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Solidago ×*snarskisii* nothosp. nov. (Asteraceae) from Lithuania and its position in the infrageneric classification of the genus

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Abstract

A natural hybrid between the native *Solidago virgaurea* and the alien invasive *S. gigantea,* recorded in South Lithuania, is described as *S.* ×*snarskisii* nothosp. nov. A new nothosubsection, *Solidago* sect. *Solidago* nothosubsect. *Triplidago* notho-subsect. nov., is proposed to accommodate this hybrid and *S.* ×*niederederi*.

Key words: alien species, fertility, hybridization, native species, nothospecies, nothosubsection, reproduction.

Introduction

The process of natural hybridization may produce genotypes that establish new evolutionary lineages (Arnold & Hodges 1995). Judging by the wide distribution of allopolyploidy among plants, many species might be of direct hybrid origin or descended from a hybrid species in the recent past (Soltis & Soltis 1995). Interspecific hybridization between a native and an invading plant species or two invading species results in a new taxon (Abbot 1992). Further hybridization of new taxa with native ones can lead to the loss of genetic integrity of native populations (Huxel 1999, Kaljund & Leht 2013). For example, an extent of hybridization between native and alien species has been evaluated in Germany. The study revealed that 75 hybrids have been already registered and 59 further hybrids can be detected as both parental species occur in the country (Bleeker *et al.* 2007).

Natural interspecific hybrids are rather frequent between species within numerous genera as well as between species of different but closely related genera of Astereae (Nesom 1994a). Natural hybrids are particularly frequent in the genera *Symphyotrichum* Nees (1832: 135) and *Solidago* Linnaeus (1753: 878) (Nesom 1993, 1994b, Semple & Cook 2006).

The genus *Solidago* comprises about 100 species, most of which are native to North America, eight species occur in Mexico, four in South America, and six to ten species are native to Europe and Asia (Semple & Cook 2006). Over a dozen of hybrids between native species of the genus *Solidago* were described in North America (Semple & Cook 2006) and one hybrid, *S.* ×*niederederi* Khek (1905: 22), was described in Europe, which originates from crosses between the native *S. virgaurea* Linnaeus (1753: 880) and the alien *S. canadensis* Linnaeus (1753: 878).

In the most widely recognized infrageneric classification of the genus *Solidago* as proposed by Nesom (1993) with later amendments and corrections (Semple & Cook 2006, Semple & Gandhi 2004), two sections (*S.* sect. *Solidago* and *S.* sect. *Ptarmicoidei* (House 1924: 710) Semple & Gandhi (2004: 756) were accepted. *Solidago* sect. *Solidago* includes most species and is divided into 10 subsections.

In September 2014, during the investigation on the population structure of *S. gigantea* Aiton (1789: 211) in Trakai district (South Lithuania), we paid attention to several individuals growing on the margin of a colony. These plants had much larger capitula and a different shape of synflorescence compared to *S. gigantea*. We initially presumed that these unusual *Solidago* plants could be *S.* ×*niederederi*, which is rather frequent in the habitats occupied by *S. virgaurea* and *S. canadensis* s.l. However, a close study of the collected specimens enabled us to conclude that they significantly differed from *S.* ×*niederederi*. Furthermore, one of the parental species of *S.* ×*niederederi*, *S. canadensis* s.l., was not recorded in the vicinity of that locality, neither naturalized nor in cultivation. After thorough studies of the specimens, we concluded that these unusual plants represent an undescribed hybrid between *S. gigantea* and *S. virgaurea*.

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Materials and methods

The investigations on hybrid plants in the field and under laboratory conditions were performed in September and October 2014 and in September 2015. The height of shoots and the length of synflorescence were measured on live plants during field studies, whereas characteristics of leaves were assessed on dry specimens. The length of the involucre, ligular and tubular florets and pappus was measured on fresh material. In each population of the hybrid and its parental species, five synflorescences were taken from different culms and six capitula from different parts of each of the synflorescence were selected for the analysis. The number of ligular and tubular flowers were counted in each of the selected capitulum as well as one ligular floret, one tubular floret and one pappus of the tubular floret were measured using binocular microscope with precision of 0.1 mm. The material for the evaluation of seed-set of hybrid plants between *S. gigantea* and *S. virgaurea* was collected in mid-October 2014 and at the end of September 2015. A total of thirty capitula were collected each year from five generative shoots and were put into separate paper bags for further analysis.

The examined specimens of *Solidago* species used for comparison (see *Additional specimens examined*) are deposited at the Herbarium of the Institute of Botany of the Nature Research Centre (BILAS) in Vilnius, Lithuania.

Taxonomic treatment

1. ***Solidago* ×*snarskisii*** Gudžinskas & Žalneravičius, **nothosp. nov.** (Figs. 1, 2A, 3A, 4) (*Solidago gigantea* Aiton × *S. virgaurea* Linnaeus)

Holotype:—LITHUANIA. Trakai district, Aukštadvaris Regional Park, environs of Zabarauskai village, in an abandoned meadow on the edge of forest (54.555191° N; 24.512987° E), 13 September 2014, *Z. Gudžinskas & E. Žalneravičius 76801* (generative shoot) and *76802* (vegetative shoot) (BILAS, on two cross-referenced sheets). **Isotypes**:—*Z. Gudžinskas & E. Žalneravičius 76803, 76804* (BILAS).

Perennial clonal herbs with long and short rhizomes, forming sparse culms or clusters. Generative shoots 140–180 cm tall, erect, dark-purplish or brown-purplish; vegetative shoots 50–100 cm tall, with numerous terminal leaves crowded into a rosette-like structure. The distal part of the stem glabrous and distinctly bluish pruinose, the apical part with very sparse hairs, branches of the synflorescence moderately densely hairy. Both surfaces of leaves glabrous, except the mid-vein and leaf-edge which is covered with sparse 0.1–0.4 mm long hairs. Lower cauline leaves subpetiolate, all or almost all withered at anthesis. Middle cauline leaves lanceolate, 10–15 cm long and 2–3 cm wide, distinctly sharply serrate, three-nerved. Upper cauline leaves lanceolate or linear lanceolate, 4–6 cm long and 0.5–1.5 cm wide, gradually reducing towards the synflorescence, with sparsely serrate or entire margins. Synflorescence paniculiform, 25–33 cm long and 6–12 cm wide, with upright branches. Peduncles 0.5–1.0 cm long, strigillose, with 3–6 linear-lanceolate 1.5–4 mm long bracteoles. Involucres campanulate, 4–6 mm long and 5–7 mm wide. Phyllaries arranged in 3–4 series. Outer phyllaries lanceolate, 2–3 mm long, sparsely pilose at base. Inner phyllaries linear-lanceolate, 4–5 mm long, glabrous or almost glabrous. Ligular florets yellow, (10)11–14(15) in a capitulum, their laminae 6.0–7.0 mm long and 0.8–1.8 mm wide. Tubular florets yellow, (11)12–18(20) in a capitulum, their corollas 4.2–5.2 mm long; corolla lobes are 0.8–1.2 mm long. Cypselae (undeveloped) 1.5–1.8 mm long, strigose. Pappi 3.5–4.0 mm long.

Etymology:—The epithet of the hybrid is dedicated to Povilas Snarskis (1889–1969), a professor of Vilnius University, for his notable contributions to the knowledge of plant diversity and distribution in Lithuania in the 20th century.

Phenology:—In Lithuania, *S.* ×*snarskisii* starts to flower at the beginning of August and continues until the middle of September; solitary capitula continue to flower to the end of September. *Solidago* ×*snarskisii* starts to flower almost simultaneously with *S. gigantea* and its flowering continues about two weeks longer, whereas *S. virgaurea* starts to flower about two weeks earlier than *S.* ×*snarskisii* and continues, depending on weather conditions, until the end of September or even until the middle of October.

Reproduction:—Production of viable seeds in *S.* ×*snarskisii* was not recorded. All achenes collected in 2014 and 2015 were empty. The hybrid reproduces by long and short rhizomes like its parental species *S. gigantea*, and, therefore, clones formed by vegetative reproduction can persist for a long time until conditions remain favourable.

FIGURE 1. Holotype of *Solidago ×snarskisii.*

FIGURE 2. Stem indumentum of *Solidago ×snarskisii* (A) and *Solidago ×niederederi* (B).

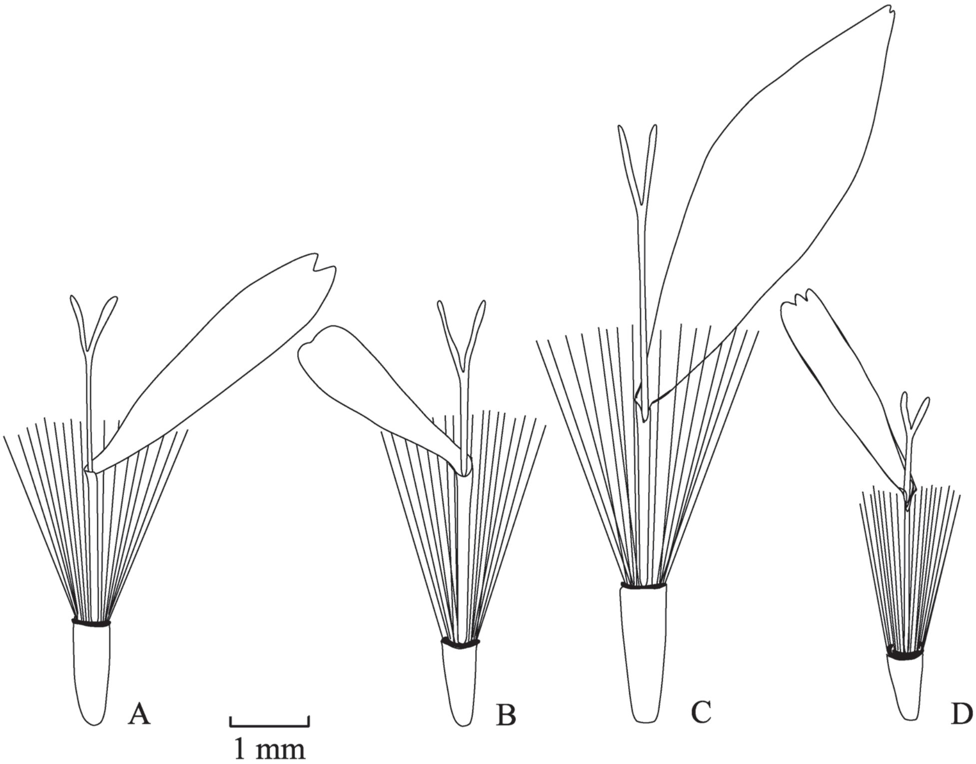

FIGURE 3. Ligular florets of *Solidago ×snarskisii* (A), *S. gigantea* (B), *S. virgaurea* (C) and *S. ×niederederi* (D) with pappi and fruits. Drawn from fresh material (see *Additional specimens examined*).

FIGURE 4. Vegetative shoot of *Solidago ×snarskisii* with condensed leaves on its apex forming a pseudorosette.

Population size:—In 2014, when *S.* ×*snarskisii* was first found, three culms were identified. One of the culms had five generative and three vegetative shoots; the other two were smaller, i.e. with two and one generative shoot and one and three vegetative shoots, respectively. In September 2015, we revisited the locality of the hybrid and recorded five culms of the generative stage of development. Culms registered in 2014 slightly expanded: the largest culm had 15 generative and three vegetative shoots, whereas two other culms had five and three generative as well as two vegetative shoots each. Two newly emerged culms were within a distance of five meters from the closest individual recorded in 2014; therefore, their emergence by means of vegetative reproduction and spread is excluded. The two new culms in 2015 probably reached the generative stage for the first time and were not noted during the investigation in 2014. One of these individuals had two generative and one vegetative shoots; another individual had a single generative shoot.

Diagnostic characters:—The hybrid *S.* ×*snarskisii* is similar to *S. gigantea* by the height and general appearance; however, its characters of capitula and florets are intermediate compared to the parental species (Table 1).

Solidago ×*snarskisii* is easily distinguished from *S. gigantea* by a paniculate synflorescence, with branches diverging at an acute angle. The synflorescence of *S. gigantea* is pyramidal or club-shaped with branches diverging at a wide angle. The capitula of *S.* ×*snarskisii* are significantly larger and the involucres are longer than those of *S. gigantea* (Table 1). The number of tubular florets in a capitulum of *S.* ×*snarskisii* is more than two times larger than in a capitulum of *S. gigantea*. The length and width of ligular florets of *S.* ×*snarskisii* is significantly larger than in *S. gigantea* (Table 1, Figure 3).

The differentiation between *S.* ×*snarskisii* and *S.* ×*niederederi* is more difficult. These hybrids primarily differ in stem characters. The stem of *S.* ×*snarskisii* is entirely glabrous and clearly bluish pruinose below the synflorescence (at least in fresh plants). The stem of *S.* ×*niederederi* is sparsely or moderately, occasionally densely hairy (Figure 2). *Solidago* ×*snarskisii* and *S.* ×*niederederi* also differ by the length of the involucre, the number of tubular florets in a capitulum and the length and width of ligular florets (Table 1, Figure 3). Another reliable character to differentiate *S.* ×*snarskisii* and *S.* ×*niederederi* is the ratio between the number of tubular and ligular florets in a capitulum. Tubular florets in well-developed capitula of *S.* ×*snarskisii* usually outnumber ligular florets (occasionally their numbers are equal), whereas in *S.* ×*niederederi* ligular florets always outnumber tubular florets.

TABLE 1. Comparison of selected morphological characteristics of a capitulum and florets of *Solidago* ×*snarskisii*, its parental species (*S. gigantea* and *S. virgaurea*) and *S.* ×*niederederi* (n=30; mean±SD). Differences of characteristics among taxa were evaluated by the results of ANOVA test. Values indicated by the same letter are significantly different (P<0.05).

Character	*S.* ×*snarskisii*	*S. gigantea*	*S. virgaurea*	*S.* ×*niederederi*
Length of the involucre (mm)	6.1±0.3[a]	4.6±0.3[a]	8.1±0.3[a]	5.5±0.2[a]
Number of ligular florets in a capitulum	12.6±0.8[a]	11.2±1.2[ab]	10.3±1.3[ab]	12.0±1.0[b]
Number of tubular florets in a capitulum	15.0±1.6[b]	6.6±1.2[ab]	15.4±2.8[a]	9.3±1.9[ab]
Length of ligular floret (mm)	6.5±0.1[a]	4.9±0.3[a]	10.8±0.7[a]	5.5±0.2[a]
Width of ligular floret (mm)	0.9±0.1[a]	0.7±0.1[a]	2.0±0.2[a]	0.5±0.1[a]
Length of tubular floret (mm)	4.6±0.2[a]	4.3±0.3[ab]	6.4±0.3[ab]	4.5±0.2[b]
Length of pappus (mm)	3.6±0.2[a]	3.0±0.1[ab]	5.2±0.2[ab]	3.7±0.2[b]

Habitat:—*Solidago* ×*snarskisii* was found growing together with one of the parental species, *S. gigantea*, in an abandoned mesic meadow, whereas another parental species, *S. virgaurea*, occupies a sandy xerothermic slope and the edge of the forest. The distance between the outermost margins of the *S. gigantea* colony and the population of *S. virgaurea* is about 50 meters.

2. ***Solidago*** sect. ***Solidago*** nothosubsect. ***Triplidago*** Gudžinskas & Žalneravičius, **nothosubsect. nov.** (*Solidago* sect. *Solidago* subsect. *Triplinerviae* × *Solidago* sect. *Solidago* subsect. *Solidago*)

Synflorescence paniculiform, its branches diverging from the axis at an acute angle. Leaves acutely serrate, with three distinct veins like in plants of *Solidago* sect. *Solidago* subsect. *Triplinerviae* (Torrey & Gray 1842: 222) Nesom (1993: 8). A characteristic feature of this nothosubsection is the formation of pseudorosettes on the apices of vegetative shoots (Figure 4) of both *S.* ×*snarskisii* and *S.* ×*niederederi*, which is never observed in *S. gigantea* or *S. canadensis*. Rosettes of leaves in *S. virgaurea* are usually formed at the ground level or on very short (1–3 cm high) vegetative shoots.

This nothosubsection includes all hybrids between species of *Solidago* sect. *Solidago* subsect. *Solidago* and *Solidago* sect. *Solidago* subsect. *Triplinerviae*. To date, two hybrids belonging to this subsection are known: *S.* ×*niederederi* and *S.* ×*snarskisii*.

Discussion

In the native range in North America, *S. gigantea* is usually represented by diploid, tetraploid and hexaploid races, however, occasionally triploid and pentaploid plants occur (Schlaepfer *et al*. 2008). In its invasive range in Europe and East Asia, only tetraploid plants are found (Schlaepfer *et al*. 2008, 2010). Studies on the ploidy level of *S. gigantea* in Lithuania also proved all plants to be tetraploids (2n=36) (Karpavičienė & Radušienė 2016). In various areas of the native distribution, *S. virgaurea* is a diploid (2n=18) (Kiełtyk & Mirek 2013). Therefore, *S. ×snarskisii* is a result of hybridization between tetraploid and diploid parental species and this fact can explain why no developed seeds were found in the investigated capitula.

Though hybrids between diploid and tetraploid species are sterile, sometimes such hybrids create opportunities for repeated hybridization. A good example of this was described in the British Isles. A triploid hybrid between the native tetraploid *Senecio vulgaris* Linnaeus (1753: 867) and the invasive diploid *S. squalidus* Linnaeus (1753: 869) is highly sterile, but has acted as a bridge for introgression and also in the formation of the allohexaploid *S. cambrensis* Rosser (1955: 228) (Abbott 1992, Lowe & Abbott 1996, 2015).

The formation of hybrids between insect-pollinated species depends on pollinators (Rieseberg 1997). Flowers of *Solidago* species are intensively visited by bees, bumblebees and other insects, therefore, formation of hybrids is possible in contact zones even if the ecology of the parental species slightly differs.

We suppose that the hybrid *S. ×snarskisii* was formed when flowers of *S. gigantea* (pollen-receptor) where pollinated by pollen of *S. virgaurea* (pollen-donor). Such presumption we have made because hybrid plants grow in a close proximity of a *S. gigantea* clone. A thorough study of *Solidago* plants enabled us to reveal no less than five individuals of *S. ×snarskisii* at the generative stage of development, which are separated by a distance from two to five meters. Significant distances among individuals enabled us to exclude the possibility of their clonal origin. Certainly, we cannot exclude the possibility that the maternal species of *S. ×snarskisii* is *S. virgaurea* and its flowers were pollinated by pollen of *S. gigantea*, which grows within a distance of ca. 50 meters. Seeds developed from cross-pollination might have been brought by wind to the proximity of the *S. gigantea* colony. However, investigations performed by Meyer & Schmid (1999) revealed that the main part of shed *Solidago* fruits fall down within a distance of several meters from parental plants and only a small fraction of fruits travel a significant distance.

Considering the number of recorded individuals of *S. ×snarskisii* in the locality, it is clear that cross-pollination of *S. gigantea* flowers with pollen of *S. virgaurea* is not a singular event. Under experimental conditions only 0.008% of produced alien *Solidago* seeds become established seedlings (Meyer & Schmid 1999) and even a lesser number of seedlings reach the generative stage. If this proportion is correct, more than 62,500 seeds need to be produced from cross-pollination between *S. gigantea* and *S. virgaurea* for five hybrid individuals to appear.

We suppose that the occurrence of *S. ×snarskisii* can increase in the future as it happened with *S. ×niederederi*. This hybrid was described in 1905 based on specimens from Austria (Khek 1905) and new records of *S. ×niederederi* were absent probably until 1920, when it was found in Austria (Pliszko 2015). Since the middle of the 20th century hybrid plants started to emerge in various European countries: Austria (Melzer 1984, Essl & Rabitsch 2002), France (Kerguélen 1999), Sweden and Denmark (Nilsson 1976), Britain (Stace 1991), Norway (Sunding 1989), Germany (Otto *et al*. 2005, Bleeker *et al*. 2007), Poland (Pliszko 2013), Lithuania (Karpavičienė & Radušienė 2016), etc. Though in many European countries *S. ×niederederi* is reported as rare, it is increasingly frequent and in some localities abundant in Lithuania.

The existence of *S. ×snarskisii* is probable in a number of localities where its parental species grow in a close proximity or in the same habitat, in fact through the whole range of *S. virgaurea* invaded by *S. gigantea*. In contact areas of both parental species attention should be paid to individuals with the capitula larger than are characteristic of *S. gigantea* and with an unusually shaped synflorescence.

Following the point of view of Pyšek *et al*. (2004), *S. ×snarskisii* should be considered as alien in Europe, because it originated by hybridization between a native and an alien species. To date, *S. ×snarskisii* can be evaluated as casual; however, it has a potential to naturalize.

Additional specimens examined. *Solidago gigantea*: Lithuania, Trakai district, Aukštadvaris Regional Park, environs of Zabarauskai village, in an abandoned meadow on the edge of forest (54.555191° N; 24.512987° E), 13 September 2014, Z. Gudžinskas & E. Žalneravičius (Nr. 76809).—*Solidago virgaurea*: Lithuania, Trakai district, Aukštadvaris Regional Park, environs of Zabarauskai village, on the edge of pine forest (54.555313° N; 24.512972° E), 26 September 2015, Z. Gudžinskas (Nr. 76810).—*Solidago ×niederederi*: Lithuania, Vilnius distr., northwestern outskirts of Pailgė village, in an abandoned xeromesic meadow, abundant (54.907076° N; 25.561001° E), 28 September

2015, Z. Gudžinskas (Nr. 76808).—*Solidago ×snarskisii*: Lithuania, Trakai district, Aukštadvaris Regional Park, environs of Zabarauskai village, in an abandoned meadow on the edge of forest (54.555191° N; 24.512987° E), 26 September 2015, Z. Gudžinskas (Nr. 76805, 76806, 76807; paratypes).

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