp.
- Pujadas-Salvà, A. & Crespo, M.B. (2004) A new species of *Orobanche* (*Orobanchaceae*) from south-eastern Spain. *Botanical Journal of the Linnean Society* 146: 97–102.
- Pujadas-Salvà, A. (2008) *Orobanche mariana* A. Pujadas (*Orobanchaceae*) sp. nov. para el sur de la Península Ibérica. *Acta Bot. Malacitana* 32: 269–274.
- Pujadas Salvà, A. (2012) Typification and characterization of *Orobanche ritro* Gren. & Godr. (*Orobanchaceae*) of central and southern Europe. *Acta Botanica Gallica* 159: 67–72.
<http://dx.doi.org/10.1080/12538078.2012.671644>
- Pusch, J. & Günther, K.-F. (2009) Familie Orobanchaceae s. str. Sommerwurzgewächse. In: Wagenitz, G.W. (ed.) *Illustrierte Flora von Mitteleuropa* VI(1A), ed. 2. Weissdorn-Verlag, Jena, pp. 1–99.
- Pusch, J. (2000) *Orobanche panicii*—Neu für Österreich und für ganz Mitteleuropa. *Floristische Rundbriefe* 34: 27–42.
- Qosja, X., Papparisto, K., Demiri, M. & Vangjeli, J. (1992) *Flora e Shqiperise*, vol. 2. Akademia e Shkencave e RPS te Shqiperise, Qendra e Kerkimeve Biologjike, Tirana, 446 pp.
- Qosja, X., Papparisto, K., Vangjeli, J. & Ruci, B. (1996) *Flore e Shqiperise*, vol. 3. Akademia e Shkencave e RPS te Shqiperise, Qendra e Kerkimeve Biologjike, Tirana, 331 pp.
- Rakaj, M. (2009) Floristic and chorological news from north Albania. *Botanica Serbica* 33: 177–183.
- Schaulo, D.N. (2006) Flora of West Sajan. *Turczaninowia* 9: 5–336.
- Schaupp, J. (2011) *Orobanche panicii*. In: Fischer, M.A. & Niklfeld, H. (eds.) *Floristische Neufunde* (99–123). *Neilreichia* 6: 385.
- Schlauer, J., Meijer, W. & Hansen, B. (2012). *Parasitic Plants Database*. Available from: http://www.omnisterra.com/bot/pp_home.cgi (accessed: 4 October 2012).
- Schneeweiss, G.M., Colwell, A., Park, J.M., Jang, C.G. & Stuessy, T.F. (2004) Phylogeny of holoparasitic *Orobanche* (*Orobanchaceae*) inferred from nuclear ITS-sequences. *Molecular Phylogenetics and Evolution* 30: 465–478.
[http://dx.doi.org/10.1016/s1055-7903\(03\)00210-0](http://dx.doi.org/10.1016/s1055-7903(03)00210-0)
- Schneeweiss, G.M., Frajman, B. & Dakskobler, I. (2009) *Orobanche lycoctoni* Rhiner (*Orobanchaceae*), a poorly known species of the Central European flora. *Candollea* 64: 91–99.
- Schönswetter, P., Gribl, N. & Frajman, B. (in press) *Orobanche lycoctoni* - (fast) neu für Österreich. *Neilreichia* 7.
- Schönswetter, P., Schneeweiss, G.M., Gutermann, W., Schratt-Ehrendorfer, L., Tribsch, A., Frajman, B., Köckinger, K., Latzin, S., Starlinger, F., Greimler, J., Hülber, K., Sinn, E., Niklfeld, H. (2011) Floristische Neufunde aus den Ostalpen. *Neilreichia* 6: 81–98.
- Stamatakis, A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690.
<http://dx.doi.org/10.1093/bioinformatics/btl446>
- Stamatakis, A., Hoover, P. & Rougemont, J. (2008) A fast bootstrapping algorithm for the RAxML web-servers. *Systematic Biology* 57: 758–771.
<http://dx.doi.org/10.1080/10635150802429642>
- Swofford, D.L. (2002) PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods), ver. 4.0 beta 10. Sinauer Associates, Sunderland.
- Teryokhin, E.S., Schibakina, G.B., Serafimovitsch, N.B. & Kravtsova, T.I. (1993) *Opredelitel Sarasychovyeh Flory SSSR* [Key to the broomrapes of the Flora of the USSR]. Nauka, St. Petersburg, 123 pp.
- Tzvelev, N.N. (1981) *Orobanchaceae* Vent. In: Fedorov, A.A. (ed.). *Flora Evropeiskoi Chasti SSSR* [Flora of Russia: The European Part and Bordering Regions], vol. 5. Nauka, Leningrad, pp. 434–461 [English translation: Balkema. A.A., India, 2001].
- Uhlich, H. (2013) *OroWiki*. Available from: <http://orowiki.org/wiki/> (accessed: 20 March 2013).
- Vangjeli, J., Ruci, B., Mullaj, A., Papparisto, K. & Qosja, X.H. (2000) *Flora e Shqiperise*, vol. 4. Akademia e Shkencave e Republikes se Shqiperise, Instituti i Kerkimeve Biologjike, Tirane, 502 pp.
- Zázvorka, J. (2010) *Orobanche kochii* and *O. elatior* (*Orobanchaceae*) in central Europe. *Acta Musei Moraviae, Scientiae biologicae (Brno)* 95: 77–119.
- Zhang, Z. & Tzvelev, N.N. (1998) *Orobanchaceae*. In: Wu Zhengyi & Raven, P.H. (eds.) *Flora of China*, vol. 18. Missouri Botanical Garden Press, St. Louis (USA), pp. 229–243.

Appendix: Plant material of *O. krylowii* used in our study.

Plant material studied morphologically (the accessions with GenBank number were analyzed molecularly).

ALBANIA: (1) Tropojë, Alpet Shqiptare, valley Valbona, along the path from Dragobi (alp Stanet e Droces) to the saddle W of Maja Hekuraves (Qaf e Droces/ Qafa Droces), at the timberline, 1611 m; clearings in beech forest, forest margins, extending slightly above timberline into lower alpine meadows, limestone; parasitizing exclusively on *Thalictrum minus*; N42.39972, E19.93861. Leg. P. Schönswetter, D. Kutnjak & B. Frajman 16.8.2010, No. 12981 (WU, JBAG, herb. Sánchez Pedraja), KF359500.

RUSSIA: (2) Irkutsk Oblast, Lake Baikal, southern vicinity of the city of Slyudyanka (above the factory of mosaic plates) [N51.66, E103.7002778]. Mixed forest with a grassy understory. Leg. M. Ivanova, 22.07.2000 (ALTB), KF359504; (3) Altaisky krai, Charyshsky district, Bashchelaksky ridge, river valley Big Maraliha at a mouth of a stream of Beketnyj; N51.67, E83.633. Leg. R.V. Kamelin, A.I. Shmakov *et al.*, 6.7.2000 (ALTB), KF359503; (4) Altaisky krai, Altaisky district, near Nikolskoye (N51.85, E85.0833), in a mine dump. Leg. T. A. Terekhina & N. V. Elekova, 21.7.1997 (JBAG, herb. Sánchez Pedraja), KF359501; (5) Krasnoyarsky krai, Mayna river valley, Mayninskoye artificial lake S of the village Sizaya, right bank, N52.95, E91.5. Leg. A. I. Shmakov, M. G. Kuczev, A. V. Vaganov & S. A. Kostyukov, 28.7.2005 (ALTB), KF359502; (6) Sverdlovskaya oblast, Nevjanskij Rayon, road from railway station Mursinka to village Taraskovo [N57.15389, E60.081944] (photos at <http://www.plantarium.ru/page/view/item/25938.html>); (7) Republic Altai, Central Altai, Sema river basin, surroundings of the village Shebalino, 1200 m, grassland. Leg. Voronina, 10.7.[19]47 (MW); (8) Krasnoyarsky krai, lake Mayninskoye, 3 km upper Mayna, right bank, N52.986684, E91.507874. Leg. A.I. Shmakov, M.G. Kursev, A.V. Vaganov & S.A. Kostyukov, 28.7.2005 (ALTB); (9) 7 km SW of the village Altai, deciduous forest on the slopes of the NW exposed slope in the valley Ushkungoy, 1700 m. Leg. Voronov, 10.8.1932 (MW №623); (10) Altai, Biyskii distr., System of the Katun River, neighborhood of the village of the Altajskoe, on the river bank Kamenka, at the road [N52.013627, E85.34729] Leg. E. Klemenzenz, 23.6.1904 (MW); (11) Krasnoshchekovskii distr., security zone of the reserve Tigiretskii, 0,5 km south of the Mt. Czerny Kamen [51.138863,83.086166], forest of *Betula* and *Larix sibirica*. Leg. S.A. Usik & M.A. Shirshov, 26.7.2002 (ALTB); (12) Charyshskii distr., neighborhood of the village of Ust-Tulatink, southern macroslope of the Mt. Mochnataja, N51.407344, E83.513603. Leg. A.I. Shmakov, S.V. Smirnov, M.G. Kutsev, I.N. Chubarov & I. Naumov, 21.6.2002 (ALTB); (13) Charyshskii distr., river valley Charysh, Mt. Mochnataja, NW exposition, N51.4167, E83.467. Leg. A.I. Shmakov, R.A. Zubov, A.V. Vaganov, 25.6.2004 (ALTB); (14) Altaiskii krai, Charyshskii distr., N of the village Pokrovka, 877.3 m, N51.158677, E83.577118. Leg. A.I. Shmakov, S.V. Smirnov, M.G. Kutsev, M.M. Silantjeva, A.A. Kechajkin & A.V. Gal'kin, 23.6.2008 (ALTB); (15) Tigiretsky ridge, between the rivers Bol. and Chesnokovka, flood plain, N51.08, E82.57. Leg. A.I. Shmakov, S.V. Smirnov, P.A. Kosachev, I.N. Chubarov & A.V. Vaganov, 10.7.2005 (ALTB).

KAZAKHSTAN: (16) Semipalatinsk [Semey] region, Altai Mts., Zaysan county, valley of the stream Baubek-Bulak [N48.24167, E83.9533]. Leg. V. Reznichenko, 24.7.1908 (LE 519).

Additional field observations from Russia by P. Kosachev: (1) Krasnojarsk (N55.776573, E93.010254), (2) Uzhur (N55.304138, E89.758301), (3) river Kija (N55.21649, E88.066406), (4) Schyra lake (N54.686534, E90), (5) city of Minusinsk (N53.730842, E91.634216), (6) village Ak-Dovurak (N51.883273, E90.43396), (7) lake Kara-Chol (N51.378638, E89.472656), (8) village Abasa (N52.897306, E90.653687 & N52.78117, E89.648438), (9) Kemerovo (N55.002826, E86.352539), (10) village Solton (N52.821023, E86.558533), (11) village Chemal (N51.42062, E85.999603), (12) village Aktasch (50.338449, 87.451172).

Literature data used for the distribution map (Fig. 4). The coordinates are only approximations for the localities given in the literature. All data with one exception (from Kazakhstan; indicated) are from Russia.

Krylov (1907): vicinity of Tomsk: village Golownino (“Zhukovka” is written by Krylov *et al.* 1939!) in the vicinity of the lake Dal’nee Peschanoe (N56.461258, E84.880857)—sub f. *puberula*; vicinity of Tomsk: Malaja Kirgizka (N56.55778, E85.072231); pine forest Gavrillovski in the vicinity of Salair mines (N54.286473, E85.928078)—both sub f. *glaberrima*. Krylov *et al.* (1939): village Voronovo (N56.045966, E83.806); between the rivers Malyi Hysas and Otkyl (Mal. Abakan; N51.96701, E88.871126); village Usnesja (N51.548043, E85.943069); between villages Kebesen’ and Troizkoe on the river Pyzha (N51.823578, E87.096319); between the rivers Malyi Chili and Ajuchekpes (N51.483521, E87.692814); river Ischtaru (N51.560638, E87.645779); city Tobol’sk (N58.236911, E68.270302); Kynovski zavod (now village Kyn; N57.868132, E58.517761); Werch-Issetski area (now city Ekaterinburg; N56.932987, E60.4953); village Il’inskoe (N56.343946, E62.582703); village Katon-Karagai on river Sarymsak (N49.146008, E85.664463); village N. Pichtovka (N49.793677, E84.538994); Kazakhstan: village Ust’ Karabolka (N56.127184, E61.681824). Popov & Busik (1966): Arschan (N52.281602, E102.392578); Baikal on the rivers Osinovka (N51.446946, E104.735756) and Snezhnaja (N51.398563, E104.647865). Kurbatskij (1979): all Russia, first four from Krasnojarskii kraj: village Najdenovo, right bank of Upper Enisej (N57.30611667, E94.39195); surroundings of the city Krasnojarsk (N55.976872, E92.866516); zapovednik “Stolby” (N55.883333, E92.766667); village Krasnogor’evka (N55.575195, E94.821619); Republic of Khakassia, Bejskii district, village Iudino [nowadays Bondarevo], river Sos (52.941914, 90.5057). Malyshev & Peschkova (1979): region Tajschetski (N55.584555, E97.646484); village Kujtun (N54.508327, E101.480713); city Irkutsk, St. Olcha, village Kiselek (N52.365118, E104.108505); village Bazhenovskoe and river Tojsuk (N53.435719, E102.744141). Alekseev *et al.* (1989): Baschkirski zapovednik (N53.363665, E57.788086); village Mesjagutovo (N55.696164, E58.238525). Gorchakovskij *et al.* (1994): Sem’ Brat’ev cliffs (N57.350237, E60.144653); Zakasnik „Zaural’e“ on the river Sylva (N57.363016, E57.154312). Ivanova (1999): Republic of Buryatia: village Arschan (N52.281602, E102.392578); rivers Bulu and Mojgoty in Tunkinski valley (N51.861109, E102.163224); Mts. Chamar-Daban, river Ossinowka (N51.446946, E104.735756); Bol. Mamaj (N51.417817, E104.815114); Baikal Lake, Tschiwyrkujski gulf (N53.357109, E107.356567); Irkutsk region: village Bazhej (Baschejewski; N53.435719, E102.744141); village Kujtun (N54.508327, E101.480713); village Kiselek on the river Oka (N52.365118, E104.108505); between Listwjanka and village Bol. Koty on the SW coast of the Baikal sea (52.113252, 104.412231). Krasnoborov (2000): village Egor’evski (N54.422126, E84.210205); village Kotorovo (N54.43331, E84.830933). Kulikov (2005): city Zlatoust (N55.186709, E59.668121); upper valley of the river Kizil (N55.928914, E60.367126); Mt. Iljmenski (N55.269728, E60.207825); village Nizhni Atljan (N55.009126, E59.874115); Bazhukovo (N56.34699, E59.282227); Mt. Mal. Irendyk (N54.870285, E59.845276); Mt. Kurkak (N53.946388, E58.952637); river Kamyschenka (N55.472627, E60.759888). Schaulo (2006): Mt. Kulumys (N52.940363, E92.828979); Mt. Kirsa (N52.558821, E89.833832). Chepinoga *et al.* (2008): river Angasolka and village Bol. Lug (N51.956961, E104.772491); city Sljudjanka (N51.663186, E103.690338); St. Kunerma (N55.76769, E108.451195). Naumenko (2008): city Stchuch’e (N55.211251, E62.75322); village Jalanskoe (N55.017001, E62.701721); village Zyrjanka (N56.216966, E62.133436). Artemov (2012): between the rivers Turgen and Zajchicha (N49.675627, E86.014709).