



Article

The Seventh Conference in Memory of Alexey K. Skvortsov

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Conference Overview

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The 7th annual Conference in Memory of Prof. Alexei Skvortsov was held at the Main Botanical Garden of the Russian Academy of Sciences on February 9, 2018. The Conference was organized by the Moscow Branch of the Russian Botanical Society and supported by the Main Botanical Garden and Moscow University. As with the previous conferences, the topic was narrowed to just one of the areas of interest of Prof. Skvortsov, this time to the “Species problem in plants and animals.” The Conference was held in the traditional format of a one-day meeting. The 7th Conference gathered mostly botanists from Moscow, 48 in all, who presented their talks and took part in discussions. The talks were mostly devoted to the problem of species delimitation in its various aspects, from morphology to molecular diversity, in populations of native, alien, and cultivated plants, and were presented in three oral sessions. Between the sessions, two photographic exhibits were presented in the hall of the laboratory building, the “Flora of South Africa” by Dr. Liudmila Ozerova and “Tulips of Southeast Russia” by the Young Naturalists’ Club *Putnik (Globetrotter)*.

The sessions were preceded by an introductory welcoming talk by the newly elected Director of the Main Botanical Garden Dr. Vladimir Upelnik.

The morning session was devoted to the species problem in native species. The first lecture by Dr. Natalya Reshetnikova dealt with changes in overall morphological habit in some plant species over the past century, as exemplified by populations of *Verbascum nigrum*, *Dianthus superbis*, *Medicago lupulina*, and some others. The second talk presented by Dr. Nina Stepanova and a high school student M. Loktev was devoted to species delimitation and volume in the *Tulipa biebersteiniana* group. Using re-evaluated morphological characters, mostly those of underground organs, and molecular markers, they demonstrated that the East European populations can be unequivocally placed into two species, mesophyllous *T. biebersteiniana* and

xerophyllous *T. scythica*. Further talks were also devoted to delimitation of species in diverse groups of plants. Drs. Julia Shner and Tatiana Ostroumova presented their work on species limits in the genus *Peucedanum* section *Peucedanum* (Apiaceae); Dr. Sergei Efimov and his co-authors from Moscow and Altai State Universities discussed the results of molecular and cytogenetic studies in the *Paeonia obovata* group; Dr. Maxim Nuraliev and his co-authors presented a talk on the evolution of the genus *Thismia* (Thismiaceae) in the light of morphological and molecular data. After a coffee break, four more talks were presented, among which two are worth special mention: one by Dr. Tatiana Kramina on molecular genetic identification of a *Silene* plant raised from a seed obtained from permafrost deposits of the late Pleistocene and Dr. Vladimir Gohman's talk on integrative taxonomy of parasitic Hymenoptera, the only zoological topic at this conference.

The afternoon session was devoted to the problems of identification and species delimitation among alien and invasive plants, exemplified by *Erigeron*, *Cuscuta*, and some other genera, followed by lectures on problems arising with species-level identification of some cultivated plants, including cultivated poplars (the talk by Dr. Marina Kostina and Natalia Vasilieva).

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

Species complex of *Paeonia obovata* Maxim. (Paeoniaceae): five species or just one?

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A complex of herbaceous peonies akin to *Paeonia obovata* Maxim. is distributed in the forests of East Asia. These peonies differ from other groups by their biternate leaves that consist of nine broad obovate entire segments, solitary terminal flowers, and glabrous follicles. Diploid plants (2n=10) occur along with tetraploids (2n=20).

The number of species recognized by various authors (Shipchinskiy, 1937; Voroschilov, 1966; Stern, 1946; Kemularia-Nathadze, 1958; Makedonskaya, 1979; Uspenskaya, 1987; Hong *et al.*, 2001) ranges from five (*P. obovata*, *P. oreogeton* S.Moore, *P. japonica* (Makino) Miyabe & Takeda, *P. vernalis* Mandl., and *P. willmottiae* Stapf) to just one, with two subspecies (*P. obovata* subsp. *obovata* and *P. obovata* subsp. *willmottiae* (Stapf) D.Y.Hong & K.Y.Pan). All the species occur in Russia, except for *P. willmottiae*, a Chinese endemic. Due to high morphological variability and the presence of polyploid

forms, identification of species in this group presents substantial difficulties. Authors disagree in their understanding of the species volume, which creates additional problems.

Species of *P. obovata* group are characterized by a large number of polymorphisms in ITS sequences of nuclear rDNA, which include two types of nucleotides (Yefimov *et al.*, 2017). Three groups of samples were segregated in accordance with the observed number of polymorphisms: those with 11, 3, and 2 polymorphisms. The groups are discreet, no hybrids found so far. The third group differs from the other two not just by the number of polymorphisms, but also by their position in the ITS sequence. It is difficult to find correlations of the segregated groups with any morphological characters. We have only found some correlation with the geographic distribution. The group with the smallest number of polymorphisms includes samples from Sakhalin Island and the Maritime Province (District of Shkotovo).

The aim of this research was to determine if there is a correlation between the observed polymorphisms and ploidy. Using the flow cytometry method, we obtained data on the relative DNA content and genome size in 16 representatives of the *P. obovata* complex. Monoploid genome size ranged within 11.57–14.70 pg; among the sampled plants there were diploids along with tetraploids. There was a good correlation between the ploidy level and number of ITS polymorphisms.

The data obtained suggested that the species complex of *P. obovata* constitutes a very heterogeneous group as regards morphological and genetic characters. Apparently, the differences at the genome level are more distinct than the morphological differences. The observed polymorphisms may depict a contemporary diversification within the group.

This work was supported by the Russian Science Foundation Grant N° 14–50–00029 *Scientific Basis for Creation of the National Depository for Living Systems* (sample collection in natural habitats and obtaining of flow cytometry data) and was also conducted within the framework of the government assignments for the Lomonosov Moscow State University N° AAAA–A16–116021660099–5 and 01201353074: *Morphological Studies and Nucleotide Sequences Analysis*.

The problem of species diagnostics in invasive *Erigeron* sect. *Conyza*: hybridogeneous taxa or ecological forms?

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Within the Mediterranean Basin, all taxa of the genus *Erigeron* sect. *Conyza* are alien; in fact, *E. canadensis* L. has been included in the ten most aggressive invasive species in Europe in the databases DAISIE and GT IBMA. During 2017, we studied the morphological features and ecological niches of *E. canadensis*, *E. bonariensis* L., and *E. sumatrensis* Retz. in Italy, Spain, and Portugal. Some of the sampled plants could not be attributed, with any certainty, to a species based on analysis of their morphological characters (inflorescence shape, type of pubescence on shoots and leaves), as they

exhibited intermediate parameters, most often a combination of characters typical of *E.canadensis* and *E.sumatrensis*, both of which are widespread in southern Europe. These individuals appear to be putative hybrids of invasive *Erigeron* species; however, their morphological peculiarities could be also caused by adverse ecologic situations or mechanical influences, such as damage to plants or severe contamination of habitats.

To help explain the observed morphological differences, we conducted a molecular-genetic study using ISSR fragment analysis. The CTAB method was used for the extraction of DNA from 34 herbarium samples and the following ISSR primers were used for PCR: (CAG)₅ [M7], (AC)₈(C/T)G [M2], (GA)₈ YG [UBC 841], and DBD(AC)₇ [UBC 889]. The obtained data were processed in the programs *Structure* (Fig. 1) and *NewHybrids* (Fig. 2).

Analysis by the program *Structure* produced three distinct groups: 1 – all those samples which, both morphologically and according to the molecular data, belonged to *E.bonariensis*, including one individual with atypical pink peripheral florets, collected in Pompei, Italy; 2 – all samples morphologically identical to *E.canadensis*, except for N° 19 collected in Madrid City Park, which had characters typical for *E.sumatrensis* but also unique spike-like head arrays not encountered in any other samples; 3 – all samples of *E.sumatrensis* along with putative hybrids *E.sumatrensis* × *E.canadensis*.

We further analyzed in *NewHybrids* the similarities between DNA fragments in the putative hybrids *E.sumatrensis* × *E.canadensis* and in their parent species. Two samples (N°s 6 and 22) were found to be of hybridogeneous origin with more than 80% probability. Remarkably, it was only N° 22 that exhibited morphological characters intermediate between those of the parents, while N° 6 did not look any different from a typical *E.sumatrensis*. Five samples (3, 5c, 8b, 10b, and 19) were found to be hybrids with a probability of no less than 25%; however, only two of those (10b and 22) could be identified as hybrids judging by the intermediacy of morphological characters, while the other three, collected in Italy, were initially attributed to *E.sumatrensis*. Sample 19, *E.sumatrensis* with the spike-like head arrangement, must also be a hybrid, *E.sumatrensis* × *E.canadensis* (with 36% probability). Samples with morphological characters intermediate between *E.sumatrensis* and *E.canadensis*, which we had considered to be hybrids, were grouped with *E.sumatrensis*, even though they (especially 8a and 8b) exhibit characters more typical of *E.canadensis*, i.e., scanty pubescence on adaxial and abaxial leaf surfaces (on average less than 5 trichomes mm²) and less turbinate involucre. The obtained data demonstrate high infraspecific variability in *E.sumatrensis* as compared with the other two representatives of sect. *Conyza*. The variation in diagnostic characters for *E.sumatrensis* is determined by both hybridization processes and environmental factors.

Apparently, the invasive *E. bonariensis* has rarely, if ever, been involved in any hybridisation in Southern Europe, while *E. sumatrensis* and *E. canadensis* hybridize with each other frequently. The overall percentage of hybrids and back-crosses in horseweed populations has been low so far, but monitoring of hybridogeneous activity in *Erigeron* sect. *Conyza* is certainly necessary to enable predictions regarding a possible expansion of their secondary ranges and the potential threat they may pose to biodiversity in the Mediterranean Region.

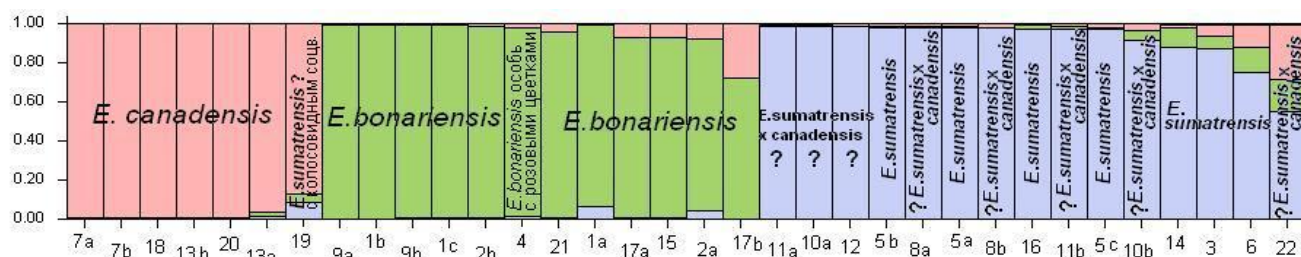


Figure 1. Samples of *Erigeron* sect. *Conyza* arranged according to similarities in their DNA, as shown by analysis in *Structure*. Provenance information (letter qualifiers signify different samples of the same species collected in the same locality): 1–6 Italy, 7 Russia (Main Botanic Garden RAS, Moscow), 8–14 Italy, 15–17 Portugal (Lisbon), 18–22 Spain (Madrid)

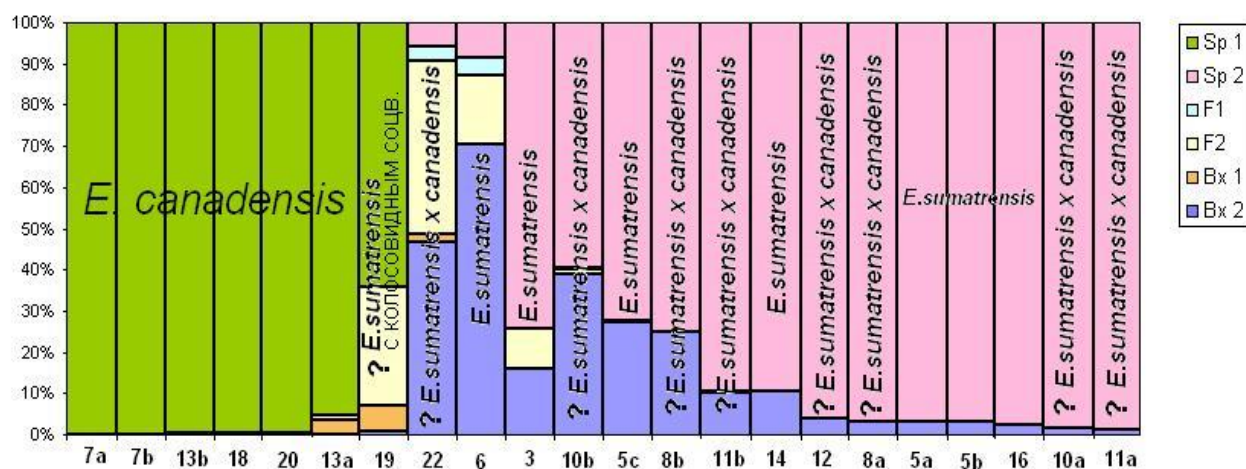


Figure 2. Samples belonging to different taxa in *Erigeron* sect. *Conyza* and probability of their placement in species, hybrids, or back-crosses based on the results of analysis in *NewHybrids*. Provenance information as in Figure 1

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Integrative taxonomy of the parasitoid Hymenoptera: major approaches, techniques, and results

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Parasitoid Hymenoptera, or parasitic wasps, are one of the most speciose and economically important insect groups. The taxonomic study of parasitoids is substantially complicated, mainly due to the morphological similarity of their closely related forms that live in ecologically analogous environments. In addition, the intraspecific morphological variation of parasitic wasps imposed on them by their hosts can be significant. Thus, it is often difficult to distinguish between different individuals of the same parasitoid species, on the one hand, and the members of several morphologically similar but different species, on the other hand. To make this distinction, intraspecific morphological variation of these insects must be differentiated from the interspecific one. In the case of parasitic wasps, this means a distinction between the environmental and genetic variations. To achieve this goal, more or less environmentally independent characters, i.e., molecular, chromosomal and similar ones, should be involved. Moreover, these characters must be employed within the framework of integrative taxonomy, which implies a combined use of various techniques for delimiting, recognizing and describing closely related species.

Molecular study is the most widespread technique used in the integrative taxonomy of parasitoids. With this kind of study, sequences of either the so-called barcoding fragment of cytochrome oxidase coded by mitochondrial DNA (*COI* mtDNA) or, less frequently, of cytochrome b (*Cytb* mtDNA) are employed. Sequences of nuclear genes, for example, ITS2 and 28S ribosomal DNA are additionally used. Study of these markers revealed cryptic taxa within many parasitoid morphospecies. It also demonstrated that species delimitation based on external characters that are subject to environmental variation could be incorrect. Chromosomal analysis is another technique that has been increasingly used in parasitoid taxonomy. Several cryptic species of parasitic wasps were initially recognized and then described as new to science based on their karyotypic differences. The use of chromosomal characters in the integrative taxonomy has some important advantages, because they are also morphological, at least in a broad sense. At the same time, many of these characters are discrete and therefore can either mark genetically isolated populations or reveal certain cases of interspecific hybridization.

The use of more classical approaches in parasitoid taxonomy has also substantially changed during the recent decades. In particular, new systems of morphological characters are now employed to distinguish between closely related species, and recently developed methods of geometric morphometry are effectively used for the same purpose. In addition, ecological and physiological studies that include testing for reproductive isolation and identification of the host range are involved in delimiting parasitic wasp species with considerable success. For example, these studies demonstrate that many widespread

polyphagous parasitoids are in fact groups of specialized cryptic species, where each species is often fully isolated from the others.

These two techniques of integrative taxonomy are complementary to each other, and integration of the results obtained by the different techniques constitutes the very essence of integrative taxonomy. Evaluation of the taxonomic rank of newly discovered cryptic lineages and formal description of new species, if appropriate, are both very important for fundamental as well as applied research. The latter painstaking and effort-consuming task can be performed only by qualified taxonomists, and nowadays the significance of these specialists is therefore substantially increasing. Paradoxically, this pattern does not exclude species descriptions based exclusively on their DNA sequences when morphological differences between these taxa cannot be found. Examples of nomenclatural decisions of this kind are already known in the taxonomy of parasitic wasps and some other invertebrates. The current edition of the International Code of Zoological Nomenclature neither explicitly prohibits nor encourages these actions, but its content is likely to be changed in the future in a way which makes both the initial designation and further maintenance of the so-called DNA-types and similar objects a routine procedure.

The obtained data therefore demonstrate that the presence of cryptic taxa within widely distributed morphospecies of parasitic wasps should be considered rather a rule than an exception. As soon as representative material on these taxa is collected and adequate techniques are used to analyze it, the detection of cryptic species becomes highly likely, if not almost inevitable. Current experience confirms that every parasitoid morphospecies must be carefully studied using modern techniques to reveal cryptic taxa. Moreover, these techniques can verify results of the morphological analysis by identifying taxonomically important information among other data.

Ecological amplitude of *Armeniaca vulgaris* Lam., *A. mandshurica* (Maximowicz) B.Skvorzov, and *Persica vulgaris* Mill. tested during the adverse weather period of 2016-2017

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During the past decade, starting from 2007, a selection nursery and an experimental garden have been established in Makhra, Vladimir Region, 120 km northeast of Moscow. The climate conditions here are harsher than in Moscow: there are less days with temperatures above freezing, and the frost is harder. All phenological phases in plants occur nearly two weeks later than in the capital. Also, the soil is extremely poor, sandy. The probability of selecting frost-resistant genotypes of apricot and peach is higher in this climate.

All the trees planted here in their permanent positions in the autumn of 2007 were lost during the next 5–7 years. This happened not only because of the cold climate, but also due to damping off. The sandy soil subsided much more than a clayey soil would, so that root collars sank lower than the soil surface and the formed holes accumulated cold water in autumn and melt water in spring, which triggered

bark damage and resulted in the death of trees. From 2010 on, two-year-old apricot seedlings have been planted on mounds up to 70 cm high. Even though these mounds also subsided with time, a height of about 20–30 cm has remained. This technique allowed all the newly planted saplings to become successfully established.

During the first eight years, four winters in Makhra were moderately cold and the other four severe, with temperatures dropping at times to about -35°C , while in Moscow it was never colder than -25°C . No losses were encountered among the nursery apricots, and even the peaches survived, though some sustained significant damage. By 2016, the experimental garden of stone fruits in Makhra contained 100 apricots, 9 peaches, and another 30 seedlings of plum, cherry plum, black cherry, and cherry.

The winter of 2016–17 started unusually early, at the end of October, when the wood in most trees was still immature. The trees did not have a chance to complete leaf abscission and some had not even started. As to be expected, this lack of preparation for winter had an adverse affect on their overwintering. Early in January 2017, for three days in a row, the temperature reached about -30°C in Moscow, while in Makhra the night temperatures were down to -35° and even -37°C .

The Makhra Experimental Garden lost 64% of its 3–10-year-old apricot saplings. A quarter of the surviving trees received 4–5 points during the evaluation; 11% – 2–3 points (the highest score of 5 was awarded to saplings with regrowth of one or more shoots to 70–100 cm; 1 point was assigned to those with poor shoot regrowth). As for the peaches, all 9 saplings aged 3–8 years old perished. In Moscow, all apricots survived the 2016/2017 winter, while among peaches aged 4–16 years old 8.5% died (their total number had been 73), although many of the peaches that lived through the winter were frost-bitten and contracted peach leaf curl.

Among the apricots that perished in Makhra during the 2016/2017 winter, 39% were 3–6-year-old saplings from Kyrgyzstan. Of 28 trees from Kyrgyzstan, only three survived, while in the Main Botanic Garden (MBG) in Moscow, 18 of 24 Kyrgyz trees survived, and in the Moscow monasteries, where the microclimate is the mildest, all the 18 planted apricot saplings lived on.

The evaluation of those apricots that survived in Makhra yielded the following results. Of the trees awarded 4–5 points, 17% were Manchurian, 46% were raised from seed originating from the Novospassky Monastery and 37% from seed collected in other monasteries and MBG.

Until recently, in the Novospassky Monastery there were 18 apricot trees, three of which were Manchurian. A dense planting resulted in cross-pollination, so that hybrids between *A.vulgaris* and *A.mandshurica* were produced. The hybrid nature of the obtained plants was confirmed through observations of morphological characters. Saplings from *A.vulgaris* seed exhibited phenotypical characters characteristic of *A.mandshurica*: lighter, pinkish-colored bark, leaf blades with long acuminate tips and coarse serration at the margin, invariably early onset of autumn foliage color, pink flower color, smallish fruit, etc. *A.mandshurica* starts and finishes its vegetation earlier. The latter feature proved to be critical in the harsh conditions of the northern Vladimir Region. It was this adaptation that resulted in the

most successful overwintering of the Manchurian apricots and their hybrids originating from the Novospassky Monastery.

In the Makhra nursery beds, the 1–2-year-old apricot seedlings/saplings of variable provenance, peaches, and nectarines all suffered a winter die-back down to the very root collar. During the subsequent growing season of 2017, they produced new shoots, whose quality was evaluated using a 5-point scale (Tables 1 and 2).

Table 1. Overwintering of one-year-old seedlings in the nursery and their recovery during the summer, 2017

Apricot seedlings Provenance	Quality of shoots regrown from root collar*			Perished
	5–4 points	3–2 points	1 point	
China	14%	6%	2%	78%
Kyrgyzstan	22.2%	3.7%	3.7%	70.4%
Tadjikistan	6.3%	9.5%	6.3%	77.8%
Slovakia	11.7%	17.6%	-	70.6%
Moscow	8.3%	17.4%	22%	52.3%
Peaches and nectarines	0%	0%	0%	100%

* 5 points – regrowth of one or more shoots to 70–100 cm; 1 point – very weak shoot regrowth; plants may be discarded.

Table 2. Overwintering of two-year-old saplings in the nursery and their recovery during the summer, 2017

Apricot seedlings Provenance	Quality of shoots regrown from root collar			Perished
	5–4 points	3–2 points	1 point	
Tadjikistan	33.3%	26.3%	13%	27.4%
Moscow	58%	25%	8%	9%
Peaches and nectarines	73%	19%	4%	4%

The data in Table 1 demonstrate that among the 1-year-old seedlings, those of the Moscow provenance overwintered, as usual, better than those of any other provenance, yet were behind during the subsequent recovery. Among the 2-year-olds (Table 2), the Moscovites overwintered and grew back the best.

Of the peaches and nectarines in Machra, all 3–8-year-olds and 1-year-olds perished, while the 2-year-olds overwintered even more successfully than the apricot 2-year-olds from Moscow (Table 2). This can be explained if one considers that, differently from older saplings, the 2-year-olds were overwintering under the snow and at the same time they had a more developed root system, as compared to 1-year-olds.

In the Makhra experimental garden, many planting spots are now vacant; the selection of the most winter-hardy individuals will be continued, while relying more heavily on Manchurian apricot.

Molecular genetic identification of a campion (*Silene*) from the Late Pleistocene age

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Beringia, the Late Pleistocene ice-free refugium, which once stretched from northeastern Siberia to western Canada, can potentially serve as a source of genetic material of extinct plants and animals, their DNA being preserved in excellent condition. Beringia thus constitutes a natural laboratory for studies of microevolution and its rate. Reconstruction of ancient plants may provide exclusive material for the understanding of evolutionary processes and detailed reconstructions of the Pleistocene environment.

Seeds of more than 30 plant species, including fruits and seeds of campion, were excavated by the staff of the Laboratory of Soil Cryology, Institute of Physicochemical and Biological Problems in Soil Science, RAS, Moscow, from the Late Pleistocene fossil burrows of the Arctic ground squirrel (*Urocitellus parryii*) in the permafrost sediments buried at a depth of 38 m at the lower Kolyma River in northern Yakutia (Gubin and Khasanov, 1996). According to the results of radiocarbon dating, the age of these samples is 31800 ± 310 years.

The genus *Silene* L. (Caryophyllaceae) includes about 700 species of herbaceous plants occurring across the world, mostly at moderate-climate latitudes of the Northern Hemisphere, with a center of diversity in the Mediterranean Region and the Middle East (Oxelman and Lidén, 1995). A number of species of campion are distributed in the Arctic tundra of northeastern Siberia and North America. Başlı and co-workers studied the morphology of the excavated seed under light and scanning electron microscopes and compared the ancient seed with those of extant *Silene* species (*S. alba*, *S. chlorantha*, *S. nutans*, and *S. stenophylla*), which occur nowadays in that and adjacent regions. The excavated seeds were identified as *S. stenophylla* Ledeb., even though they were smaller than those of contemporary plants (Başlı *et al.*, 2009).

Using the placental tissue of immature fruit and applying the methods of tissue culture along with clonal micropropagation, the staff of the Laboratory of Cryobiology and Water Biophysics, Institute of Cell Biophysics, RAS, succeeded in producing plants that flowered and yielded highly viable seed (Yashina *et al.*, 2012). The authors identified the plants as *S. stenophylla*; however, B.Oxelman and his colleagues disagreed and, relying on a number of morphological characters, proposed the ancient plant's placement in the group of *S. linnaeana* Vorosch. (Oxelman *et al.*, 2012). According to its geographical distribution, they further identified it as *S. samojedora* (Sambuk) B.Oxelman, particularly emphasizing the fact that *S. stenophylla* and *S. linnaeana* are related rather distantly (Oxelman *et al.*, 2012).

Therefore, the proper attribution of the ancient campion to a species using methods of molecular genetics presented a critical task.

The DNA of plants regenerated from tissues of the ancient plant served as material for the current study. Samples from twelve herbarium specimens preserved in the Moscow State University Herbarium (MW) served as sources of DNA for comparisons. The specimens were identified as follows: *S. stenophylla* (Khabarovsk Province, Magadan Region, and Chukotka); *S. linnaeana* (Yakutia/Sakha Rep., Rep. of Buryatia, and Amur Region); *S. samojedora* (Taimyr Pen. in Krasnoyarsk Province); *S. ajanensis* (Regel & Tiling) Vorosch. (Khabarovsk Province, Magadan Region). The identification of these samples was confirmed by S.R.Mayorov. Markers for the molecular genetic analysis, *rps16* intron of cpDNA and ITS1–2 of the nuclear rDNA, were chosen as the ones best studied for the genus *Silene* (Oxelman *et al.*, 2013). DNA markers representing the entire genus *Silene* were obtained from GenBank. These included 58 sequences of *rps16* and 73 of ITS1–2. Two species of the genus *Lychnis* were used as outgroups. Phylogenetic reconstructions were conducted separately for *rps16* and ITS1–2 using the methods of Maximum Likelihood (ML) in *MEGA 6.0* and Bayesian Analyses in *MrBayes* Program. For the ML method, we used the GTR+G model for *rps16* and GTR+G+I model for ITS.

The alignment length was 984 bp for *rps16* and 778 bp for ITS. The sequence obtained from the reconstructed campion was practically identical, for both markers, to those of *S. samojedora* and *S. linnaeana* (both with our own samples and those obtained from GenBank). Within the sequences of *rps16* belonging to *S. linnaeana*, *S. samojedora*, *S. ajanensis*, and *S. villosula*, there was only one variable region, C/T at position 281. Also, one *S. villosula* sample had an insertion, and one of *S. samojedora* had a deletion. With the ITS marker, the sequence in the regenerant also matched those in the species of *S. linnaeana* group in which we observed practically no variability, except for some polymorphism at certain sites. The degree of polymorphism was somewhat higher in the regenerant sequences: ten polymorphic sites in ITS1 and six in ITS2.

Phylogenetic analysis based on both markers demonstrated the division of the genus *Silene* into two subgenera, *Silene* and *Behenantha*, and also revealed uncertain positions of some sections and species. Two large clades were most supported with both markers. Clade One included sect. *Siphonomorpha* and sect. *Sclerocalycinae* of subg. *Silene*. Clade Two contained sect. *Physolychnis* and sect. *Viscosae* of subg.

Behenantha. *S. stenophylla* was placed in Clade One with high support, while the regenerated campion together with species of the *S. linnaeana* group was placed in Clade Two. This confirms the point of view expressed by Oxelman and co-workers (Oxelman *et al.*, 2012).

Due to a nearly complete lack of differences in ITS and *rps16* sequences in the species of the *S. linnaeana* group, one may even question the reasons for segregation of several species in this group. However, differences have been demonstrated among these species in their low-copy nuclear genes, and polyploidy has also been observed within this complex (Popp *et al.*, 2005). Low variability of the studied sequences in the *S. linnaeana* group may be interpreted as proof of the reliability of the markers chosen for barcoding. Low variability may also indicate a young evolutionary age of this group and a low evolutionary rate in the Arctic environment. Full-genome studies along with employment of variable SSR and AFLP markers may accelerate the study of microevolutionary processes in the group.

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Morphometric variability of species occupying narrow ecological niches within peatland habitats

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Peatlands are unique habitats requiring specific adaptation mechanisms from all inhabiting organisms (Nitsenko, 1967; Rydin and Jeglum, 2006). Special environmental conditions there include high water levels, inundation, significant temperature fluctuations on the surface of the substrate, low oxygen content, impeded access to nutrients, predominantly high acidity, and so on. In these situations, intense competition for space and nutrients takes place among mire inhabitants including those belonging to different life forms, such as vascular plants and the constantly expanding moss cover (Minayeva and Sirin, 2012).

A limited number of vascular plant species is typical for bogs along with high ecosystem diversity: vegetation here is characterized by discrete complexes and mosaics, which is a well-known phenomenon (Masing, 1974). Microcoenosis has been considered by many authors as the basic structural unit of bog vegetation cover (Masing, 1982, 1984), an indicator of ecological conditions (Antipin, 1991; Blagoveshchenskiy, 1992), as well as a unit of vegetation dynamics (Zobel, 1988). Horizontal differentiation of vegetation and formation of nanotopography elements, including those within limits of hollows, have been attributed to ecological factors (Loopman, 1988).

Spatial isolation of mire massifs, abrupt, ecologically caused boundaries between peatlands and uplands, and internal patterns within peatlands (mosaics) promote morphological radiation, i.e., intraspecific variability in vascular plants. This could be a compensatory mechanism offsetting limitations in the number of species. Using examples of herbaceous vascular plants typical for bogs, we tested the hypothesis that suggests compensation of low species diversity through high morphological intraspecific diversity in the bog environment.

Pod-grass (*Scheuchzeria palustris* L.), mud sedge (*Carex limosa* L.), and white beak-rush (*Rhynchospora alba* (L.) Vahl) were used as model species. The former two species are obligate helophytes (perennial wetland plants whose overwintering buds remain under water). The study took place in bog hollows at different slope levels on two different sites located within ridge-hollow complexes on the Staroselsky Mokh Bog in the Central Forest Biosphere Reserve (Tsentrarno-Lesnoi Zapovednik), Tver Region.

Upon recording natural boundaries within bog hollows by cartographic methods, the author segregated vegetation mosaic elements differing from each other by habitat parameters. These elements were grouped in six types of microcoenoses: dry *Sphagnum* moss carpets, intermediate *Sphagnum* moss carpets, moist *Sphagnum* moss carpets, semi-inundated and inundated parts of hollows, and quaking bog carpets in degraded parts of hollows. All the microcoenoses reliably differed from each other by the ground water level, dissolved oxygen content in water, and temperature regime. Electric conductivity and pH measurements did not reveal any meaningful differences.

For each studied species, the following measurements were taken *in situ* on a series of permanent plots located within the natural boundaries of microcoenoses twice a year during two vegetation seasons: number of ramets (originating either from seed or vegetatively); for each ramet, the recorded parameters included the stem height, number of leaves, length of flowering shoots, ontogenetic stage, and phenological stage (8 times per season). Genets were not distinguished from ramets when taking *in situ* measurements. Additionally, model individuals were chosen outside permanent plots, within the respective microcoenoses. Morphological parameters of model plants were considered in more detail including the lengths of all leaves, length of inflorescence, and other parameters referring to reproductive morphology.

While the studied microcoenoses practically did not differ from each other with respect to their vascular species composition, the differences in shoot density and the habits of plants were quite significant. It was speculated that certain plant morphs may correlate with certain habitats. On the other hand, shoots significantly differing in measurements and/or color could be connected, originating from the same rhizome or isolated due to particulation only recently.

A number of statistically valid differences were revealed between genets and/or ramets inhabiting different microcoenoses in their key morphometric parameters including reproductive morphology. The tallest plants inhabited inundated parts of hollows, while the shortest ones were recorded on quaking carpets of degraded hollows. In other microcoenoses, height differences were more pronounced in *Scheuchzeria palustris* than in the other two species. The same trend was revealed in the measurements of leaf and stem length: distinct morphs whose segregation was based on a complex of characters were identified only in *Scheuchzeria palustris*. The other two species produced a continuum along the habitat gradient with respect to their morphometric parameters, so that it was impossible to segregate distinct morphs.

While *Scheuchzeria palustris* did not exhibit any differences between microcoenoses as regards the ontogenetic structure of their coenopopulation loci or reproductive morphology, the

other two species appeared to actively employ population regulatory mechanisms in their adaptive strategy. The portion of plants originating from seed in pod-grass populations was invariably insignificant in all habitats. Solitary immature genets were observed within the entire span of ecologically optimal habitats (ranging from dry *Sphagnum* moss carpets to semi-inundated areas). Also, the density of flowering shoots was tens of times lower than that of vegetative ones.

Rhynchospora alba was shown to be a total opposite of *Scheuchzeria palustris* in this respect. Depending on the type of microcoenosis, its coenopopulation structure varied so drastically that it formed a full ontogenetic spectre. Regeneration from seed was the most successful in the poorest conditions, on degraded quaking carpets, where other species were abundant as well, although in a depressed status.

Carex limosa was observed taking over habitats with challenging conditions, which helps it to avoid intense competition taking place in more favourable situations. To sustain populations in the extreme settings (inundated hollows, dry *Sphagnum* moss carpets), the sedge resorts to seed regeneration.

The three species appeared to utilize contrasting adaptive strategies in the ever-changing dynamic setting of the bog microcoenoses mosaics. Due to their specific environment, bog habitats presumably are the stage for microevolutionary processes in at least some species. Therefore, bog plants are to become a subject of more careful examination, which should employ genetic research.

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**Floral morphology and the species problem in some Asian representatives of
Sect. *Myrianthus* (Blakelock) Leonova (*Euonymus* L., Celastraceae)**

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East and Southeast Asia are major hotspots for species diversity in the genus *Euonymus*. Among the largest taxonomic groups within the genus in the region, there is the section *Myrianthus* (Blakelock) Leonova, which, according to various assessments, comprises 25 to 45 species (Blakelock, 1951; Ma, 2001). The important diagnostic character for the section is the four-lobed pyriform capsule. Delimitation and identification of a number of closely related species within the section *Myrianthus* (*E. cochinchinensis*, *E. glaber*, *E. indicus*, *E. laxicymosus*, *E. laxiflorus*, and others) is challenging. These species feature an unusual shape of sepals and petals (the so-called elaborate design) along with variable morphology of margins in the parts of the perianth. The margins can be entire, fimbriate, or else dentate. Descriptions of the floral structure in the species of this section produced by different authors are often incomplete and contradict each other. Discrepancies exist particularly in interpretation of terminology referring to the morphology of the sepal and petal margin: dentate, denticulate, and fimbriate. These terms have been often confused. The information concerning the shape and color of the perianth parts

is often missing completely, as these characters can be only observed when working with living material. Due to this, the number of species accepted by different experts varies greatly. At the same time, the employment of characters describing the capsule for the species identification presents significant challenges due to similarities in the fruit morphology in a number of species; besides, the fruiting specimens are not always available. Additional complications arise from the fact that similar characters are occasionally present in representatives of other sections in the genus.

The authors conducted critical analysis of herbarium material and live samples including their own collections from natural habitats in Vietnam, Cambodia, and Thailand with the purpose of revelation of the set of critical morphological characters and their conditions in certain taxa along with evaluation of their significance for the species taxonomy within the section *Myrianthus* in the genus *Euonymus*.

We have identified the most constant and most variable floral morphological characters and determined which are essential for resolving the species problem in the group in question. The stable (species-specific) characters are flower color, calyx shape, sepal and petal margin structure, petal shape, stamen size, and length of filaments. At the same time, the number of flowers in the inflorescence and flower meristem may vary within species and even in individual plants.

The identified stable characters, some of which are in need of terminology unification, provide substantial help when attributing living material or photographs of living plants to species. These characters are to be considered in the taxonomic review of a group of species that have traditionally been placed in the section *Myrianthus*. For example, in *E. cochinchinensis* and *E. indicus*, lateral margins of petals are revolute, while in *E. glaber*, *E. laxicymosus*, and *E. laxiflorus* petals are flat. Petals are blotched red in *E. glaber*, *E. indicus*, and probably also in *E. cochinchinensis*. Stamens feature long filaments in *E. cochinchinensis* and *E. indicus*, while in *E. glaber*, *E. laxicymosus*, and *E. laxiflorus* anthers are sessile. Sepal margin is fimbriate in *E. cochinchinensis* and nearly entire in *E. glaber*, *E. indicus*, *E. laxicymosus*, and *E. laxiflorus*. Finally, petals are denticulate in *E. glaber*, *E. laxicymosus*, and *E. laxiflorus*, while in *E. cochinchinensis* and *E. indicus* they are fimbriate.

Morphological diversity and evolution of *Thismia* (Thismiaceae) in the light of molecular phylogeny

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Thismiaceae is a family of mycoheterotrophic non-photosynthetic plants belonging to the monocot order Dioscoreales. This family was traditionally treated as a tribe, Thismieae, of the family Burmanniaceae and the precise relationship of Thismiaceae and Burmanniaceae s.str. still remains unclear. Thismiaceae are subdivided into five genera, of which *Thismia* is the only species-rich genus, comprising about ¾ of all the species in this family. At least 71 species of *Thismia* are currently known, and this figure grows rapidly due to the intensive field studies of various researchers throughout the world's tropical regions. For instance, seven new species were described during the year 2017. The new findings drastically change earlier assumptions about the morphological diversity and geographical distribution of *Thismia*; a number of new combinations of morphological features are now recognized. For these reasons, traditional taxonomic delimitations and phylogenetic views on this genus are no longer applicable to its known species diversity.

Like most mycoheterotrophic angiosperms, representatives of *Thismia* are low terrestrial herbs with flowers at ground level or raised on a short scaly whitish stem. The flowers are terminal, solitary, or in a multi-flowered monochasial inflorescence. The floral morphology of *Thismia* is especially complex and intriguing. Flowers are actinomorphic (rarely zygomorphic), epigynous, pentacyclic, and trimerous. Outer floral elements are arranged on an elongated campanulate hypanthium (floral tube). Two whorls of perianth are equal to strongly unequal. While the outer tepals are invariably free, the inner tepals of some species are fused postgenitally by their distal parts to form a dome-shaped structure called the mitre. The outer tepals, or the inner tepals (including those fused into a mitre), or both can bear long filiform appendages. At the base of the tepals, there is a diaphragm called the annulus, which forms the roof of the hypanthium and possesses a narrow orifice in the center. Stamens of both whorls are attached to the inner surface of the annulus and hang down to the inner space of the hypanthium. They thus expose their adaxial surface outside and abaxial surface inside. The anther connectives are very broad; they bear thecae at their abaxial side and various hairs and appendages of complex shape at long apical prolongations. All six stamens are usually fused postgenitally into a single stamen tube leaving six narrow slots between the free filaments; in some species the stamens are free. The ovary is unilocular with three central or parietal placentas, bearing a style with three stylodia at its top.

In our study, we have reconstructed the evolution of several key characters of *Thismia* floral structure based on molecular phylogenetic data. Our molecular phylogenetic tree comprises 24 species and represents the first reliable reconstruction at the scale of the whole genus *Thismia*. We used the mitochondrial *atp1* and nuclear 18S rRNA genes for the main tree and the nuclear ITS region for elaboration of particular groups. We confirmed that the Old World species of *Thismia* form a well-supported clade, while the only New World species included in the analysis is distantly related to them. Within the Old World clade, we recognize four subclades with good support. These subclades correspond well with the geographical distribution of the species and their flower morphology. Subclade I comprises three species from Taiwan and Thailand which share several common features of stamen structure. Subclade II comprises five mitre-bearing Australian species, whose high morphological similarity was shown earlier. Subclade III consists of six species from Thailand and Vietnam characterized by the absence of tepal appendages and presence of mitres, all recently discovered and sharing the combination of features which does not fit into traditional systems of the genus. Subclade IV comprises six Southeast Asian species with equal inner and outer tepals which are free and bear long filiform appendages.

Among eight floral characters which were studied by mapping their conditions onto the molecular tree, most appeared to show some homoplastic evolution. For instance, the mitre appeared at the base of the Old World Clade and was lost once in its evolution; in addition, the loose dome of inner tepals (mitre-like structure without any fusion) evolved from the mitre in two species independently. Appendages of inner tepals, whose presence is a plesiomorphy of the Old World Clade, were lost twice. Appendages of outer tepals show even more complicated evolution with at least four homoplastic events. The presence of the adaxial appendage of the stamen connective appears to be a character whose variation perfectly agrees with phylogenetic reconstruction: all the species of Clade I, which is the basal subclade of the Old World Clade, lack appendages, while in the rest of the Old World species the appendages are present.

Thus, we have provided the first skeletal phylogenetic reconstruction which, after some additions and amendments, can be used as the basis for the construction of a modern taxonomic system of the genus *Thismia*. The subclades of the Old World clade are likely to be treated as subgeneric taxa. Each of them can be provided with a unique morphological description. We propose four characters whose combination allows the clades to be easily distinguished. These are the presence of the mitre, inner tepal appendages, stamen appendages, and hypanthium bars.

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On species delimitation in the genus *Peucedanum* L. sect. *Peucedanum* (Apiaceae)

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Among those species that have been placed in the type section *Peucedanum* L. (*Peucedanum* s.str.) 8 to 15 are polycarpics with twice or more times tripinnatifid leaf blades, linear or narrow linear, entire ultimate segments, and mostly yellow petals. Species of this section are distributed in Central and Southern Europe, the Caucasus, Southwest and Central Asia, Western China, and Siberia.

In fact, only quantitative characters, such as width and length of the ultimate segment in the basal leaf or the number of rays in the central umbel along with the provenance information, have been used for attribution to species within this group. These species can be provisionally divided into two groupings: ‘narrow-leaved,’ (*P. calcareum* Albov, *P. guvenianum* Yildirim & H.Duman, *P. longifolium* Waldst. & Kit., *P. paniculatum* Loisel., and *P. vourinense* (Leute) Hartvig), in all of which the ultimate leaf segment does not exceed 1 mm in width, and ‘broad-leaved,’ i.e., with the ultimate leaf segment wider than 1 mm (*P. coriaceum* Rchb., *P. morisonii* Besser ex Schult., *P. officinale* L., *P. rochelium* Heuff., *P. ruthenicum* M.Bieb., and *P. tauricum* M.Bieb.).

All of the eight species of this group that we have had an opportunity to study have a similar fruit structure and morphology: fruit glabrous, significantly contracted dorsally, lateral ribs wing-like, dorsal ribs filiform, calyx teeth short triangular, stylopodium low conic, stylodia recurved to dorsal side, commissure broad; exocarp cells small, mesocarp parenchymatous, except for lateral wings filled with ligneous cells that have porous walls; inner mesocarp with thin (1–2-cell-thick), intermittent layer of ligneous fibers (hypendocarp); furrow vittae 13-lingular, commissure vittae 2; vittae on ribs small, singular; cell boundaries on fruit surface indistinguishable under SEM; cuticle striate. Of the studied *Peucedanum* segregates, only *Cervaria rivinii* Gaertn. Has similar fruit.

Three different methods of phylogenetic tree construction for *Peucedanum* s.l. based on the ITS rDNA analysis invariably yielded results where five species of *Peucedanum* s.str. were grouped in a single subclade with the bootstrap support of 83% (Spalik *et al.*, 2004). Similar results had been obtained in a study that confirmed the segregation of *Taeniopetalum* Vis. From within *Peucedanum* s.l. (Ostroumova *et al.*, 2016). Among the species of the studied group, there are diploids ($2n=22$) as well as hexaploids ($2n=66$). We have also revealed polyploid series ($2n=22$, 44, and 66) in two species, *P. longifolium* and *P. ruthenicum* (Pimenov *et al.*, 2002; Shner *et al.*, 2017).

There is always a temptation to treat extreme ecological forms and chromosome races in any such group as distinct species. For example, exceptionally large specimens of *P. longifolium* from Turkey, growing there on volcanic soil, have been named *P. guvenianum* (Yildirim and Duman, 2017) and diploid narrow-leaved races from Abkhazia and northern Greece were once described as *P. calcareum* and *P. vourinense*, respectively.

We undertook a morphometric study of more than 400 samples at the following herbaria: E, H, LE, MHA, MOSM, MW as well as our own collections attributed to 12 species within the section. The characters that have traditionally been employed for species delineation and identification are the number

of rays in the central umbel, the length of ripe fruit along with its length-to-width ratio, the ratio of ripe fruit length and that of its pedicel, the division order of basal leaf as well as the length and width of its ultimate segment. None of the studied characters allowed for unequivocal species delimitation, character variability ranges considerably overlapping and not matching the ranges mentioned in floras, field guides, and the monograph of the genus within Europe (Frey, 1989). Provenance remains the most important criterion for attribution of a sample to a certain species. Of two similar broad-leaved samples, one originating from Austria, the other from near Novosibirsk (southern West Siberia), the former would be identified as *P. officinale*, the latter as *P. morisonii*. The problem requires further investigation employing methods of both classical and molecular systematics.

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Dodders of the Penza Region: species composition and distribution

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Dodders (*Cuscuta*) are a taxonomically challenging genus of vascular plants embracing from 150 to 274 species, depending on the view of the author (Vasyutin *et al.*, 2002; Dankvert *et al.*, 2009). As obligate parasitic plants, members of the genus are included in the Quarantine Item listing for the Russian Federation. Eight dodder species have been designated as posing a considerable threat to Russian agriculture (Vasyutin *et al.*, 2002). The species composition of the genus in Penza Region was last revised

by V.M.Vasyukov in 2004, so an update of data on the species composition and monitoring of their distribution dynamics is now urgently needed.

According to the data accumulated by 2016–2017 in the Penza Branch of the All-Russian Center for Plant Quarantine, of a total of 27 districts in Penza Region, 11 are known to have had *Cuscuta* infestations – a total of 25 loci.

During 2017, the author collected dodder as herbarium specimens and flower samples preserved in alcohol from six districts of the Penza Region (Kolyshlei, Serdobsk, Zemetchino, Tamala, Bashmakovo, and Penza). Corresponding records included detailed notes on habitat types and host plants.

The following five dodder species had previously been included in the flora of the Penza Region at different times: *Cuscuta epilinum* Weihe, *C. lupuliformis* Krock., *C. monogyna* Vahl, *C. europaea* L., and *C. campestris* Yunck. (Solyanov, 2001; Vasyukov, 2004).

The distribution of *C. epilinum* in the Penza Region is not yet clear (Solyanov, 2001).

C. lupuliformis was infrequently recorded in river floodplains, forested gullies, and riparian willow thickets within the Penza Region (Solyanov, 2001; Vasyukov, 2004).

C. monogyna was rarely encountered on shrubs at forest margins and openings (Vasyukov, 2004).

C. europaea has been known since 1905 when it was first recorded by I.I.Sprygin (data from the Sprygin Herbarium). Later on (1908–1928), it was collected by N.V.Dyukina, E.K.Stuckenberg, A.I.Vvedensky, E.A.Gorodkova, and B.P.Satzerdotov within territories currently corresponding to the following districts of the Penza Region: Bashmakovo, Nizhny Lomov, Pachelma, Mokshan, Kuznetsk, Serdobsk, Kolyshlei, Narovchat, Penza, Gorodishche, and Belinsky). *Urtica dioica* L. was the host plant in most cases; occasional hosts were *Coronilla varia* L. (*Securigera varia* (L.) Lassen), *Impatiens noli-tangere* L., *Lysimachia vulgaris* L., *Artemisia vulgaris* L. The plant occurred most often in moist, damp areas in floodplains, on gully bottoms, in alder and aspen stands along brooks, in linden/oak forests, and amidst willow thickets. Solitary samples were collected on nettles in a garden and in another anthropogenic situation.

In the surveyed districts, the author did not locate a single plant of *C. europaea*, *C. epilinum*, *C. lupuliformis*, or *C. monogyna*.

C. campestris, field or golden dodder is an alien species discovered in the Penza Region by Vasyukov (2004). It now frequents railway embankments and is quite common in areas of human habitation. While in the Sprygin Herbarium it is represented by just a single collection made at a roadside by T.V.Razzhivina in 2008, all of the author's collections have been identified as *C. campestris*. Field dodder frequently occurs at roadsides, near human dwellings and at field margins. Its host plants are *Polygonum aviculare* L. (the majority of cases), *Erigeron canadensis* L., *Echinochloa crus-galli* (L.) Beauv., *Amaranthus retroflexus* L., *Plantago major* L., *Medicago sativa* L., *Lactuca tatarica* (L.) C.A.Mey., *Setaria glauca* L., or *Atriplex sagittata* Borkh.

The situation with *C. epilinum*, *C. lupuliformis*, *C. monogyna*, and *C. europaea* is to be clarified during future surveys. Apparently, *C. lupuliformis* and *C. monogyna*, which may occur only sparingly and only in natural habitats, so far do not pose any threat to agriculture in the region. *C. europaea* was recorded in significant amounts in the early 20th century, mostly in natural habitats, but recently it has not been registered. More thorough searches may result in relocating this species. In some of its habitats, *C. europaea* could have been displaced by the alien *C. campestris*, which is now frequent in the region, definitely posing a serious threat for agricultural crops. Populations of this plant must be managed and controlled.

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