



Typification of Kerner names in *Gentiana* sect. *Endotricha* Froel. (currently classified as *Gentianella* Moench, Gentianaceae)

DIETER REICH^{1,3*}, WALTER GUTERMANN^{1,4}, DAVID PREHSLER^{2,5} & JOSEF GREIMLER^{1,6}

¹ Division of Systematic and Evolutionary Botany, University of Vienna, Rennweg 14, Vienna, 1030, Austria.

² Core Facility Botanical Garden, University of Vienna, Rennweg 14, Vienna, 1030, Austria.

³ ✉ dieter.reich@univie.ac.at; <http://orcid.org/0000-0003-0784-0048>

⁴ ✉ walter.gutermann@univie.ac.at; <https://orcid.org/0000-0002-9201-6872>

⁵ ✉ david.prehslar@univie.ac.at; <https://orcid.org/0000-0003-1821-8051>

⁶ ✉ josef.greimler@univie.ac.at; <https://orcid.org/0000-0002-5823-0007>

Abstract

Anton Kerner together with his brother Joseph Kerner described five taxa of *Gentianella*, then classified as species within *Gentiana* sect. *Endotricha*. Of these, four were based on material distributed in his seminal *Flora exsiccata Austro-Hungarica* series. In the following decades a multitude of names was created in this intricate group due to ecotypic polymorphism. We here provide the lectotypes, currently accepted names and synonymies of these five names coined by the Kerner brothers: *Gentiana austriaca*, *G. norica*, *G. praecox*, *G. rhaetica* and *G. sturmiana*.

Keywords: Austria, *Flora exsiccata Austro-Hungarica*, lectotypes, nomenclature, typification, WU

Introduction

Within *Gentianella* Moench (1794: 482), formerly classified as *Gentiana* sect. *Endotricha* Froel. (1796: 86) a multitude of names has been created for the European flora throughout the last more than 200 years but only few are still accepted as correct. Among those authors, whose scientific names are still used is Anton Kerner, ennobled as “Ritter von Marilau” (1831–1898). Kerner became the head of the Botanical Museum (later the herbarium WU) and Garden in 1878. At about this time the entire collection of the Botanical Museum was transferred to the newly founded “Naturhistorische Hofmuseum” (now herbarium W) and Kerner started re-building the herbarium collection of the Botanical Museum from the scratch. To this end he distributed a large-scale series of exsiccatae, the *Flora exsiccata Austro-Hungarica*, from 1881 onwards, in exchange for material from other national and international herbaria (Schönbeck-Temesy 1992). His younger brother, Josef Kerner, himself a lawyer, shared his botanical interests and was also involved in both the *Flora exsiccata Austro-Hungarica* series as well as in A. Kerner’s research on *Gentiana* sect. *Endotricha* (= *Gentianella*) (Kronfeld 1908). After A. Kerner’s death Karl Fritsch (1864–1934) (Kronfeld 1908) and later Richard Wettstein (1863–1931) continued the series, that was finalized with no. 3601–4000 in 1913 (Anonymous 1915). Both his interest in the genus *Gentianella* as well as seasonal dimorphism in general influenced R. Wettstein, his son-in-law and successor as professor of botany at the University of Vienna (cf. Wettstein 1891, 1892a–g, 1896, 1897, 1900). Kerner’s private herbarium of approx. 40,000 vouchers with a focus on the Austro-Hungarian Empire was purchased by the ministry of education (Ministerium für Kultus und Unterricht) and handed over to the Botanical Institute (Schönbeck-Temesy 1992), where it now is integrated in the main collection of WU (WU generale) but kept in separate folders.

The Kerner brothers described five taxa in *Gentiana* sect. *Endotricha*, four of these i.a. based on material distributed in the *Flora exsiccata Austro-Hungarica* series. *Gentianella* has received a great deal of taxonomic interest because of its high degree of morphological variation, as have other short-lived taxa in genera such as *Euphrasia* L. (1753b: 604) (Wettstein 1896, Zopfi 1997, Svobodová *et al.* 2016), *Melampyrum* L. (1753b: 605) (Soó 1929a, Štech 2000), *Odontites* Ludw. (1757: 120) (Waisbecker 1899, Koutecký *et al.* 2012) or *Rhinanthus* L. (1753b: 603) (Sterneck 1901, as “*Alectorolophus*”, Soó 1929ab, Pleines *et al.* 2013). Both, enhanced phenotypic plasticity (Bradshaw 1965, Winn 1996)

and local adaptation to environmental constraints (Suní *et al.* 2020) may be responsible for high variation within and among populations of these short-lived plants. The occurrence of early and late flowering “cohorts” within a population was already observed by Kerner (1882ab, 1888, 1893) in distinguishing aestival and autumnal variants, e.g. the pair of *Gentiana norica* and *G. sturmiana*. The still widely used term of seasonal dimorphism (“Saisondimorphismus”) was soon thereafter introduced by Wettstein (1895, 1900). However, already Soó (1929ab) noted many other factors apart from flowering time influencing the intricate morphological patterns in these taxa and thus coined the term pseudoseasonal polymorphism. Studies based on statistical approaches found morphological continuities between seasonal variants/ecotypes (e.g., Karlsson 1974, Campion-Bourget 1982, Štech 2000, Pleines *et al.* 2013) and genetic clusters rather according to geography than to ecology (Pleines *et al.* 2013). Hypothesized reasons for the origin of seasonally separated ecotypes are recent adaptations to different management regimes (e.g., Wettstein 1900, Ronniger 1910, Karlsson 1974, Reisch & Poschlod 2009) or pre-adapted ecotypes secondarily colonizing anthropogenic habitats (e.g., Soó 1929ab, Bollinger 1989).

Interestingly, Lennartsson (1997) found a clear temporal separation between aestival and autumnal variants in Scandinavian populations of *Gentianella amarella* (L.) Börner (1912: 543; *Gentiana amarella* L., 1753a: 230) and *G. campestris* (L.) Börner (1912: 543; *Gentiana campestris* L. 1753a: 231) whereas Zopfi (1991) found more complex patterns of ecotypes in *G. campestris* and *G. germanica* s.l. in the Alps. In *Gentianella praecox* populations within the Austrian part of the Bohemian Massif a shallow genetic coherence of the few remnant early flowering morphs was observed (Plenk *et al.* 2016, as *G. bohémica*). However, especially the Central European lowland populations of *Gentianella* spp. dramatically decreased during the last half-century due to drastic changes in land-use (Zopfi 1991, Křenová *et al.* 2019, Reich *et al.* 2020), thus the processes leading to early and late flowering cohorts in these taxa will probably never be fully understood.

The aim of this article is to present the available original herbarium material and to designate lectotypes for five names described by the Kerner brothers based on material collected within Austria. Two of those names, *G. austriaca* and *G. rhaetica*, are presently accepted according to the Austrian field flora (Fischer *et al.* 2008); two, *G. austriaca* and *G. praecox* according to Euro+Med PlantBase (Marhold 2011). Furtheron, we provide a comprehensive synonymy for this nomenclatorial and taxonomic pandemonium causing confusion not only in historical publications.

Material and Methods

Based on the corresponding protologues all original material was pulled from the herbaria BOZ, IBF, PR, PRC, W and WU; additionally, material in BRNU recorded during a previous visit by J.G. was consulted and online databases of the herbaria AMD & L (<https://biportal.naturalis.nl/?language=en&back>), B (<http://ww2.bgbm.org/herbarium/default.cfm>), BM (<https://data.nhm.ac.uk/search>), C (<http://www.daim.snm.ku.dk/search-in-types>), E (<https://data.rbge.org.uk/search/herbarium/>), G (<https://www.ville-ge.ch/musinfo/bd/cjb/chg/advanced.php?lang=en>), GB, LD, OHN S, UME & UPS (<http://herbarium.emg.umu.se/>), GOET ([https://gwdu64.gwdg.de/pls/herbar/typen\\$.startup](https://gwdu64.gwdg.de/pls/herbar/typen$.startup)), GZU & JE (<http://jacq.org/>), K (<https://apps.kew.org/herbcat/gotoSearchPage.do>), LI (<https://www.zobodat.at/arten.php>), MW (<https://plant.depo.msu.ru/?d=P>), P (https://science.mnhn.fr/institution/mnhn/collection/p/item/search/form?lang=en_US) and Z (<https://www.herbarien.uzh.ch/de/belegsuche.html>) were searched for further material. The current type status was assigned following the *International Code of Nomenclature for algae, fungi, and plants* (Turland *et al.* 2018), and for each name an appropriate lectotype was chosen in accordance with the morphological characters and geographical indications given in the protologue. A. Kerner’s herbarium is stored in WU (Stafleu & Cowan 1979), this material was therefore given priority in typification. Material found in W and WU was databased in JACQ (JACQ consortium 2004 onwards) following the corresponding good practice manual (http://jacq.nhm-wien.ac.at/dokuwiki/doku.php?id=export_documentation) and photographed using a Phase One iXR reproduction camera and a Phase One Credo 80 digital back (Phase One, Copenhagen, Denmark). Complying with the *Recommendation on the digitisation and online accessibility of cultural material and digital preservation* (European Commission 2011) label information, type status, high-resolution photographs and geo-referenced collecting localities are publicly available via Virtual Herbaria JACQ (JACQ consortium 2004 onwards). Acronyms of the herbaria follow Thiers (2020), standard forms of nomenclatorial authors follow IPNI (2020).

The relevant literature (taxonomic treatments, national and local floras, nomenclatorial notes, etc.) was consulted for synonyms and corresponding protologues were analysed. Given assignments to the synonymy of the taxa in this intricate group do not necessarily reflect the taxonomic treatment in recent national or international floras and databases

but are always based on the morphological description, the localities cited in the protologue and personal expertise. The same holds true for given current names.

Results and discussion

It is important to note that Kerner's printed schedae were distributed in sets of 100 numbers each (Centurien), thus new names coined in this series were effectively published (Art. 30.8; Turland *et al.* 2018) prior to the publication of the subsequently printed books (cf. Svojtka 2020). Therefore both references, the distributed series and the printed book, are cited when referring to taxa described within the *Flora exsiccata Austro-Hungarica* series. In the case of the below discussed material the title page of Kerner's second volume of the printed book comprising no. 401–800 gives 1882 as publishing year and the preface is dated with December 1882. A hand-written note in the personal copy of W. Gutermann that corrects the publication date to April 1883 probably refers to the latest date given in Stafleu & Cowan (1979) but could not be verified otherwise despite thorough literature research in book reviews and announcements in relevant journals dating back to this time.

The physical herbarium search for the corresponding original material yielded three syntypes in BOZ, five syntypes in PR, 26 syntypes in PRC, four syntypes in IBF, 23 syntypes plus five vouchers representing possible other original material in WU, ten syntypes in W plus one voucher representing possible other original material as well as three syntypes in BRNU; online search yielded 63 additional syntypes stored in various herbaria plus two possible types, eight vouchers representing other original material and three ones representing possible other original material. All taxa described by Kerner except *Gentiana praecox* were based i.a. on gatherings distributed in the *Flora exsiccata Austro-Hungarica* series and are thus well-represented in other herbaria whereas original material of *G. praecox* is restricted to the herbarium WU (plus two vouchers representing possible other original material in P). A. Kerner's personal herbarium is deposited in WU with well-preserved specimens clearly in line with the protologue available, therefore all five lectotypes were chosen from material in this herbarium.

As expected, literature analysis yielded a high number of synonyms, many of which are to be classified as *pro parte* synonyms due to the changing taxonomic concepts and species delimitations in the group whereas some remain ambiguous due to inaccuracy of their protologues.

Typifications

1. *Gentiana austriaca* A. Kern. & Jos. Kern. in Kerner (1882a: no. 648 & 1882b: 123) \equiv *Gentiana germanica* var. *austriaca* (A. Kern. & Jos. Kern.) Beck (1893: 940) \equiv *Gentiana polymorpha* subsp. *austriaca* (A. Kern. & Jos. Kern.) Wettst. (1900: 314) \equiv *Gentiana germanica* subsp. *austriaca* (A. Kern. & Jos. Kern.) Hayek (1930: 423) \equiv *Gentianella austriaca* (A. Kern. & Jos. Kern.) Holub (1965: 102)

Ind. loci [habitat]: Austria inferior [Lower Austria]. In declivibus graminosis ad Gisshübel prope Perchtoldsdorf in agro Vindobonensi; solo calc[areo]; 300^m s. m., Woloszczak. In pratis paludosis planitei ad W[iener] Neustadt; solo turfoso; 280^m s. m. J. Kerner. In declivibus graminosis ad pedem montis Gösing ad Sieding prope Neunkirchen; solo calc[areo]; 500^m s. m. J. Kerner.

Type (lectotype designated here):—AUSTRIA. Austria inferior. In declivibus graminosis ad Gisshübel prope Perchtoldsdorf in agro Vindobonensi; solo calc.; 300^m s.m., [s.d.], [E.] Woloszczak [Fl. Exs. Austr.-Hung. no. 648 I], WU [WU 0080248, !].

Isolectotypes:—BM [BM 000752306], BRNU [BRNU 75544, !], GJO [GJO 3199, GJO 8065, !], GZU [GZU 000273683, digital image !], JE [JE 00001726, digital image !], L [L 2705477, digital image !], MW [MW 0594207, digital image !], OHN [OHN 244102], P [P 03989344, digital image !], PR [PR 971343, digital image !], PRC [PRC s.n., PRC s.n., PRC s.n., PRC s.n., digital image !], W [W 1887-0004467, !], WU [WU 0080242, WU 0080243, !].

Remaining syntypes:—AUSTRIA. Austria inferior. In pratis paludosis planitiei ad W. Neustadt; solo turfoso; 300^m s.m., [s.d.], J. Kerner [Fl. Exs. Austr.-Hung. no. 648 II], BM [BM 000752307], BRNU [BRNU 75544, !], GJO [GJO 3200, GJO 8065, !], GZU [GZU 000273684, digital image !], JE [JE 00001725, digital image !], LD [LD 1701517B], MW [MW 0595599, digital image !], PR [PR 971344, digital image !], PRC [PRC s.n., PRC s.n., PRC s.n., PRC s.n., digital image !], W [W 1887-0004467, !], WU [WU 0080244, !].

—AUSTRIA. Austria inferior. In declivibus graminosis ad pedem montis Gösing ad Sieding prope Neunkirchen; solo calc.; 500^m s.m., [s.d.], J. Kerner [Fl. Exs. Austr.-Hung. no. 648 III], BM [BM 000752308], GJO [GJO 3201, !], GZU [GZU 000273685, digital image !].

!], JE [JE 00001724, digital image !], LD [LD 1701517C], MW [MW 0595600, digital image !], PR [PR 971345, digital image !], PRC [PRC s.n., PRC s.n., PRC s.n., digital image !], W [W 1887-0004467, !], WU [WU 0080245, WU 0080246, WU 0080247, !]. Isolectotype or syntype:—[Fl. Exs. Austr.-Hung. no. 648 but not indicated if this belong to gathering *I*, *II*, or *III*] P [P 03989342, digital image !].

Possible other original material:—[lacking a detailed label, but according to the calyx features clearly belonging to *G. austriaca* and indicated with a label giving *II*, probably referring to Fl. Exs. Austr.-Hung. no. 648 *II*] L [L 2705478, digital image !].

Current name: ***Gentianella austriaca***

Synonymy:

- = *Gentiana amarella* [var. *grandiflora*] f. *acutifolia* Neilr. (1858: 479) p.p. quoad loci cit. but excluding syn. *Gentiana germanica* Willd.
- = *Gentiana stiriaca* var. *castanetorum* Borbás (1892a: 186) ≡ *Gentiana castanetorum* (Borbás) Borbás (1892b: 286) ≡ *Gentiana austriaca* var. *castanetorum* (Borbás) Wettst. (1897: 349) ≡ *Gentiana austriaca* [unranked] *castanetorum* (Borbás) Jáv. (1925: 829)
- = *Gentiana austriaca* var. *montana* Wiesb. ex Wettst. (1892d: 128)
- = *Gentiana austriaca* var. *paludosa* Wiesb. ex Wettst. (1892d: 128)
- = *Gentiana austriaca* var. *praeflorens* Wettst. (1892d: 128) ≡ *Gentiana praeflorens* (Wettst.) Wettst. (1892g: 234)
- = *Gentiana neilreichii* Dörf. & Wettst. in Dörf. (1898: no. 3766) ≡ *Gentiana austriaca* subsp. *neilreichii* (Dörf. & Wettst.) Wettst. ex Hayek (1912: 355) ≡ *Gentiana germanica* [subsp. *austriaca*] var. *neilreichii* (Dörf. & Wettst.) Hayek (1930: 423) ≡ *Gentianella austriaca* subsp. *neilreichii* (Dörf. & Wettst.) Holub (1967: 118)
- = *Gentiana austriaca* var. *brachyodonta* Waisb. (1903: 70) ≡ *Gentiana austriaca* var. *brachyodonta* (Waisb.) Jáv. (1925: 829)
- = *Gentiana austriaca* [var. *montana*] f. *humilis* Waisb. (1903: 70)
- = *Gentiana austriaca* [var. *montana*] f. *prolificata* Waisb. (1903: 70)
- *Gentiana amarella* [var. *grandiflora*] f. *obtusifolia* auct.: Neilr. (1858: 479) p.p. (quoad loc. cit. solum) [the cited localities refer to either *Gentianella austriaca* (“...Gans, ...am Oetscher, ...”) or *Gentianella praecox* (“...Urgebirge der Kreise O. W. W. und O. M. B. ...”)]
- *Gentiana germanica* [unranked] *albiflora* Schur (1861: 89) *nom. nud.* [based on material from “Wiesen im Halterthale”]
- *Gentiana polymorpha* Wettst. (1897: 373), *nom. illeg.* [*nom. superfl. pro Gentiana germanica* Willd. (1798: 1346)] p.p. (quoad subsp. *austriaca*)

Notes:—The Kerner brothers described *Gentiana austriaca* based on the three gatherings that were distributed in the *Flora exsiccata Austro-Hungarica* series as numbers 648 *I*, *II* and *III* (Kerner 1882ab). Additional material is cited indirectly by listing *Gentiana amarella* sensu Jacquin (1762), sensu Sauter (1826) and sensu Dolliner (1842) as well as *Gentiana germanica* sensu Neilreich (1846) in the synonymy. The latter refers to localities of *Gentianella austriaca* in the Wiener Becken and Kalk-Wienerwald regions (cf. Reich *et al.* 2020). None of this additional original material could be traced in the consulted herbaria.

All original specimens of *Gentiana austriaca* found in WU are well preserved and most of them exhibit the typical narrow, linear, and elongated calyx lobes lacking papillae, with rounded sinuses. Some specimens of all three gatherings show a certain variation in the calyx lobe shape towards broader lobes, which, however, represents well the morphological variation within the taxon. A voucher from gathering 648 *I* (WU 0080248) was chosen as lectotype. This gathering represents best the average state of characters in this taxon occurring from nowadays almost lost lowland habitats, where it is typically found in wetlands up to various types of still widespread subalpine grassland (Reich *et al.* 2020).

The current name, *Gentianella austriaca*, is widely accepted in floristic and taxonomic literature (e.g., Pritchard & Tutin 1972, Fischer *et al.* 2008, Marhold 2011, Bartha & Király 2015). However, in Pritchard & Tutin (1972) and Marhold (2011) plants referring to *Gentianella praecox* are included, which is in contrast to our opinion that this name should be applied only to plants from north-eastern Austria and northern Hungary (Reich *et al.* 2020).

2. *Gentiana norica* A. Kern. & Jos. Kern. in Kerner (1892: no. 2190 & 1893: 56–57) ≡ *Gentiana polymorpha* subsp. *norica* (A. Kern. & Jos. Kern.) Wettst. (1900: 318) ≡ *Gentiana aspera* subsp. *norica* (A. Kern. & Jos. Kern.) Ronniger (1910: 304) ≡ *Gentianella obtusifolia* subsp. *norica* (A. Kern. & Jos. Kern.) Holub (1967: 120)

Ind. loci [habitat]: Stiria superior [Styria]. In pratis humidis ad lacum Grundlsee; solo calcareo; 800^m s.m., A. Kerner. Austria superior [Upper Austria]. In pratis alpium vallis Hinterstoder; solo calcareo; J. Kerner.

Type (lectotype designated here):—AUSTRIA. Austria superior. In pratis alpium vallis Hinterstoder; solo calcareo, [s.d.], J. Kerner [Fl. Exs. Austr.-Hung. no. 2190 *II*], WU [WU 0080233, !].

Isolectotypes:—B [B 100277733, B 100277734, digital image !], BM [BM 000752303], BOZ [BOZ 37677, !], GJO [GJO 3171, !], GOET [GOET 004016, digital image !], IBF [IBF 119191, !], KFTA [KFTA 0002618, digital image !], L [L 2705628, digital image !], LD [LD 1715404], MW [MW 0595601, digital image !] P [P 04016656, digital image !], PR [PR 971342, digital image !], PRC [PRC s.n., PRC s.n., PRC s.n., digital image !], W [W 1892-0005642, W 1894-0003530, !].

Remaining syntypes:—AUSTRIA. Stiria superior. In pratis humidis ad lacum Grundlsee; solo calcareo; 800^m s.m., [s.d.], A. Kerner [Fl. Exs. Austr.-Hung. no. 2190 I], B [B 100277735, digital image !], BM [BM 000752304], BOZ [BOZ 37671, !], GJO [GJO 3170, !], GOET [GOET 004017, digital image !], L [L 2705627, digital image !], LD [LD 1715468], MW [MW 0594228, digital image !], P [P 04016655, digital image !], PR [PR 971341, digital image !], PRC [PRC s.n., PRC s.n., PRC s.n., digital image !], W [W 1894-0003529, W 1892-0005643, !], WU [WU 0080234, WU 0080235, !].

Isolectotype or syntype:—[Fl. Exs. Austr.-Hung. no. 2190 but not indicated if this belong to gathering I or II] B [B 100277736, digital image !], P [P 03988790, digital image !]

Remaining other original material:—AUSTRIA. In Oberösterreich: auf dem Pyrgas [Pyhrngaß: Oberhalb Hofalpe], s.d. [August 1884], Dürnberger s.n., LI [LI 295942, digital image !].

—AUSTRIA. In Oberösterreich: auf den Bergen bei Gmunden, s.d., Degen s.n. LI [s.n., +/- Gmunden: Kranabethsattel].

—AUSTRIA. In Salzburg: um Lofer, s.d., Spitzel s.n. L [L 2700566, L 2705862, L 2700344, digital image !].

—AUSTRIA. In Kärnten: bei Heiligenblut, s.d., Hoppe s.n., AMD [AMD 72382, digital image !], L [L 2695603, L 2705852, digital image !], W [W 0106800, !]

Current name: *Gentianella obtusifolia* (F.W. Schmidt) Holub (1967: 118) ≡ *Hippion obtusifolium* F.W. Schmidt (1793: 27)

Notes:—*Gentiana norica* was described based on two gatherings that were distributed in the *Flora exsiccata Austro-Hungarica* as numbers 2190 I and II and including a large number of additional vouchers from the Austrian federal states of Carinthia, Salzburg, Styria, Tyrol and Upper Austria (Kerner 1892, 1893), of which only a part could be traced. Additionally, in the synonymy *Hippion obtusifolium* p.p. was cited. The protologue is followed by an elaborate essay discussing whether the newly described *G. norica* might be the same as *Hippion obtusifolium*. This reasoning, however, remains indecisive as at no point it is clearly indicated that *G. norica* is identical with *H. obtusifolium*. In contrast to Holub (1967), who commented “an nomen illegit. ?” with respect to *Gentiana norica*, we thus consider it a fully legitimate name.

All corresponding specimens of *G. norica* in WU are well preserved and they all show the unequal calyx lobes broadened at the base and with revolute margins as described in the protologue, but in gathering 2190 I specimens on the sheet WU 0080235 have acute rather than obtuse cauline leaves as would be in line with the protologue whereas specimens on WU 0080234 are small, untypical individuals. We thus designated the voucher of 2190 II (WU 0080233) as lectotype, as individuals collected from this locality are well developed and show obtuse leaves (also the duplicates given above!) and thus better represent the morphological description. However, in our opinion this aestival variant is of no taxonomic relevance and should be included in *G. obtusifolia*.

For details on the identity and typification of *G. obtusifolia* see Reich *et al.* (in prep.).

3. *Gentiana praecox* A. Kern. & Jos. Kern. in Kerner (1888: 669–670) ≡ *Gentiana polymorpha* subsp. *praecox* (A. Kern. & Jos. Kern.) Wettst. (1900: 318) ≡ *Gentiana germanica* [subsp. *carpatica*] var. *praecox* (A. Kern. & Jos. Kern.) Hayek (1930: 423) ≡ *Gentianella austriaca* subsp. *praecox* (A. Kern. & Jos. Kern.) Holub (1967: 119) ≡ *Gentianella praecox* (A. Kern. & Jos. Kern.) Dostál ex E. Mayer (1968: 26)

Ind. loci [habitat]: Austria inferior [Lower Austria]. Copiose in pratis montium ad Bergern prope Mautern, in monte Jauerling, Ostrong etc.

Type (lectotype designated here):—AUSTRIA. Nied.Oesterr. – auf dem Jauerling, 1871, J. Kerner s.n., WU [WU-Kern 0080250, !]

Isolectotype:—WU [WU-Kern 0080249, !]

Remaining syntypes:—AUSTRIA. Wiesen des Burgstock am Jauerling, June 1853, anonymous s.n., WU [WU-Kern 0080254, !]

AUSTRIA. Am Ostrang [Ostrong], s.d., H. Kalbruner s.n., WU [WU-Kern 0080251, !]

Possible other original material:—AUSTRIA. Austria inf. Rossatz ad Danubium; in pratis subsilvaticis, s.d., [A.] Kerner s.n., P [P 03988800, P 03990012, digital image !] [these specimens clearly belong to *G. praecox* (cf. W 1953-0003327), though still labelled as *G. germanica*.]

—AUSTRIA. Niederösterreich. Rossatz, 1867, [J.] Kerner s.n., WU [WU-Kern 0129161, !] [these specimens clearly belong to *G. praecox* (cf. W 1953-0003327), though still labelled as *G. germanica*.]

Current name: ≡ *Gentianella praecox*

Synonymy:

- = *Gentiana amarella* [var. *grandiflora*] f. *acutifolia* Neilr. (1858: 479) p.p. quoad loc. cit. but excluding syn. *Gentiana germanica* Willd.
- = *Gentiana carpatica* Wettst. (1892a: 4–6) *nom. illeg.* (non *Gentiana carpatica* Kit. in Schultes, 1814: 443) p.p. ≡ *Gentiana germanica* var. *carpatica* Beck (1893: 940, quoad *Gentiana carpatica* Wettst.) p.p. ≡ *Gentianella carpatica* (Beck) Börner (1912: 542) p.p. ≡ *Gentiana* [*praecox*] [unranked] *carpatica* (Beck) Jáv. (1925: 828) p.p. ≡ *Gentiana praecox* var. *carpatica* (Beck) Braun-Blanq. (1927: 2043) p.p. ≡ *Gentiana germanica* subsp. *carpatica* (Beck) Hayek (1930: 423) p.p. ≡ *Gentianella lutescens* subsp. *carpatica* (Beck) Holub (1967: 119) p.p. [in respect to the given localities in the protologue Wettstein's name is partly a synonym of (i) *Gentianella praecox* (“Ex Moravica:…Mährisch-Trübau [Moravská Třebová]…Kiritein [Křtiny]…Hardeg in valle Thajatal…”, “Ex Bohemia septentrionali…”, “Ex Austria inferiore: Prope Sallingstadt”), and of (ii) *Gentianella lutescens* (all other cited localities); homotypical combinations variously refer to the first or to the second species.]
- = *Gentiana praecox* var. *flavicans* Borbás ex Wettst. (1897: 351)
- = *Gentiana praecox* [var. *carpatica*] f. *albiflora* Krist (1934: 126)
- = *Gentianella bohémica* Skalický (1969: 144) ≡ *Gentianella praecox* subsp. *bohémica* (Skalický) Holub (1998: 105)
- = *Gentianella gabretae* Skalický (1969: 146)
- *Gentiana amarella* [var. *grandiflora*] f. *obtusifolia* auct.: Neilr. (1858: 479) p.p. (quoad loc. cit. solum) [the cited localities refer to either *Gentianella austriaca* (“…Gans, …am Oetscher, …”) or *Gentianella praecox* (“…Urgebirge der Kreise O. W. W. und O. M. B. …”)]
- *Gentiana polymorpha* Wettst. (1897: 373), *nom. illeg.* [*nom. superfl. pro Gentiana germanica* Willd. (1798: 1346)] p.p. (quoad subsp. *praecox*)

Notes:—*Gentiana praecox* was described based on material from the southern Waldviertel region (Jauerling, Ostrong) and Dunkelsteiner Wald region (Bergern prope Mautern) (Kerner 1888), both belonging to the Bohemian Massif. According to the protologue (and the name) it refers to the aestival variant. Besides Lower Austria, where very few extant populations were only recently reported by Plenk *et al.* (2016), these early flowering morphs were only known from the Šumava mountains in SW Bohemia, where they are reported to be extinct (Kaplan *et al.* 2018). Kirschner & Kirschnerová (2000) reported them for Upper Austria without specification, although no further evidence for this occurrence could be found. V. Skalický in 1991 (pers. comm.) considered the entire original material of *G. praecox* as conspecific with his *Gentiana gabretae*, that he had described as aestival variant based on material from the Šumava mountains. In our opinion the shallow genetic differentiation but clear reproductive isolation between early and late flowering variants (Plenk *et al.* 2016) may justify a separation as subspecies. Kerner's original material represents the southernmost edge of a species with its centre of distribution in the Czech Republic (Kaplan *et al.* 2018), however in its early flowering variant.

Additional confusion was caused by Wettstein's (1897) application of the name *Gentiana praecox* as an aestival variant of his *Gentiana carpatica*, which comprises early flowering variants of *Gentianella praecox* as well as *Gentianella lutescens* (Velen.) Holub (1967: 117) [≡ *Gentiana lutescens* Velen. (1888: 29–30)]. The latter taxon of the Carpathians and at least the northern mountain ranges of the Balkan Peninsula (Kirschner & Kirschnerová 2003) is not completely understood but it is definitely found outside the distribution range of *Gentianella praecox*.

All of the four original gatherings of *Gentiana praecox* in WU are well-preserved and in line with the morphological description given in the protologue, but two of them (WU-Kern 0080251, WU-Kern 0080254) are mounted together on one herbarium sheet and thus prone to confusions between the localities. We therefore designated one of the vouchers collected from Mt. Jauerling (WU-Kern 0080250) as lectotype.

The current name, *Gentianella praecox*, is widely accepted in literature (e.g., Kirschner & Kirschnerová 2000, Fischer *et al.* 2008, Kaplan *et al.* 2018), though sometimes erroneously considered an aestival variant of *Gentianella austriaca* (e.g., Pritchard & Tutin 1972, Marhold 2011). In our opinion it applies to plants originating from the Bohemian Massif in southeastern Bavaria (Germany), Bohemia (Czech Republic) and northern Austria (Reich *et al.* 2020).

4. *Gentiana rhaetica* A. Kern. & Jos. Kern. in Kerner (1882a: no. 649 & 1882b: 124) ≡ *Gentiana polymorpha* subsp. *rhaetica* (A. Kern. & Jos. Kern.) Wettst. (1900: 318) ≡ *Gentiana germanica* subsp. *rhaetica* (A. Kern. & Jos. Kern.) Braun-Blanq. in Hegi (1927: 2039) ≡ *Gentianella rhaetica* (A. Kern. & Jos. Kern.) Löve & Löve (1961: 42) ≡ *Gentianella germanica* subsp. *rhaetica* (A. Kern. & Jos. Kern.) Holub (1967: 119)

Ind. loci [habitat]: Tirolia centralis [Tyrol]. In pratis subalpinis ad Trins in valle Gschnitz, solo schistoso et calcareo; 1200–1600^m s.m., A. Kerner.

Type (lectotype designated here):—AUSTRIA. Tirolia centralis. In pratis subalpinis ad Trins in valle Gschnitz, solo schistoso et calcareo; 1200–1600^m s.m., s.d., A. Kerner [Fl. Exs. Austr.-Hung. no. 649], WU [WU-Hal-E 0078399, !].

Isolectotypes: BM [BM 000752305], BOZ [BOZ 048148, !], BRNU [BRNU 75547, !] E [E 00025250], GJO [GJO 3193, GJO 8070, !], GOET [GOET 004173, digital image !], IBF [IBF 119613, IBF 119614, IBF 119619, !], L [L 2700428, digital image !], MW [MW 0594229, digital image !], P [P 03988762, digital image !], PRC [PRC s.n., PRC s.n., PRC s.n., PRC s.n., digital image !], W [W 2005-0016017, !], WU [WU 0080240, WU 0080241, !]

Possible isolectotypes:—AUSTRIA. Ad Trins in valle Gschnitz (Tirolia centralis), s.d., A. Kerner [Fl. Exs. Austr.-Hung. no. 649 I, II], P [P 03988767, P 03988766, digital image !] [these were probably erroneously annotated as number I and II as Kerner (1882ab) only gives one locality.]

Possible other original material:—AUSTRIA. Tirol. Trins im Gschnitzthale, 1873, A. Kerner s.n., WU [WU-Kern 0080237, !]

—AUSTRIA. Tirol. Schneeberg bei Trins, September 1870, A. Kerner s.n., WU [WU-Kern 0080238, !]

—AUSTRIA. Tirol. Lärchwiesen bei Schneeberg im Gschnitzthale, September 1870, A. Kerner s.n., WU [WU-Kern 0080239, !]

Current name: ***Gentianella rhaetica***

Synonymy:

= *Gentiana stiriaca* Wettst. (1892a: 1–4) p.p. [excluding the material from Ennstaler Alpen, Hochschwab and Lower Austria, which belongs to *G. obtusifolia* introgressed by *G. austriaca* (Greimler & Jang 2007)] ≡ *Gentiana rhaetica* f. *stiriaca* (Wettst.) Wettst. (1897: 343) p.p. ≡ *Gentiana rhaetica* var. *stiriaca* (Wettst.) Hayek (1912: 354) p.p. ≡ *Gentiana germanica* f. *stiriaca* (Wettst.) Braun-Blanq. in Hegi (1927: 2040) p.p.

= *Gentiana solstitialis* Wettst. (1897: 337) p.p. [described as aestival variant of *G. rhaetica* and *G. wettsteinii* Murb. (1892: 14; a superfluous *nom. nov.* for *G. germanica*)] ≡ *Gentiana rhaetica* subsp. *solstitialis* (Wettst.) Wettst. ex Hayek (1912: 354) p.p. ≡ *Gentiana germanica* subsp. *solstitialis* (Wettst.) Vollm. (1914: 599) pp. ≡ *Gentiana germanica* var. *solstitialis* (Wettst.) Krist (1934: 116) p.p.

= *Gentiana kernerii* Dörf. & Wettst. in Dörf. (1898: no. 3757) ≡ *Gentiana rhaetica* subsp. *kernerii* (Dörf. & Wettst.) Wettst. ex Hayek (1912: 353) ≡ *Gentiana germanica* subsp. *kernerii* (Dörf. & Wettst.) Schinz & Thell. in Schinz & Keller (1923: 532)

= *Gentiana kernerii* f. *mixta* Nevole (1906: 161) p.p. ≡ *Gentiana rhaetica* [subsp. *kernerii*] var. *mixta* (Nevole) Hayek (1912: 354)

= *Gentiana rhaetica* [subsp. *kernerii*] var. *calpicola* Hayek (1912: 353)

? = *Gentiana anisodonta* var. *glabrescens* Hayek (1912: 351) [Hayek described this as a transitional form towards *Gentiana austriaca*, with less broadened outer calyx lobes and almost glabrous calyx based on plants from “Sulzbach” (Solčava, Slovenia). According to the given locality this could correspond to *Gentianella rhaetica* (Greimler (2010).)]

- *Gentiana rhaetica* var. *frondisepala* auct.: Pacher (1892: 109, quoad *Gentiana frondosepala* Borbás) p.p. (quoad loc. cit.), non quoad syn. Borbás [nom. inval. pro *Gentiana obtusifolia* var. *calpicina* W.D.J. Koch (1844: 356); Borbás described this taxon as aestival variant of *G. rhaetica* (“Sommerform der *G. Rhaetica* mit sehr ungleichen und blattähnlichen Kelchzähnen”) but listed it in the synonymy of *G. obtusifolia* β *calpicina*]

- *Gentiana polymorpha* Wettst. (1897: 373), *nom. illeg.* [*nom. superfl. pro Gentiana germanica* Willd. (1798: 1346)] p.p. (quoad subsp. *rhaetica*)

Notes:—The description of *Gentiana rhaetica* is based on a single gathering from Gschnitztal E of Stubai Alps in Tyrol distributed as number 649 in the *Flora exsiccata Austro-Hungarica* (Kerner 1882ab), however covering a large altitudinal range between 1,200 and 1,600 m a.s.l. In addition to the protologue Kerner discussed the identity of *Gentiana germanica* Willd. (1798: 1346) [≡ *Gentianella germanica* (Willd.) Börner (1912: 542)] and gave an identification key including related taxa. The proposed discriminating characters between *G. germanica* and *G. rhaetica* (length/width ratio of leaves, their length relative to the internodes, corolla length, gynophore length relative to calyx tube) are often blurred by high morphological variation. However, genetic data to some extent supports the separation of *Gentianella germanica* as a taxon occurring in W and NW Europe, and *G. rhaetica* as its vicariant in the Alps (Jang *et al.* 2005). This geographic concept was already anticipated by Kerner (1882ab) but more clearly sketched by Wettstein (1892c). Additionally, an aestival variant, *Gentiana solstitialis*, and a montane to alpine variant, *Gentiana kernerii*, were discriminated from the autumnal *Gentiana rhaetica* by Wettstein (1897) and Dörf. (1898), thus already broadening the classical dimorphism of early and late flowering variants. Zopfi (1991) concluded that there may be far more ecotypes, each showing its own morphological and seasonal characteristics. However, in our opinion a taxonomic separation of any of these from *Gentianella rhaetica* is not justified.

Morphologically divergent morphs at the eastern margin of the species' distribution range were described as *Gentiana stiriaca* Wettst. (1892a: 1–4). Initially, Wettstein (1892a) hypothesized that these are transitional forms between *G. sturmiensis* and *G. austriaca*. However, later Wettstein (1897) argued, that these variants represent a transition between *G. austriaca* and *G. rhaetica*. Genetic analyses showed that they actually fall into two groups, within *G. obtusifolia* and *G. rhaetica*, both introgressed by *G. austriaca* (Greimler & Jang 2007).

The entire original material of *Gentiana rhaetica* in WU is well preserved and fits the morphological description given in the protologue. As the three vouchers originating from Kerner's herbarium are not indicated as *G. rhaetica*, we

thus chose one of the vouchers from Halácsy's *Herbarium Europaeum* carrying the original *Flora exsiccata Austro-Hungarica* label (WU-Hal-E 0078399) as lectotype.

Although often included in *Gentianella germanica* (e.g., Pritchard & Tutin 1972, Marhold 2011) we here follow Jang *et al.* (2005) and the Austrian field flora (Fischer *et al.* 2008). The distribution area of the taxon remains somewhat unclear but obviously is restricted to the Alps (Greimler *et al.* 2011, Reich *et al.* unpublished data).

5. *Gentiana sturmiana* A. Kern. & Jos. Kern. in Kerner (1882a: no. 647 & 1882b: 122–123) ≡ *Gentiana germanica* var. *sturmiana* (A. Kern. & Jos. Kern.) Beck (1893: 940) ≡ *Gentiana polymorpha* subsp. *sturmiana* (A. Kern. & Jos. Kern.) Wettst. (1900: 318) ≡ *Gentiana aspera* subsp. *sturmiana* (A. Kern. & Jos. Kern.) Ronniger (1910: 304) ≡ *Gentianella sturmiana* (A. Kern. & Jos. Kern.) Börner (1912: 542) ≡ *Gentiana aspera* var. *sturmiana* (A. Kern. & Jos. Kern.) Schinz & Thell. (1914: 275) ≡ *Gentianella obtusifolia* subsp. *sturmiana* (A. Kern. & Jos. Kern.) Holub (1967: 120)

Ind. loci [habitat]: Austria inferior [Lower Austria]. In collibus graminosis ad Baumgarten et Bergern prope urbem Mautern ad Danubium; solo argilloso-arenaceo; 300^m s.m., J. Kerner. Austria superior [Upper Austria]. In graminosis lapidosis ad pedem montis Sarstein ad Hallstatt; solo calc[areo]; 500^m s.m., Stapf.

Type (lectotype designated here):—AUSTRIA. Austria inferior. In collibus graminosis ad Baumgarten et Bergern prope urbem Mautern ad Danubium; solo argilloso-arenaceo; 300^m s.m., s.d., J. Kerner [Fl. Exs. Austr.-Hung. no. 647 I], WU [WU 0080230, !].

Isolotypes: BM [BM 000752300], GJO [GJO 3191, GJO 8062, !], L [L 2705635, digital image !], LD [LD 1714764], MW [MW 0594234, digital image !], PRC [PRC s.n., PRC s.n., digital image !], W [W 1887-0004514, !], WU [WU 0080227, !].

Remaining syntypes [and/or isolotypes]:—AUSTRIA. Austria superior. In graminosis lapidosis ad pedem montis Sarstein ad Hallstatt; solo calc.; 500^m s.m., s.d., [O.] Stapf [Fl. Exs. Austr.-Hung. no. 647 II], BM [BM 000752301], GJO [GJO 3192, !], L [L 2705634, digital image !], MW [MW 0594235, digital image !], PRC [PRC s.n., PRC s.n., digital image !], W [W 1887-0004516, !], WU [WU 0080226, WU 0080229, WU 0080231, WU-Hal-E 0078400, !].

Isolotype or syntype [Fl. Exs. Austr.-Hung. no. 647 but not indicated if this belongs to gathering I or II]: BRNU [BRNU 75640, !], GOET [GOET 004014, GOET 004015, digital image !], P [P 03988723, digital image !], PRC [PRC s.n., PRC s.n., digital image !].

Possible other original material:—AUSTRIA. Am Fuße des Sarstein in Obersee bei Hallstatt, 1882, O. Stapf s.n., WU [WU 0080228, !] [it remains unclear if this is a duplicate of Fl. Exs. Austr.-Hung. no. 647 II or was collected only later].

Current name: = *Gentianella obtusifolia* (F.W. Schmidt) Holub (1967: 118) ≡ *Hippion obtusifolium* Schmidt (1793: 27)

Notes:—The description of *Gentiana sturmiana* is based on material distributed as numbers 647 I and II of Kerner's *Flora exsiccata Austro-Hungarica*, one collected from Wachau region in Lower Austria and one from the area N of Mt. Dachstein in Upper Austria (Kerner 1882ab). The pair of aestival *G. norica* and autumnal *G. sturmiana* today is usually assigned to a single species (Pritchard & Tutin 1972, Fischer *et al.* 2008, Marhold 2011; all as *Gentianella aspera*), which by priority has to be named *Gentianella obtusifolia*. Both type localities of *G. sturmiana* are well situated within the distribution range of *G. obtusifolia* (Greimler *et al.* 2011). All specimens originating from Wachau region clearly show (i) acute leaves, short internodes and long corollas in accordance with the protologue, as well as (ii) long cylindrical papillae on the margin and the midrib of the calyx lobes, a significant character of *Gentianella obtusifolia*, though neither mentioned in protologue of *Gentiana sturmiana* nor by Schmidt (1793). Unexpectedly, some of the specimens supposedly originating from Upper Austria exhibit shorter, more cone-shaped papillae on the margins of the calyx lobes, some are even glabrous on the midrib of the lobes and some show narrow and elongated calyx lobes. Whereas these variants are not known to us from the Upper Austrian populations that show the typical features of *G. obtusifolia* (see for example WU 0083486), transitions approaching *Gentianella austriaca* are sometimes found in the few remnant populations of *Gentianella obtusifolia* in Lower Austria in the surroundings of the *locus classicus* (see for example WU 0083486). These divergent populations seem to be within the morphological variation in the eastern part of the distribution area. We thus can assume an erroneous assignment of these specimens to the gathering of *Flora exsiccata Austro-Hungarica* 647 II, either already during the process of distribution or when the material was mounted. Interestingly, similar narrow calyx lobes could also be observed on the digital images of some of the specimens on the vouchers belonging to gathering 647 II in L (L 2705634) and MW (MW 0594235). We therefore chose one of the vouchers representing gathering 647 I (WU 0080230) as lectotype.

For details on the identity and typification of *G. obtusifolia* see Reich *et al.* (in prep.).

Acknowledgements

We are grateful to the curators Marc Appelhans (GOET), Roxali Bijmoer (L), Christian Bräuchler & Bruno Wallnöfer (W), Jiří Danihelka (BRNU), Patrik Mráz (PRC), Ota Šída (PR), Michael Thalinger (IBF), Walter Till (WU) and Thomas Wilhalm (BOZ) for their help and advice, to Matthias Svojtka (Vienna University Library, Departmental Library Botany) for his help in recovering rare literature, to Ruth Sander for her critical comments, to the anonymous reviewer who considerably helped to improve this manuscript and to the Austrian Science Fund (FWF) for financial support (grant P22716-B16 to J.G.).

References

- Anonymous (1915) Sammlungen. *Magyar botanikai lapok* 13: 164–165.
- Bartha, D. & Király, G. (2015) *Atlas florae Hungariae. Magyarország edényes növényfajainak elterjedési atlasza* [Distribution atlas of vascular plants of Hungary]. Nyugat-magyarországi Egyetem Kiadó, Sopron, 330 pp.
- Beck von Managetta, G.E. (1893) *Flora von Nieder-Österreich*. 2 (2). Carl Gerold's Sohn, Wien, 575 pp.
- Bollinger, M. (1989) *Odontites lanceolata* (Gaudin) Reichenbach – ein formenreicher Endemit der Westalpen. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 111: 1–28.
- Borbás, V. von (1892a) Flora von Oesterreich-Ungarn. II. West-, Nord- und Mittelungarn. (Fortsetzung). *Österreichische botanische Zeitschrift* 42: 184–187.
<https://doi.org/10.1007/BF01794238>
- Borbás, V. von (1892b) Flora von Oesterreich-Ungarn. II. West-, Nord- und Mittelungarn. (Fortsetzung und Schluss.). *Österreichische botanische Zeitschrift* 42: 286–288.
<https://doi.org/10.1007/BF01798530>
- Börner, C.J.B. (1912) *Eine Flora für das deutsche Volk mit Unterstützung von L. Lange und P. Dobe bearbeitet von Carl Börner. Ein Hilfsbuch zum Bestimmen der heimischen Pflanzen ohne botanische Vorkenntnisse*. R. Voigtländer, Leipzig, 864 pp.
- Bradshaw, A.D. (1965) Evolutionary Significance of Phenotypic Plasticity in Plants. In: Caspari, E.W. & Thoday, J.M. (Eds.) *Advance in Genetics*. Vol 13. Academy Press, New York, London, pp. 115–156.
[https://doi.org/10.1016/S0065-2660\(08\)60048-6](https://doi.org/10.1016/S0065-2660(08)60048-6)
- Campion-Bourget, F. (1982) Influence de l'hémiparasitisme du *Rhinanthus alectorolophus* (Scop.) Pollich sur son dimorphisme saisonnier. *Revue générale de Botanique* 89: 3–77.
- Dolliner, G. (1842) *Enumeratio plantarum phanerogamicarum in Austria inferiori crescentium*. Sumptibus et Typis Caroli Gerold, Vindobonae [Vienna], 160 pp.
- Dörfler, I. [Ed.] (1898) *Herbarium normale, Schedae ad Centuriam XXXVIII*. E typographia O. Hensel, Vindobonae [Vienna], pp. 245–294.
- European Commission (2011) Recommendation of 27.10.2011 on the digitisation and online accessibility of cultural material and digital preservation. Available from: https://ec.europa.eu/digital-single-market/sites/digital-agenda/files/en_4.pdf (accessed 6 July 2020)
- Fischer, M.A., Oswald, K. & Adler, W. (2008) *Exkursionsflora für Österreich, Liechtenstein und Südtirol*. 3. Aufl. Biologiezentrum der Oberösterreichischen Landesmuseen, Linz, 1392 pp.
- Froelich, J.A. (1796) *De Gentiana Dissertatio*. Typis Kunstmannianis, Erlangae [Erlangen], 142 pp.
- Greimler, J. (2010) Revision of *Gentianella austriaca* s.l. and *G. rhaetica* in Slovenia. *Hladnikia* 25: 3–12.
- Greimler, J. & Jang, C.G. (2007) *Gentianella stiriaca*, a case of reticulate evolution in the northeastern and eastern Central Alps. *Taxon* 56 (3): 857–870.
<https://doi.org/10.2307/25065867>
- Greimler, J., Park, J.M. & Schneeweiss, H. (2011) *Gentianella* (Gentianaceae): A model taxon for evolution in the Alps. *Taxon* 60 (2): 427–435.
<https://doi.org/10.1002/tax.602012>
- Hayek, A. von (1912) *Flora von Steiermark, eine systematische Bearbeitung der im Herzogtum Steiermark wildwachsenden oder im Grossen gebauten Farn- und Blütenpflanzen nebst einer pflanzengeographischen Schilderung des Landes mit Benutzung eines vom naturwissenschaftlichen Verein für Steiermark angelegten Standortskataloges*. 2 (1). Gebr. Bornträger, Berlin, 480 pp.
- Hayek, A. (1930) Prodromus florae peninsulae balcanicae. *Repertorium specierum novarum regni vegetabilis. Beiheft* 30 2 (Lief. 4): 337–576.

- Hegi, G. (1927) *Illustrierte Flora von Mittel-Europa*. 5 (3). J.F. Lehmann, München, pp. 1563–2250.
- Holub, J. (1965) Příspěvek k poznání vegetačních a floristických poměrů okolí Železné Rudy [Beitrag zur Kenntnis der Vegetations- und floristischen Verhältnisse in der Umgebung von Železná Ruda (Eisenstein)]. *Preslia* 37: 95–110.
- Holub, J. (1967) Neue Namen innerhalb der Gattungen *Gentianella* Moench, *Gentianopsis* Ma und *Comastoma* (Wettst.) Tokoyuni. *Folia Geobotanica et Phytotaxonomica* 2: 115–120.
<https://doi.org/10.1007/BF02851756>
- Holub, J. (1998) Reclassifications of new names in vascular plants 1. *Preslia* 70: 97–122.
- IPNI (2020) International Plant Names Index. Available from: <http://www.ipni.org> (accessed 6 July 2020)
- JACQ consortium (2004) Virtual Herbaria Website. Available from: <https://jacq.org> (accessed 7 July 2020)
- Jacquín, N.J. von (1762) *Enumeratio stirpium plerarumque, quae sponte crescunt in agro vindobonensi, montibusque confinibus. Accedunt observationum centuria et appendix de paucis exoticis*. Joannis Pauli Kraus, Vindobonae [Vienna], 322 pp.
<https://doi.org/10.5962/bhl.title.125456>
- Jang, C.G., Müllner, A.N. & Greimler, J. (2005) Conflicting patterns of genetic and morphological variation in European *Gentianella* section *Gentianella*. *Botanical Journal of the Linnean Society* 148 (2): 175–187.
<https://doi.org/10.1111/j.1095-8339.2005.00406.x>
- Jávorka, S. (1925) *Magyar flóra*. 3. Magyar Nemzeti Múzeum Növénytára, Budapest, 506 pp.
- Kaplan, Z., Danihelka, J., Chrtek, J. Jr., Prančl, J., Ducháček, M., Ekrť, L., Kirschner, J., Brabec, J., Zázvorka, J., Trávníček, B., Dřevojan, P., Šumberová, K., Kocián, P., Wild, J. & Petřík, P. (2018) Distributions of vascular plants in the Czech Republic. Part 7. *Preslia* 90: 425–531.
<https://doi.org/10.23855/preslia.2018.425>
- Karlsson, T. (1974) Recurrent ecotypic variation in Rhinanthae and Gentianaceae in relation to hemiparasitism and mycotrophy. *Botaniska notiser* 127: 527–539.
- Kerner, A. (1882a) *Flora Exsiccata Austro-Hungarica*. Vol. II. Printed schedae, nos. 401–800.
- Kerner, A. (1882b) *Schedae ad floram exsiccata austro-hungaricum*. Vol. II. Guilielmum Frick, Vindobonae [Vienna], 175 pp.
<https://doi.org/10.1007/BF01647425>
- Kerner, A. (1888) Beiträge zur Flora von Niederösterreich. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* 38: 669–670.
- Kerner, A. (1892) *Flora Exsiccata Austro-Hungarica*. Scheda no. 2190.
- Kerner, A. (1893) *Schedae ad floram exsiccata austro-hungaricum*. VI. E typographia M. Salzeri, Vindobonae [Vienna], 135 pp.
- Kirschner, J. & Kirschnerová, L. (2000) Gentianaceae Juss. – hořcovité. In: Slavík, B., Chrtek, J. jun. & Štěpánková, J. (Eds.) *Květena České republiky [Flora of the Czech Republic]* 6. Academia, Praha, pp. 72–110.
- Kirschnerová, L. & Kirschner, J. (2003) Změny v rozšíření *Gentianella lutescens* subsp. *lutescens* a subsp. *carpatica* v České republice [Changes in the distribution of *Gentianella lutescens* subsp. *lutescens* and subsp. *carpatica* in the Czech Republic]. *Zprávy České botanické společnosti* 38: 205–216.
- Koch, W.D.J. (1844) *Taschenbuch der deutschen und Schweizer Flora*. Gebhart und Reisland, Leipzig, 604 pp.
- Koutecký, P., Tuleu, G., Baďurová, T., Košnar, J., Štech, M. & Těšitel, J. (2012) Distribution of cytotypes and seasonal variation in the *Odontites vernus* group in central Europe. *Preslia* 84 (4): 887–904.
- Křenová, Z., Brabec, J., Rössler, S. & Kindlmann, P. (2019) Can we learn from the ecology of the Bohemian gentian and save another closely related species of *Gentianella*? *Plos one* 14 (12): e0226487.
<https://doi.org/10.1371/journal.pone.0226487>
- Krist, V. (1934) Hořce Československé republiky (Gentianae Reipublicae čechoslovenicae). *Sborník Klubu Přírodovědeckého v Brně* 16: 60–139.
- Kronfeld, E.M. (1908) *Anton Kerner von Marilaun. Leben und Arbeit eines deutschen Naturforschers*. Tauchnitz, Leipzig, 392 pp.
- Lennartsson, T. (1997) Seasonal differentiation - a conservative reproductive barrier in two grassland *Gentianella* (Gentianaceae) species. *Plant Systematics and Evolution* 208 (1–2): 45–69.
<https://doi.org/10.1007/BF00986082>
- Linnaeus, C. von (1753a) *Species plantarum, exhibentes plantas rite cognitatas ad genera relatas, cum differentiis specificis, nominibus trivialibus, synonymis selectis, locis natalibus, secundum systema sexuale digestas*. Tomus I. Impensis Laurentii Salvii, Holmiae [Stockholm], pp. 1–560.
<https://doi.org/10.5962/bhl.title.669>
- Linnaeus, C. von (1753b) *Species plantarum, exhibentes plantas rite cognitatas ad genera relatas, cum differentiis specificis, nominibus trivialibus, synonymis selectis, locis natalibus, secundum systema sexuale digestas*. Tomus II. Impensis Laurentii Salvii, Holmiae [Stockholm], pp. 561–1200.
<https://doi.org/10.5962/bhl.title.669>

- Löve, Á. & Löve, D. (1961) Some nomenclatural changes in the European flora. I. Species and supraspecific categories. *Botaniska Notiser* 114: 33–47.
- Ludwig, C.G. (1757) *Institutiones historico physicae regni vegetabilis praelectionibus academicis accommodatae*. Ed. 2. Joh. Fridericum Gleditsch, Lipsiae [Leipzig], 274 pp.
- Marhold, K. (2011) Gentianaceae. *The Euro+Med PlantBase*. Available from: <http://ww2.bgbm.org/EuroPlusMed> (accessed 4 July 2020)
- Mayer, E. (1968) Zur Kenntnis der Gattung *Gentianella* Moench in Jugoslawien. II. Der *G. aspera*-, *G. germanica*- und *G. austriaca*-Komplex. *Biološki vestnik* 16: 23–28.
- Moench, C. (1794) *Methodus plantas horti botanici et agri marburgensis, a staminum situ describendi*. In officina nova libraria academiae, Marburgi cactorum [Marburg], 780 pp.
<https://doi.org/10.5962/bhl.title.304>
- Murbeck, S.S. (1892) Studien über *Gentianen* aus der Gruppe *Endotricha* Froel. *Acta Horti Bergiani* 2 (3): 1–28.
- Neilreich, A. (1846) Flora von Wien. *Eine Aufzählung der in den Umgebungen Wiens wild wachsenden oder im Grossen gebauten Gefässpflanzen, nebst einer pflanzengeographischen Uebersicht*. Fr. Beck, Wien, 706 pp.
- Neilreich, A. (1858) *Flora von Niederösterreich*. Carl Gerold's Sohn, Wien, 1010 pp.
- Nevole, J. (1906) Übergangsformen zwischen geographischen Arten der endotrichen *Gentianen*. *Österreichische botanische Zeitschrift* 56 (4): 158–162.
<https://doi.org/10.1007/BF01791798>
- Pacher, D. (1892) Systematische Aufzählung der in Kärnten wildwachsenden Gefässpflanzen. II. Nachtrag. *Jahrbuch des naturhistorischen Landesmuseums von Kärnten* 22: 25–160.
- Pleines, T., Esfeld, K., Blattner, F.R. & Thiv, M. (2013) Ecotypes and genetic structure of *Rhinanthus alectorolophus* (Orobanchaceae) in southwestern Germany. *Plant Systematics and Evolution* 299 (8): 1523–1535.
<https://doi.org/10.1007/s00606-013-0816-8>
- Plenk, K., Göd, F., Kriechbaum, M. & Kropf, M. (2016) Genetic and reproductive characterisation of seasonal flowering morphs of *Gentianella bohemica* revealed strong reproductive isolation and possible single origin. *Plant Biology* 18 (1): 111–123.
<https://doi.org/10.1111/plb.12354>
- Pritchard, N.M. & Tutin, T.G. (1972) *Gentianella* Moench. 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*. Vol. 3. Cambridge University Press, Cambridge, pp. 63–67.
- Reich, D., Wrška, T., Plutzer, C. & Greimler, J. (2020) The impact of land-use change on the distribution of *Gentianella austriaca* and *G. praecox* in Austria. *Preslia* 92: 213–234.
<https://doi.org/10.23855/preslia.2020.213>
- Reich, D., Mráz, P. & Gutermann, W. (in Prep.) A long story in a short note – identity and typification of *Hippion obtusifolium* F.W. Schmidt, and synonymy of *Gentianella obtusifolia* (Gentianaceae). *Phytotaxa*.
- Reisch, C. & Poschold, P. (2009) Land use affects flowering time: seasonal and genetic differentiation in the grassland plant *Scabiosa columbaria*. *Evolutionary ecology* 23 (5): 753–764.
<https://doi.org/10.1007/s10682-008-9270-4>
- Ronniger, K. (1910) Die schweizerischen Arten und Formen der Gattung *Melampyrum* L. *Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich* 55: 300–330.
- Sauter, A.E. (1826) *Dissertatio inauguralis geographico-botanica de territorio vindobonensi. Versuch einer geographisch-botanischen Schilderung der Umgebung von Wien*. Typis Antonii de Haykul, Vindobonae [Vienna], 50 pp.
- Schinz, H. & Thellung, A. (1914) *Flora der Schweiz. II Teil: Kritische Flora*. Ed. 3. Albert Raustein, Zürich, 582 pp.
- Schinz, H. & Keller, R. (1923) *Flora der Schweiz. I Teil: Exkursionsflora*. Ed. 4. Albert Raustein, Zürich, 792 pp.
- Schmidt, F.W. (1793) *Flora boëmica inchoata exhibens plantarum regni Boëmiae indigenarum species*. Centuria secunda. I.G. Calve, Pragae [Prague], 97 pp.
<https://doi.org/10.5962/bhl.title.124860>
- Schönbeck-Temesy, E. (1992) Zur Geschichte des Herbars der Wiener Universität. *Abhandlungen der Zoologisch-Botanischen Gesellschaft in Österreich* 26: 69–95.
- Schultes, J.A. (1814) *Österreichs Flora. Ein Handbuch auf botanischen Excursionen, enthaltend eine kurze Beschreibung der in den Erbstaaten des österreichischen Kaiserthumes wildwachsenden Pflanzen*. ed. 2, 1. C. Schaumburg & Compagnie, Wien, 700 pp.
- Schur, P.J.F. (1861) Beiträge zur Flora von Wien. *Oesterreichische botanische Zeitschrift* 11 (3): 81–98.
<https://doi.org/10.1007/BF01963022>
- Skalický, V. (1969) Die Sammelart *Gentianella germanica* (Willd.) E. F. Warburg s. l. im Böhmischem Massiv (Vorläufige Mitteilung). *Preslia* 41: 140–147.
- Soó, R. de (1929a) Sur les caractères morphologiques des genres *Melampyrum* et *Rhinanthus* et leur valeur systématique. *Bulletin de la*

- Société Botanique de France* 76 (3): 611–622.
<https://doi.org/10.1080/00378941.1929.10837194>
- Soó, R. de (1929b) Die mittel- und südosteuropäischen Arten und Formen der Gattung *Rhinanthus* und ihre Verbreitung in Südosteuropa. *Repertorium specierum novarum regni vegetabilis* 26: 179–219.
<https://doi.org/10.1002/fedr.4870262704>
- Stafleu, F. & Cowan, R.S. (1979) *Taxonomic Literature*. Vol. II: H–Le. Bohn, Scheltema and Holkema, Utrecht, 991 pp. [*Regnum Vegetabile* 98].
- Štech, M. (2000) Seasonal variation in *Melampyrum nemorosum*. *Preslia* 72: 345–368.
- Sterneck, J. von (1901) Monographie der Gattung *Alectorolophus*. (Mit 3 Karten anschließend und einem Stammbaume). *Abhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* 1 (2): 1–150.
- Suni, S.S., Ainsworth, B. & Hopkins, R. (2020) Local adaptation mediates floral responses to water limitation in an annual wildflower. *American Journal of Botany* 107: 209–218.
<https://doi.org/10.1002/ajb2.1434>
- Svobodová, Š., Košnar, J., Koutecký, P. & Štech, M. (2016) Microsatellite analysis of four similar *Euphrasia* (Orobanchaceae) species changes the traditional view of this group. *Plant Ecology and Evolution* 149 (1): 45–58.
<https://doi.org/10.5091/plecevo.2016.1128>
- Svojtka, M. (2020) Die *Flora exsiccata Austro-Hungarica* des Anton KERNER VON MARILAUN (1831–1898): ein europäisches Sammelprojekt und antinationalistischer Vermittler zwischen den Völkern der Habsburgermonarchie. In: Seidl, J. & Kästner, I. (Eds.) *Tauschen und Schenken. Wissenschaftliche Sammlungen als Resultat europäischer Zusammenarbeit*. Shaker Verlag, Düren, pp. 213–228.
- Thiers, B. (2020) Index herbariorum: a global directory of public herbaria and associated staff. *New York: New York Botanical Garden's Virtual Herbarium*. Available from: <http://sweetgum.nybg.org/ih> (accessed 5 July 2020)
<https://doi.org/10.12705/Code.2018>
- Turland, N.J., Wiersema, J.H., Barrie, F.R., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Kusber, W.-H., Li, D.-Z., Marhold, K., May, T.W., McNeill, J., Monro, A.M., Prado, J., Price, M.J. & Smith, G.F. (Eds.) (2018) *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017*. Koeltz Botanical Books, Glashütten. [*Regnum Vegetabile* 159].
<https://doi.org/10.12705/Code.2018>
- Velenovský, J. (1888) Resultate der zweiten botanischen Reise nach Bulgarien. *Sitzungsberichte der Königlichen Böhmisches Gesellschaft der Wissenschaften. Mathematisch-naturwissenschaftliche Classe* 1888/3: 19–74.
- Vollmann, F. (1914) *Flora von Bayern*. Ulmer, Stuttgart, 840 pp.
- Waisbecker, A. (1899) Beiträge zur Kenntniss der Gattung *Odontites*. *Österreichische Botanische Zeitschrift* 49 (12): 437–442.
<https://doi.org/10.1007/BF01794972>
- Waisbecker, A. (1903) Új adatok Vas vármegyé flórájához. [Neue Beiträge zur Flora des Eisenburger Comitats in West-Ungarn]. *Magyar botanikai lapok* 2 (3): 63–71.
- Wettstein, R. (1892a) Die Arten der Gattung *Gentiana* aus der Section “*Endotricha*” Fröl. (Fortsetzung). *Österreichische botanische Zeitschrift* 42 (1): 1–6.
- Wettstein, R. (1892b) Die Arten der Gattung *Gentiana* aus der Section “*Endotricha*” Fröl. (Fortsetzung). *Österreichische botanische Zeitschrift* 42 (2): 40–45.
- Wettstein, R. (1892c) Die Arten der Gattung *Gentiana* aus der Section “*Endotricha*” Fröl. (Fortsetzung). *Österreichische botanische Zeitschrift* 42 (3): 84–88.
- Wettstein, R. (1892d) Die Arten der Gattung *Gentiana* aus der Section “*Endotricha*” Fröl. (Fortsetzung). *Österreichische botanische Zeitschrift* 42 (4): 125–130.
<https://doi.org/10.1007/BF01798130>
- Wettstein, R. (1892e) Die Arten der Gattung *Gentiana* aus der Section “*Endotricha*” Fröl. (Fortsetzung). *Österreichische botanische Zeitschrift* 42 (5): 156–161.
- Wettstein, R. (1892f) Die Arten der Gattung *Gentiana* aus der Section “*Endotricha*” Fröl. (Fortsetzung). *Österreichische botanische Zeitschrift* 42 (6): 193–196.
<https://doi.org/10.1007/BF01798523>
- Wettstein, R. (1892g) Die Arten der Gattung *Gentiana* aus der Section “*Endotricha*” Fröl. (Schluss). *Österreichische botanische Zeitschrift* 42 (7): 229–235.
<https://doi.org/10.1007/BF01791046>
- Wettstein, R. (1895) Der Saison-Dimorphismus als Ausgangspunkt für die Bildung neuer Arten im Pflanzenreiche. *Berichte der Deutschen Botanischen Gesellschaft* 13: 303–313.
- Wettstein, R. (1896) *Monographie der Gattung Euphrasia*. W. Engelmann, Wien, 316 pp.

- Wettstein, R. (1897) Die europäischen Arten der Gattung *Gentiana* aus der Section *Endotricha* Froel. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Wien. Mathematisch-naturwissenschaftliche Klasse* 64: 309–382.
- Wettstein, R. (1900) Descendenztheoretische Untersuchungen. 1. Untersuchungen über den Saison-Dimorphismus im Pflanzenreiche. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Wien. Mathematisch-naturwissenschaftliche Klasse* 70: [305]–346.
- Willdenow, C.L. von (1798) *Species plantarum, Editio quarta*. 1 (2). G.C. Nauk, Berlin, 1071 pp.
- Winn, A.A. (1996) Adaptation to fine-grained environmental variation: An analysis of within-individual variation in an annual plant. *Evolution* 50: 1111–1118.
<https://doi.org/10.1111/j.1558-5646.1996.tb02351.x>
- Zopfi, H.J. (1991) Aestival and autumnal vicariads of *Gentianella* (Gentianaceae): A myth? *Plant Systematics and Evolution* 174 (3–4): 139–158.
<https://doi.org/10.1007/BF00940336>
- Zopfi, H.J. (1997) Ecotypic variation of *Euphrasia rostkoviana* Hayne (Scrophulariaceae) in relation to grassland management. *Flora* 192 (3): 279–295.
[https://doi.org/10.1016/S0367-2530\(17\)30793-4](https://doi.org/10.1016/S0367-2530(17)30793-4)