

Revision of *Gentianella austriaca* s.l. and *G. rhaetica* in Slovenia.

Revizija skupine avstrijskega (*Gentianella austriaca* s.l.) in retijskega (*G. rhaetica*) sviščevca v Sloveniji

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Abstract

In a revision of *Gentianella austriaca* s.l. and *G. rhaetica* in Slovenia *G. obtusifolia*, *G. lutescens*, and *G. rhaetica* could be confirmed. Individual plants resemble *G. austriaca* s.str., however, there is not a single sample consisting entirely of *G. austriaca* s.str. and most samples were judged as intermediates between *G. austriaca* s.l. and *G. rhaetica*. *Gentianella lutescens*, the taxon with the shorter calyx lobes of *G. austriaca* s.l., and *G. rhaetica* are the most frequent taxa and the highest number of intermediates were found among these two. Both taxa as well as their intermediates show roughly the same distribution. These geographical patterns do not point to a distinct introgression zone among them in Slovenia.

Izvleček

Med revizijo skupine *Gentianella austriaca* s.l. and *G. rhaetica* smo za ozemlje Slovenije potrdili pojavljanje hrapavega (*G. obtusifolia*), zgodnjega (*G. lutescens*) in retijskega sviščevca (*G. rhaetica*). Posamezne herbarizirane rastline so sicer podobne vrsti *G. austriaca* s.str., vendar noben nabirek v celoti ne predstavlja te vrste, zato je bila večina nabirkov določenih kot prehodna oblika med *G. austriaca* s.l. in *G. rhaetica*. *Gentianella lutescens*, vrsta s krajšimi čašnimi krpami iz skupine *G. austriaca* s.l., in *G. rhaetica* sta najbolj pogosti vrsti in med njima obstaja v herbarijskih zbirkah tudi največ prehodnih oblik. Oba taksona kot tudi njune prehodne oblike imajo v Sloveniji približno enak vzorec razširjenosti, kar ne kaže na to, da bi med obema vrstama v Sloveniji obstajalo razločno, geografsko omejeno prehodno (introgresijsko) območje. Pri prehodnih oblikah med *G. lutescens* in *G. rhaetica* gre morda za zelo variabilen takson, morfološko podoben *G. lutescens* in *G. rhaetica*, ki je ohranil staro variabilnost, pozneje izgubljeno pri potomcih, vodečih h *G. rhaetica* in *G. austriaca*.

1. The problem

Delimitation and distribution of the European taxa of *Gentianella* Moench section *Gentianella* is a long-standing and yet poorly resolved problem. PRITCHARD & TUTIN (1972) lamented that much of the confusing taxonomy in this section results from mixing morphological variation due to seasonal dimorphism or ecological polymorphism with other more definite characters. This is especially true for South-Eastern Europe, where identification of taxa has suffered from such intersections. Regarding Slovenia the distribution maps in JOGAN (2001) illustrate the problem by displaying four variants of *G. austriaca* and two of *G. lutescens*. Considering all variants the

distributions of these two taxa widely overlap, which may indicate that there is some disagreement on how to distinguish basically the two taxa *G. austriaca* and *G. lutescens*.

WRABER (2007) distinguishes *G. austriaca* and *G. lutescens* by the calyx, corolla and inflorescence features (details below) given by WETTSTEIN (1896). After a large scale morphological revision, however, GREIMLER & al. (2004) included these two taxa into an informal taxon because of the high variation in all characters across their distribution area. This informal group of *G. austriaca* s.l. altogether includes *G. austriaca*, *G. lutescens*, and *G. fatrae*, an endemic of the Western Carpathians. This group can be distinguished from the two wide-spread taxa of *G. germanica* s.l., i. e. *G. germanica* (Willd.) Börner and *G. rhaetica* (A.&J. Kern.) A.&D. Löve only by the calyx features as other characters applied occasionally for this purpose (inflorescence, corolla length) are too variable. These calyx features are (WETTSTEIN 1896, GREIMLER & al. 2004): Calyx lobes narrow-linear, sinus between lobes rounded in *G. austriaca* s.l. versus calyx lobes (broad-) triangular, sinus between lobes acute in *G. germanica* s.l.

To gain more insight into variation and distribution of *G. rhaetica* (the only taxon of *G. germanica* s.l. present in the Alps and south of them) and *G. austriaca* s.l. in Slovenia collections from the herbarium LJU were examined and revised. Additionally samples from KL, WU, and TSB from contact regions were examined. The latter samples were included mostly for gaining more insight into variation of those taxa on a larger regional scale. A list of all revised LJU specimens is given in appendix 1.

2. Results of the revision

Samples with a *G. lutescens* like appearance are frequent in Slovenia, however, in only a minority of all examined samples exhibiting the clear character sets according to WRABER (2007), as there are: Calyx lobes as long or shorter than tube, corolla 18-25 mm long, inflorescence \pm racemose (*G. lutescens*) versus calyx lobes longer than tube, corolla 24-45 mm long, inflorescence \pm umbel-shaped (*G. austriaca*). The samples with mostly short and narrow calyx lobes were determined as *G. lutescens* although on the larger terminal flowers of those plants occasionally broad triangular calyx lobes and acute sinuses (as in *G. rhaetica*) can be found. Single individuals in *G. lutescens* samples showing aberrant broad and short calyx lobes are often damaged with the main stem cut or bitten. These individuals also compensate the damage with a rich ramification. For the purpose of searching possible biogeographic patterns plants with calyx lobes clearly longer than the tube ($>1.3\times$) were assigned to *G. austriaca* despite the reservations given above.

The majority of samples has been identified as intermediate or mixed samples, whereby "mixed" in this respect has the following meanings:

(i) Samples (sheets) with plants showing features of *G. rhaetica* and *G. lutescens*, either within single flowers (e.g. many plants of *G. praecox*, LJU10026726) or among single flowers of an individual (also in LJU10026726) indicating morphological intermediates were revised as *G. rhaetica-lutescens*. The same is true for such variation among individuals (*G. carpatica*, LJU10026821: 3 *rhaetica*, 3 *lutescens*). They were also revised as *G. rhaetica-lutescens*.

(ii) Samples showing features of *G. rhaetica* and *G. austriaca*, again within flowers/ individuals and among individuals were revised as *G. rhaetica-austriaca*. All those mixture combinations can be found, e.g., within and among the more than 30 plants of *G. austriaca* sample LJU10026486. In some of those samples also features of *G. lutescens* can be found additionally. However, this was ignored unless these features were very clear in single plants.

(iii) More complex samples with plants of various intermediate features. This problem is exemplified for instance by LJU10026818 (det. *G. carpatica*), which contains mostly intermediate plants (4 *rhaetica-austriaca*, 1 *rhaetica*, 2 *rhaetica-lutescens*); LJU10026820 (*G. carpatica*): 3 *rhaetica-austriaca*, 1 *rhaetica-lutescens*; LJU10026601 (*G. germanica*) 2 *austriaca*, 10 *rhaetica-austriaca*, 1 *rhaetica*, 1 *rhaetica-lutescens*).

Further peculiarities:

(i) There is one sample (eight individuals) inserted under *G. carpatica* from Kum, LJU10026734, that resembles *G. amarella* with very small flowers mostly below 15 mm long, however, with an unsuitable ovary character. Checking two flowers revealed one stalked (2-3 mm) and one sessile ovary. The assignment of this sample is unclear.

(ii) Samples that have been determined as *G. obtusifolia*, could be confirmed entirely in two cases. In a third sample a mixture of *G. obtusifolia* and *G. rhaetica* was collected with one intermediate individual regarding size and shape of papillae on the margin of the calyx lobes.

(iii) A few samples are so poor or in such a bad condition, that a determination is hardly possible.

I agree with MAYER (1968) and PRITCHARD & TUTIN (1972) in not regarding seasonal dimorphism as a relevant phenomenon for taxonomic purposes on the level investigated here. Seasonal or ecological differentiation is part of intraspecific variation that is not considered here. Although such dimorphism exists in lower elevations and extra-montane parts of Middle Europe (e.g. SKALICKY 1969, PREKORŠEK 1972, pers. obs.) it is often intermingled with ecological polymorphism (ZOPFI 1991, GREIMLER & DOBEŠ 2000).

To sum up the following taxa were identified:

- *G. lutescens* (Velen.) Holub [incl. *Gentiana praecox* auct.; *G. carpathica* Wettst.]
- *G. obtusifolia* (F.W.Schmidt) Holub [*G. aspera* (Hegetschw.) Dostal ex Skal., Chrték & Gil.; incl. *Gentiana norica* A.&J. Kern., *G. sturmiana* A.&J. Kern.]
- *G. rhaetica* (A.&J. Kern.) A.&D. Löve [incl. *Gentiana germanica* auct.; *G. kernerii* Dörfel. & Wettst.; *G. solstitialis* Wettst.]
- ?*G. austriaca* (A.&J.Kern) Holub [incl. *Gentiana praeflorens* Wettst.; *G. neilreichii* Dörfel. & Wettst.], very doubtful as there is obviously no sample consisting entirely of this taxon.

The informal combinations assigning the mixed or intermediate samples are indicated by the joint epitheta as explained above, e. g. *G. rhaetica-lutescens*.

3. Discussion

The tremendous amount of samples that had to be considered mixed or intermediate is irritating. However, I have often noticed disagreement in determinations in the revised material and in earlier revisions including samples from those parts of the southern Alps that are included here, which is obviously due in part to the fuzzy character puzzle reported above. In principle there can be two scenarios explaining these findings: (i) There is one yet unrecognised highly variable taxon with morphological affinities to *G. lutescens* and to *G. rhaetica*. This taxon may have conserved an ancient polymorphism that was lost in the descendent lineages leading to *G. rhaetica* and *G. austriaca* s.l. (ii) A wide-spread taxon of *G. austriaca* s.l. (most likely *G. lutescens*) shows a varying introgression from *G. rhaetica* and probably other taxa.

A puzzling result from this revision is that not a single unambiguous population of *G. austriaca* may exist in Slovenia. From my experience a variant that clearly matches the improved diagnosis for *G. austriaca* in WETTSTEIN (1896, p. 40: *Calyx dentibus tubo evidenter longioribus linearibus sensim acuminatis, ... sinibus inter dentes rotundatis ...*) is present in the north-eastern Alps, the western Carpathians and the western Hungarian region. Towards the east and south, however, the situation becomes unclear based on field observations in Romania and studying herbarium samples from southern and eastern Europe (WU, ZA, and ZAHO). According to the distribution map in WETTSTEIN (1896) *G. lutescens* follows essentially the Carpathian mountain ranges and occurs also in the southern Dinarids thus delimiting the distribution of *G. austriaca* towards north, east and parts of southwest. From this map one could conclude that *G. lutescens* is essentially a taxon of higher elevations whereas *G. austriaca* occurs in the plains and (mostly) lower mountain ranges. JOVANOVIĆ-DUNJIĆ (1973) reports both taxa for Serbia; DOMAC (1994) only *G. austriaca* for Croatia. I am, however, not aware of any detailed information on distribution patterns in these countries. Among Slovenian authors commenting on *G. austriaca* MAYER (1954) assumed that this taxon is not rare in Slovenia and PREKORŠEK (1971) noticed many transitional or intermediate variants between *G. austriaca* and *G. lutescens* (= *G. praecox* sensu auct.). To me the many intermediate samples between *G. austriaca* s.l. and *G. rhaetica* appear more problematic.

In this context it is important to remember again WETTSTEIN (1892, 1896) who separated a variant *G. stiriaca* on several taxonomical levels from *G. rhaetica*. This taxon was thought

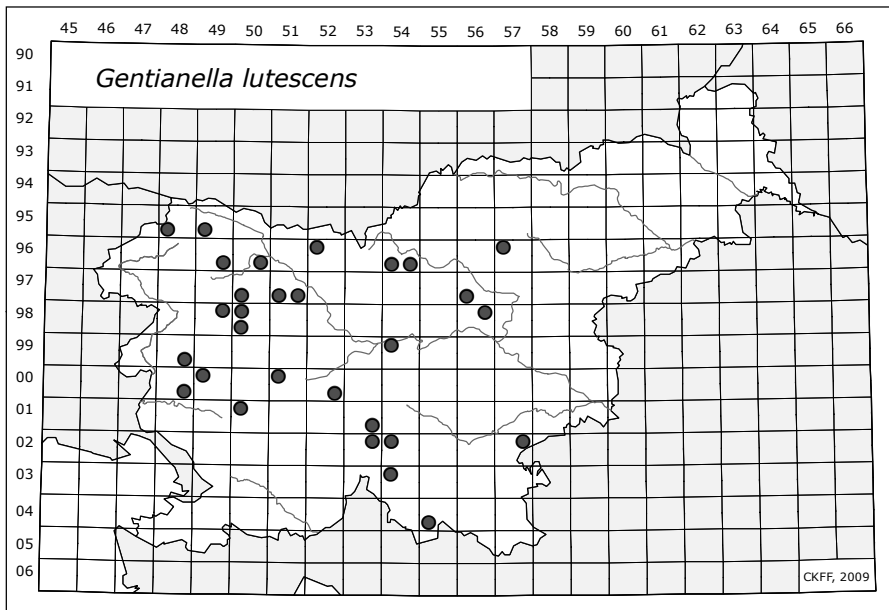


Figure 1: Distribution of *Gentianella lutescens* in Slovenia
Slika 1: Razširjenost vrste *Gentianella lutescens* v Sloveniji

initially to link *G. obtusifolia* and *G. austriaca* in the Northern Alps (WETTSTEIN 1892). Later WETTSTEIN (1896) considered this taxon a transition between *G. rhaetica* and *G. austriaca*. More recently this taxon was recognised by MAURER (1998) for the flora of Styria. However, GREIMLER & JANG (2007) could show that even within Styria this “taxon” is nested in a northern gene pool of *G. obtusifolia* which confirms WETTSTEIN’s (1892) initial assumption as well as in a southern gene pool of *G. rhaetica*. These *G. stiriaca* samples of both gene pools show some genetic admixture from *G. austriaca*. To come to the point here: It may well be that such introgressive patterns play a much stronger role in the southern parts of Europe that provided refugial areas during glaciations. The major components of such a mass can only be identified on a larger sampling scale and by including genetic methods.

Judged from morphology *G. rhaetica* is obviously the major component contributing to the mixed samples. For instance among the three plants collected and reported by ACCETTO (2008, LJU10134395) one displays entirely the features of *G. rhaetica* whereas the other two are intermediate between this taxon and *G. lutescens* regarding calyx features. Yet there is a high number of samples representing *G. rhaetica* without or with only little character contamination from other taxa. The occasionally strongly rolled back margins of the calyx lobes may point to some introgression from *G. anisodonta*. The separation of the mixtures *rhaetica-lutescens* from *rhaetica-austriaca* is often problematic due to the high variation in the calyx characters within the samples. However, this distinction was made to identify possible biogeographical patterns despite a high probability of error.

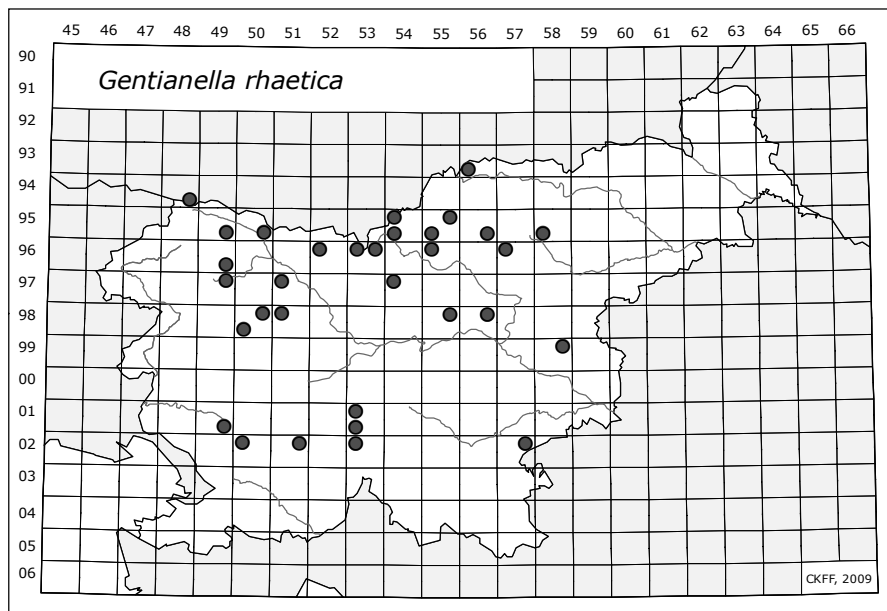


Figure 2: Distribution of *Gentianella rhaetica* in Slovenia

Slika 2: Razširjenost vrste *Gentianella rhaetica* v Sloveniji

To recognise such introgressive patterns or any patterns that might be responsible for the many intermediate or mixture samples the revisions were mapped onto a Slovenian grid-map. The results, however, are disappointing in this respect as the intermediate samples appear all over the range of the two taxa *G. rhaetica* and *G. lutescens*, which show a rather similar pattern (Fig. 1 and 2) with the mixed samples (Fig. 3) between these two covering their whole distribution area. Furthermore, all mixture samples assigned to *G. rhaetica-austriaca* may belong to variants of *G. rhaetica-lutescens* with longer calyx lobes. So from these patterns there is no indication of a distinct introgression zone within Slovenia. Despite the many intermediate samples there can be some ecological separation of the two taxa, however, detailed habitat information is not available from the sampling data. Temporal separation is unlikely as both taxa show a bimodal seasonal pattern of flowering. This may point to another above discussed scenario with an unrecognised highly variable taxon with morphological affinities to *G. lutescens* and to *G. rhaetica*, which may have conserved an ancient polymorphism that was lost in the descendent lineages leading to *G. rhaetica* and *G. austriaca* s.l.. Again: A larger sampling scale and applying genetic methods is necessary to resolve this puzzle.

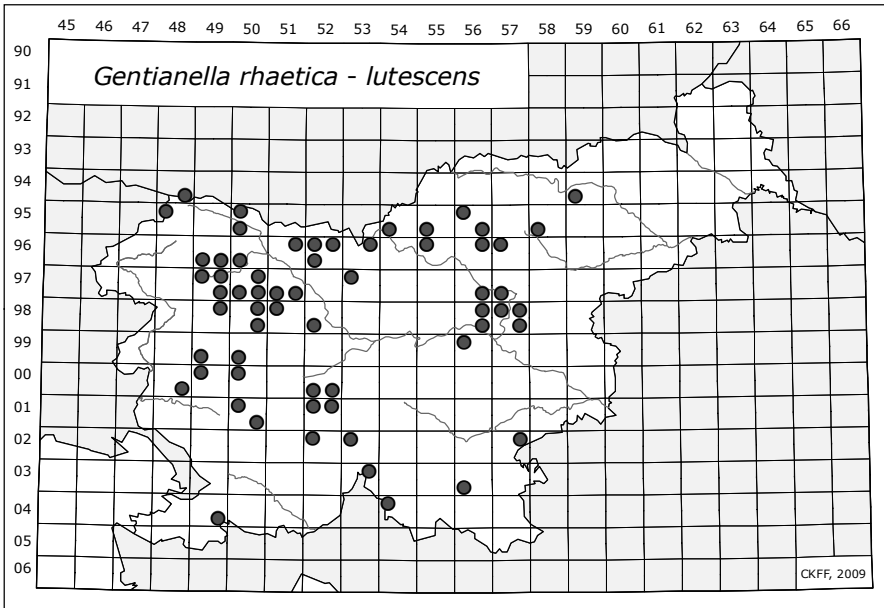


Figure 3: Distribution of intermediates between *Gentianella lutescens* and *G. rhaetica* in Slovenia including sampling sites with both taxa

Slika 3: Razširjenost prehodnih oblik med vrstama *Gentianella lutescens* in *G. rhaetica* v Sloveniji vključno z nahajališči z obema taksonoma

Determination key for *Gentianella* s.str. (without *Gentianopsis* and *Comastoma*):

- | | | |
|---|--|-----------------------------|
| 1 | Margin of calyx lobes usually with long-conical or long-cylindrical papillae | 2 |
| * | Margin of calyx lobes glabrous or with short-conical papillae | 4 |
| 2 | Midrib of calyx lobes without papillae; calyx lobes usually strongly revolute and very unequal, margin usually with long-conical (occasionally long-cylindrical or short-conical) papillae | <i>G. anisodonta</i> -group |
| * | Midrib of calyx lobes often with papillae; calyx lobes revolute or not, usually subequal, margin with long-cylindrical or long-conical papillae (occasionally short-conical) papillae | 3 |
| 3 | Calyx lobes usually broadly-lanceolate, (1-)1.3-2(-2.5) × as long as tube; margin of calyx lobes usually with long-cylindrical, occasionally with long-conical or short-conical papillae | <i>G. obtusifolia</i> |
| * | Calyx lobes narrowly-lanceolate, (1.5-)2-3 × as long as tube; margin of calyx lobes with long-conical or long-cylindrical, occasionally with short-conical papillae or rarely glabrous | <i>G. pilosa</i> |
| 4 | Calyx sinus acute; calyx lobes (triangular-) lanceolate, margin of calyx lobes always with short-conical papillae | <i>G. rhaetica</i> |
| * | Calyx sinus obtuse; calyx lobes linear or narrowly-lanceolate; margin of calyx lobes without or with short-conical papillae | <i>G. austriaca</i> s.l. 5 |
| 5 | Calyx lobes at least 1.3 × as long as tube | <i>G. austriaca</i> |
| * | Calyx lobes shorter or about as long as tube | <i>G. lutescens</i> |

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Appendix 1. Vouchers seen (all numbers below with prefix LJU).

G. anisodonta s.l.

- Podobnik A. 10026516; Simonič M. 10026607.
G. anisodonta-rhaetica
 Jezernik D. 10026579; Justin R. 10026505; Paulin A. 10026479.
G. anisodonta-austriaca
 Mavrič P. 10026581.

G. obtusifolia (= *G. aspera*)

- Martinčič A. 10026476; Batič F. 10026477; Wraber T. 10026478.

G. lutescens

- Mayer E. 10026506; Drobnič M. 10026631; Bavcon J. 10026632; Seljak G. 10026671; Martinčič A. 10026672; Prekoršek B. 10026698; Zirnich C. 10026699; Wraber M. 10026701; Martinčič A. 10026707; Dolšak F. 10026717; Wraber M. 10026719; Prekoršek B. 10026738; Prekoršek B. 10026741; Prekoršek B. 10026747; Prekoršek B. 10026749; Paulin A. 10026760; Mayer E. 10026766; Prekoršek B. 10026776; Mayer E. 10026780; Wraber M. 10026784; Wraber M. 10026785; Wraber T. 10026788; Wraber M. 10026789; Peterlin S. 10026791; Wraber T. 10026793; Wraber M. 10026794; Wraber M. 10026795; Wraber M. 10026797; Wraber M. 10026799; Wraber M. 10026800; Wraber M. 10026803; Wraber M. 10026821; Jan L. 10060955.G.

G. lutescens-austriaca

- Peterlin S. 10026688; Prekoršek B. 10026735; Prekoršek B. 10026736; Paulin A. 10026762; Wraber T. 10026792.

G. rhaetica

Wraber T. 10026478; Paulin A. 10026480; Paulin A. 10026481; Martinčič A. 10026482; Martinčič A. 10026484; Prekoršek B. 10026490; Prekoršek B. 10026491; Wraber M. 10026499; Dolšak F. 10026501; Dolšak F. 10026502; Martinčič A. 10026507; Mayer E. 10026508; Prekoršek B. 10026515; Prekoršek B. 10026518; Prekoršek B. 10026520; Volčič M. 10026578; Wraber M. 10026583; Wraber T. 10026591; Wraber M. 10026592; Wraber M. 10026593; Wraber M. 10026594; Wraber M. 10026597; Wraber M. 10026599; Accetto T. 10026604; Wraber M. 10026605; Peterlin S. 10026606; Wraber M. 10026608; Wraber M. 10026611; Wraber M. 10026616; Wraber M. 10026619; Wraber T. 10026621; Seljak G. 10026670; Wraber M. 10026680; Justin R. 10026711; Justin R. 10026715; Dolšak F. 10026716; Prekoršek B. 10026757; Mayer E. 10026766; Prekoršek B. 10026769; Prekoršek B. 10026774; Wraber M. 10026811; Wraber M. 10026821; Accetto M. 10134972; Accetto M. 10134974; Accetto M. 10134977; Accetto M. 10134394.

G. rhaetica-aspera

Keglevič Z. 10026582.

G. rhaetica-austriaca

Prekoršek B. 10026497; Martinčič A. 10026483; Martinčič A. 10026485; Martinčič A. 10026486; Wraber T. 10026487; Prekoršek B. 10026488; Prekoršek B. 10026489; Prekoršek B. 10026495; Prekoršek B. 10026496; Wraber T. 10026498; Wraber T. 10026500; Justin R. 10026503; Justin R. 10026504; Prekoršek B. 10026509; Strgar V. 10026510; Prekoršek B. 10026511; Ravnik V. 10026512; Martinčič A. 10026513; Wraber T. 10026514; Wraber M. 10026585; Wraber M. 10026590; Wraber M. 10026595; Wraber M. 10026601; Wraber M. 10026618; Wraber T. 10026690; Prekoršek B. 10026695; Prekoršek B. 10026696; Zirnich C. 10026700; Justin R. 10026705; Wraber M. 10026720; Prekoršek B. 10026723; Prekoršek B. 10026724; Prekoršek B. 10026725; Prekoršek B. 10026731; Prekoršek B. 10026737; Prekoršek B. 10026744; Prekoršek B. 10026746; Prekoršek B. 10026750; Prekoršek B. 10026752; Prekoršek B. 10026753; Prekoršek B. 10026773; Prekoršek B. 10026779; Wraber T. 10026805; Wraber T. 10026808; Wraber T. 10026812; Wraber M. 10026813; Wraber M. 10026814; Wraber M. 10026818; Wraber M. 10026820; Accetto M. 10134975; Accetto M. 10134976; Accetto M. 10134973. Wraber M. 10026584.

G. rhaetica-lutescens

Prekoršek B. 10026751; Wraber T. 10026807; Justin R. 10026709; Wraber T. 10026633; Filipič A. 10026693; Prekoršek B. 10026492; Prekoršek B. 10026494; Prekoršek B. 10026519; Wraber M. 10026586; Wraber M. 10026587; Wraber M. 10026588; Wraber M. 10026596; Wraber M. 10026598; Leskovar I. 10026602; Leskovar I. 10026603; Wraber M. 10026609; Wraber M. 10026614; Wraber M. 10026615; Simonič M. 10026620; Družkovič B. 10026673; Wraber T. 10026674; Wraber T. 10026675; Knez T. 10026676; Wraber M. 10026677; Wraber M. 10026679; Wraber M. 10026681; Wraber M. 10026682; Wraber M. 10026683; Wraber M. 10026684; Wraber M. 10026685; Wraber M. 10026686; Plemel V. 10026687; Podobnik A. 10026689; Wraber T. 10026691; Filipič A. 10026694; Prekoršek B. 10026697; Wraber M. 10026702; Wraber M. 10026703; Wraber T. 10026706; Justin R. 10026708; Martinčič A. 10026710; Justin R. 10026712; Martinčič A. 10026714; Martinčič A. 10026718; Wraber M. 10026721; Wraber M. 10026722; Prekoršek B. 10026726; Prekoršek B. 10026727; Prekoršek B. 10026728; Prekoršek B. 10026729; Prekoršek B.

10026732; Prekoršek B. 10026733; Prekoršek B. 10026740; Prekoršek B. 10026742; Prekoršek B. 10026743; Prekoršek B. 10026745; Prekoršek B. 10026754; Prekoršek B. 10026755; Prekoršek B. 10026756; Prekoršek B. 10026758; Paulin A. 10026759; Paulin A. 10026761; Paulin A. 10026763; Paulin A. 10026764; Paulin A. 10026765; Martinčič A. 10026767; Wraber T. 10026768; Martinčič M. 10026770; Mayer E. 10026771; Prekoršek B. 10026772; Prekoršek B. 10026775; Prekoršek B. 10026777; Prekoršek B. 10026778; Zirnich C. 10026781; Zirnich C. 10026782; Prekoršek B. 10026783; Wraber M. 10026786; Wraber T. 10026787; Wraber T. 10026790; Wraber M. 10026796; Wraber M. 10026801; Wraber M. 10026802; Wraber T. 10026806; Wraber T. 10026809; Wraber M. 10026810; Wraber M. 10026815; Wraber M. 10026816; Wraber M. 10026817; Wraber M. 10026819; Accetto M. 10134395; Accetto M. 10134971.

Unclear samples

Prekoršek B. 10026734; Prekoršek B. 10026493; Keglevič Z. 10026517; Jogan N. 10026580; Wraber M. 10026589; Wraber M. 10026600; Wraber M. 10026610; Wraber M. 10026612; Wraber M. 10026613; Wraber M. 10026617; Justin R. 10026678; Prekoršek B. 10026692; Justin R. 10026704; Justin R. 10026713; Prekoršek B. 10026730; Prekoršek B. 10026739; Prekoršek B. 10026748; Wraber M. 10026798; Wraber M. 10026804