

Ann. Naturhist. Mus. Wien, B	113	109–117	Wien, April 2012
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***Gentianella insubrica* and *G. germanica* s.l. (Gentianaceae) in the western Alps**

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Abstract

In this article we investigate the relationships of *Gentianella insubrica*, a narrow endemic of the Insubrian Alps, with *G. germanica*, *G. rhaetica*, and the *G. anisodonta* group. Based on statistical data we discuss variation in diacritical morphometric characters and provide a determination key for these taxa, which are only weakly differentiated from *G. insubrica* and that, therefore, have been occasionally confused with it. We show that *G. insubrica* is not related to the *G. anisodonta* group and is rather an isolated variant of *G. germanica*. Finally we select a lectotype for *Gentiana insubrica* from samples collected on Mte. San Giorgio at the type locality according to Hans Kunz in his original publication.

Keywords: *Gentianella germanica* s.l., *G. insubrica*, Gentianaceae; taxonomy, determination key, nomenclature, lectotype.

Zusammenfassung

In diesem Beitrag untersuchen wir die Beziehungen der in den insubrischen Alpen endemischen *Gentianella insubrica* zu *G. germanica*, *G. rhaetica* und zur *G. anisodonta*-Gruppe. Anhand statistischer Daten untersuchen wir die Variation in diakritischen morphometrischen Merkmalen und erarbeiten aufgrund der Unterschiede einen Bestimmungsschlüssel für die oben erwähnten Arten, die nur schwach von *G. insubrica* differenziert sind und mit welchen dieses Taxon manchmal verwechselt wird. Wir zeigen, daß *G. insubrica* mit der *G. anisodonta*-Gruppe nicht näher verwandt ist und daß der insubrische Endemit vermutlich eine isolierte Variante von *G. germanica* ist. Schließlich selektieren wir einen Lectotyp für *Gentiana insubrica* aus den Aufsammlungen vom Mte. San Giorgio, von wo das Typenmaterial stammt, das Hans Kunz in seiner Originalarbeit zitiert.

Introduction

The genus *Gentianella* MOENCH (in Central Europe represented only by section *Gentianella*) shows a high level of diversity in the Alps, especially around presumed refugial areas in the southern Alps. There is some evidence from molecular data (VON HAGEN & KADEREIT 2001; JANG & al. 2005) for a very young evolutionary history of section *Gentianella*. The geographical setting provided by the Alps and the climatic changes during the Pleistocene were certainly the major factors shaping the patterns of diversity in *Gentianella* that we see today. For example, the *G. anisodonta* group exhibits at least two geographically distinct entities besides the widespread *G. anisodonta* (BORBÁS) A.LÖVE & D.LÖVE, from which the narrow endemics *G. engadinensis* (WETTST.) HOLUB (SW Alps) and *G. liburnica* E.MAYER & KUNZ (SE Alps) are morphologically somewhat differentiated. Another differentiation concerns the widespread *G. germanica* s.l.: KERNER & KERNER (1882) separated plants from the eastern Alps as a new species, now

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G. rhaetica (A.KERN. & JOS.KERN.) A.LÖVE & D.LÖVE. The delimitation of this species has remained controversial in the floristic literature (HESS & al. 1972; PRITCHARD & TUTIN 1972; LAUBER & WAGNER 2007; FISCHER & al. 2008) due to somewhat cryptic diagnostic characters. In a recent investigation, however, we found a surprisingly high molecular differentiation between populations of *G. germanica* (WILLD.) BÖRNER (= *G. germanica* s.str.) from western and northern Central Europe and the Swiss Jura mountains and populations from the Alps corresponding to *G. rhaetica* (JANG & al. 2005).

Seasonal dimorphism (WETTSTEIN 1986; LENNARTSSON 1997) and ecological polymorphism (ZOPFI 1991) can complicate identification in the genus. These factors are, however, not relevant to the species dealt with in the present study; hybridization and introgression instead provide sources of confusion. Variants showing intermediate morphology do occur among adjacent taxa and have occasionally been treated as taxonomic entities. Such reticulate evolution leading to an intermediate “species” among *G. rhaetica*, *G. austriaca* (A.KERN. & JOS.KERN.) HOLUB, and *G. obtusifolia* (F.W.SCHMIDT) HOLUB in the eastern Alps (WETTSTEIN 1892, 1896; MAURER 1998) could be confirmed by molecular markers (GREIMLER & JANG 2007).

Regarding the western Alps two major problems have remained unresolved: (i) The delimitation of the narrow endemic *G. insubrica* (KUNZ) HOLUB and (ii) the geographical boundaries between *G. germanica* and *G. rhaetica*. Concerning problem (ii), most samples of *G. germanica* s.l. in the Swiss herbaria (G, Z, ZT) cannot clearly be assigned to one of these two taxa, due to the lack of sufficient morphological differentiation between *G. rhaetica* and *G. germanica* and the high variation found in all characters that have been used for diagnosis (GREIMLER & al. 2004). This remains an open question and needs further investigation including a search for genetic relationships in an extensive sample across the western Alps and surrounding areas. In this article we want to focus on the first problem, i.e. we (1) investigate relationships of *G. insubrica* with other members of the genus, especially with *G. germanica* s.l.; (2) provide a determination key for the taxa that can be confused with *G. insubrica*; and (3) select a lectotype for *G. insubrica* from the specimens cited by KUNZ (1940).

Methods

Morphometric data (calyx and corolla lengths and lobe/tube ratios, and the ratio of corolla/calyx length) were collected from *G. insubrica* vouchers at the herbaria BAS-BG, G, WU, Z, ZT. Calyx length was measured on the longest (visible) lobe, which was also used for calculating the lobe/tube ratio. Additionally, calyx lobe shape (equal/different; flat/revolute) and types of papillae on those lobes were recorded according to Greimler & al. (2004). These data were combined with the corresponding data from GREIMLER & al. (2004). SPSS for Windows 10.0 was used to calculate descriptive statistics. Post-hoc comparisons (significance tests) in Table 1 were Bonferroni corrected. The determination key is based exclusively on the investigated samples ignoring (often-questionable) data from the botanical literature. Measures and ratios include minimum and maximum (in parentheses) and the range covered by the standard deviation; measures are rounded to the nearest millimetre. Information on specimens is given in the paragraph on lectotypification and in Appendix 1.

Results and discussion

(1) Relationships among *G. germanica*, *G. rhaetica*, *G. insubrica* and other taxa

In the very detailed diagnosis of *G. insubrica*, KUNZ (1940) stressed the differences between this taxon and *G. anisodonta*, which is obviously the reason why PIGNATTI (1982) mentioned a variant *G. insubrica* under *G. anisodonta*. This created some uncertainty about this taxon, and has led to some misidentifications of variants belonging to the *G. anisodonta* group (Greimler, pers. obs.). However, KUNZ also pointed out that the calyx lobes are slightly unequal in size and shape and rarely distinctly unequal, showing variation “like in *G. germanica*”. He also noticed that in *G. insubrica* only the short papillae on the calyx lobes and upper leaves are found, again “like in *G. germanica*”. Despite these obvious similarities with *G. germanica* KUNZ suggests (1940: p12) “*G. insubrica* [hat] ... mit dem Formenkreis der *G. germanica* s. lat. nichts zu tun [...has no relation to the group of *G. germanica*]”. We disagree for several reasons: (i) We have never found the typical elongated papillae of the *G. anisodonta* group in *G. insubrica* samples (as KUNZ himself had pointed out); (ii) Unequal calyx lobes do occur also in *G. germanica* s.l., again in accordance with observations by KUNZ (this alone is not a strong criterion for classification); (iii) The shape of the calyx lobes and how they are revolute are more similar to *G. germanica* s.l.; and finally (iv) genetic evidence does not support any relation to the *G. anisodonta* group but a close relationship with *G. germanica* s.str.

The major surprise in the genetic analysis of European *Gentianella* was the high molecular differentiation found between *G. germanica* and *G. rhaetica* at a level as high or even higher than between other morphologically well separated taxa (JANG & al. 2005). From the AFLP data of this investigation we further noticed that *G. insubrica* is closely related to *G. germanica* s.str. and not to the geographically closer taxon *G. rhaetica* (Fig. 1). No genetic evidence was found for *G. anisodonta* being involved in a reticulate genesis of *G. insubrica*. The taxon found next to *G. germanica* and *G. insubrica* was *G. campestris* in this analysis. However, there are some caveats: (i) The lack of resampling support for the basic structure of the AFLP trees although the nodes combining *G. germanica* and *G. insubrica* had supports of 94 and 76 BP in the NJ and MP analyses, respectively; (ii) Only one population of *G. insubrica* (five individuals from Mte. Generoso) was included in the analysis. We were not able to find any *Gentianella* on Mte. San Giorgio, the locus classicus from which also most specimens were cited by KUNZ (1940).

What are the morphological differences between *G. insubrica* and the two taxa of *G. germanica* s.l., namely *G. germanica* (s.str.) and *G. rhaetica*? HESS & al. (1972) used the smaller flowers of *G. insubrica*, quantitatively expressed by 5–10 mm long corolla lobes, to distinguish it from *G. germanica* (including *G. rhaetica*) with corolla lobes 9–15 mm long. This quantitative character is also given by LAUBER & WAGNER (2007) among other qualitative ones. In fact there are significant differences between *G. insubrica* and *G. germanica/rhaetica* in several quantitative floral characters (Table 1). In *G. insubrica* we found the longest calyces and largest calyx lobe/tube length ratio (Fig. 2), and the smallest corolla length and corolla/calyx length ratio. *G. insubrica* also has the shortest corolla lobes, slightly exceeding however the range given by HESS & al. (1972) and LAUBER & WAGNER (2007). A closer inspection of those differences (Table 1) reveals (i) high standard deviations and (ii) wide total ranges of variation, which render the characters of low discriminative power despite significant mean differences. High variation in

G. insubrica was especially found in samples of Monte Generoso and Monte Pravello, where single plants often approach *G. germanica* s.l. Significant mean differences in floral characters were also found between *G. germanica* and *G. rhaetica*, again with high variation. Vegetative characters (e.g. plant size, number of internodes, leaf size and shape) as well as ramification and inflorescence sizes do not provide sufficiently strong clues for separating those taxa due to their very high variation (see GREIMLER & al. 2004).

Table 1. Descriptive statistics (number of individuals, mean, standard deviation, minimum, maximum) of flower characters for the three taxa. Significant mean differences ($P < 0.05$) between pairs of taxa are indicated by a (*G. rhaetica*), b (*G. germanica*), and c (*G. insubrica*). Post-hoc comparisons were Bonferroni corrected.

Character	Taxa	N	Mean	Sd.	Min.	Max.
Calyx length, mm	<i>G. rhaetica</i>	75	15.91 ^b	2.76	11.00	24.00
	<i>G. germanica</i>	54	12.74 ^{a, c}	2.75	6.00	21.00
	<i>G. insubrica</i>	56	17.13 ^b	3.51	11.00	27.00
Ratio calyx lobe/tube	<i>G. rhaetica</i>	67	1.36 ^c	0.28	0.78	2.40
	<i>G. germanica</i>	41	1.32 ^c	0.21	0.83	1.67
	<i>G. insubrica</i>	50	1.94 ^{a, b}	0.51	1.14	3.50
Corolla length, mm	<i>G. rhaetica</i>	92	27.39 ^c	4.71	20.00	50.00
	<i>G. germanica</i>	52	28.04 ^c	5.43	18.00	43.00
	<i>G. insubrica</i>	62	24.70 ^{a, b}	2.79	15.00	30.00
Corolla lobe length, mm	<i>G. rhaetica</i>	82	12.16 ^{b, c}	2.42	9.00	23.00
	<i>G. germanica</i>	44	11.07 ^{a, c}	2.49	7.00	16.00
	<i>G. insubrica</i>	36	9.39 ^{a, b}	1.32	6.00	12.00
Ratio corolla lobe/tube	<i>G. rhaetica</i>	82	0.83 ^{b, c}	0.14	0.59	1.30
	<i>G. germanica</i>	44	0.66 ^a	0.10	0.50	0.91
	<i>G. insubrica</i>	36	0.64 ^a	0.07	0.50	0.83
Ratio corolla/calyx	<i>G. rhaetica</i>	72	1.70 ^{b, c}	0.31	1.13	2.94
	<i>G. germanica</i>	52	2.23 ^{a, c}	0.39	1.63	3.50
	<i>G. insubrica</i>	54	1.48 ^{a, b}	0.24	0.81	1.92

The finding that *G. insubrica* (at least one population) is closely related to *G. germanica* (Fig. 1) stimulates some speculation on the distribution of the *G. germanica* group in the western Alps. KERNER & KERNER (1882) provided a very general picture for *G. germanica* (from northern Germany to the eastern Carpathians) and *G. rhaetica* (western Central Alps) that was later refined by WETTSTEIN (1896) for both *G. germanica* (mainly Central Europe west and north of the Alps) and *G. rhaetica* (Graubünden, Switzerland eastwards to Styria, Austria). Since then *G. rhaetica* has been either ignored (HESS & al. 1972), included in *G. germanica* without comment (AESCHIMANN & al. 2004), included

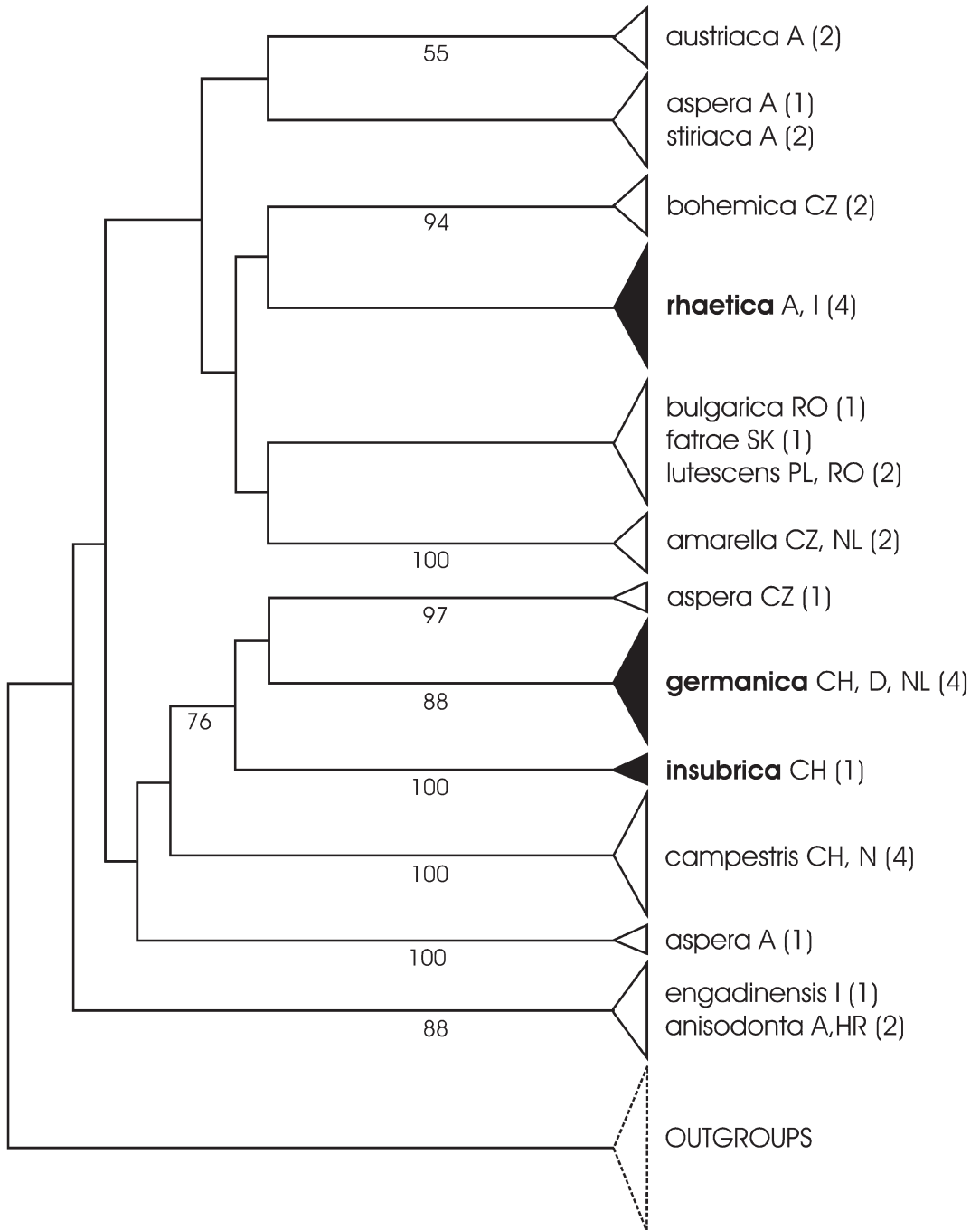


Fig. 1: *Gentianella germanica* agg. in an MP tree (AFLP data, modified from JANG & al. 2005). Numbers below branches indicate bootstrap support. A, Austria; CH, Switzerland; CZ, Czech Republic; D, Germany; HR Croatia; I, Italy; NL, Netherlands; PL, Poland; RO, Romania. Numbers of populations are given in parentheses.

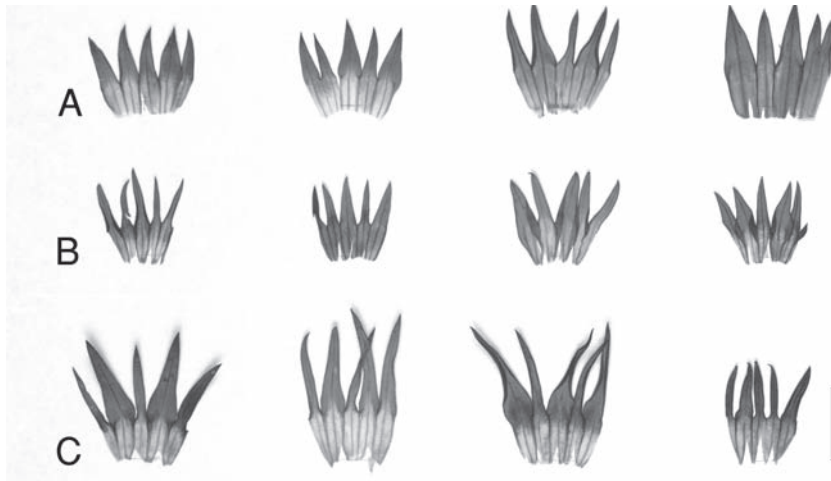


Fig. 2: Calyx shapes of (A) *Gentianella rhaetica* (I, Plawenn; A, Vent, two samples each); (B) *G. germanica* (CH, Dittingen; Tannmatt); (C) *G. insubrica* (CH, Mte. Generoso). Bar: 1 cm.

as an ecotypic variant (PRITCHARD & TUTIN 1972) or distinguished at the subspecific level from *G. germanica* (LAUBER & WAGNER 2007), in each case without precise information on distribution. It is not mentioned in the French flora by GUINOCHET & DE VILMORIN (1975). Studying herbarium collections at Z, ZT, and G did not provide a clear picture due to the limited diacritical value of morphological characters. Statistics on metric flower characters including samples investigated in GREIMLER & al. (2004) are given in Table 1. Non-metric characters like “calyx lobes curved outwards” (LAUBER & WAGNER 2007) in *G. germanica* do not occur with sufficient frequency and may be related to habitat variation. Assigning plants with many short internodes and a relatively delicate calyx (GREIMLER & al. 2004) to *G. germanica*, however, provides a scenario in which this taxon is more abundant and does often occur in the Alps even towards their more central regions. This is also well illustrated by two samples (with duplicates in G and Z) edited by BRAUN-BLANQUET in *Flora Raetica Exsiccata*. Both were collected in Graubünden, Switzerland: Number 470 labelled *G. germanica* subsp. *eugermanica* in semi-dry grassland (Mesobrometum), 750 m, near Trimmis (“Föhrenbezirk”); and number 1173 labelled *G. germanica* subsp. *rhaetica* var. *kernerii* in the Central Alps, pasture near Vals, 1300-1700 m, at a distance of about 50 km SW from the former. From these findings it may well be that *G. rhaetica* is only present in the more eastern and central parts of the Swiss Alps and that *G. germanica* is the common taxon north and west of the Central Alps. In the south *G. germanica* may at least be present in a morphologically weakly differentiated “variant” *G. insubrica*.

Given the high variation and thus poor separation of the three taxa one may ask whether it makes sense to distinguish *G. insubrica* on the specific level from *G. germanica* s.l., as still applied in the recent *Flora Helvetica* (LAUBER & WAGNER 2007). Summarizing the present evidence we notice that there is some differentiation that seems to correlate with distribution. Clearly we are facing the problem of cryptic species in *G. germanica* agg. Such species show poor morphological differentiation despite high levels of reproduc-

tive isolation or genetic differentiation. Genetic distance between pairs of cryptic species may indicate sufficient divergence to treat them as distinct evolutionary entities. Using artificial crosses and nuclear ribosomal DNA sequences OKUYAMA & KATO (2009) for example revealed three additional reproductively isolated groups in line with genetic divergence and thus cryptic species within the morphologically well-studied Asian genus *Mitella*. In our ongoing research project we are currently collecting data from a representative sample across the western Alps and surrounding areas to address again morphological as well as genetic variation and differentiation in *G. germanica* agg.. Based on more detailed evidence from these analyses we will hopefully be able to resolve this question in the future. Therefore we do not want to propose any formal changes in taxonomy at present.

(2) Determination key

Additional descriptive characters of lower discriminative power are given in inserted paragraphs following the stronger diacritical characters. The term “usually” with respect to measures or counts covers the range given by the standard deviation.

- 1 Margin of calyx lobes with long-conical, occasionally short-conical or long-cylindrical papillae; larger calyx lobes tapering from rounded egg-shaped base into a narrow apex, margins strongly revolute. Corolla often dark reddish-violet outside *G. anisodonta* group (*G. anisodonta*, *G. engadinesis*)
- 1* Margin of calyx lobes with short conical papillae or nearly glabrous; larger calyx lobes long-triangular with revolute or flat margins. Corolla bluish-violet outside as a rule (*G. germanica* agg.) 2
- 2 Calyx lobes (1.1–) 1.4–2.5 (–3.5) × as long as calyx tube; unequal in size and shape: 1 or 2 (3) lobes usually much larger, often approaching corolla length. Larger calyx lobes triangular, often with revolute margins, smaller ones often nearly linear; corolla (15–) 22–28 (–30) mm long; corolla lobes (6–) 8–11 (–12) mm long; corolla (0.8–) 1.2–1.7 (–1.9) × as long as calyx. *G. insubrica*
- 2* Calyx lobes (0.8–) 1.1–1.7 (–2.4) × as long as calyx tube; subequal in size and shape, larger ones rarely approaching corolla length. Larger calyx lobes triangular, their margins revolute or not, smaller ones narrowly-triangular; corolla (18–) 22–34 (–50) mm long; corolla lobes (7–) 8–15 (–23) mm long. (*G. germanica* s.l.) 3
- 3 Gynophore (0–) 0.1–0.5 (–0.8) × as long as calyx tube; corolla (1.1–) 1.4–2.0 (–2.9) × as long as calyx. Plants of late summer and autumn often branched from base, usually with 4–8 internodes. *G. rhaetica*
- 3* Gynophore (0.4–) 0.6–1.1 (–1.4) × as long as calyx tube; corolla (1.6–) 1.8–2.6 (–3.5) × as long as calyx. Plants of late summer and autumn often simple, usually with 6–11 internodes. *G. germanica* s.str.

(3) Lectotypification of *Gentianella insubrica*

Gentianella insubrica (KUNZ) HOLUB, Folia Geobot. Phytotax. 2: 117 (1967)

≡ *Gentiana insubrica* KUNZ, Verh. Naturforsch. Ges. Basel 51 (2): 6–19 (1940).

Lectotype (hic designatus): Schweiz, Tessin, „Meriggio“ am Mte. San Giorgio auf Waldwiese westlich vom Weg über Meride. Exp. WSW., ca. 860 m.s.m., Kalk, 3. 7. 1940 W. Koch 40/188 [ZT 7544].

Isolectotypes: Two further sheets of the same collection (without labels, see remarks): 3. 7. 1940 W. Koch 40/188 [ZT 7545]; – 3. 7. 1940 W. Koch 40/188 [ZT 7546].

Further Syntypes: Schweiz, Tessin, „Meriggio“ am Mte. San Giorgio auf Waldwiese westl. vom Weg über Meride, Exp. WSW., ca. 860 m. s. m., Kalk, 3. 7. 1940 W. Koch [BAS-BG]; – Schweiz, Tessin, Bergwiese am östl. Wege zwischen Meride und Alla Cassina auf dem M. s. Giorgio, Luganersee, 11. 7. 1938 H. Kunz [BAS-BG]; – Schweiz, Tessin, Waldwiesen auf dem Mte. San Giorgio, besonders „Meriggio“, westl. des Weges nach Meride, Luganersee, 31. 7. 1940 H. Kunz [BAS-BG]; – Schweiz, Tessin, Südhang des Monte San Giorgio ob Meride, Trockenwiese, Kalk, ca. 850 m.s.m, 7. 7. 1935 W. Koch [ZT 7539-7542]; – Schweiz, Tessin, Waldwiese auf „Meriggio“ am Mte. San Giorgio, Exp. WSW, ca. 860 m.s.m, 3. 7. 1940 W. Koch [ZT 7538].

Remarks: Although KUNZ (1940) had seen herbarium material of *G. insubrica* from the herbaria G-Delessert, Z, ZT (incl. RUEB), and his own herbarium (now kept in BAS-BG), in the protologue he clearly restricted his diagnosis and the type material to his private collection and the specimens from ZT. This results in 11 eligible sheets. We selected ZT 7544, being part of a large series of plant individuals in excellent preparative state. This series is mounted on three sheets of which sheet 7544 bears the label, two mounted individuals, and a capsule with 13 unmounted individuals while the other sheets bear no labels: On sheet 7545 we found three mounted and 17 unmounted individuals, and on sheet 7546 three mounted and 16 unmounted individuals. All three sheets have been numbered “568” at bottom right and more recently with the cited barcode numbers (7544-46) top left. As it cannot be decided whether the author had this collection as a specimen with more than one preparation (Art. 8.3 ICBN) in hand at the time he prepared the publication, we restricted the lectotype to the labelled sheet.

Acknowledgements

We want to thank the herbaria BAS-BG, G, Z, and ZT for providing vouchers and the colleagues there that helped during visits and in tracking specific collections or single vouchers as well as Anton Russell, University Vienna, for improving the English of the manuscript. This research was supported by grant P22716-B16 of the Austrian Science Fund (FWF).

References

- AESCHIMANN D., LAUBER K., MOSER D.M. & THEURILLAT J.-P., 2004: Flora alpina 2. – Bern, Stuttgart, Wien: Haupt Verlag.
- FISCHER M.A., OSWALD K. & ADLER W., 2008: Exkursionsflora für Österreich, Liechtenstein und Südtirol. 3. Aufl. – Linz: Biologiezentrum der Oberöstr. Landesmuseen.
- GREIMLER J., HERMANOWSKI B. & JANG C.-G., 2004: A re-evaluation of morphological characters in European *Gentianella* section *Gentianella* (Gentianaceae). – Pl. Syst. Evol. 248: 143–169.
- GREIMLER J. & JANG C.-G., 2007. *Gentianella stiriaca*, a case of reticulate evolution in the north-eastern and eastern Central Alps. – Taxon 56: 857–870.
- GUINOCHET M. & DE VILMORIN R., 1975: Flore de France, Fasc. 2. – Paris: Anatole-France.
- HESS H.E., LANDOLT E. & HIRZEL R., 1972. Flora der Schweiz 3. – Basel, Stuttgart: Birkhäuser.
- JANG C.-G., MÜLLNER A.N. & GREIMLER J., 2005: Conflicting patterns of genetic and morphological variation in European *Gentianella* section *Gentianella*. – Bot. J. Linn. Soc. 148: 175–187.

- KERNER A. & KERNER J., 1882: 649. *Gentiana Rhaetica*. – In: KERNER A. (ed.): Schedae ad Fl. exsicc. Austro-Hung. 2: 122–128. – Vindobona: Frick.
- KUNZ H., 1940. Beitrag zur Revision einiger Gentianen. – Verh. Naturforsch. Ges. Basel 51: 1–20.
- LAUBER K. & WAGNER G., 2007: Flora Helvetica. 4. Aufl. – Bern, Stuttgart, Wien: P. Haupt.
- LENNARTSSON T., 1997: Seasonal differentiation, a conservative reproductive barrier in two grassland *Gentianella* (Gentianaceae) species. – Pl. Syst. Evol. 208: 45–69.
- MAURER W., 1998: Flora der Steiermark vol II/1. – München: IHW-Verlag.
- OKUYAMA Y. & KATO M., 2009: Unveiling cryptic species diversity of flowering plants: successful biological species identification of Asian *Mitella* using nuclear ribosomal DNA sequences. – BMC Evol. Biol. 9: 105–120.
- PIGNATTI S., 1983: Flora d'Italia 2. – Bologna: Edagricole.
- PRITCHARD N.M. & TUTIN T.G., 1972: 6. *Gentianella* Moench. – In: TUTIN T.G. & HEYWOOD V.H. (eds.): Flora Europaea 3: 63–67. – Cambridge: Cambridge University Press.
- VON HAGEN K.B. & KADEREIT J.W., 2001: The phylogeny of *Gentianella* (Gentianaceae) and its colonization of the southern hemisphere as revealed by nuclear and chloroplast DNA sequence variation. – Organisms Div. Evol. 1: 61–79.
- WETTSTEIN R., 1892: Untersuchungen über Pflanzen der österreichisch-ungarischen Monarchie. Die Arten der Gattung *Gentiana* aus der Section „*Endotricha*“ FRÖL. – Österr. Bot. Z. 42: 1–6, 40–45, 84–88, 125–130, 156–161, 193–196, 229–235.
- WETTSTEIN R., 1896: Die Europäischen Arten der Gattung *Gentiana* aus der Section *Endotricha* FRÖEL. und ihr entwicklungsgeschichtlicher Zusammenhang. – Wien: C. Gerold.
- ZOPFI H.J., 1991: Aestival and autumnal vicariads of *Gentianella* (Gentianaceae): a myth? – Pl. Syst. Evol. 174: 139–158.

Appendix 1: Additional collections investigated

Gentianella insubrica

24.07.1901 P. Chenevard [G, 2 sheets], 18.08.1908 P. Chenevard [G 162577], 30.06.1902 M. Jaeggli [G 162579], 30.08.1955 H. Seitter [G 165598, 2 sheets], 22.10.1920 H. Fruhstorfer [Z 65099, Z 65100], 15.09.1931 E. Schmid [Z 65103], 06.10.1910 F. Rohrer [Z 65105], 06.07.1930 A. Perti [BAS-BG], 13.07.1943 A. Huber-Morath [BAS-BG], 15.10.1978 P. Güntert [BAS-BG], 13.07.1943 A. Huber-Morath [BAS-BG], 1879 F. Kaeser [Z 691], 1917 Jacquet [Z 690], 1894 J. Coaz [ZT 7551], 1936 W. Lüdi [ZT 7550], 1948 H. Dübi [ZT 7547, ZT 7548]. 22.08.2001 J. Greimler [WU].

Unclear and mixed samples

24.07.1948 H. Kunz [BAS-BG], 28.06.1960 A. Becherer [BAS-BG], 1937 G. Kummer [ZT 7549], 21.08.1905 J. Bär [Z 65102], 10.06.1904 M.L. Aubert [G 162578], 20.09.1903 Schweingruber [Z 65101], 23.08.1977 W. Baumgartner [BAS-BG], 1940 W. Koch [ZT 7543].

Collection not found (cited in KUNZ 1940): 1928 W. Koch.

