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RESEARCH ARTICLE

Notes on the taxonomy of the species complex *Symphytum tuberosum* (*Boraginaceae*) and on the interpretation of the name *S. microcalix*

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Abstract. The name *Symphytum microcalix* originally published by P.M. Opiz is currently interpreted in two different ways, namely as a synonym of *Symphytum officinale* or as a name of a taxon from the *S. tuberosum* aggregate. The application of the name is discussed based on the analysis of Opiz's protologue, with notes on the origin of the authentic material, and on the spelling of the name. It is concluded that Opiz's description was most likely based on an anomalous plant of *Symphytum bohemicum* and thus it is not applicable to any representatives of the *S. tuberosum* aggregate. Further nomenclatural and taxonomic issues within the *S. tuberosum* aggr. are discussed, with a special emphasis on the status of Ukrainian representatives of this species complex.

Keywords: comfrey, history of botany, nomenclature, Opiz, polyploidy

History of the name *Symphytum microcalix*

The name *Symphytum microcalix* Opiz (*Boraginaceae*) was first published by the Czech botanist Philipp (Filip) Maximilian Opiz in 1839 (Berchtold, Opiz, 1839). The taxonomic application of that name is currently interpreted in two different ways: it is either placed in the synonymy of *Symphytum officinale* L. (POWO, 2024) or, alternatively, is applied to a taxon from the *Symphytum tuberosum* aggregate occurring in the Podillya region and adjacent areas of Ukraine (Dobrochaeva,

1981; Mosyakin, Fedoronchuk, 1999; Valdés, von Raab-Straube, 2011–onward). An attempt to resolve this controversy is made based on the analysis of Opiz's original description and other available information.

In his 1839 work, Opiz mentioned three species of *Symphytum* L. naturally occurring in Bohemia (nowadays part of the Czech Republic): *S. officinale*, *S. microcalix* and *S. tuberosum*. He provided detailed morphological descriptions of those species, together with notes on their phenology and ecology, and listed their known occurrences

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in Bohemia. He also provided an account of intraspecific variability within *S. officinale*. The species was divided into three unranked infraspecific entities (α *villosum* Opiz, β *hirsutum* Opiz and γ *hispidum* Opiz), with the former two subdivided further into lower-rank groups. Thus, Opiz was well aware of the considerable morphological variability of *S. officinale*, and his species concept was rather broadly defined. He placed *Symphytum bohemicum* F.W. Schmidt in the synonymy of *S. officinale* β *hirsutum* d. *flavescens* Opiz. Nevertheless, *S. microcalix* was recognized by Opiz as a species of its own, distinct from both *S. officinale* and *S. tuberosum*. Notably, the specific epithet has been spelled in the protologue as “*microcalix*”. That spelling was changed by later authors to “*microcalyx*”. In fact, words “calyx” and “calix” do coexist in Latin, the first one being mainly applied in descriptive morphology and the second one meaning “cup” or “chalice”. Indeed, there are several other plant names in current use having the word or stem element “calix” in their specific epithets, e.g. *Justicia nematocalix* Lindau, *Masdevallia calocalix* Luer and *Rosmarinus eriocalix* Jord. & Fourr. Thus, in my opinion, the spelling “*microcalix*” does not constitute an orthographic error and is thus not correctable to “*microcalyx*” (see Art. 60 of the ICN: Turland et al., 2018).

Symphytum microcalix received little attention by following authors, and there is only a limited number of publications where it was specifically mentioned. Čelakovský (1871) reduced it to the unranked infraspecific taxon (supposedly a variety) under *S. officinale*, namely *S. officinale* γ *stenophyllum* Čelak. The exclamation mark in Čelakovský’s work indicated that he had an opportunity to examine the original Opiz’s collection of *S. microcalix*. Few years later, Nyman (1881) treated Opiz’s taxon as a subvariety of *S. officinale*, whereas Beck von Mannagetta (1893) included it into *S. officinale* β *angustifolium*. Afterwards, Opiz’s name largely remained out of use, until it was applied by Dobrochaeva (1981) in a very different sense, namely to plants of the *S. tuberosum* aggregate occurring in the Podillya (earlier often Latinized as Podolia) region and adjacent areas of Ukraine. That view was largely followed by later Ukrainian authors, and the name *S. microcalix* (spelled as “*microcalyx*”) appeared in national and regional checklists (e.g., Mosyakin, Fedoronchuk, 1999; Kricsfalusy, Budnikov, 2007; Danylyk,

Volodymyrets, 2020) and was taken over, in the sense used by Dobrochaeva, into the *Euro+Med checklist* (Valdés, von Raab-Straube, 2011–onward). An attempt to resolve the existing controversy over the application of the name *S. microcalix* Opiz is presented below.

Tracing the original material of *Symphytum microcalix*

Doubtlessly, examination of the authentic material of *S. microcalix* Opiz (if extant and available) would help in unambiguously revealing its true identity. Thus, an attempt was made to trace any extant original material. In the protologue, Opiz cited a collection number (as “Opiz! herb. n. 6016”) and indicated a single locality as “Auf nassen Wiesen. Bei Pardubic (1807. Opiz!)”, i.e. on wet meadows near the town of Pardubice, Czech Republic. Thus, the geographic origin, collection date, and collection number of the original material of *S. microcalix* were clearly defined by the author in the protologue. This protologue of *S. microcalix* also includes the following reference: “*Symphytum officinale* (patens) Besser fl. galic. 1. p. 152. n. 206 ?”. However, since this citation was accompanied by a question mark, this material has not been definitely included by Opiz in his concept of this species and thus it cannot be considered as part of the original material of *S. microcalix*. According to Stafleu and Cowan (1981), most of Opiz’s collections are kept in three Czech herbaria, namely PR, PRC and PRM. Thus, requests about the existence of original specimens of *S. microcalix* Opiz have been sent to the curators of the mentioned herbaria. Additionally, a recent comprehensive revision of all *Symphytum* specimens collected in the Czech Republic and currently preserved in Czech herbaria (Kobřlová et al., 2016b; Kobřlová, 2017; Kobřlová, Hroneš, 2017) greatly assisted in the identification of possible original material. Among all the collections investigated in the course of this revision, there is just a single extant specimen (PR) that was collected by Opiz in Pardubice. Further information on that specimen and its digital image were kindly provided by Otakar Šída (PR), who was able to locate it in the PR collection. Even if the specimen in question (barcode PR 751948; Fig. 1) might have been collected by Opiz near Pardubice, it is unlikely to be part of the original material of *S. microcalix*. The label of this specimen in Opiz’s handwriting reads as follows (Fig. 2):



Fig. 1. Image of the herbarium specimen of *Symphytum officinale* from Opiz's herbarium preserved in the herbarium of the National Museum (Národní muzeum) in Prague (PR751948)

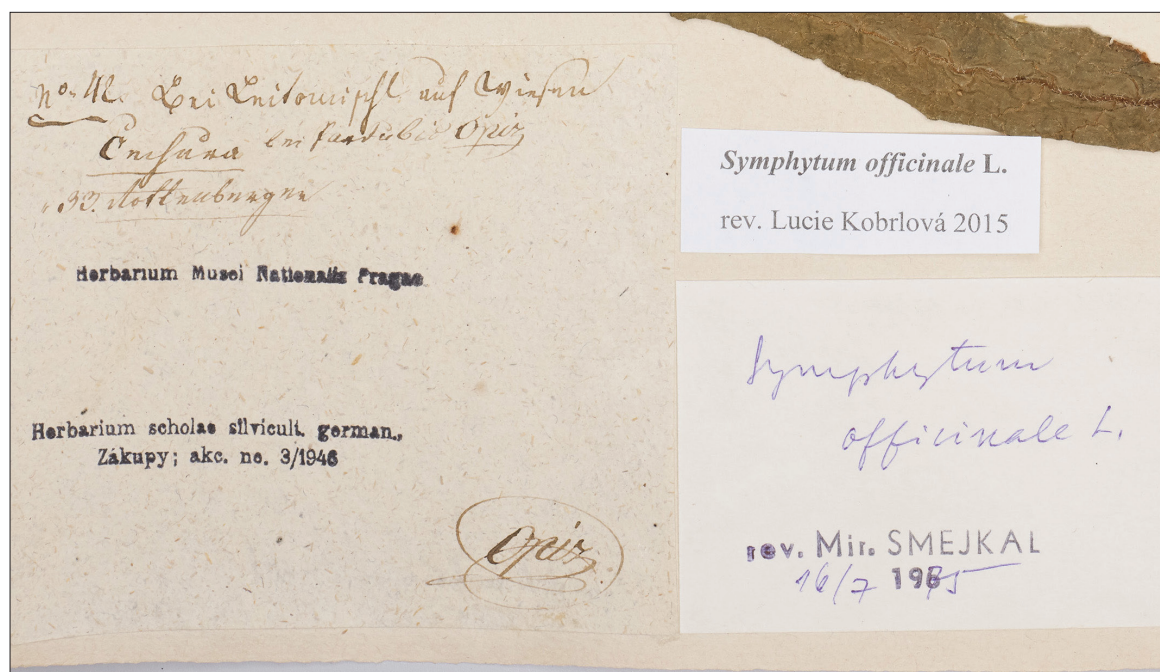


Fig. 2. Crop of Figure 1 showing labels attached to the herbarium specimen PR751948

no. 42. Bei Leitomischl auf Wiesen
 Čechura Bei Pardubic. Opiz
 „33 Rottenberger

According to Otakar Šída (personal communication), the label was originally a part of a herbarium cover (double sheet) that likely included several specimens of different origin. It explains the fact that three collector names (underlined on the original label) and two different localities are mentioned on the same label. The sheet also bears Opiz's signature and two identification labels by M. Smejkal and L. Koblřová (both with the name *Symphytum officinale* L.). There are no further labels or markings that would allow the identification of this specimen as original material of *S. microcalix*. There is no collection date indicated, and the number 6016 mentioned in the protologue could not be found anywhere on the sheet. Without those details, the indication of the collection locality ("Padubic") is not sufficient for the positive identification of this specimen as the original collection of *S. microcalix*, as Opiz mentioned the existence of several collections of another species, *S. officinale*, from the same locality (Berchtold, Opiz, 1839). Furthermore, according to O. Šída, the sheet is not a part of Opiz's original herbarium and comes from a set of his duplicates. Thus, its identification with *S. microcalix* would be highly speculative.

Because no other material matching the protologue of *S. microcalix* could be identified in any of Czech herbaria, there is apparently no extant original material of *S. microcalix* in existence. In the opinion of O. Šída (personal communication), Opiz's "herb. n. 6016" referred to Opiz's "Authentisches Herbarium". Opiz's original collections were donated to PR where they were partly destroyed in the second half of the 19th century, and it seems plausible that the original material of *S. microcalix* was lost around that time. Designation of a neotype for *S. microcalix* could potentially affix the application of the name and resolve the existing controversy. However, it should be kept in mind when designating the neotype that Opiz specifically emphasized a distinctive feature of *S. microcalix* in the protologue, i.e. that its filaments were nearly equal to anthers. This is indeed very uncommon for the species of *Symphytum* naturally occurring in Czech Republic, as their filaments are usually much shorter than anthers (Koblřová, 2022). Thus, a specimen with filaments nearly equal to anthers would be a preferred choice for the neotype in order not to be in serious conflict with the protologue. As no information about contemporary occurrence of such plants in the vicinity of the type locality of *S. microcalix* is available to the author of these notes, he refrains from designating a neotype.

Analysis of Opiz's protologue

In the absence of any extant original material, conclusions about the identity of *S. microcalix* are to be drawn from the analysis of its protologue. Currently, the name *S. microcalix* is interpreted either as a synonym of *S. officinale* or as a name of a taxon from the *S. tuberosum* species complex. Thus, the main question to be answered is in fact to which of the two species aggregates, *S. officinale* aggr. or *S. tuberosum* aggr., the plant described by Opiz does belong to. The main features distinguishing those groups are as following (Kobrlóvá, 2022):

Symphytum officinale aggr.: rhizome fusiform, ± vertical; mericarps (“nutlets”) smooth, shiny; stamens with connective projecting beyond thecae; leaves strongly decurrent; corolla purple-violet or white;

Symphytum tuberosum aggr.: rhizome horizontal or oblique, tuberous, with alternate thick (tuberous) and thin portions; mericarps (“nutlets”) verrucose or wrinkled; stamens with connective not projecting beyond thecae; leaves not or shortly decurrent; corolla pale yellow.

As can be concluded from the detailed descriptions of *S. officinale* and *S. tuberosum* published by Berchtold and Opiz (1839), Opiz was well aware of the differences between those two species aggregates. All of the distinguishing features of those groups were correctly described by him except for the differences in connective length that have not been explicitly mentioned. *Symphytum microcalix* was described by Opiz as having fusiform rhizome (Opiz used the term “möhrenförmig” that can be translated as “carrot-shaped”, both for *S. officinale* and *S. microcalix*), narrowly decurrent cauline leaves and white flowers (whereas flowers of *S. tuberosum* were described by Opiz as pale yellow). Connective and fruit features have not been mentioned in the original description of *S. microcalix*. Nevertheless, the description provided in the protologue, in particular, the vertical fusiform (“carrot-shaped”) rhizome without tuberous thickenings, strongly indicates that the species described by Opiz most probably belongs to the *S. officinale* species complex. Furthermore, Opiz compared his species with *S. officinale*, *S. bohemicum* and *S. patens*, i.e. with the taxa belonging to *S. officinale* aggr., but no attempt has been made to compare it with *S. tuberosum*. Notably, Čelakovský (1871), who apparently had an opportunity to examine the

original material of *S. microcalix*, also reduced it to a variety of *S. officinale*. Additionally, according to the protologue, *S. microcalix* was collected by Opiz in wet meadows. This is a typical habitat of the representatives of *S. officinale* aggr. (Kobrlóvá, 2017, 2022), whereas taxa of *S. tuberosum* aggr. are predominantly forest plants growing in the Czech Republic in deciduous woodlands or occasionally (*S. tuberosum* subsp. *angustifolium* (A. Kern.) Nyman) in semi-dry grasslands (Kobrlóvá et al., 2016b).

It seems most plausible that plants described by Opiz as *S. microcalix* represent an anomalous (aberrant) form of *S. bohemicum*. Plants of *S. bohemicum* are usually slenderer than *S. officinale*, with narrower wings formed by decurrent cauline leaves (Kobrlóvá, 2022). Those differences from *S. officinale* were indeed highlighted in the original description of *S. microcalix*. Relative length of anthers and filaments is an additional distinguishing feature specifically emphasized by Opiz. According to the protologue, filaments of *S. microcalix* were nearly equaling anthers. As filaments of both *S. officinale* and *S. tuberosum* are normally much shorter than anthers, it seems likely that Opiz described an aberrant deviating plant. A similar opinion was expressed by Čelakovský (1871), who linked abnormal length of filaments to the shorter than normal length of the corolla tube in *S. microcalix*, and further added that it was unclear whether the variety described by Opiz occurred constantly and frequently within certain populations or if such plants emerged only sporadically among normal ones.

It remains uncertain why the name *S. microcalix* was applied by Dobrochaeva (1981) in a different sense, namely to plants from *S. tuberosum* aggr. Notably, Dobrochaeva (1968) provided a discussion on the previously published names that might be potentially applicable to members of *S. tuberosum* aggr. naturally occurring in Ukraine, but the name *S. microcalix* has not been mentioned there. Furthermore, the type locality of *S. microcalix* was cited by Dobrochaeva (1981) as “In Laubwäldern an der Ufern [des] Dniester bei Czernelica”. The same type citation was later repeated by Krytzka et al. (2000). This citation is obviously erroneous. As discussed above, the only original material of *S. microcalix* cited in the protologue was collected by Opiz in the vicinity of Pardubice. The citation used in Dobrochaeva (1981) in fact corresponds to the type locality of *Symphytum foliosum* Rehm (1868). Thus, there is no reason to assume that any type

material of *S. microcalix* was collected in the territory of Ukraine. Additionally, there is an apparent conflict between the type locality of *S. microcalix* (Pardubice in the Czech Republic) on one hand and the known distribution range of *S. microcalix* and its status as an endemic species of Ukraine as outlined in Dobrochaeva (1981) on the other hand.

Taking into account all of the above considerations, it is concluded that the name *S. microcalix* Opiz is neither applicable to plants of *S. tuberosum* aggr. occurring in the Podillya region of Ukraine nor to any other representatives of the *S. tuberosum* species complex. However, finding the nomenclaturally and taxonomically correct name for the taxon listed as “*S. microcalyx*” in the contemporary Ukrainian botanical literature is not a trivial task. Providing an answer to this question is beyond the scope of the current publication as it should be addressed in a broader context of the taxonomy of the *S. tuberosum* species complex over its entire distribution range. Further studies involving a combination of morphometric, cytological and molecular analyses might be required to resolve intricate relationships within *S. tuberosum* aggr. Some of the existing taxonomic and nomenclatural issues within this species aggregate are discussed below.

Overview of the species complex *Symphytum tuberosum* aggr.

As currently understood, the species complex *S. tuberosum* is widely distributed in Europe from the British Isles and the Iberian Peninsula to the Eastern Carpathians, the Podillya region of Ukraine, Moldova, Balkan Peninsula and northwestern Turkey. Members of the complex show great variation in their ploidy level (Murín, Májovský, 1982), with the morphological differences between different cytotypes and their geographical distribution not being satisfactory resolved yet. This situation is reflected in the complicated taxonomy and nomenclature within the complex (Table 1).

The founding species of this aggregate, *S. tuberosum* L., was described by Carl Linné in the first edition of his “Species Plantarum” in 1753. Several names assignable to this species complex were published in the 19th century (e.g., *S. mediterraneum* W.D.J. Koch, *S. angustifolium* A. Kern., *S. nodosum* Schur, *S. foliosum* Rehmman, *S. gussonei* F.W. Schultz). However, all those species were described from areas located at the limits of the continuous

distribution of *S. tuberosum* aggr., and they were predominantly considered as local forms of limited distribution. Despite the description of those species, the status of *S. tuberosum* as a single and fairly uniform species has remained largely unquestioned, and little attention was given to its intraspecific variation at that time. At the beginning of the 20th century, the vast majority of plants from large areas of West, Central and East Europe were still regarded as belonging to one and the same species, i.e. *S. tuberosum*. This view is reflected in the revision of Bucknall (1913), who treated *S. tuberosum* as a species with very broad distribution: “From Britain, France and Spain to Turkey, and from Germany and S.W. Russia to Italy and Greece”. However, the concept of *S. tuberosum* as a fairly uniform species showing little variation over its distribution range has been challenged by Pugsley (1931). He was the first author who draw attention to the morphological heterogeneity within the species *S. tuberosum* as circumscribed by earlier authors. Pugsley pointed out that plants of *S. tuberosum* from West Europe (France, Spain and the British Isles) show remarkable morphological differences from plants known under the same name but occurring further eastwards. Plants from West Europe are generally taller and stouter, with thicker and closely spaced tuberous rhizomes; their cauline leaves are narrower and more numerous (6–12). In contrast, plants from Central and East Europe are lower and slenderer, with longer and thinner rhizomes; cauline leaves are broader and fewer (3–6). Importantly, Pugsley examined original specimens of *S. tuberosum* from the Linnaean herbarium (LINN) and came to the conclusion that they correspond to the western morphotype with narrow leaves. As a consequence, he applied the Linnaean name *S. tuberosum* exclusively to western plants with narrower cauline leaves. Pugsley was aware of earlier names published for the representatives of *S. tuberosum* species complex from Central and Eastern Europe (e.g., *S. angustifolium*, *S. nodosum* and *S. foliosum*). However, in his opinion, none of those names could be applied with confidence to the Central European morphotype of *S. tuberosum* with broader leaves. Thus, he described a new species, *S. leonhardtianum* Pugsley, and designated as its type the specimen collected by Kerner in Haltertal near Vienna, Austria.

The concept of dividing *S. tuberosum* into two geographical races was generally followed by later

Table 1. Treatment of the *Symphytum tuberosum* species complex by selected authors

Reference	Accepted taxa and their distribution ranges
Bucknall, 1913	<ol style="list-style-type: none"> <i>Symphytum tuberosum</i> L. (including <i>S. foliosum</i> Rehmann) — western, central and southern Europe <ol style="list-style-type: none"> <i>S. tuberosum</i> var. <i>angustifolium</i> (A. Kern.) Buckn. — Hungary, Galicia (nowadays western Ukraine) <i>Symphytum mediterraneum</i> W.D.J. Koch — France <i>Symphytum gussonei</i> F.W. Schultz — Sicily, Galicia (nowadays western Ukraine); the latter occurrence cited with a question mark.
Pugsley, 1931	<ol style="list-style-type: none"> <i>Symphytum tuberosum</i> — France, Spain, Italy and the British Isles <i>Symphytum leonhardtianum</i> Pugsley — central and southern Europe from France and Italy eastwards <ol style="list-style-type: none"> <i>S. leonhardtianum</i> var. <i>longifolium</i> (Beck) Pugsley — Trencsén (nowadays western Slovakia) <p><i>Symphytum mediterraneum</i>, <i>S. angustifolium</i>, <i>S. nodosum</i>, <i>S. foliosum</i> and <i>S. gussonei</i> have been mentioned by Pugsley without drawing definitive conclusions on their taxonomic status. <i>Symphytum mediterraneum</i> was regarded as doubtful due to the absence of the type material, and <i>S. foliosum</i> was considered as a possible hybrid between <i>S. officinale</i> and <i>S. tuberosum</i>.</p>
Dobrochaeva, 1968	<ol style="list-style-type: none"> <i>Symphytum tuberosum</i> — western Europe <i>Symphytum leonhardtianum</i> — central Europe <i>Symphytum besseri</i> Zaver. — Podillya region of Ukraine <i>Symphytum popovii</i> Dobrocz. — the Ukrainian Carpathians and adjacent regions <p><i>Symphytum mediterraneum</i>, <i>S. angustifolium</i> and <i>S. gussonei</i> are not discussed by Dobrochaeva. <i>Symphytum foliosum</i> is treated as a hybrid between <i>S. officinale</i> and <i>S. tuberosum</i> s. l. <i>Symphytum nodosum</i> is mentioned without drawing conclusions on its taxonomic status.</p>
Pawłowski, 1972	<ol style="list-style-type: none"> <i>Symphytum tuberosum</i> L. <ol style="list-style-type: none"> <i>S. tuberosum</i> subsp. <i>tuberosum</i> — western Europe <i>S. tuberosum</i> subsp. <i>nodosum</i> (Schur) Soó (including <i>S. leonhardtianum</i>, <i>S. popovii</i>, <i>S. tuberosum</i> subsp. <i>angustifolium</i>) — central and southeastern Europe <i>Symphytum gussonei</i> — Sicily <p><i>Symphytum mediterraneum</i> is synonymized with <i>S. tuberosum</i> without being assigned to one of the two subspecies.</p>
Murín, Májovský, 1982	<ol style="list-style-type: none"> <i>Symphytum mediterraneum</i> ($2n = 144$) — western Europe (corresponds to <i>S. tuberosum</i> of previous authors) <i>Symphytum tuberosum</i> (including <i>S. leonhardtianum</i>) ($2n = 96$) — central Europe <i>Symphytum angustifolium</i> ($2n = 32$) — Hungary and Slovakia <i>Symphytum gussonei</i> — Sicily <p><i>Symphytum nodosum</i> is mentioned as a taxon of uncertain status.</p>
Valdés, von Raab-Straube, 2011–onward	<ol style="list-style-type: none"> <i>Symphytum tuberosum</i> (including <i>S. mediterraneum</i>) <ol style="list-style-type: none"> <i>S. tuberosum</i> subsp. <i>tuberosum</i> (including <i>S. ambiguum</i> Pau) — Spain, France, the British Isles, Germany, Switzerland, Slovakia, Italy (questionable) <i>S. tuberosum</i> subsp. <i>angustifolium</i> (including <i>S. leonhardtianum</i>, <i>S. nodosum</i>, <i>S. popovii</i>) — Albania, Austria, Bulgaria, Croatia, Czech Republic, France, Germany, Greece, Hungary, Italy, Moldova, Poland, Romania, Serbia, Slovakia, Slovenia, Switzerland, Turkey, Ukraine (Crimea only) <i>Symphytum gussonei</i> — Sicily <i>Symphytum besseri</i> — Ukraine <i>Symphytum microcalyx</i> — Ukraine.
POWO, 2024	<ol style="list-style-type: none"> <i>Symphytum tuberosum</i> <ol style="list-style-type: none"> <i>S. tuberosum</i> subsp. <i>tuberosum</i> (including <i>S. leonhardtianum</i>, <i>S. mediterraneum</i>, <i>S. minus</i> Bubani, <i>S. tuberosum</i> var. <i>grandiflorum</i> Sennen, <i>S. tuberosum</i> var. <i>variegatum-superbum</i> J. Dix) — Austria, France, Germany, Great Britain, Spain (incl. Balears) <i>S. tuberosum</i> subsp. <i>angustifolium</i> (including <i>S. foliosum</i>, <i>S. nodosum</i>, <i>S. popovii</i>) — Albania, Austria, Belarus, Bulgaria, Czechoslovakia, Germany, Greece, Hungary, Italy, Poland, Romania, Switzerland, Turkey, Ukraine, Yugoslavia <i>Symphytum gussonei</i> — Sicily <p>Both <i>S. besseri</i> and <i>S. microcalyx</i> are placed in the synonymy of <i>S. officinale</i>.</p>

authors. However, those races were predominantly given the rank of subspecies instead of the specific rank proposed by Pugsley. Consequently, the western race was recognized as the type subspecies, *S. tuberosum* subsp. *tuberosum*, whereas the eastern race appeared under the names *S. tuberosum* subsp. *nodosum* (Schur) Soó (Pawłowski, 1972; Wickens, 1978) or *S. tuberosum* subsp. *angustifolium* (A. Kern.) Nyman (Stearn, 1985; Bottega, Garbari, 2003). However, not all authors accepted the interpretation of specimens from the Linnaean herbarium proposed by Pugsley (1931) and, consequently, some botanists have questioned the application of the Linnaean name, *S. tuberosum*, to plants from West European populations. Murín and Májovský (1982) argued that the type specimens of *S. tuberosum* from the Linnaean herbarium are incomplete as they are represented solely by upper fragments of flowering shoots and do not include lower parts of stems and rhizomes. For this reason, those authors believed that type specimens cannot be unambiguously assigned neither to the western nor to eastern race of *S. tuberosum* s. l. Additionally, the origin of the type specimens in the Linnaean herbarium remains unknown. The above authors also pointed out that the only locality indicated by Linné in the protologue of *S. tuberosum* was southern Germany (“*Habitat in Germania australi*”). Thus, Murín and Májovský (1982) came to the conclusion that the name *S. tuberosum* in a narrow sense should be applied to the eastern race, as it is the only race known to occur in Germany. This point of view was recently followed by Koblrová et al. (2016a), who have applied the name *S. tuberosum* subsp. *tuberosum* to the eastern subspecies. At the same time, numerous authors continue using the name *S. tuberosum* subsp. *tuberosum* for the western subspecies (Rodríguez Gracia, Castroviejo, 2012; Jäger, 2017). Thus, there are two conflicting opinions on the identity of the type specimen of *S. tuberosum*, and the taxonomy within this species complex can only be stabilized when this controversy is resolved. Possible solutions for this taxonomic issue include assigning an epitype or conserving the name *S. tuberosum* with a new conserved type of the known origin and ploidy level (see below for the importance of the ploidy level in this species complex). The conservation of the name *S. tuberosum* with the conserved type might be a preferred option, as it would provide a nomenclaturally binding solution. For the purposes of nomenclatural stability, it might

be advisable to fix the application of the Linnaean name to the western race, to which it has been traditionally applied by the majority of authors since the revision by Pugsley (1931).

Polyploidy within *Symphytum tuberosum* aggr.

Another important aspect that contributed to the taxonomic complexity of the species aggregate of *S. tuberosum* is that it encompasses a great diversity of cytotypes and ploidy levels. Chromosome numbers reported so far for representatives of *S. tuberosum* aggr. include $2n = 18, 32, 64, 72, 96, 120, 144$ (Rice et al., 2015). Out of those, the chromosome number $2n = 18$ has been reported only once by Tarnavski (1948), and this old record is in need of verification. Additionally, a recent report of $2n = 24$ for *S. tuberosum* from Turkey (Inceer et al., 2007) might be in fact referable to *S. ibericum*, as the investigated material was collected in the region of Trabzon, where *S. ibericum* is relatively common (and the chromosome number $2n = 24$ has been reported for this species earlier), whereas *S. tuberosum* has not been reported before from that area (Wickens, 1978). Notably, the chromosome number $2n = 144$ is the highest reported value for the entire family *Boraginaceae* (Weigend et al., 2016).

The reported chromosome numbers (except for $2n = 18$) agree with the proposed basic chromosome number for *S. tuberosum* $x = 8$ (Murín, Májovský, 1982). Thus, ploidy levels in the investigated populations correspond to $4x, 8x, 9x, 12x, 15x$ and $18x$. The existence of plants with odd numbers of chromosomal sets ($9x$ and $15x$) is quite remarkable, as those are expected to encounter problems with the segregation of chromosomes in meiosis due to the chromosomal imbalance (Shepherd, 2017). It is not known whether $9x$ and $15x$ *S. tuberosum* plants are fertile and if they are able to produce viable seeds. Plants with $2n = 120$ potentially could arise from hybridization between plants with $2n = 96$ and $2n = 144$. This hypothesis is indirectly supported by their geographic distributions — such plants have been reported only from France and Italy (Jaarsma et al., 1990; Bottega et al., 2001), i.e., the contact zone between the distribution areas of dodecaploids and octodecaploids. However, as detailed information on plants with $2n = 120$ is lacking, their tentative hybrid nature requires verification. In addition to more frequent ploidy levels listed above,

several minor ploidy levels (e.g., $6x$, $10x$, and $14x$) have been reported by Kobrlová et al. (2016a) without exact chromosome counts. Those ploidy levels were found only in a few individual plants growing in populations dominated either by tetraploids ($4x$) or by dodecaploids ($12x$), and they never formed pure stands.

A certain pattern of geographic distribution of individual cytotypes is apparent from the available data. Thus, tetraploids ($2n = 4x = 32$) are known from the Czech Republic, Slovak Republic and Hungary (Murín, Májovský, 1982; Kobrlová et al., 2016a); octaploids ($2n = 8x = 64$) — from Bulgaria, Greece, and Turkey (van Loon, Oudemans, 1982; Markova, 1983; Jaarsma et al., 1990); nonaploids ($2n = 9x = 72$) have been reported only from Bulgaria (Markova, Ivanova, 1970); dodecaploids ($2n = 12x = 96$) have the widest distribution area and are known from Germany, Austria, Czech Republic, Slovak Republic, Poland, Hungary, Slovenia, Italy and Spain (Grau, 1968; Luque Palomo, 1982; Murín, Májovský, 1982; Jaarsma et al., 1990; Kobrlová et al., 2016a, 2018); plants with $2n = 15x = 120$ occur in Italy and France (Jaarsma et al., 1990; Bottega et al., 2001), and octodecaploids ($2n = 18x = 144$) have been reported from France and Italy (Grau, 1968; Jaarsma et al., 1990).

As discussed by Murín and Májovský (1982), at least three cytotypes of *S. tuberosum* aggr. (tetraploids, dodecaploids and octodecaploids) can be characterized morphologically and show certain ecological preferences. Octodecaploid plants ($2n = 144$) match the western race (subspecies), whereas dodecaploids ($2n = 96$) largely correspond to the eastern race (subspecies) as defined by Pawłowski (1972). In agreement with that, dodecaploid plants were reported from the type locality of *S. leonhardtianum* (Kobrlová et al., 2018). However, correct naming of those two subspecies depends on the interpretation of the Linnaean type material, and their nomenclature can only be stabilized once the application of the Linnaean name is fixed. In addition to those two races that received wide recognition following the publication of Pugsley (1931), Murín and Májovský (1982) convincingly showed the existence of an additional morphologically distinct race represented by tetraploid plants. They associated this tetraploid race with the taxon previously described as *S. angustifolium* A. Kern. (1863). The type of *S. angustifolium* was collected by Kerner in the Pilis Mountains (northern Hungary). Before the

publication of Murín and Májovský (1982), those plants have been largely considered being an aberrant form of the eastern race (Stearn, 1985). However, as they differ in their ploidy level, morphological features, ecological preferences and have defined distribution areas, they might deserve the status of a distinct subspecies (Kobrlová et al., 2016a). As a consequence, the application of the name *S. tuberosum* subsp. *angustifolium* should be restricted to the tetraploid plants, and not to be extended to the eastern subspecies as a whole (as it is often the case, e.g., Valdés and von Raab-Straube, 2011–onward; POWO, 2024), which is largely represented by dodecaploid plants. Thus, if the traditional application of the name *S. tuberosum* subsp. *tuberosum* to the western octodecaploid race is maintained, a different name needs to be found for the dodecaploid plants instead of *S. tuberosum* subsp. *angustifolium*. The first option that comes into question is the name *S. tuberosum* subsp. *nodosum* based on *S. nodosum* Schur. In fact, the name had been used in that sense before by some authors (Pawłowski, 1972; Wickens, 1978). However, *S. nodosum* was described by Schur from Romania and, as noted by Murín and Májovský (1982), dodecaploid plants have not yet been reported from that country. At the same time, the type of *S. nodosum* could not be traced so far (Cecchi, Selvi, 2015). Should it be shown by future studies that the name *S. tuberosum* subsp. *nodosum* is not applicable to dodecaploid race, the next name in the chronological order would be *S. leonhardtianum*. The latter name is undoubtedly referable to Central European dodecaploid plants, as shown by Kobrlová et al. (2018). However, this name was published at the rank of species, and a new combination will be needed if the dodecaploid plants are treated at the subspecies rank. There is currently no information on the morphological distinctiveness of other cytotypes of *S. tuberosum* and, consequently, no names have been proposed for them. In this respect, octoploid plants reported from Bulgaria, Greece and Turkey and not known elsewhere might deserve detailed investigation.

Naming of Ukrainian representatives of *Symphytum tuberosum* aggr.

Ukrainian botanists initially followed the view of Pugsley (1931) and referred all Ukrainian populations of *S. tuberosum* aggr. to *S. leonhardtianum* (Barbarych, 1950; Dobrochaeva, 1957). However,

Zaverucha (1962) published the description of a new species, *S. besseri* Zaver. based on material collected in the vicinity of Kremenets (Ternopil Region, Ukraine). He distinguished this new species from West European *S. tuberosum* and from Carpathian plants, which he referred to as *S. popovii* Dobrocz., a name not yet validated at the time of Zaverucha's publication. A few years later, Dobrochaeva (1968) validly published the name *S. popovii* Dobrocz., which she considered being distinct from *S. leonhardtianum*. *Symphytum popovii* was characterized by Dobrochaeva as a forest plant of the Ukrainian Carpathians, but, somewhat unexpectedly, a specimen collected in Ternopil Region (Ukraine) has been chosen as the type. In the same publication, Dobrochaeva (1968) provided a detailed discussion of the names that might be potentially applicable to Ukrainian plants of *S. tuberosum* aggr. However, the name *S. angustifolium* A. Kern. has been regrettably omitted in that discussion. In her following treatment of *S. tuberosum* aggr., Dobrochaeva (1981) applied the name *S. popovii* to Carpathian broad-leaved forest plants, but the name *S. besseri* was placed in the synonymy of *S. microcalix* Opiz. As discussed above, the name *S. microcalix* is not applicable to any taxon within *S. tuberosum* aggr. Nevertheless, later authors largely followed the nomenclature proposed by Dobrochaeva (1981) and listed two species of the *S. tuberosum* aggr. for the flora of Ukraine, i.e., *S. popovii* and *S. microcalix* (the latter as "*S. microcalyx*"). In this respect, the *Euro+Med* treatment (Valdés, von Raab-Straube, 2011–onward) stands out as it accepts both *S. microcalix* and *S. besseri* as two distinct species supposedly endemic to Ukraine, whereas the name *S. popovii* is placed in the synonymy of *S. tuberosum* subsp. *angustifolium*, but its distribution area within Ukraine is erroneously shown as being limited to Crimea, from where no representatives of the *S. tuberosum* species complex are known.

The name *S. foliosum* Rehmman had been occasionally applied to the eastern race of *S. tuberosum* aggr., and it is still listed as a synonym of *S. tuberosum* subsp. *angustifolium* in POWO (2024). The name was published by Rehmman (1868) based on materials collected by Hölzl near Chernelytsya (spelled as Czernelica in the protologue), nowadays within Ivano-Frankivsk Region of Ukraine. Later collections distributed under the name *S. foliosum* in the series "Flora exsiccata Austro-Hungarica" (No. 3709) and "Flora polonica exsiccata" (No.

851.a) indeed agree with the concept of *S. tuberosum* subsp. *angustifolium* (Pugsley, 1931; Pawłowski, 1961; Smejkal, 1978). However, the description provided by Rehmman in the protologue gave some indications that the described plants might be of hybrid origin (Pugsley, 1931; Popov, 1953). Pawłowski was able to locate a specimen from the original Hölzl's gathering (in fact, the only collection mentioned in the protologue) in the herbarium of the Polish Academy of Sciences in Krakow (KRAM). After examination of Hölzl's specimen, Pawłowski came to the conclusion that it indeed represents a hybrid between *S. tuberosum* subsp. *nodosum* (i. e., the eastern race of *S. tuberosum*) and *S. officinale* (Pawłowski, 1961). The concept of *S. foliosum* as a taxon of the hybrid origin was followed by Dobrochaeva (1968) and Smejkal (1978).

The recent publications of Koblrová et al. (2016a, 2016b, 2018) have greatly contributed to the understanding of the diversity within *S. tuberosum* species complex in Central Europe. It has been convincingly demonstrated that this complex is represented in Central Europe by two dominant cytotypes (4x and 12x) that are morphologically and ecologically distinct and have distinct distribution patterns. Arguably, both cytotypes are best treated at the rank of distinct subspecies. Koblrová and coauthors have analyzed *S. tuberosum* aggr. populations from Austria, Czech Republic, Slovak Republic, Hungary and Poland. A critical comparison of Ukrainian populations with material from other Central European countries seems to be appropriate to establish their taxonomic status.

It should be noted that Carpathian plants known as *S. popovii* show considerable morphological similarity with Central European dodecaploid plants. According to the protologue (Dobrochaeva, 1968), the differences between *S. popovii* and *S. leonhardtianum* are merely quantitative: broader cauline leaves (length to width ration 2.2 : 1 in *S. popovii* versus 3 : 1 in *S. leonhardtianum*), narrower corolla tube (up to 4 mm in *S. popovii* versus 4.5–5.0 mm in *S. leonhardtianum*) and narrower mericarps (2–3 mm in *S. popovii* versus 3.5 mm in *S. leonhardtianum*). The holotype of *S. popovii* (KW000008138, online image!) indeed is represented by a plant with relatively broad cauline leaves. However, the reported leaf length to width ratio of 2.2 : 1 falls well within the variation range observed for this character in natural populations of dodecaploid plants from Central Europe

(Kobrolová et al., 2016a). Additionally, the plants observed by the author in Zakarpattya (Transcarpathia) Region of Ukraine and formally referable to *S. popovii* had narrower cauline leaves than holotype of *S. popovii* (Fig. 3) and were morphologically indistinguishable from Central European dodecaploids presented in the publications of Murín and Májovský (1982) and Kobrolová et al. (2016a). No published data on the natural variability of two other characters indicated by Dobrochaeva could be found in literature, and their significance should be critically re-evaluated. At the same time, narrow-leaved plants known either as “*S. microcalyx*” or as *S. besseri* resemble Central European tetraploids referable as *S. tuberosum* subsp. *angustifolium*. Neither Zaverucha (1962) nor Dobrochaeva (1968) made a direct comparison between those two taxa. However, the holotype of *S. besseri* (KW000008137, online image!) appears to be remarkably similar to the lectotype of *S. angustifolium* (WU0069897, online image!). The author nevertheless refrains from drawing any definitive conclusions about the identity of Ukrainian populations of *S. tuberosum* aggr. before their karyological status is determined. No data on chromosome counts or ploidy levels for Ukrainian populations of *S. tuberosum* aggr. could be traced in literature. However, Murín and Májovský (1982) have expressed an opinion that tetraploid plants of *S. tuberosum* aggr. might occur in Ukraine and, specifically, within populations growing in the Vihorlat area in Zakarpattya Region. Also, it appears reasonable to expect the occurrence of dodecaploid plants in Ukraine, as this cytotype is by far the most common in the neighboring countries of the Carpathian region (Poland, Slovak Republic and Hungary).

Conclusions

In conclusion, an attempt to resolve the identity of the name *S. microcalix* Opiz has been made in this publication. The history of the name has been reviewed. No extant original material for this name could be traced and, in all likelihood, the only Opiz’s specimen (or gathering) cited in the protologue has been lost. Analysis of the original description led to the conclusion that Opiz’s description is not applicable to any member of *S. tuberosum* species complex and the name *S. microcalix* should be placed in the synonymy of *S. bohemicum*.

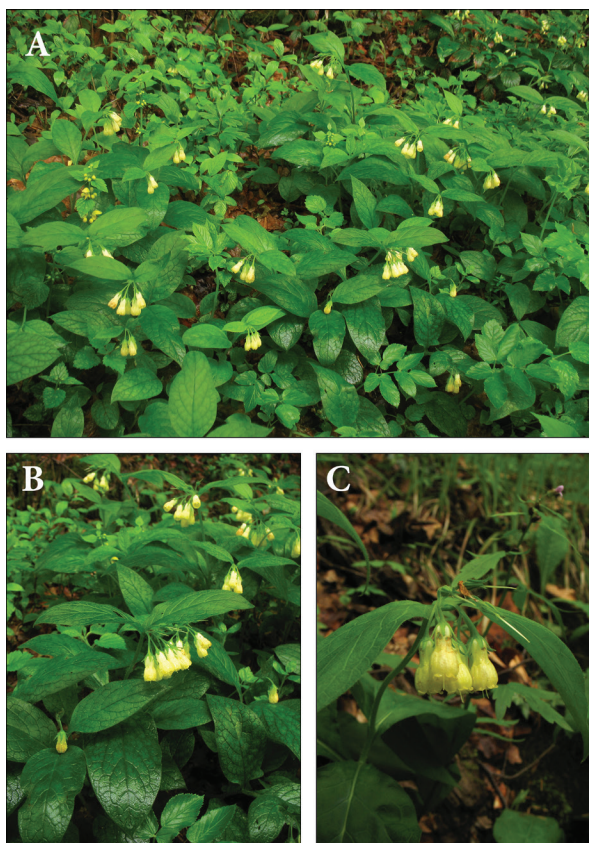


Fig. 3. Flowering plants of *Symphytum popovii* observed in the Kuziy Protected Area, part of Carpathian Biosphere Reserve (Rakhiv District, Zakarpattya (Transcarpathian) Region, Ukraine). A: flowering plants in their habitat; B: a flowering plant; C: the upper part of a flowering shoot with the inflorescence

Recent advances in nomenclature and taxonomy of the species complex have been reviewed with a special emphasis on the status of Ukrainian populations. It is concluded that the controversy surrounding the status of the Linnaean type of *S. tuberosum* has a destabilizing effect on the nomenclature of the entire group. Conservation of this name with a new conserved type that would affix the traditional application of the name to the octodecaploid race of *S. tuberosum* aggr. is proposed as a preferred solution towards nomenclatural stability. At the same time, the applicability of the name *S. nodosum* to dodecaploid plants within the species complex *S. tuberosum* aggr. needs to be evaluated. Two species described from Ukraine, *S. besseri* and *S. popovii*, are shown to have considerable morphological similarity with Central European tetraploid

and dodecaploid plants, respectively. A critical comparison of Ukrainian populations with populations from Central Europe is essential for establishing their taxonomic status. This comparison should be based on thorough morphometric and cytological analysis of plants from Ukrainian populations. It is important to include into such analysis the material from the type localities of the species described from the territory of Ukraine, i.e., *S. foliosum*, *S. popovii* and *S. besseri*. This publication is expected to attract interest of researchers to the intricate species complex *S. tuberosum* aggr. and in this way contribute to better understanding of its taxonomy and evolutionary history.

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Нотатки щодо таксономії видового комплексу *Symphytum tuberosum* (Boraginaceae) та щодо інтерпретації назви *S. microcalix*

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Реферат. Назва *Symphytum microcalix*, що була вперше запропонована Ф.М. Опіцем, у сучасних джерелах має дві різні інтерпретації — як синонім *Symphytum officinale* або ж як назва таксону з комплексу *Symphytum tuberosum*. Використання даної назви обговорюється на основі аналізу протологу, опублікованого Опіцем. Наводяться дані щодо походження автентичного матеріалу та нотатки щодо написання видового епітету. Наявні дані дозволяють зробити висновок, що рослина, описана Опіцем як *S. microcalix*, найімовірніше являла собою аномальний екземпляр *Symphytum bohemicum*, а її застосування до рослин з комплексу *S. tuberosum* є необґрунтованим. При обговоренні подальших номенклатурних і таксономічних проблем, пов'язаних з таксонами комплексу *S. tuberosum*, особлива увага приділена статусу популяцій рослин, що ростуть на території України.

Ключові слова: *Symphytum*, живокіст, історія ботаніки, номенклатура, Опіц, поліплоїдія