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New hybrid *Salix* × *setifera* (*Salicaceae*) from northern Yakutia

Новый гибрид *Salix* × *setifera* (*Salicaceae*) из северной Якутии

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Abstract. A new hybrid *Salix* × *setifera* Efimova, T. A. Poliak. et I. V. Belyaeva from northern Yakutia (Russia) is described and its characteristics are given. Hybrid individuals show diagnostic features of both parental species, *S. hastata* L. and *S. reptans* Rupr. Both vegetative and generative organs have intermediate characteristics. No plants with male flowers were found. Based on the detected nucleotide variability of the ITS rDNA region, the hybrid origin of *S.* × *setifera* was confirmed. A species-specific transversion (T→A) was detected in ITS2 for *S. reptans* and *S.* × *setifera*, which is absent in *S. hastata*. It is possible that the hybrid mentioned above occurs in areas where both parental species grow together in the tundra and forest-tundra of northern Eurasia.

Keywords: *Salix hastata, Salix reptans*, new hybrid, subarctic tundra, northern Eurasia, ITS-region, rDNA, single nucleotide polymorphism, species-specific transversion.

Аннотация. Приводится описание нового гибрида *Salix* × *setifera* Efimova, T. A. Poliak. et I. V. Belyaeva из северной Якутии (Россия) и обсуждаются его характеристики. Морфология гибридных растений демонстрирует промежуточные диагностические признаки генеративных и вегетативных органов обоих видов. Мужские особи не найдены. Обнаруженная нуклеотидная изменчивость области ITS рДНК подтверждает гибридное происхождение *S.* × *setifera*. В ITS2 *S. reptans* и *S.* × *setifera* обнаружена видоспецифичная трансверсия (T→A), отсутствующая у *S. hastata*. Возможно нахождение гибрида в местах совместного произрастания обоих родительских видов в субарктических тундрах и лесотундрах северной Евразии.

Ключевые слова: *Salix hastata*, *Salix reptans*, новый гибрид, субарктическая тундра, северная Евразия, ITS-регион, рДНК, однонуклеотидная замена, трансверсия.

Representatives of the genus *Salix* L. (*Salicaceae* Mirb.) are among the most polymorphic plants, widespread in the Northern Hemisphere. High intraspecific variability and frequent interspecific hybridization complicate the already complex taxonomy of this genus. Actual data on hybridization and introgression within the genus are given in multiple publications which point out the difficulties in identifying hybrids (Meikle, 1975; Belyaeva, 1998; Elven, Karlson, 2000; Hardig et al., 2000; Jessen, Lehman, 2000; Ohashi, 2001; Triest, 2001; Koropachinsky, Milyutin, 2006; Belyaeva, 2009; Efimova et al., 2009; Kailis, Eleftheriadou, 2011; Van Puyvelde, 2013; Efimova et al., 2015; Stace et al., 2015; Wu et al., 2015; Gramlich, Hörandl, 2016; Gramlich et al., 2016; Kuzovkina et al., 2016a, b; Belyaeva et al., 2018; Efimova et al., 2019; Belyaeva, 2020; Belyaeva et al., 2020; He et al., 2020; Wagner et al., 2020; Belyaeva et al., 2021; Wagner et al., 2021; Epanchintseva, Belyaeva, 2022; Wagner et al., 2023).

In August 2011, during an expedition to the delta of the River Lena studying the flora and vegetation of the region, a willow with an unusual combination of characters was found in a shrub-green-moss mixed community located on a terrace above the floodplain. The

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willows that were growing in the area belong to six different sections and two subgenera. The first subgenus, *Chamaetia* (Dumort.) Nasarow, is represented in the studied area by *S. nummularia* Andersson (sect. *Herbella* Ser.) and *S. reptans* Rupr. (sect. *Glaucae* Pax). The second subgenus, *Vetrix* Dumort., is represented in this area by *S. alaxensis* Coville (sect. *Villosae* (Andersson) Rouy), *S. hastata* L. (sect. *Hastatae* A. Kern.), *S. lanata* L. (sect. *Lanatae* (Andersson) Koehne) and *S. pulchra* Cham. (sect. *Phylicifoliae* Pax). The comparative morphological analysis of the unknown willow with all the other species mentioned above led us to conclude the hybrid origin of the willow in question because it has a unique combination of characters intermediate between *S. hastata* and *S. reptans*.

A. K. Skvortsov (1968, 1999) noted that the two subgenera, *Chamaetia* and *Vetrix*, to which the parental species of the new hybrid belong, are generally close to each other, and the boundary between them can be drawn only as a convention. He believed that subg. *Chamaetia* was not derived from the boreal groups of subg. *Vetrix*; sections of the former subgenus have a common root only with the most primitive sections of the latter, and their formation may have occurred in the highlands during pre-glacial times. The core of subg. *Vetrix* to which the first parental species, *S. hastata*, belongs consists mainly of forest, valley, and swamp species which generally do not grow beyond the northern taiga and forest-tundra, and are represented by the life forms of large trees, multi-stemmed trees and shrubs. The subgenus, *Chamaetia*, to which the second parent species, *S. reptans*, belongs is mainly composed of semi-prostrate and dwarf shrubs mostly having shorter shoots, narrowly adapted to extreme arctic conditions of tundra, forest-tundra and mountains. Some species of these two subgenera are found growing together in the forest-tundra and southern hypoarctic tundra, and hybridization between them is possible. *S. reptans* is one of the most widespread species of willows in the tundra of the River Lena delta although *S. hastata* is not a widespread species there, occasionally growing as solitary plants or in small groups in shrub thickets. The hybrids occur directly where *S. reptans* and *S. hastata* grow together.

To our knowledge there is only a brief note by M. I. Nasarow (1935: 117) in which he listed all hybrids that *S. hastata* can make with other species and mentioned, in one sentence, a hybrid between the latter and *S. reptans*. However, he did not give a name, description or distribution for any of the hybrids.

Materials and methods

Comparative morphological analysis of the herbarium specimens with the following description and identification were made with a binocular microscope, LOMO with 2–40× magnification, using traditional comparative-morphological methods and morphological characters as described by Skvortsov (1968, 1974, 1999), N. M. Bolshakov (1992), V. A. Nedoluzhko (1995), I. V. Belyaeva et al. (2006), G. W. Argus et al. (2010) and E. T. Valyagina-Malyutina (2018). Herbarium specimens of the species mentioned in the text were studied at BM, E, H, K, LE, MHA, MW, NS, NSK, PERM, S, SASY, SVER (Herbarium codes follow Thiers, 2024).

For DNA isolation, young leaves were collected from 2-year-old shoots from the same plant that was used for morphological analysis, and which is cited here as the holotype specimen. The leaves were dried on silica gel and DNA was isolated from 20–25 mg of the dry material using standard techniques for plant tissues (Doyle, Doyle, 1990). Primers ITS6 and ITS9, designed for East Asian species of the tribe *Spiraeeae*, were used to amplify the ITS operon (Potter et al., 2007). The amplification cycle included denaturation at 94 °C for 1 min, primer annealing at 58 °C for 50 s and extension at 72 °C for 1 min, with the number of cycles being 30. The resulting PCR fragments were purified using Diatom DNA Elution reagent kit for rapid elution of DNA from agarose gels (Izogen LLC, Russian Federation). Sequencing of ITS fragments was performed in both directions (Evrogen CJSC, Russian Federation). Sequences were aligned in pairs using BioEdit software, and multiple alignments were performed using ClustalW2 software with subsequent verification of ambiguous positions on the chromatograms. The ITS hybrid sequence was deposited in GenBank NCBI (PQ604647.1).

Results and discussion

Comparative morphological analysis

Comparison of morphological characters of the hybrid with those of possible parental species showed the intermediate characters such as pubescence of the ovaries which are semi-naked, i. e. naked in the middle part and pubescent on the distal and proximal ends (Fig. 1: *e*). This unusual hairiness is because one parent, *S. hastata*, has glabrous ovaries, while the other parent, *S. reptans*, has densely pubescent ovaries. The shape of stipules and leaf blades is also intermediate. The stipules in *S. hastata* are ovate, narrowly ovate, oblique, glandular-serrate along the edge, in *S. reptans* they are narrowly lanceolate with hardly noticeable glands on the entire edge. Hybrid plants have narrowly ovate or elliptical stipules with entire or glandular-toothed edges.

The intermediate shape of the leaf blades is shown within the same shoot: there are blades that correspond in shape to both, *S. reptans* and *S. hastata* — from

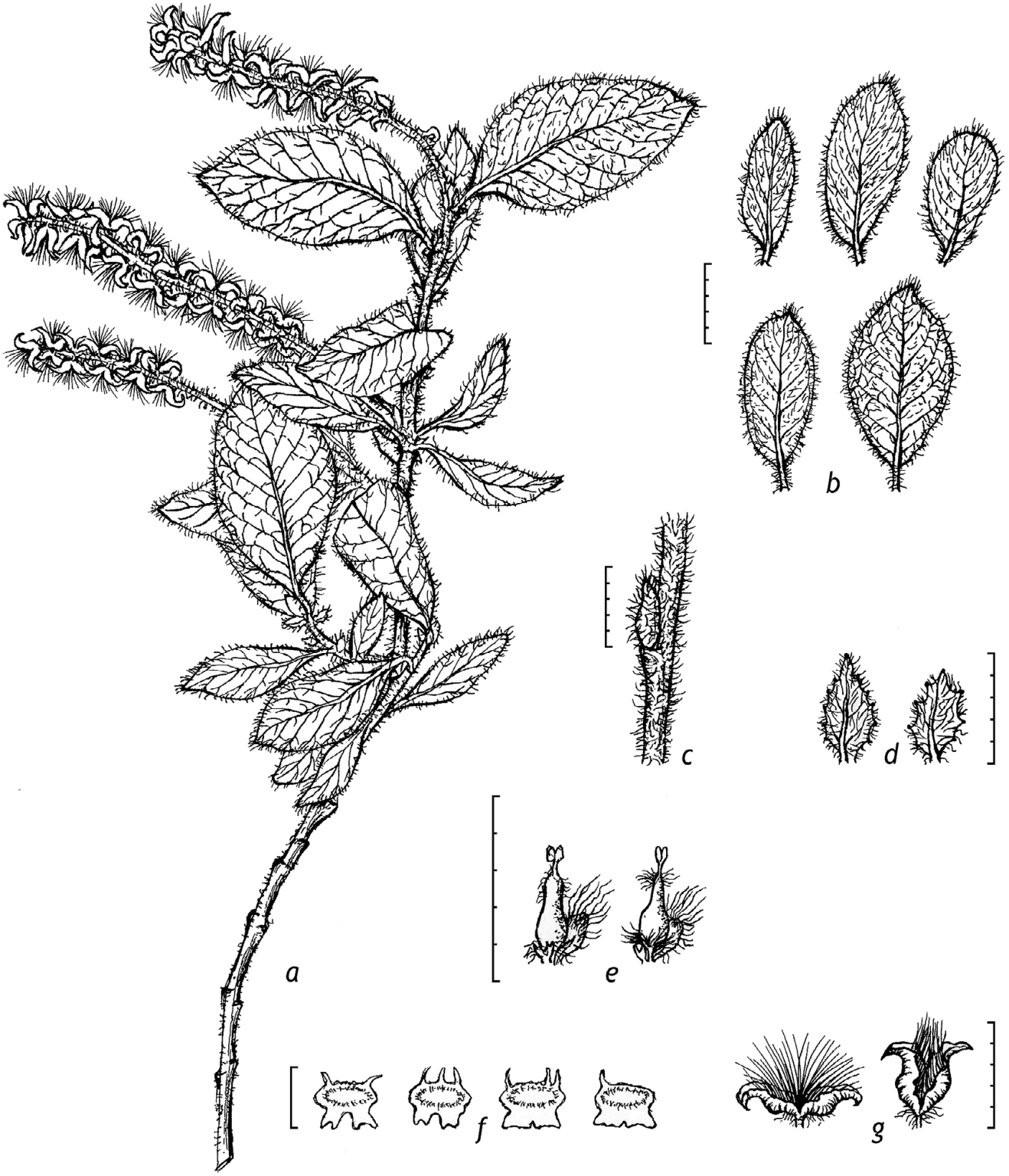

Fig. 1. *Salix* × *setifera*: *a* — branch with fruiting catkins; *b* — leaves; *c* — fragment of shoot with floriferous bud; *d* — stipules; *e* — female flowers; *f* — nectaries; *g* — capsules with seeds. Scale bars: *b*–*e*, *g* — 5 mm; *f* — 1 mm.

lanceolate to broadly ovate. Such dimorphism of leaf blades is characteristic of hybrid plants.

The structure of nectaries is also intermediate: the general appearance is similar to *S. reptans* (adaxial nectary bilateral, fused, broadly rectangular; abaxial nectary 2-partite, or with uneven edges with 1–2–3 lobes, but the abaxial lobes are 3–6 times shorter than those of *S. reptans*, mostly straight, not tortuous).

Molecular genetic analysis

To confirm the hybrid origin of *S.* × *setifera*, nucleotide sequences of the ITS region of the rDNA, which is the claimed marker for species identification (Efimova et al., 2019) and recently emerged plant hybrids (Alvarez, Wendel, 2003; Efimova et al., 2019), were included. In a comparative study of ITS in the studied pure species and the hybrid *S. hastata* × *S. reptans*, a single nucleotide polymorphism (substitution, SNP), T→A at position 581, was detected in the ITS2 intergenic spacer. This transversion is species-specific for *S. reptans* according to our long-term studies (Efimova, Poliakova, unpubl.). The low variability of the ITS region of rDNA in the family *Salicaceae* and genus *Salix* has been reported previously (Leskinen, Alström-Rapaport, 1999; Efimova et al., 2019). Thus, the detected hybrid individuals were found to be related to *S. reptans*. Since *S. hastata* lacks the species-specific SNP in ITS2 detected in our studies, it is not possible to directly prove its relationship with the hybrid. At the same time, phenotypic traits of the neighbouring *S. hastata* are present in the morphology of the hybrid plants, and intermediate traits between *S. hastata* and *S. reptans* are observed.

Taxonomy and nomenclature

Salix × setifera Efimova, T. A. Poliak. et I. V. Belyaeva, nothosp. nova (*S. hastata* L. × *S. reptans* Rupr.). — Figs. 1, 2.

A gnarled low upright shrub up to 40 cm high with coarse dark chestnut or dark grey to blackish branches (Figs. 1: *a*; 2). One- and two-year-old shoots densely pubescent with long, ragged, tangled white hairs. Mature shoots up to 0.5 cm thick, densely woolly, covered with tangled white hairs. Generative buds 5–6 mm long, densely pubescent with wavy white hairs, pressed to the shoot, with a bent apex (Fig. 1: *c*). Leaves 1.5–4 cm long and 0.7–2 cm wide, lanceolate, narrow to broad oval, narrowly obovate to broad obovate, green above, light green below with entire edges without noticeable glands, cuneate base and blunt or sharp tips (Figs. 1: *b*; 2). Petioles 2–5 mm, pubescent (Fig. 1: *b*), grooved adaxially. The main and lateral veins protrude abaxially, parallel, veins of secondary and tertiary orders finely reticulate. Stipules large, up to 5 mm long, 3–5 mm wide, narrowly oval or elliptical, equilateral or inequilateral, entire or glandular-toothed, with slightly curled edges, densely pubescent on the upper side (Fig. 1: *d*). Female catkins up to 7 cm long and up to 1 cm wide on hairy peduncle 1.2–2.5 cm with 2–4 leaflets up to 3 cm long and up to 1.2 cm wide, catkin rachis hairy (hairs curl when dry) (Fig. 1: *a*). Ovaries up to 3 mm long, semi-glabrous (glabrous in the middle, pubescent with a tuft of white wavy hairs on the side and above, or only below) becoming glabrous, on a short stalk 0.1–0.3 mm. Bracts 1.5–2 mm long, ovoid or oblong, red, dark red, densely pubescent with long wavy hairs, exceeding the apex of the scale by 3 mm. Styles fused 0.4–0.7 mm, stigmas entire, 0.4–0.7 mm (Fig. 1: *e*), dark burgundy, velvety. Mature capsules up to 1 cm long, red, pale red, glossy, glabrous, with wavy hairs at very bottom and stalk, the valves curl slightly when drying, stalks 0.5–1 mm long (Fig. 1: *g*). Nectaries 0.5–0.7 mm long, fused, broadly rectangular on the adaxial side, bipartite or with uneven apices, on the abaxial side with 1–2–3 narrow short lobes (Fig. 1: *f*). Seeds up to 1.5 mm long. The number of seeds in capsule is 24–26. Male plants were not found.

H o l o t y p e (Fig. 2): Russia, northern Yakutia, Bulunsky ulus (district), lower reaches of the Lena River delta, Tit-Ary Island, second floodplain terrace, 100 m south of the fishing village Bykovsky Nasleg, 71.986897° N, 127.094674° E, 4 VIII 2011, A. P. Efimova (SASY: SASY0055955!; isotype — LE 01305974!).

D i a g n o s i s . *Salix* × *setifera* differs from *S. hastata* (see descriptions by Bolshakov, 1992; Nedoluzhko, 1995; Belyaeva et al., 2006; Valyagina-Malyutina, 2018; Efimova, 2020) in having gnarled, rough shoots with short internodes, densely pubescent generative buds, leaf blades with entire edge vs serrate in *S. hastata* and short (2–5 mm), deeply grooved petioles vs shallowly grooved in *S. hastata*, heteromorphic hairy leaves vs monomorphic and glabrous in *S. hastata*, more densely hairy bracts, hairy capsule vs glabrous, short dark red coloured stigmas and more complex morphological structure of nectaries vs longer yellowish stigmas and one simple nectary in *S. hastata*. The new hybrid differs from *S. reptans* (see descriptions by Bolshakov, 1992; Nedoluzhko, 1995; Belyaeva et al., 2006; Valyagina-Malyutina, 2018; Efimova, 2020) in having light green coloured less hairy leaves vs green and more hairy in *S. reptans* and ochre colour partly hairy becoming glabrous capsules vs densely hairy in *S. reptans*. The number of seed scars in capsule of *S.* × *setifera* is 24–26, while in *S. hastata* it is 16–18, and in *S. reptans* it is 18–20. It is possible that the increased number of seeds in the hybrid may represent a residual phenomenon of

Fig. 2. Holotype of *Salix* × *setifera* (SASY0055955).

heterosis. There are no obvious signs of heterosis in the detected hybrid individuals, which can be explained by the fact that they are probably produced by back crossing.

E t y m o l o g y . The epithet "setifera" means bristle-bearing (Stearn, 2004: 493) and refers to the type of hairiness of the ovaries of the hybrid (Fig. 1: *e*).

D i s t r i b u t i o n . Described from Bulunsky ulus (district), lower reaches of the Lena River delta, Tit-Ary Island, northern Yakutia (Russia). Several specimens of *S.* × *setifera* from the vicinity of the village of Chokurdakh, Allaikhovsky ulus in Yakutia, were studied at SASY. The hybrid individuals from there have predominantly characteristics of *S. hastata*. The hybrid can be found in places where both parent species grow together in the subarctic tundra of Eurasia.

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