



Article

The Sixth Conference in Memory of Alexey K. Skvortsov

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Conference Overview

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It has become a tradition for Moscow botanists to celebrate the birthday of the late Prof. Alexei Skvortsov at conferences organized in his memory at the Main Botanical Garden of the Russian Academy of Sciences. The 6th Conference held on March 9-10, 2017 was organized by the Moscow Branch of the Russian Botanical Society and supported by the Main Botanical Garden and Moscow University. This time the Conference gained partial support from the Russian Foundation for Basic Research. As it was with the preceding conference, and in contrast to the earlier ones, the topic was limited to just one of Prof. Skvortsov's areas of interest. The 2017 Conference was entitled *Microevolution and hybridization among plants and animals*. While the previous conferences were just brief one-day meetings, this one was held in a two-day format. Appreciating the fact that Prof. Skvortsov was not only a famous botanist, but had started his scientific career as a medical man and zoologist, the organizers decided to widen the conference format, inviting zoologists to discuss the shared common problems of organic evolution. The 6th Conference gathered botanists, zoologists, and ecologists, 58 in all, from Moscow, St. Petersburg, Chelyabinsk, and Paris (France), who presented their talks and took part in discussions. The talks were dedicated to subjects spanning microevolution per se to phylogeography, phylogeny at low taxonomic levels, and spontaneous and artificial hybridization. Most of the speakers were, as usual, from the Main Botanical Garden and Moscow University, the institutions where Alexey Konstantinovich worked for most of his life.

The Conference talks were presented in seven oral sessions that lasted for two days and started with a plenary session: two general talks devoted to Skvortsov's heritage. One of them, given by Dr. Ekaterina Tkacheva from the Main Botanical Garden Library, was entitled *The works by A.K. Skvortsov in the world's informational space*. This was an analysis of references to Skvortsov's works and the impact of his ideas upon modern science. The other one, by Dr.

Larisa Kramarenko, dealt with the microevolution of *Prunus persica* Mill. in Moscow Region during a 33-year period.

The following three sessions were devoted to various aspects of microevolution, phylogeography, and hybrid speciation in plants. The first day finished with an exciting talk by Dr. Liudmila Ozerova on a trip to Madagascar, a hotspot of species diversity, followed by the conference dinner.

The second day started with a session on hybridization in natural populations of native and alien plants. The second session of the day was mostly zoological and included excellent talks by Dr. Natalia Abramson on differentiation and cryptic speciation in rodents in Northeastern Palearctic and by Dr. Vladimir Gokhman on problems of the species-level taxonomy in parasitoid Hymenoptera. The remaining two sessions dealt mostly with hybridization and cryptic speciation in plants, including hybridization in cultivation.

Abstracts of all the talks, translated from Russian by Irina Kadis, are presented below.

BOTANY

Hybridogeneous plant species at Moscow railroads

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Metadata pertaining to herbarium specimens (MHA, MW) collected from 1851 to 2016 at Moscow railroads have been organized in the database. The total length of railroads in the City of Moscow (its limits defined as of 2012) is about 300 kilometres. The flora of the central junction is represented by 1087 species from 447 genera and 94 families. Railroads are well known as an important vector for the advancement of alien species; meanwhile, the stressful ecological situation may provoke micro-evolutionary processes that can critically affect a species' genome.

Fifty-eight hybridogeneous species belonging to 36 genera and 20 families have been recorded at the railroads. A proportion of the hybrids (5% from the total species amount) must be attributed to the specificity of the habitat. The family that has yielded the most hybrids is Rosaceae (14 species) followed by Asteraceae (7 species), Salicaceae (7), Lamiaceae (4), Onagraceae (4), and Poaceae (3). Another 14 families are known to contain 1–2 hybridogeneous species.

Most hybrids (74%) are cultigeneous, reaching the railroad through anthropochory or zoochory. Examples of these are *Malus* × *robusta* Rehder, *Rosa* × *viarum* A.K.Skvortsov, *Populus* × *canescens* (Aiton) Sm., *Symphytotrichum* × *versicolor* (Willd.) G.L.Nesom, *Mentha* × *wirtgeniana* F.W.Schultz, *Lolium* × *hybridum* Hausskn. Cultigeneous hybrids dominate over spontaneous hybrids in plants of every major life form: among annuals and biennials (65%), perennials (70%), and woody plants (89%).

Along with hybridization, other types of mutational variability have been detected at railroads: segregation of parental species (e.g., *Fragaria moschata* Duchesne ex Weston from *F.* × *ananassa* (Duchesne ex Weston) Duchesne ex Rozier), reversion from cultivated forms back to wild ancestral types (*Beta vulgaris* L., *Raphanus sativus* L., *Secale cereale* L., *Triticum aestivum* L., *Malus domestica* Borkh., *Prunus domestica* L.), malformations, such as branching of inflorescences in *Secale cereale*. Apparently, wild forms are better adapted than cultivated forms to the specific railroad environment with its alkaline soil, rather high nutritional levels, and organic and inorganic contaminants that include widely applied herbicides.

Polymorphism of the ITS1 and ITS2 of nuclear ribosomal DNA in *Paeonia lactiflora* Pall. (Paeoniaceae) determined using next-generation sequencing technology

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The genus *Paeonia* L. constitutes a convenient case study of reticulate evolution. The hybrid species are mostly identified by full or partial ITS sequence additivity of the putative parental species (Sang *et al.*, 1995, 1997; Punina *et al.*, 2012). One of the few species whose hybridogeneous nature has not been demonstrated is *Paeonia lactiflora* Pall. distributed in China, Mongolia, and in the adjacent Russian territory. This diploid species is quite distinct morphologically. The geographical area of *P. lactiflora* overlaps with that of *P. veitchii* Lynch in the south and with species from the *P. obovata* Maxim. complex in the east. Hybrids between these species have not been recorded in natural habitats. Yet there is a cultivar *Paeonia* 'Fan Tan,' a putative hybrid *P. lactiflora* × *P. obovata* (Smirnow, 1975). Recently, there appeared new data on the hybrid nature of *P. anomala* L. (*P. lactiflora* × *P. veitchii*) (Pan *et al.*, 2007).

The next-generation sequencing approach has brought about new technical opportunities for obtaining ITS haplotypes of nuclear rDNA for a representative sample that would include rare variants. We have determined ITS1 and ITS2 sequences using the *Illumina HiSeq 2000* platform (USA) with read length of 101 bp from the terminus of each fragment. The alignment of the sequence reads with the assembled ribosomal operon has allowed us to reveal random polymerase errors along with polymorphic positions. A total of 13 polymorphic positions have been found: 8 in ITS1 (69, 93, 117, 125, 145, 158, 212, and 217) and 5 in ITS2 (25, 35, 90, 189, and 199). Polymorphism at these positions, (except for 125, 145 and 217) is not of hybridogeneous origin but may be explained by the presence of additive nucleotides not registered in other species. We assume that the observed additive polymorphism of nuclear ribosomal transcribed spacers could be attributed to the genetic differentiation within the species.

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***Chenopodium glaucum* L. – one species or two? Polytopic species: their taxonomy and the challenge of identification**

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Oakleaf goosefoot *Chenopodium glaucum* L. is widespread across the European part of Russia from its northern extremities to the Caucasus. The species is also ubiquitous in West Europe and known from Africa, Australia, and North America. Its tremendous polymorphism has resulted in descriptions of a wide variety of forms, a few subspecies, and interspecific hybrids, such as *C. schulzeanum* Murr (*C. glaucum* L. × *C. rubrum* L.). Some authors treat the subspecies in the rank of distinct species (*C. salinum* Standl., *C. wolffii* Simonk.). Because the species was described from West Europe, its type, which is preserved in London, fits West European samples both morphologically and genetically.

We conducted a comparative study of nucleotide sequences of the segment ITS1–5.8S–ITS2 nrDNA from samples identified as *Chenopodium glaucum* collected in European Russia (Moscow). Phylogenetic analyses of the same sequences ITS1–5.8S–ITS2 nrDNA in closely related species *C. rubrum* L., *C. urbicum* L., and *C. glaucum* from West Europe have shown (gene bank NCBI) that the sequence belonging to the *C. glaucum* sample from Moscow clusters with *C. rubrum*, while those obtained from plants collected from West Europe (Spain and Italy) and identified as *C. glaucum* cluster with *C. urbicum*.

The analysis of the sequences revealed the absence of nucleotides unique for *Chenopodium urbicum* in *C. glaucum* from Moscow, while nucleotides unique for *C. rubrum* were present (and numbered 11). On the contrary, in West European *C. glaucum*, 8 nucleotides unique for *C. urbicum* were found versus just 3 of those unique for *C. rubrum*.

Therefore, it is logical to assume that the *Chenopodium glaucum* from West Europe is of an independent hybridogeneous origin. Its genome donors could have been *C. rubrum* and *C. urbicum*. The *C. glaucum* from central European Russia appears to also be of an independent hybridogeneous origin, and one of the genome donors in this case also could have been *C. rubrum*. To find out which the second donor was, one must study closely related species, such as *C. chenopodioides* L. The discovery of taxa having a polytopic origin makes it possible to expect findings of other new taxa in situations where these four species coexist. Pure *C. glaucum* has not been found so far. If it exists, then all the other known taxa involving this species must constitute its hybrids with other species.

Within *Chenopodium glaucum* there is a great variety of forms. A few subspecies and a large number of forms have been described:

C. glaucum L. subsp. *glaucum*

C. glaucum L. subsp. *ambiguum* (R.Br.) Murr & Thell., Mém. Soc. Sci. Nat. Math. Cherbourg 38: 196. 1912.

C. glaucum L. subsp. *salinum* (Standl.) Aellen, Repert. Spec. Nov. Regni Veg., 26: 46. 1929.

C. glaucum L. subsp. *parodii* (Aellen) Aellen, Amer. Midl. Naturalist 30: 60. 1943.

C. glaucum L. subsp. *orientale* Vorosch., Byull. Glavn. Bot. Sada, Moscow, 130: 36, 1984. This subspecies was described from Russia and later as a distinct species, *C. amurense* Ignatov. However, both these taxa appear to be synonymous with *C. ambiguum* R.Br. (\equiv *C. glaucum* subsp. *ambiguum* (R.Br.) Murr & Thell.).

Another study of phylogeny and possible hybridization in which participating samples would be collected from across the entire species range would help to find out whether *C. glaucum* from central European Russia is synonymous with any previously known subspecies or constitutes a distinct hybridogeneous species.

Modes of morphological evolution and their role in adaptive radiation of biomorphs in willows

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The history of the genus *Salix* L. and habitat restraints of its species allow one to assume that the somatic radiation of willows has taken place within three adaptive zones, with manifestation of several morphological evolutionary modes.

According to A.K.Skvortsov, ancestral life forms in willows were tall shrubs or alluvial trees. Their ecological evolution went in the direction of the enhancement of winter hardiness. The evidence for this is the presence of multiple boreal sections of the phylogenetically young subgenera *Vetrix* and *Chamaetia* in the Holarctic.

Advancement to high altitudes resulted in transformation of shrubs into shrublets. At the level of barren heights, *Salix glauca* L., *S. berberifolia* Pall., and *S. tschuktschorum* A.K.Skvortsov are represented by taproot epigeneous xylorhizomatous shrublets. Habit

changes have been accompanied by a number of deviations: reduction in the duration of the onthomorphogenesis (OMG) phase, annual shoot die-off occurring on more than one-third of shoot length, oligomerization, nanyzm, and bryophylization (migration of dormant buds into moss layer). During the process of diversification and translocation of ecological niches, some tundra willows (*Salix fuscescens* Andersson, *S. lapponum* L.) were preserved at oligotrophic wetlands attaining features of reduced biomorphs. These are rather low shrubs with few stems, their shoot origins sunk in the thick moss layer. They are characterized by a storeyed structure and active formation of adventitious roots, which results in constant renovation of the root system (terminal prolongation).

When *Salix alba* L. and *S. ×fragilis* L. inhabit river valley terraces, they form single-trunk trees. Yet due to anthropogenic stresses, this habit is becoming extremely rare. A much more frequent habit is tree-shrub, an intermediate form combining characters of both biomorphs. Development of intermediate habits is due to the early activation of dormant buds on the trunk, which constitutes the OMG increment (terminal prolongation) of a single-stem tree. This morphological mode must have constituted the essence of the transformation of the tree life form into a geoxylous shrub, the most frequent biomorph in the genus.

Both flooding and drought result in terminal abbreviations in willows, so that single-stem small trees or aeroxylous shrubs are formed. On the other hand, basal abbreviations in situations of severe shading produce epigeogenic, xylorhizomatous, facultative and semiprostrate trees.

***Impatiens glandulifera* Royle (Balsaminaceae) in the secondary range: Efficiency of pollination**

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Impatiens glandulifera Royle is an annual of mostly wet habitats that can grow to 2.5 meters in height. Within its native range in the Western Himalayas, it occurs on river banks and in ruderal habitats (Polunin and Stainton, 1984). Its secondary range includes practically all of Eurasia, North America (Vinogradova *et al.*, 2010), and New Zealand (Weber, 2003). This work is a study of pollinator species and an evaluation of seed production rate in *I. glandulifera* within its secondary range. The assessment was undertaken in 2009–2013 in 5 populations

located in two regions of temperate European Russia: Tver (Tver and Andreapol) and Moscow (Zelenograd). Anthecological observations demonstrated the quantitative dominance of *Bombus pascuorum* Scopoli among pollinators. *B. hortorum* L. and *B. lucorum* L. were also recorded. Pollinator species diversity in *I. glandulifera* was practically identical to that known for native species with similar coloration, such as *Stachys officinalis* (L.) Trevis. or *Epilobium hirsutum* L. My observations yielded results similar to those obtained in Ireland (Nienhuis and Stout, 2009) and Siberia (Tomsk) (Konusova *et al.*, 2016). Reproduction in *I. glandulifera* is exclusively by seed. The smallest average number of seed per individual plant (609) was recorded for the population at Malino Railroad Station, while the maximal seed productivity was found in the population at Zelenograd-2: on average 1354 seed per individual plant, which is twice as large. Depending on population densities, the crop varied from 6158 to 37705 seed m⁻². Such a high rate of seed production in the secondary range is achieved through active visitations by long-tongue bumblebees during the flowering time. It is the adaptation of *I. glandulifera* to pollination by wide-ranging insect species that has allowed this plant to successfully conquer new territories.

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***Prunus persica* (L.) Batch: thirty-three years of introduction work in Moscow Region; its physiological traits, as compared to *Prunus armeniaca* L. grown in similar conditions**

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Among peaches, there are 6 species, all of them growing wild in China (Kostina, 1941). Only one of these, *Prunus persica* (L.) Batch has been in cultivation. Within the species, one can distinguish three groups: true peaches (those with pubescent fruit), nectarines (those with glabrous fruit), and flat or donut peaches (those with compressed fruit). The number of horticultural varieties in the world approaches 5 thousand (Ryabov, 1956; Yeremin, 2010; Sychov, 2016).

Peach was first brought to European Russia in the 17th century and initially grown in greenhouses. Occasionally peasants would plant peaches outdoors, close to their houses, on a south-facing wall and keep them flat against the wall on trellises over the winter. In the Far East and southern Siberia, they cultivate the tender plant by bending it down to the ground and covering for the winter. Similar techniques have been also attempted in Moscow Region.

In 1984 the author obtained peach seed from Latvia. Of three dozen seed, only a single seedling survived in the Main Botanic Garden in Moscow. It was named *P. persica* 'Pizhon' (*Prunus* 'Dandy'). This tree was grown outdoors without any protection for 13 years, producing a few fruits nearly annually.

Scions of the cultivar, 'Dneprovskiy', were received by the author in the late 90's. This variety had originated in the mid-20th century in Kiev (Shaitan *et al.*, 1989) as a selected seedling from another cultivar, 'Druzhba.' The latter had been obtained through germinating seed from China. Scions taken from *Prunus* 'Dneprovskiy' and *P.* 'Pizhon' were grafted onto seedlings of *P. domestica* L. and *P. besseyi* L.H.Bailey and planted in Moscow monasteries.

In the early 2000's the grafted trees started fruiting, and the fruits turned out to be very juicy and tasty. Seed from these cultivars were sown along with seed from the Crimea and imported varieties of peaches and nectarines.

Then came the year 2006. During mid-January, there were three nights in a row when the temperature in Moscow reached -31°C (-24°F), while daytime temperatures were -25 to -28°C. This cold wave was followed by a second one at the start of February: minimal temperatures dropped to -27°C (-17°F) for three nights, with daytime temperatures -22 to -26°C. None of seedlings or grafted trees survived, except for two small grafts (one *Prunus*

'Dneprovskiy,' the other *P.* 'Pizhon') whose lower branches were protected under snow. The entire upper parts of both plants died off, while the lower branches not only survived under the snow, but even produced some flowers in spring. They recovered during the summer of 2006 and then flowered and produced fruit in 2007. Currently small peach orchards consisting of seedlings of the first and second generations grown in Moscow exist in monasteries of the City of Moscow, Moscow suburbs, and also around Vladimir, a city 180 kilometers east of Moscow. When planting a peach, one has to find the warmest, well-lit spot that is protected from wind and be ready to provide some kind of winter cover. A two-year-old seedling from *P.* 'Pizhon' was planted in the fall of 2010 in northern Vladimir Region (Makhra, Alexandrov District). The chosen spot was not just a south-facing wall but actually a niche in the wall, so the plant was well protected from wind. This seedling has lived, with some frost damage, through a few severe winters with minimal temperatures dropping to -30 – -35°C (-22 – -31°F). It first flowered in 2016. There were not that many flowers, yet practically all of them yielded fruits, the plant thus demonstrating high self-compatibility. The fruits weigh 50–90 g, have intensive dark red flush, and are exceptionally tasty and juicy. They ripen early in August. This peach has never been covered in winter, as the extremely beneficial spot provides conditions for successful overwintering.

While cultivating apricots and peaches in the same conditions for many years, I have had an opportunity to compare the two related genera.

Drawbacks of peaches in comparison with apricots.

1. The most problematic quality of peaches is their low frost hardiness. Peach shoots often have to overwinter while they have not yet hardened. Temperatures of -25 – -30°C (-13 – -22°F) can kill not just flower buds, but entire trees.

2. Peach seed (when sown in the fall) have low germination rate: 15–30%, while apricot has 70–80% germination rate, not infrequently even up to 100%. However, the second-year germination in peaches is up to 30%, while apricots produce only 0.5%, occasionally up to 4% germination during the second year.

3. Peaches yield to apricots as regards longevity. In Middle Asia, there are 100-year-old and even older apricots, and in China (according to Chinese authors), some apricots have attained the age of 300. As to peaches, even in favorable conditions they hardly live older than 30. In the Far East, horticulturalists arrange for 'peach lines': while a certain group of trees is in the reproductive age, another group is being started, so that the older ones can be timely

replaced. In the challenging conditions of the north, a peach only lasts until the next cold winter.

Advantages of peaches over apricots.

1. Peaches flower 6 to 12 days later than apricots. The dormancy period in peach is longer, and more heat is needed to trigger the start of growing processes; therefore, peaches don't respond to thaws as apricots do. Peaches can better adjust to abrupt temperature jumps and suffer less from root rot. This makes it possible to cover peaches over winter. Apricots cannot be protected this way, as they will almost certainly rot under a cover.

2. Peaches are self-compatible, at least partially. Most apricots are not; they require cross-pollination.

3. The root system in peach seedlings is more extensive than in apricots, so peaches are transplanted more successfully.

4. Apricots cannot be propagated from cuttings, while peach softwood cuttings root well.

5. Apricots can only be grafted onto certain rootstocks; there are many more rootstock choices for peach scions. A peach can be grafted onto a seedling of *Prunus persica*, *P. armeniaca* L., *P. cerasifera* Ehrh., *P. domestica* L., *P. tomentosa* Thunb., *P. besseyi*, *P. dulcis* Rouchy, and a number of clonal rootstocks: OP-23-23, 140-2, SVG-11-19, etc. Since peach has softer wood, cuts are made more easily, which positively affects grafting results. Summer budding is also more successful in peaches.

6. One important advantage of peach over apricot is reduced susceptibility to fungal diseases (at least as of today, while there are not that many peach trees in Moscow Region and the infection has not been accumulated). Peach is far less subject to peach scab (peach freckles) and peach blight (moniliosis) than apricot. However, peach is subject to peach leaf curl, a fungal disease that does not attack apricots.

7. Apricot does not have peak fruiting years at regular intervals. A superfluous number of flower buds is started annually – even during a peak fruiting year. As a result of this, trees don't rest and exhaust their potential, if only the abundant buds are not killed during adverse weather episodes. Peaches, on the contrary, have periodical mast years, although this periodicity is only moderate, not as pronounced as in apples. During a peak year, a peach produces less flower buds for the following season. Plants thus have an opportunity to rest and recover.

In a nutshell, the comparison reveals the firm, unyielding nature of apricots: these plants are just as tough as their wood. Peaches can be described as a soft, flexible, agreeable plants, amenable objects that are a pleasure to work with.

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Hybridization of cultivated bearded irises in the Department of Ornamental Horticulture at the Main Botanic Garden

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Selection work at the Department of Ornamental Horticulture, Main Botanic Garden cannot be called a new direction; however, the work was suspended for a while for objective reasons and then restarted in 2011. Representatives of the genus *Iris* L., mostly subg. *Iris* and the namesake section have become important objects of this work. The outline of the selection work with irises highlights three major directions. The first one is hybridization of cultivars belonging to the same horticultural group and featuring some unique or uncommon characters (flower color, general habit, morphological traits of perianth, etc.). The next direction of work is crossings among the most promising cultivars from different groups, as judged by results of introduction trials. This direction has been implemented most consistently: source populations for the selection have been created. Finally, the third outlined work direction is hybridization of cultivars with plants from natural populations.

The hybridization nursery is one of the key units within the classic outline of the selection process. The nursery is to be formed utilizing the living collection resources. This principle has been fully retained when working with irises: 30% of the total number of *Iris* × *hybrida* hort. varieties in the contemporary (2011–2016) garden collection have been used for crossings. The number of hybrid combinations tried yearly during this period varies from 13 in 2011 to 30 in 2012 and 2016.

The frequency of participation of certain cultivars in the hybridization varies in the following manner: 69.2% of cultivars have participated not more than 2 times and 18.9% not more than 4. Those cultivars that are most frequently used in the hybridization schemes present the most interest. Currently there are 7 varieties that have been involved in crossings more than 6 times. These are 4 low-growing Standard Dwarf Bearded (SDB) cultivars: *Iris* 'Cimarron Rose,' *I.* 'Vesenniy Salat' ('Spring Salad'), *I.* 'Celsius,' and *I.* 'Gingerbread Man' with respective participation frequencies of 17, 7, 6, and 6; also 2 Intermediate Bearded cultivars: *I.* 'Honey Glazed' (16 times) and *I.* 'Red Zinger' (10) and a single Tall Bearded – *I.* 'Pallida Perfecta' (8).

For cultivars of complex hybrid origin, the critical trait is compatibility during cross-pollination. Cultivated bearded irises are not an exception: pro- or post-gamous incompatibility can develop even during hybridization between cultivars belonging to the same group. This can influence the outcome when various hybrid combinations are tried. During the analyzed work period, 63.9% of cultivars (of the total number used) produced only a single combination that yielded seed. 18 cultivars did not produce any productive specimens. At the same time, there are 4 cultivars in the contemporary collection that appear to be most promising for the creation of source populations. These are *Iris* 'Cimarron Rose,' *I.* 'Gingerbread Man,' *I.* 'Orange Tiger,' and *I.* 'Honey Glazed.' *I.* 'Honey Glazed' appears most efficient as the maternal parent, while *I.* 'Cimarron Rose' is universal.

At this stage, 28 cultivars have been infrequently used in crossings. This group includes 4 categories: cultivars participating in the collection for more than 20 years; those whose cultivation period is 15–20 years (though older cultivars of SDB irises still have good potential); those whose cultivation time in the collection does not exceed 3 years; and finally those at the stage of propagation/introduction trials.

At the Department, we believe that repetitive employment of the most promising parent combinations in hybridization schemes must be useful when dealing with a large-assortment taxon. In order to identify those advantageous combinations, the author has been assessing hybrid combinations of SDB irises historically used at the Department of Ornamental

Horticulture. Two characters were chosen as selection criteria in this analysis: the number of seed per fruit and that of normally developed seed (by visual assessment). According to the preliminary result, the following 6 pairs are of interest: *Iris* 'Beau' × *I. aphylla* L., *I.* 'Add It Up' × *I. aphylla*, *I.* 'Cimarron Rose' × *I.* 'No Contest', *I.* 'Pumpin' Iron' × *I. aphylla*, as well as reciprocal combinations of *I.* 'Music' and *I.* 'Cimarron Rose.'

Selection nurseries have been assembled at the Department on a regular basis, starting from 2013 (as the dormancy period for the seed of bearded irises is about 3 years). Resulting from the undertaken trials, 3 promising selections have been identified in the formed populations:

I 5–2011–2014 (*Iris* 'Vesennyi Salat' × *I. aphylla*), I 22–2012–2015 (*I.* 'C48' × *I.* 'Pallida Perfecta'), and I 17–2012–2016 (*I.* 'Mini Dynamo' × *I. aphylla*).

Phylogeography of *Ophiorrhiza* L. (Rubiaceae) in Thailand

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The genus *Ophiorrhiza* L. (Rubiaceae, Ophiorrhizeae) is represented by mostly herbaceous plants distributed in Indomalaya. It comprises about 150 species (Darwin, 1976). The genus remains poorly known from the systematic standpoint; no phylogenetic studies have been undertaken so far.

We made an attempt to investigate the phylogeny in the genus *Ophiorrhiza* using sequences of nuclear ribosomal internal transcribed spacer (ITS) and chloroplast rpS16 intron sequences.

Dry leaf samples collected by I.A.Schanzer during his trips to Thailand, herbarium samples of *Ophiorrhiza* from Thailand, China, and other countries preserved in L, AAU, BKF, and QBG, as well as DNA sequences from the GenBank have served as material for the study.

Geographical locations for the samples participating in the study were plotted on the map. The samples had been collected mostly from forested areas in mountainous regions of northern, central, and southern Thailand. A total of 115 samples, 123 ITS sequences, and 106 rpS16 intron sequences were analyzed in the study.

DNA was isolated using the CTAB method (Doyle and Doyle, 1987). Amplification and sequencing for the ITS was undertaken using the primers NNC18s10 and C26A (Mort *et al.*,

2007) and *rpsF* /*rpsR2* primer pair for *rpS16* intron (Oxelman *et al.* 1997). Alignment was conducted through *BioEdit* Program. Phylogenetic trees based on aligned sequences were then created with *SplitsTree4* Program using the neighbor-joining method and also with the *TreeFinder* employing the method of maximum likelihood. Haplotype genealogy for nuclear, ITS, and *rpS16* intron sequences was created using the method of statistical parsimony in the TCS Program. The resulting trees and haplotype networks for nuclear and chloroplast segments were not congruent: samples belonging to the same species according to taxonomic characters ended up occupying different branches of the phylogenetic tree. This was especially true for *O. pseudofasciculata* Schanzer and *O. trichocarpos* Blume.

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Genomic composition of polyploid species in the genus *Catabrosa* P.Beauv. (Poaceae) as revealed by molecular phylogenetic analysis

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Water whorlgrass (*Catabrosa* P.Beauv.) is a small genus of riparian grasses widespread across the world. For a long time it was considered monotypic, represented only by *Catabrosa aquatica* (L.) P.Beauv. (brookgrass), a species described from Europe (Palisot de Beauvois, 1812). *C. capusii* Franch. was described in 1884 from Middle Asia differing in its very narrow panicle and nearly black spikelets. The species was accepted by R.Rozhevitz in the *Flora of the USSR*. Later on, it was demonstrated that this taxon actually constitutes more than

a dozen species differing from one another in their morphological characters, geographical ranges, and chromosome numbers.

The basic chromosome number in water whorlgrasses is 5. The species form a polyploid series ranging from diploids *Catabrosa pseudairoides* (J.Herrm.) Tzvelev and *C. atrata* (Tzvelev) Tzvelev to octoploids ($2n=40$) from the Altai Mountains, which we described in 2016 as *C. ledebourii* Punina & Nosov and *C. bogutensis* Punina & Nosov (Punina *et al.*, 2016). Octoploids have not been previously known in the genus. These facts prove that the genus *Catabrosa* is not at all monotypic; moreover, similarly to other related grass taxa, it most probably contains hybridogeneous species.

In search of such hybridogeneous species, we conducted molecular-phylogenetic analysis of nuclear ITS1-gene 5.8S rRNA-ITS2 and chloroplast trnL-trnF genes. We also paid close attention to ambiguous regions in the sequences ITS1 5.8S rRNA-ITS2, which are evidence of the presence of two sequence versions originating from different parental taxa amplified from the general genome pool. Phylogenetic trees were built using the maximum likelihood method with the employment of the model GTR+I+G (1000 bootstrap replications). In naming of putative nuclear and chloroplast genome variants in polyploid *Catabrosa* species, we follow Soreng *et al.* (2010) and Nosov *et al.* (2015).

The genus *Catabrosa* belongs to the subtribe *Coleanthinae* (= *Puccinellinae*), which appears to be quite ancient (R.Soreng, pers. comm.) within *Poeae* s.str. (= *Poeae* chloroplast type, Soreng *et al.*, 2007). According to the sequences of the ITS1-gene 5.8S rRNA-ITS2, this is a sister genus to the clade *Hyalopoa* + *Paracolpodium*, while *Puccinellia* forms a separate clade. We call nuclear genomes of the subtribe *Puccinelliinae* C-genomes, and the version characteristic of *Catabrosa* – C_c . The octoploid species from the Altai *C. ledebourii* and *C. bogutensis* are the ones most remote from the rest of the whorlgrasses, their version of nuclear genome named as $C_{c-ledebourii}$.

The montane Altai species *Catabrosa bogutensis* differs from *C. ledebourii*, the South Siberian species entering China, by the diminutive stature of the whole plant and the nearly complete absence of stolons. Apparently, *C. bogutensis* constitutes a high-elevation derivative of *C. ledebourii* and clearly differs from the hypoarctic *C. minor* (Bab.) Tzvelev, also a miniature plant with mostly caespitose habit. So far no closely related diploids have been known for these species; their hypothetical ancestor could very well be of Asian origin.

The rest of the studied *Catabrosa* species form a weakly supported clade (BS=59%), which may be attributed to a closer relationship among the other species and also may be due to

concerted evolution of ITS-sequences in a polyploid genome. ITS-sequences in *C. aquatica* s.l. from Nevada, USA occupy an indeterminate position. Morphologically this sample does not differ much from European samples of the same species, yet according to its genome composition (or at least the genome represented mostly in its polyploid set), it may constitute a separate evolutionary line, a cryptic species. ITS-sequences of other American species, the Canadian *C. aquatica* s.l. and the South American high-elevation species *C. werdermannii* (Pilg.) Nicora & Rúgolo, also occupy indeterminate positions within the tree.

An ancient Mediterranean diploid ($2n=10$) *Catabrosa pseudairoides* (J.Herrm.) Tzvelev described from Astrakhan (our sample originating from Lenkoran, Azerbaijan) is monophyletic with the coastal Baltic species *C. kneuckeri* Tzvelev and hypoarctic *C. minor* ($2n=20$) (Probatova *et al.*, 2015). Our data confirm N.N.Tzvelev's hypothesis regarding the close affinity between *C. kneuckeri* and *C. minor*. Most probably *C. minor* evolved in Pleistocene from *C. kneuckeri* on the arctic sea coasts. Both species characteristically have single-flowered spikelets dominating in the panicle over two-flowered ones. On the other hand, the affinity of these species with the Mediterranean diploid, which we have detected, appears rather unusual. We cannot exclude that the diploid *C. pseudairoides* could be close to some carrier of the genome that was ancestral to both northern species and that expanded its range northward during a warmer period either before or between the glaciations. We assigned this variant of the genome the name $C_{c-pseudairoides}$.

A separate, moderately supported (BS=86%) branch on the phylogenetic tree is formed by the Middle Asian montane species *Catabrosa capusii* along with some *C. aquatica* s.l. samples. Morphologically, *C. capusii* differs very well from all other whorlgrasses in its very contracted panicles with dark-colored, nearly black spikelets. This is a tetraploid species with $2n=20$. Closely related are ITS-sequences of *C. aquatica* from Spain, which may be attributed to *C. ochroleuca* Dumort., a species from South Europe. Also in this group there are ITS-sequences of an unusual Irish sample, which greatly resembles the seaside species *C. kneuckeri*, though differing from it in pubescent lemmas. ITS-sequences from a Caucasian *C. aquatica* s.l. sample, which is characterized by a rather spreading panicle but at the same time smallish and rather dark-colored spikelets, are also akin to *C. capusii*. Plants from Dagestan and some other regions of the Northern Caucasus differing by a special shape and size (and frequently also pubescence) of their lemmas might be segregated in a separate species related to *C. capusii*. We have been calling the genomes belonging to this ancient

Mediterranean/European clade $C_{c-capusii}$. Morphologically, plants of this clade may be close to *C. aquatica* s.l. Apparently, they are ancestral to the high-elevation isolate *C. capusii*.

Genome sequences of ITS1-gene 5.8S rRNA-ITS2 in *Catabrosa aquatica* s.str. and related forms are characterized by significant number of polymorphic sites, an evidence of their allopolyploid, perhaps recent origin. Due to that, they form two weakly supported branches. A very large sample of *C. aquatica* from a Moscow suburb that demonstrated the highest substitution polymorphism must be probably attributed to a distinct species. The sister relationship between the branches of the phylogenetic tree is indeterminate (BS=46%), although there are anthropomorphic sites with polymorphism Y (C and T) in positions 105 (ITS1) and 480 (ITS2). Along with the mentioned large-sized sample from near Moscow, one of the branches includes another non-typical sample from the Republic of Kalmykia featuring a large number of three-flowered spikelets in the panicle and also a putative hybrid whose characters are intermediate between *C. kneuckeri* and *C. aquatica*. The other group contains samples of the typical *C. aquatica* s.str. from Belgorod and Georgia. Genome variants identified with *C. aquatica* s.str. may be called $C_{c-aquatica}$.

These facts not only demonstrate that *Catabrosa* is not a monotypic genus, but also that it includes complex hybridogeneous species—just like many other related grass taxa. Making progress in our understanding of the genus, we have discovered a more significant morphological variability of its species than it was found in our previous taxonomic treatments and more character combinations inherited from a number of parents in the hybridogeneous complex. We anticipate that even more genome variants are going to be discovered in polyploid species of whorlgrasses in addition to the ones we are now aware of, which is going to further clarify the relationships within the genus and its origin.

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Madagascar: A hotspot of speciation. Notes from a field trip undertaken in June 2016

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Madagascar has been classified by the IUCN (International Union for Conservation of Nature and Natural Resources) as a hotspot of biodiversity by three different criteria: a high level of species diversity, large percentage of endemic species (160 genera and 7 families), and habitats threatened due to human activity. As of today, only 2.7% of Madagascar territory is protected.

The isolation of Madagascar started about 165 million years ago, upon its separation from Gondwana. Due to natural isolation, the species inhabiting the island evolved independently, without competition or genetic exchange with any of the continents. The large size of the island, a great variety of habitats, and the tropical climate facilitate evolutionary processes, so that Madagascar has been considered the world's largest natural laboratory for speciation. The flora of Madagascar enumerates 14000 species.

The island with its climatic diversity (moist tropical climate in the east, cool Mediterranean in the mountains, and desert in the central and southern parts) constitutes a distinct microcontinent. Due to variable topography, climate, and geology, there exist contrasting vegetation types. The major one in the east is tropical rainforest; the Central High Plateau is mostly covered with extensive steppes and savannas; there are dry deciduous forests in the west.

Ranomafana National Park in the southeastern part of the island exemplifies virgin cloud- and rain-forest, in which 90% of species are endemic. The understory is mostly composed of pandans and ferns; one can also find here a very rare palm *Dyopsis bosseri* J.Dransf. The endemic giant bamboo *Cephalostachyum viguieri* A.Camus forms thickets that provide food and shelter to the rarest lemur species, *Haplemur aureus* Meier *et al.* (golden bamboo lemur), whose population was discovered in 1983. The number of these lemurs does not exceed one thousand. Due to special food requirements, the population cannot expand beyond the bamboo grove. DNA analyses have demonstrated that these are direct descendants of African lemurs, which are now extinct. Lemurs play an important role in forest regeneration, since they take part in seed dispersal.

The Central Highland is mostly covered with extensive steppes and savannas, many of which have been formed as a result of human impact. A few species of alien eucalyptus and acacias dominate the tree canopy here; however, there are also some native plants: endemic palms *Bismarckia nobilis* Hildebr. & H.Wendl. and *Ravenala madagascariensis* Sonn. Granite outcrops along the road toward Morondava would appear most interesting to any botanist. Here at the elevation of 1400–1600 meters one can encounter species of *Pachypodium* Lindl. (Apocynaceae): *P. brevicaule* Baker together with *P. densiflorum* Baker and/or *P. rosulatum* Baker, which form natural hybrids differing by the length of their pedicels. One can also find the endemic *Senecio crassissimus* Humbert and *S. meuselii* Rauh, whose leaves are quite unusual: ensiform (sword-shaped), subunifacial, vertically flattened. This vertical leaf contraction is perceived as an adaptation to the warm climate.

Dry deciduous forests of western Madagascar constitute an example of a forest that is one of the richest of its type in the world. The forest flora is characterized by staggering numbers: 100–200 species of vascular plants per hectare. Some plants reach enormous sizes, for example, baobabs (*Adansonia grandidieri* Baill., *A. suarezensis* H.Perrier, *A. za* Baill.). Both *A. grandidieri* and *A. suarezensis* have been deemed endangered. The DNA sequences of these two baobabs have much in common. Baobabs are sacred trees in the Malgasy culture. They believe their entire population will be gone with the last baobab.

More than one expedition is necessary in order to research the great biodiversity of Madagascar. The study effort has to be prompt though, as the natural communities have been catastrophically shrinking and degrading.

Molecular-genetic studies of *Salix* L. (Salicaceae) and *Spiraea* L. (Rosaceae) from Yakutia

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With the purpose of species identification and detection of interspecific hybrids in willows and meadowsweets, the authors have been studying polymorphism of the ITS region in nuclear ribosomal DNA sequences and also the second intron in *cyp73* gene family of nuclear DNA in willows.

In willows, the total alignment sequence of the analyzed ITS region (which includes ITS1 spacer, gene 5.8s, and ITS2 spacer) was 597 positions, of which 24 were variable and 13 parsimony-informative. The length of ITS1 spacer was 222–223 nucleotides, ITS2 spacer – 212 nucleotides, and 5.8s gene – 163 nucleotides. We detected species-specific genetic differences in the ITS-region within subgenus *Salix*: single-nucleotide substitutions (*S. alba* L. – 4, *S. pseudopentandra* Flod. – 1, *S. triandra* L. – 2) and deletions (*S. triandra*). These include 6 substitutions marking the subg. *Salix*. Nucleotide sequences within the ITS region were found to be identical in most species of the subgenera *Chamaetia* and *Vetrix*. 5 species of willows were verified and 5 putative hybrids were identified within these subgenera.

The second intron of *cyp73* gene family was informative for hybrid identification. The origin of *Salix* × *zhataica* Efimova, Shurduk & Ahti (*S. brachypoda* (Trautv. & C.A.Mey.) Kom. × *S. pyrolifolia* Ledeb.) was confirmed.

Within the ITS-region in *Spiraea* L. species, in addition to species-specific single-nucleotide substitutions, we found insertions/deletions and single-nucleotide deletions having taxonomic values at the section, cycle, and series levels. In *Spiraea*, the total alignment sequence of the analyzed ITS region was 660 positions, of which 572 were constant, 85 were variable, though not informative, and 74 parsimony-informative. A comparative study of ITS fragments in the studied species of meadowsweet has demonstrated the presence of substitutions (transversions and transitions). In central and southeastern Yakutia, in those habitats where *Spiraea* species occur sympatrically, we found putative introgressive hybrids *S. salicifolia* L. × *S. humilis* Pojark. and *S. media* Schmidt × *S. dahurica* Maxim. Samples having specific substitutions in ITS region also exhibit combinations of morphological characters intermediate between these closely related species, which confirms our conclusions.

The research was conducted within the framework of the Project 52.1.11 Plant Biodiversity in the Taiga Biome of Yakutia: Structure, Dynamics, and Conservation in the Institute for Biological Problems of Cryolithozone, Siberian Branch RAS and with the financial support of the Russian Foundation for Fundamental Research (projects 15-44-05103 r_east_a and 15-04-03093).

Hybrid speciation among wild roses (*Rosa* L., sect. *Rosa*) in North America and Europe

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The genus *Rosa* L. comprises ca. 150 species and is naturally distributed throughout the temperate zone of the Northern Hemisphere and mountain areas in subtropics and tropics. The European section *Caninae* is best known in the genus for its hybridization ability and hybrid speciation due to balanced heterogamy and apomixis. The entire section is polyploid, thought to be of hybridogeneous origin. Examples of hybridization in other sections are less well documented, though all of them include both di- and polyploids.

The type section, *Rosa*, is distributed in temperate Eurasia and North America. In North America it is represented by 17 native species unevenly distributed between the western and the eastern parts of the continent. This is all that remains from about one hundred species described in earlier taxonomic works after a series of revisions by W.H.Lewis and several molecular studies by A.Bruneau and co-authors. In particular, in their work on the origin of polyploid species in eastern North America (Joly *et al.*, 2006) they analyzed the haplotype network of a low-copy nuclear gene GADPH from a representative sample of populations of all the species recognized in this area, both di- and polyploid. They were able to clearly show that the three tetraploid species, *R. arkansana* Porter, *R. carolina* L., and *R. virginiana* Mill., evolved through numerous reciprocal hybridizations between the diploids *R. blanda* Aiton, *R. woodsia* Lindl., *R. nitida* Willd., *R. palustris* Marshall, and *R. foliolosa* Nutt.

Similarly, the analyses of morphological characters (Schanzer and Klinkova, 2001) and molecular ISSR markers variation (Schanzer and Voilokova, 2008) in populations of East European *Rosa cinnamomea* L. enabled us to demonstrate that *R. glabrifolia* C.A.Mey. & Rupr., *R. gorenkensis* Besser, and *R. pratorum* Sukaczew often recognized in the Russian taxonomic literature as separate species are nothing but forms of *R. cinnamomea*. This species is distributed from southwestern Siberia throughout East Europe, reaching the Carpathians and Danube Valley in the west. As far as it is known, the species is diploid throughout its area. *R. pendulina* L. is a tetraploid confined to mountainous areas of Central and West Europe. Its phylogeography has been recently studied by T. Fér and co-authors (2007) using the chloroplast intergenic spacer *trnL-trnF*. It was shown that the most ancient haplotype is confined to the glacial refugial areas in the Balkans, Apennines, and Pyrenees, while two of its

descendants occur in the Alps and Carpathians, correspondingly. The authors hypothesized that during the last glacial maximum the species survived in the major Mediterranean refugial areas as well as on the southern slopes of the Alps and in the southern Carpathians, where from it spread to its modern area by the end of the last glacial period.

Rosa oxyodon Boiss. from Dagestan and the northern macro-slope of the Greater Caucasus is another species sparking controversial opinions regarding its relations. A number of segregate species have been recognized in the literature. We studied a single *trnL-trnF* spacer from a set of populations of this species, *R. cinnamomea* from European Russia and the Urals, and *R. pendulina* from the East Carpathians, adding to the data set sequences of *R. pendulina* available from GenBank (Schanzer and Abakarova, 2012). The analysis of the resulting haplotype network showed that *R. cinnamomea* is represented by a single widely distributed haplotype not related to those of *R. pendulina* throughout the Eastern Europe, with several minor descendant haplotypes occurring in several populations at random. On the contrary, the samples of *R. oxyodon* all bear either this most frequent haplotype of *R. cinnamomea* or the Carpathian haplotype of *R. pendulina*, some specimens, however, possessing minor private haplotypes descendant from both. We hypothesize that *R. oxyodon* may have originated during the last glacial maximum through reciprocal hybridizations between *R. cinnamomea* and *R. pendulina*. The latter species may have migrated eastward from the Carpathians to the Caucasus during the glaciation time via the plain north of the Black Sea, where it came into contact with *R. cinnamomea* populations. Nowadays neither of the parental species occur in the Caucasus.

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Cryptic and pseudocryptic species in Hydatellaceae (Nymphaeales)

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Hydatellaceae is a family of aquatic and wetland plants occurring in Australia, New Zealand, and India. Twelve species are currently recognized in a single genus *Trithuria* Hook.f. (Sokoloff *et al.*, 2008). Molecular phylogenetic data and fruit morphology allowed recognition of four sections (Iles *et al.*, 2012). Current data indicate the occurrence of polyploid series in at least two sections, and the most widespread species *T. submersa* Hook.f. is an octoploid (Kynast *et al.*, 2014).

Due to the discoveries of cryptic species during microevolutionary studies of the Australian Hydatellaceae, it has been demonstrated that the existing taxonomic concept underestimates the species diversity within the family. Using sequences of nuclear and plastid markers, Iles *et al.* (2012) found that two of the three currently recognized species of section *Trithuria* (*T. bibracteata* Stapf ex D.A.Cooke and *T. submersa*) are not monophyletic, each splitting in two groups. Using microsatellite data, Marques *et al.* (2016) found the same two groups of *T. submersa*, one restricted to the southwest of Western Australia the other to Southeastern Australia. These groups likely represent two cryptic species. Two morphotypes based on fruit morphology are found in *T. bibracteata*, but it is yet unclear if they fit the two groups found through molecular analyses. Phylogenetic analysis based on plastid and nuclear data as well as microsatellite data revealed a split between northern and southern populations of the Western Australian *T. australis* s.l., a self-pollinating member of section *Hydatella*. This division is consistent with differences in fruit micromorphology, and the two groups can be

recognized as distinct species. The phylogenetic placement of a specimen of unknown geographical provenance suggests the existence of a third species in the *T. australis* complex, but fruit micromorphology provides no diagnostic characters. Furthermore, there is a distinct morphotype within the *T. australis* complex based on fruit characters for which molecular data are not currently available.

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Selection within the genus *Fragaria* L. in Yakutia: Employment of interspecific hybridization—the most efficient method for production of locally adapted varieties

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Oriental strawberry, *Fragaria orientalis* Losinsk. features a number of characters important and valuable for cultivation, which allows for selection of varieties that are locally adapted to Yakutian climatic conditions. A hybrid seedling 37-03, the one that has proved to be the most winter hardy, represents progeny from hybridization of common (woodland) strawberry (Cv 'Alexandra') with Oriental. The hybrid surpasses Oriental strawberry in winter hardiness.

The seedlings inherited high productivity from *Fragaria orientalis* with its many-flowered inflorescence as well as fruits of large size from the maternal parent. All hybrid progeny from *F. orientalis* whose other parent is the cultivated strawberry are more or less large-fruited; those whose maternal parent is wild woodland strawberry are small-fruited, just like the parent.

The taste in all hybrid seedlings is well balanced, with a pronounced muscat grape aroma, which is typical for *Fragaria orientalis*. High vitamin C content (more than 100 mg g⁻¹) has been recorded for all hybrid seedlings obtained through crosses of garden strawberry with

Oriental. However, when woodland remontant strawberry is crossed with Oriental, the vitamin C content in the resulting seedlings does not exceed 80 mg g⁻¹ (just as in *F. orientalis*).

Interspecific hybridization also paves an avenue for elevating resistance to such fungal diseases as gray mold, common spot, or strawberry leaf scorch. The highest fungal resistance that even exceeds that in the parent species has been recorded in the hybrids of woodland and Oriental strawberry.

The following cultivars of Oriental strawberry have been developed in the Safronov Institute: in 2007, 'Pokrovskaya' (with productivity of 56600 kilogram/hectare) and 'Bogdalena' (61400 kg/ha); in 2009, 'Sadovo-Spasskaya' (9500 kg/ha) and 'Bersenevskaya' (71700 kg/ha); in 2013, 'Vladyka Zosima' (79800 kg/ha) and 'Alexandra' (50700 kg/ha).

During selection work with the goal of creating locally adapted varieties, *Fragaria orientalis* has proved to be the best material providing utmost winter hardiness of interspecific hybrid progeny (the most desirable quality in Yakutia) and ensuring the success of selection process.

Fine taxonomic identification of orchids using microstructure of anther caps and pollen dispersal units (PDU)

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In the absence of criteria suitable for a universal orchid identification key, I initially resorted to a review of the historical classification systems proposed for this family. The review showed that the number of genera and species significantly varied from one classification to another: from eight genera in the first monograph (Linnaeus, 1753) to 736 in the classification based on cladistic analysis of DNA data (Chase *et al.*, 2015). As of 1799, *Dendrobium* Sw. comprised approximately 800 species; currently it contains 1459 taxa (Schuiteman, 2014). R.Dressler (1981) used orchid-pollinator relationships for his classification (*The orchids. Natural history and classification*). Clearly the most important part of that book is a discussion of approaches to orchid identification. An apparent challenge to orchid taxonomy is the abundance of amateur books on the market. Although the problem with orchid identification is not going to be resolved immediately, the path toward the solution has been specified: a deeper

study of the androecium and pollination process. The current work is an effort to move in that direction.

The orchid family is characterized by a striking morphological variation in floral structures corresponding to various pollination strategies. The variation in the androecium (column, anther cap, and pollinia) is particularly prominent (Dressler, 1993; Freudenstein and Rasmussen, 1996; Telepova-Texier, 2011). Types of pollen dispersal units (PDU) are crucial for the pollen germination, whether these are monads, tetrads single pollen grains, or other types of units (Pacini and Hesse, 2002). Variation in PDU contributes in a number of ways to current evolutionary trends: (1) differentiation of cell walls around a single microspore or tetrad; (2) contiguous tetrad types (linear, decussate, square, tetrahedral, rhomboid, T-shaped); (3) variation in external shapes of pollinaria; (4) pollen longevity; etc. As a result, some important characters, such as the number and consistency of pollinia, have been included in the key to genera (Seidenfaden, 1991). The author has published a typology for PDU in the orchid genera (Telepova-Texier, 2012, 2013).

However, data for this huge family comprising some 20000 species are still sketchy, and taxonomic treatments have not been uniformly developed across the family. During the past 13 years, I have been collecting material on floral microstructure for about 300 orchid taxa from Southeast Asia. Here I present the comparative morphology of PDU and anther caps for Asian taxa, their fine structure and typology complemented by a study of some American orchids.

Variability of morphological characteristics within the hybrid complex

***Reynoutria × bohemica* Chrtek & Chrtková**

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Among plants naturalized in Europe, there are *Reynoutria sachalinensis* (F.Schmidt) Nakai, *R. japonica* Houtt., and their cultigeneous hybrid *R. ×bohemica* Chrtek & Chrtková, which has evolved in the secondary distribution range of the parent species. Material for the study of *R. ×bohemica* was collected from five different local populations (or clones) in the City of Moscow, nine populations from around Moscow, and also two populations in Luxembourg. Samples of *R. japonica* from Japan and *R. sachalinensis* from the living collection of the Main Botanic Garden RAN were also included in the analysis.

Plants belonging to the genus *Reynoutria* flower late in their secondary distribution range, and leaf characteristics have mostly been used as diagnostic characters. However, we have observed individual intraclonal and interclonal variability of leaf blade shape as well as micromorphological leaf characters (presence/absence of trichomes on leaf abaxial surface). The habit of *R. japonica* from its native range (rather low, ascending plants) appeared in conflict with the existing key to *Reynoutria* in its secondary distribution range, and thus the key was in need of correction. We proposed rejection of references to the considerable (1–4 m) height of the plant and instead describe it as 1–1.5 m tall. Besides, the presence of conical hairs on the midrib does not appear to be a diagnostic character; this condition was only recorded for some clones within *R. ×bohemica* hybridogeneous complex.

Flowers of *Reynoutria ×bohemica* are perfect from the morphological standpoint and have a three-locular three-ribbed ovary and three-lobed fimbriate stigma. It was in just 20% of all populations that exclusively typical P(5)A5+3G(3) flowers were found, that is, only those with a five-parted perianth, five stamens in the outer series and three in the inner. As to the rest of the samples, various deviations were detected there in a number of flowers within inflorescences. These deviations concerned the number of perianth parts and androecium structure: P(5)A7G(3); P(5)A7+(2)G(3); P(5)A9G(3); P(6)A7G(3); P(6)A5+(2)G(3) (a pair of stamens completely connate); P(6)A6+(2)G(3) (two stamens connate along two-thirds of filament length); P(6)A8+1G(3) (one stamen underdeveloped); P(6)A7+(2)G(3) (two stamens connate along two-thirds of filament length); P(6)A9G(3); P(7)A11G(3). Interclonal variability as regards relative lengths of style and stamens was also observed. In all the samples, anthers were colorless and contained only some few pollen grains (sized on average 24×17 mkm).

Restoration of sexual reproduction in *Reynoutria japonica* by way of hybridization with closely related taxa and polyploidy has resulted in considerable diversity of the species in its secondary distribution range. This appears to be a major strategy for the advancement of alien species and elevation of their invasive potential. Significant improvement of plants' adaptation abilities in the conditions of their new homeland may be attributed to the stabilization of newly formed genotypes within *Reynoutria* complex through intensive vegetative regeneration.

Plants with intermediate characters or hybrids?

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The identification of alien species is challenging due to genetic drift and the possibility of hybridization with indigenous or even other closely related alien species. When using conventional diagnostic characters, it is not always possible to conclude whether the object constitutes a new race that has evolved through some microevolutionary process or a hybrid, which may have a higher invasion potential as compared to the parent species and then require special attention and invasion control measures.

The objective of the current work is prediction of the rate at which new hybridogeneous taxa that have evolved within the secondary range are going to penetrate the natural plant communities. An important part of such a study is a taxonomic revision of the taxa in question and providing evidence of their hybrid origin with the help of experimental, cytological, phytochemical, and molecular methods as well as testing the hypothesis that suggests a higher invasion potential of a hybrid when compared with parent species.

Hybridogeneous origin of the so-called *Bidens* ×*garumnae* Jeanj. & Debray, which is said to be naturalizing in the middle Volga reaches, has not been proved by experimental or molecular genetic methods. Characters that have been used to identify this taxon (prostrate habit and entire leaves) are not inherited; more than that, they are not pronounced in the type specimen of *Bidens* ×*garumnae* [P]. The plant in question may constitute a complex of microspecies within *B. tripartita* L.

We have also shown that the alien beggar-ticks recorded during the past decades in Eastern Europe under the name *Bidens connata* Muhl. ex Willd. actually constitute a complex of hybrids and back-crosses that have been formed in the secondary range by the invasive species of North American origin, *B. frondosa* L. with the native *B. cernua* L. This taxon was described as *B. decipiens* Warnst. as early as in 1895, its type preserved in Edinburg [E]. Remarkably, cypselae of *B.* ×*decipiens* are hirtellous with hairs of two types: duplex ones, consisting of two cells, like those in *B. frondosa*, and simple multicellular, like those in *B. cernua*. Additionally, in *B.* ×*decipiens* cypselae are 4-angled and 4-awned, like those of *B. cernua*, yet tuberculate, like those of *B. frondosa*. The heads in *B.* ×*decipiens* are similar to those in *B. frondosa* as far as their size and shape, while the leaves are entire, like those in *B.*

cernua. When plants were grown at an experimental plot, all of the named characters were inherited, and the molecular-genetic analyses have confirmed the hypothesis suggesting the hybridogeneous origin of *B. ×decipiens*.

In Europe, alien North American goldenrods have produced hybrids with the native *Solidago virgaurea* L. When grown at experimental plots, these hybrids have demonstrated stability of their diagnostic macro- and micromorphological characters. Similarly to *S. canadensis* L., *S. ×niederederi* Khek (*S. canadensis* × *S. virgaurea*) features smallish heads in paniculiform arrays and pubescent stems. At the same time, it has large basal leaves similar to those in *S. virgaurea*. *S. ×snarskii* Gudž. & Žaln. (*S. gigantea* Aiton × *S. virgaurea*) differs from *S. ×niederederi* in glabrous stems and larger heads. Molecular-genetic analyses have confirmed hybridogeneous origin of the studied plant samples.

Differently from such classic examples of aggressively naturalizing hybrids as *Reynoutria ×bohemica* Chrtek & Chrtková or *Spartina ×anglica* C.E.Hubb., the hybrids that we have studied are not yet widespread and occur as solitary specimens. It is just *Solidago ×niederederi* that has exhibited a more persistent naturalization tendency during the past five years in Central Europe, its range somewhat expanded in Poland, Lithuania, and Austria.

ZOOLOGY

Differentiation and cryptic speciation in rodents of Northeastern Palearctic as inferred from DNA sequence data: Case studies of genera *Lemmus* and *Stenocranius* (Rodentia, Arvicolinae)

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True lemmings (*Lemmus* Link, 1795) are the most common rodents of the Arctic tundra in the Old and New World that play a very important role in the functioning of the Arctic biota; however, their taxonomy, distribution patterns, and species delimitation are still a matter of hot discussions. The least known are lemmings from the vast territory of Northeastern Siberia (also known as Western Beringia). Three *Lemmus* species: *L. sibiricus* Kerr, 1792 *L. amurensis* Vinogradov, 1924 and *L. trimucronatus* Richardson, 1825 inhabit different parts of this territory; the exact boundaries of their ranges are poorly known. These species are

indistinguishable by cranial characters and skeletal structure but differ by coat color and sizes. However, the body size and coloration are subject to high intraspecific, seasonal, and age variation. *L. sibiricus* and *L. amurensis* have identical karyotypes (2N=50, NF=50) and in laboratory experiments produce fertile offspring, whereas *L. trimucronatus* differ from these species by the karyotype structure (2N=50, NF=52), so that hybrid males obtained in crossings of *L. trimucronatus* with the other two species are sterile (Rausch and Rausch, 1975; Gileva *et al.*, 1984; Chernyavskiy *et al.*, 1993; Chernyavskiy and Kartavtseva, 1999). Molecular studies based on comparison of cytochrome b sequences have been in good agreement with karyological and hybridological data but they included only samples from the Arctic tundra and one from the eastern coast of the Kamchatka Peninsula (Fedorov *et al.*, 1999; Abramson, *et al.*, 2008). Previous studies did not use the type material or any samples from *terra typica*. Meanwhile, the proper use of species names entirely depends on determination whether additional specimens are conspecific with the specimen with which the species' name is associated (Santos *et al.*, 2016). Here we report the results of molecular studies using cytochrome b as molecular marker and aiming at elucidating the taxonomy, phylogenetic relations, and nomenclature within g. *Lemmus* in the eastern sector of the Palearctic. We have been examining museum collections with special attention to type material. It is especially important in the case of Amur lemming, as *terra typica* of this species was flooded when the Zeya Reservoir was formed in 1974 and it has become impossible to obtain new topotypes since then. It is important that all the museum samples originating from both the upper Kolyma River basin and the eastern coast of Kamchatka Peninsula, including one paralectotype of *L. flavescens* Vinogradov, 1925 and holotype of *L. amurensis ognevi* Vinogradov, 1933 from Verkhoyanskiy Region, identified earlier as *L. amurensis* now are phylogenetically placed within the eastern clade of *L. sibiricus*. This split within the eastern clade along the 60° N into the northern and southern group is a new one on the *Lemmus* tree. Consequently, only the southern subdivision can taxonomically correspond to *L. amurensis*. We have found that the lectotype and the second paralectotype of *L. flavescens* trapped by baron von Kittlitz in 1826 belong to the Nearctic branch, i.e., to *L. trimucronatus*. Thus the first record for the species from the Kamchatka Peninsula has been made with the help of molecular tools. Phylogenetic analyses demonstrated that the range of Amur lemming is dramatically smaller than it had been previously assumed, limited to the territories of Transbaikalia, southern Yakutia, and Amur Region. The species is not only rare, but also has disappeared from most places where it used to be distributed in the first half of the past century including *terra typica* now flooded by the

Zeya Reservoir. Since the first half of 20th century when Fetisov trapped several specimens at various sites in southeastern Transbaikalia (deposited in ZMMU), no one was able to trap these animals anymore, despite numerous undertaken field studies. The only sustainable population of this species remains in the area of the Chulman River, southern Yakutia. In our opinion, the conservation status of Amur lemming undoubtedly has to be reclassified as Vulnerable/Near Threatened (VU/NT).

The narrow-headed vole *Lasiopodomys (Stenocranius) gregalis* Pall., 1779 is a widely distributed rodent species inhabiting tundra, steppe, and mountainous landscapes across the Palearctic. Currently its range is highly fragmented but in the Late Pleistocene it was continuous. Recent phylogeographic research using the mitochondrial cytochrome *b* gene has shown that there are four clear mitochondrial lineages with differences exceeding the species level (Petrova *et al.*, 2015). The most divergent was the clade confined to southeastern Transbaikalia (p-distance 11.4%). Multilocus analysis, analysis of m1 and M3 tooth structure and breeding experiments carried out earlier, showed that narrow-headed vole is represented by at least two cryptic species – the widespread *L. gregalis* and *L. raddei* Poljakov, 1881 with distribution range restricted to southeastern Transbaikalia and northeastern Mongolia. (Petrova *et al.*, 2016). Results of both molecular and morphological analyses showed that the territory of eastern Mongolia and adjacent Transbaikalia is inhabited by the true narrow-headed vole – *L. gregalis*. Southern boundary of *L. raddei* range follows the Uldzya River, which actually does not constitute a barrier, as the population of *L. raddei* was found at its right (southern) bank.

The Argun' River probably marks the eastern limit of *L. raddei*. Along the Argun' the species must be reaching the area north of Lake Dalainor. There are no visible barriers between Lake Zun-Torey and the Argun' River.

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A single generalist vs. multiple specialists: implication of modern techniques for species-level taxonomy of parasitoid Hymenoptera

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The world fauna of parasitoid Hymenoptera harbours far more than 600000 potentially recognized species. Since parasitic wasps attack many agriculture and forestry pests, these entomophagous insects are of considerable economic importance. Nevertheless, the species-level taxonomy of this group is substantially complicated due to the frequent presence of cryptic taxa within single morphospecies, especially within those reportedly having wide host

ranges and/or geographic distributions. To reveal these taxa, certain modern techniques, e.g. molecular and chromosomal analyses, are increasingly used. Recently, a number of specialized cryptic species have been detected within presumably well-studied groups of parasitoid Hymenoptera. The discovery of *Anisopteromalus quinarius* Gokhman et Baur (Pteromalidae), a cosmopolitan parasitoid of stored-product pests, represents a convincing example of that kind. Specifically, this species was often confused with the apparently well-studied *A. calandrae* Howard which has similar biology and distribution. However, haploid chromosome numbers (n) of 5 and 7, respectively, determined in these two forms unambiguously demonstrated the presence of cryptic species. As soon as the taxonomic status of *A. quinarius* was established, numerous differences between this species and *A. calandrae* in terms of morphology, molecular markers and bionomics began to accumulate. Interestingly, another ecologically similar member of the family Pteromalidae, *Lariophagus distinguendus* Förster, also appeared to harbour populations with different biologies. These populations represent two lineages that strongly differ in molecular characters. Again, chromosomal analysis of this morphospecies revealed two different karyotypes with $n = 5$ and 6. Nevertheless, these species seem to be more closely related than those of *Anisopteromalus*, because their chromosome sets presumably differ by two consecutive rearrangements, i.e., a centric fission in a particular metacentric and a pericentric inversion in a derived acrocentric chromosome. In addition, species of the *L. distinguendus* complex lack diagnostic morphological characters and can produce hybrid offspring under certain conditions, as opposed to complete reproductive isolation between *A. calandrae* and *A. quinarius*.