REVIEW ARTICLES
ОБЗОРНЫЕ СТАТЬИ

REMNANT POPULATIONS OF *CYPRIPEDIUM MACRANTHOS* (ORCHIDACEAE) IN EASTERN EUROPE: EVIDENCE OF ALMOST COMPLETE EXTINCTION AND WIDESPREAD INTROGRESSION WITH *CYPRIPEDIUM CALCEOLUS*

Petr G. Efimov[1,*], Nikolay N. Panasenko[2], Aleksey V. Gornov[3]

[1]*Komarov Botanical Institute of RAS, Russia*
**e-mail: efimov@binran.ru*
[2]*Bryansk State University, Russia*
[3]*Center for Forest Ecology and Productivity of RAS, Russia*

Received: 18.01.2022. Revised: 24.02.2022. Accepted: 26.02.2022.

The distribution of *Cypripedium macranthos* and *C.* × *ventricosum* in Eastern Europe is described in the literature controversially. At the same time, *Cypripedium* species are legally protected plants of the highest conservational importance, and detailed knowledge about their historic and current distribution is essential for correct setting of conservation priorities. In the present article, we have assembled primary information about localities of *C. macranthos* and *C.* × *ventricosum* in Russia and Ukraine by referring to the original information sources, mostly to old herbaria and literature. As a result, 19 localities have been estimated as incorrect, 11 as doubtful and only 12 as reliable. Historical absence of *C. macranthos* and *C.* × *ventricosum* in the Republic of Chechnya, Republic of Mari El, Ulyanovsk Region and Kursk Region has been confirmed, whereas its presence in the Republic of Udmurtia, Nizhniy Novgorod Region, Vologda Region, Yaroslavl Region, Republic of Komi, and Voronezh/Lipetsk Regions is questioned. Original herbarium specimens confirming its locality in the Samara Region have been found in the herbarium. The existence of the species in Ukraine is being discussed in view of the information published by V.G. Sobko in 1989, but omitted in later publications. A sharp decrease in the number of localities has been proven. The only extant locality of *C. macranthos* is situated in the Republic of Chuvashia, and that of *C.* × *ventricosum* (1–4 subpopulations) in the Bryansk Region. The amount of hybridisation between *C. macranthos* and *C. calceolus* in Eastern Europe was previously underestimated. In the part of the species' distribution centered in Bryansk Region, only hybrids have been recorded since 1903. This fact determines the need for corresponding changes in floristic data and in documents which establish local plant protection.

Key words: flora of Russia, floristic change, hybridisation, lady's slipper orchid, old records, plant conservation, relict elements, threatened vascular plants

Introduction

Cypripedium macranthos Sw., along with its more common congeners *C. calceolus* L. and *C. guttatum* Sw., are remarkable and belonging to the most widely known orchid species in North-Temperate Eurasia. Their peculiar brightly-coloured flowers and diversity of hybrid cultivars attract both plant hunters and gardeners. The involvement of these plants into illegal trade is considered as one of the causes for their rarity or even complete extirpation in many localities in the current time (Averyanov, 1999, 2000; Rännbäck, 2007; Jakubska-Busse et al., 2021). All species of the genus *Cypripedium* are included into the Red Data Book of the Russian Federation (Bardunov & Novikov, 2008) and are legally protected in all Russian regions where they occur.

The natural ranges of *C. macranthos* and *C. guttatum* are spread mainly in Asia, within Russia covering vast territories in Siberia and the Far East. But they also extend westwards from the Urals to Europe, where both species are becoming substantially rarer than in Asia (Averyanov, 1999, 2000; Vakhrameeva et al., 2014). *Cypripedium macranthos* is known for its ability to produce hybrids with the more widespread *C. calceolus*, which were described taxonomically under the name of *C.* × *ventricosum* Sw. (Averyanov, 1999, 2000; Knyasev et al., 2000a,b). This hybrid was similarly reported from a few localities in European Russia, but not so frequently as *C. macranthos*.

In Europe, many localities of *C. macranthos* are historical, due to the shrinkage of its natural

range (Averyanov, 1999, 2000). Accordingly, many of them are based on old and imprecise literature reports and/or old herbarium specimens without indication of detailed localities. Therefore, the information about the distribution of *Cypripedium macranthos* and *C.* × *ventricosum* is full of various sorts of confusion, incorrect determinations and even fraud. The situation has been further entangled by changes in the administrative division of the USSR, which took place in the first half of the XX century. It proves to be problematic or even impossible to apply some of the old records to the present-day Russian regions. As a result, there are misleading interpretations for some Russian regions, including Kursk Region, Ulyanovsk Region, Starodub District and Brasovo District of the Bryansk Region and possibly for some other localities as well. The overall situation is similar to that with another rare orchid of Russia, *Gymnadenia odoratissima* (L.) Rich, which was also reported from many localities according to old incorrect data (Kulikov & Filippov, 2011). Another additional factor is that the reports of *C. macranthos*, widely known as an ornamental plant, both now and in the past, may belong to cultivated individuals, not being properly indicated as such.

As a result, without addressing to the original sources of information, floristical treatments tend to accumulate incorrect information. The examples are essays about *C. macranthos* in the second edition of the Red Data Book of the Republic of Tatarstan (Shchepovskikh, 2006), and the first edition of the Red Data Book of the Republic of Chuvashia (Dimitriev, 2001). Republic of Chuvashia is an example where recent sources are gradually replacing the previously unconfirmed data (Gafurova, 2014, 2019). The distributional data about *Cypripedium* species in various editions of the Mayevskiy's flora (1917, 1933, 1941, 1954, 1964, 2006, 2014) are strongly different from each other. In the detailed review of the *Cypripedium* of Russia associated with its mapping, Averyanov (1999, 2000) treated all localities of *C. macranthos* and *C.* × *ventricosum* to the west from the River Volga as doubtful. In contrast, Vakhrameeva et al. (2014) assumed that at least *C. macranthos* is present as a native element in the Bryansk Region, Belgorod Region, and Orel Region.

Material and Methods

In the course of the present study, we have assembled the original data about *C. macranthos* and *C.* × *ventricosum* in Eastern Europe from literature sources and herbarium collections, and where possible, supplemented them with the unpublished data after direct observations in the field. The field studies were undertaken in the Bryansk Region in 2021 focusing on the taxonomy of plants, which still occur there under natural conditions.

The study is largely based on the data from the database «Orchids of Russia», in prospect aimed to prepare detailed maps of all orchid species known in Russia (Efimov, 2020). The currently assembled information includes complete or almost complete data from 82 herbarium collections of Russia (Appendix), including the 25 largest ones in Russia (excluding RV and MOSM). In this article, we give full citations of all herbarium specimens of *Cypripedium macranthos* and *C.* × *ventricosum* from Eastern Europe we managed to discover.

In the current study, in the west, «European Russia» is limited by administrative regions which do not include the Ural Mountain Range, except for the Republic of Komi. Administrative Regions of Russia are understood here as the 1st-level administrative units of the country. The federal cities (Saint-Petersburg and Moscow) are included into their largest nearest regions, namely Leningrad Region and Moscow Region, respectively. In relation to the herbarium specimens, abbreviation «*C.m.*» was used for *Cypripedium macranthos*, and «*C.v.*» for *C.* × *ventricosum* in the review of their localities.

Results and Discussion

Review of Cypripedium macranthos and C. × *ventricosum localities in European Russia*

Republic of Chechnya and Caucasus in general. In reference to the Caucasus, *C. macranthos* is known from two collections: «Caucasus, herb. N.K. Sredinsky» (LE 1071964!, *C.m.*); «Chechnya, Gobi-Shaudanskiye Hills [near Belorechye village], Lagowski» (LE 1038274!, *C.m.*). Both collections of Lagowski and Sredinsky from the Caucasus are considered to be not trustworthy. Possibly, both specimens in fact originated from Lagowski's collections in the time of his stay in Siberia, and mislabelled afterwards (Lipschitz, 1952). Before Averyanov (1994, 2006), both collections were incorrectly determined as *C. calceolus*, and they have been mentioned like that in many literature sources about the Caucasian flora, and even in some more recent contributions as

well (e.g. Grossheim, 1940; Ivanov & Kovaleva, 2005; Ivanov, 2019).

Vologda Region. In the Vologda Region, *C. macranthos* was reported only in 1972 in the Protected Area «Severnye Orkhidei», in the vicinity of the village of Boyarskaya, Vozhegodskiy District (Konechnaya & Suslova, 2004). Vakhrameeva et al. (2014) claimed that this record is based on a herbarium specimen. Possibly, the record is based on an incorrect determination, because the later biodiversity description of the Protected Area «Severnye Orkhidei» (Sobolev & Belonovskaya, 2013) does not mention this taxon among other orchids. The re-determined vouchers for this record may be kept in the herbarium of the Vologda State University. Unfortunately, the curator of this collection (Andrey Chkhobadze) was unable to provide us with an access to examine the herbarium in 2020–2021.

Republic of Komi. There are several reports from the Republic of Komi.

Pechora District or nearby districts. In many literature sources (e.g. Perfiljev, 1934; Goworuchin, 1937; Yudin, 1963; Bolotova et al., 1962; Martynenko, 1976), *C. macranthos* was reported for the River Synya, which was correctly questioned by Averyanov (1999, 2000). Indeed, this report was based on the incorrect determination of a *C. calceolus* herbarium specimen collected in fruits: «Komi Region, Izhma-Pechorskiy County, the River Bol'shaya Synya, limestone rock, 14.08.1926, S. Naumova» (MW 294921!). Re-determination of this specimen did not take place until 2009 (by Petr G. Efimov). In addition, there is another identically re-determined collection: «Komi-Zyryan Region, Ust'-Kulomskiy County, River Bol'shaya Soplesa [Bol'shoy Soplesk] (left tributary of the River Pechora), spruce and fir forest on the limestone slope, 03.08.1928, S. Naumova, N 356» (MW 294912!).

Troitsko-Pechorsk District. In addition to the locality along River Bol'shaya Synya, Yudin (1963) reported *C. macranthos* from the limestone outcrops along the River Ilych, which was subsequently repeated by Martynenko (1976). This is possibly a misprint because, judging by the other place of the same report (in page 531), it is clear that the locality along the River Bol'shaya Synya was the single locality of *C. macranthos* known to this author in the Republic of Komi.

Ust'-Tzil'ma District. Bolotova et al. (1962) guided by some unspecified information source also reported *C. macranthos* from the River Tzil'ma basin. This was subsequently repeated by Martynenko (1976), but reasonably questioned by Averyanov (1999, 2000).

Yaroslavl Region. «Pereslavl' District, Nagor'evskoye bog, «islands», 09.07.1980, Senatskaya» (USPIY!, *C.m.*). The plant is rather typical in appearance, but there is no determination on its label. The species was never reported from the Yaroslavl Region in the literature (e.g. Tikhomirov, 1986; Marakaev, 2015; Nyankovskiy, 2015). Here, this locality is formally treated as doubtful, but it can also mark a true isolated locality in the peripheral part of the species range.

Republic of Udmurtia. The only source is a herbarium specimen with the incomplete label, originally bearing only the name of the species: «sandy places in coniferous forests, possibly Sarap.[ul]?» (UDU!, *C.m.*). This locality was referred to the 1960s in the Red Data Book of the Republic of Udmurtia (Baranova, 2012), and it is repeated several times in the literature (Efimova, 1972; Baranova & Puzyrev, 2012), but absent in Baranova et al. (1992). The information about this locality in Udmurtia that it was still extant in the 2000s (Vakhrameeva et al., 2014), is an incorrect interpretation of the data by Baranova (2000). Subsequently published sources did not confirm this information either (Baranova, 2006; Baranova et al., 2011; Baranova & Puzyrev, 2012; Nazirov, 2016). Due to the absence of the original label and questionable interpretation of the locality, the corresponding locality is treated as unconfirmed.

Republic of Tatarstan. There are several reports from the Republic of Tatarstan.

Vysokogorskiy District. A locality near the Semiozernaya Pustyn' monastery on the slope near the village of Semiozerka is widely known, being visited by several generations of botanists (Wirzen, 1839; Claus, 1851; Ruprecht, 1866; Kryshtofovich, 1929), but there is only one herbarium specimen with a plain label. It has been only recently incorporated into the main herbarium collection, and it included both hybrid and non-hybrid individuals («grows in the forest of Semiozernaya Pustyn' in Kazan, 23.05.1818» (LE 01107814!, *C.v.*; LE 01107815!, *C.m.*). A herbarium specimen «Kazan Gub., 1894» (MW 295230!, *C.m.*) also most likely originates from this locality, the same as four specimens in the herbarium of P.Ya. Kornukh-Trotzky dating back to the 1830s: «Gub. Kazan, Korn.-Tr., N 541 [2 sheets], N 542 [2 sheets]» (KAZ!, *C.m.*). The

last record from this locality is ascribed to Korzhinsky (Shchepovskikh, 2006), but no data which confirm this, are traced in Korzhinsky's publications, which means that it might already have gone extinct by that time.

The former Menzelinsk County. «Gub. Ufa, distr. Menselinsk, in the forests, 1871, Lossiewski, N 353» (LE 01107811! and LE 01107812!, both *C.v.*). The exact locality is unknown, and theoretically, it may be referable to the present-day territory of the Republic of Bashkiria. The information in Smirnov (1979) and subsequently in three editions of the Red Data Book of the Republic of Tatarstan (Shchepovskikh, 1995, 2006; Nazirov, 2016) is different and possibly incorrect: here the locality is associated with the Krasnoborskoye Forestry of the present-day Menzelinsk District, dated on 1934.

Tukayev District. The locality was reported from Shaytanovskoye Forestry by Smirnov (1979), and subsequently by Plaksina (2001), Shchepovskikh (1995, 2006) and Nazirov (2016). Shchepovskikh (2006) incorrectly refers to Markov (1939) and Fardeeva (2006) concerning this and the preceding localities.

Elabuga District. A report from «Bol'shoye Pole» of the Elabuga District has appeared only in the 2nd edition of the Red Data Book of the Republic of Tatarstan (Shchepovskikh, 2006) as if it was originally published by Krylov (1885), but no original information can be traced in this publication.

Republic of Chuvashia. There are several reports from the Republic of Chuvashia.

Marposadsky District. «Chuvashia, Marposadskiy District, near Urakovo village, steep slope to the River Volga, the afforested slope with marl, 16.06.1997, M.M. Gafurova» (Herbarium of the Chuvashia Natural History Museum, 36050/103!, *C.m.*). The locality was revisited in 2008 by Margarita M. Gafurova (pers. comm.).

Poretskiy District. It was reported by Dimitriev (2001) and Gafurova (2014, 2019) after it was incorrectly determined *C. calceolus* specimen «Ulyanovsk Gub., Alatyr' County, Siyava village, in a boggy spruce forest at the bottom of the slope of the river valley, 30.07.1916, A.P. Shennikov, N 355» (Herbarium of the Ulyanovsk Natural History Museum!). Its duplicate and some other A.P. Shennikov collections kept in the herbarium LE were also originally determined incorrectly in the same way.

Cheboksarskiy District. A locality near Cheboksary was based on the personal communication of L.P. Teplova (Dimitriev, 2001; Gafurova, 2014). This locality was excluded from the new edition of the Red Data Book of the Republic of Chuvashia (Gafurova, 2019), as a dubious record, because L.P. Teplova did not remember the case (Margarita M. Gafurova, pers. comm).

Alatyr' District. This locality is reported by Dimitriev (2001). It is possibly a mistake based on the aforementioned collection from the village of Siyava, belonged to the former Alatyr' County according to the old administrative division. This record is omitted in the later reviews of Chuvashian flora (e.g. Gafurova, 2014, 2019).

Shumerlya District. This locality is also reported by Dimitriev (2001). In this publication, it is marked on the map but not mentioned in the text corresponding to it. It is most probably a mistake because this record is absent from the later reviews of Chuvashian flora (Gafurova, 2014, 2019).

Nizhniy Novgorod Region. It was reported from the Pustynskiy Hunting Sanctuary in the former Arzamas County (Okhapkin, 2005; Biryukova et al., 2014). This record needs confirmation.

Samara Region. «Simbirskaya Gub., Sengileevsk. County, Beloklyuchye, pine forest on the chalk slopes, 24.05.1903, D. Yanishevskiy, N 147» (KAZ!, *C.m.*); «Simbirskaya Gub., Sengileevsk. County, Zhiguli Mountains, Rustovskiye Klyuchi, a pine forest on the steep slope with a substantial admixture of broad-leaved trees, 25.05.1903, a student excursion along the River Volga, N 148» (KAZ!, *C.m.*); «Simbirsk. Gub., Sengil. [County], the only locality: the chalk slope with a pine forest near «Rustovskiye Klyuchi», 1903, Yanishevskiy, N 149» (KAZ!, *C.m.*). These typical *C. macranthos* herbarium specimens were possibly not consulted for years, and the species was cited according to the literature data, originally by Smirnov (1904), which caused some confusion in the subsequently published literature. Although Smirnov (1904) correctly reported *C. macranthos* for this locality, many later published literature sources reported hybrids *C.* × *ventricosum* instead (e.g. Mayevskiy, 1917, 1933, 1941, 1954, 1964, 2006; Plaksina, 2001; Saksonov & Koneva, 2006) or both *C. macranthos* and *C.* × *ventricosum* (Saksonov & Senator, 2012; Mayevskiy, 2014). This may be incorrect, as far as all herbarium specimens are attributable only to the species *C. macranthos*. Some confusion has also been created by the problematic attribution of the locality to the exact geographic place. Litvinov (1927) roughly

attributed it to the vicinity of the town of Sengiley, which was probably the reason why, in Mayevskiy (1954), the locality was incorrectly understood as belonging to the Ulyanovsk Region, which was later repeated by Rakov et al. (2014) as well. In contrast, in Mayevskiy (2014), the locality was moved to another direction, namely the Zhiguli Mountains. In fact, Rustovskiye Klyuchi village, later renamed to Smyslovo (Mayevskiy, 1917, 1933, 1941), was situated between the villages of Novodevichye and Klimovka, belonging to the present-day Shigony District of the Samara Region (Stepan A. Senator, pers. comm.). The village is absent on the public maps, probably due to a very short time of its existence, being flooded in the 1950s by the Kuybyshevskoe Reservoir. However, in this locality, plants may have perished long before the building of the Kuybyshevskoe Reservoir because, almost 100 years ago, Litvinov (1927), while discussing the depletion of his «mountainous» type of the pine forest in the steppe zone, stated «by rumour» that the forest in the *Cypripedium*'s locality had already been «cut down by the time of this publication. It should also be taken into account that there may have been not one but two localities: one herbarium label bears the name of «Beloklyuchye», which is a village different from the village Rustovskiye Klyuchi. Certain doubts about the correctness of the collection in Beloklyuchye may be traced from Smirnov (1904), who referred *C. macranthos* only from Rustovskiye Klyuchi, and from the text of Yanishevsky's herbarium label.

Ulyanovsk Region. All reports of both *C.* × *ventricosum* and *C. macranthos* from the Ulyanovsk Region are in fact based on the incorrect interpretation of the *C. macranthos* locality in the Samara Region (see above).

Penza Region. The record of *C.* × *ventricosum* in the Bessonovka District in July 2018 (Ueda, 2021b) obviously belongs to a cultivated individual judging by an image, although not labelled as such.

Republic of Mari El. As far as we are aware, the report for the Republic of Mari El appears only in the description of the overall species distribution in the Red Data Book of the Republic of Tatarstan (Nazirov, 2016). This is possibly a mistake.

Orel Region. There are several reports from the Orel Region.

Shablykino District, near Molodovoye: «Orel Gub., Karachevsk. County, Molodovoye, Teplov, N 1321» (MW 295227!, *C.m.*); «Flora of the Orel Region, forest near Molodovoye, 01.06.1909, V. Khitrovo» (OHHI!). The hybrid origin of the latter specimen cannot be checked, because the flower is lost. The report from the western part of the Karachev County by Zinger (1886) «in sandy places in coniferous forests» is most likely based on the same record.

Shablykino District, near Navlya. Khitrovo (1910) described this locality quite vaguely as «near Shablykino village», but, in the unpublished review of plants of the former Orel Province, Khitrovo (1923) gave more details, i.e. «forest near village Navli, 1.VI.09».

Uritskiy District. It was reported from «Chernevye forests of the Naryshkino District» in Ammosov et al. (1978). «Chernevye lesa» stand for broad-leaved forests, and their interpretation, as the local name «Chernevskiye lesa» (Bondartseva & Prisnyi, 2021), is incorrect. This locality falls into the present-day Uritskiy District (Kiseleva et al., 2021). It should be taken into account that the time period, when this record was made, is unknown. Moreover, the information about this locality cannot be verified, as it seems to be based on personal memoirs, which may be incorrect.

Belgorod Region. It was reported by Maltsev (1907) for the former Korocha County: «7/VI 1905, solitary specimens in the state forest near the village Likhaya Polyana, on the road to Zimovnoye; very rare». This locality belongs to the present-day Shebekino District, the village of «Likhaya Polyana» renamed to «Krasnaya Polyana». In the subsequently published sources, the taxon was reported for the Belgorod Region without detailed localities by Mayevskiy (1933, 1964, 2006, 2014), and in the Red Data Book of the Belgorod Region (Prisnyi, 2005), as an extinct taxon.

Kursk Region. *Cypripedium macranthos* was reported by Mayevskiy (1941, 1954) from the Kursk Region based on the incorrect georeference of the previously discussed locality in the former Korocha County, which was previously located within the former Kursk Province («Kurskaya Gouberniya»). But now it belongs to the Belgorod Region.

Voronezh / Lipetsk Regions. There are two specimens in the Herbarium of Voronezh State University (VOR 24316!; VOR 24338!) without original labels, inscribed as collected «possibly in Voronezh or Lipetsk Regions». Both represent large *C. macranthos* specimens in fruits

and seem to have been collected not long ago, possibly in the last 10–40 years, and they may originate from cultivation or from some distant Asiatic parts of Russia.

Bryansk Region. There are several reports from the Bryansk Region.

Karachev District. It was reported by Bosek (1975) without detailed locality and by Bosek (1982) for the vicinity of the town of Karachev. We consider those data as not reliable, because the original source of this information is unclear. They may be based on the incorrect interpretation of the localities from the former Karachev County, which in fact belong to the present-day Orel Region (see above).

Surazh District. From Surazh District, only doubtful information exists. It was reported in the Red Data Books of the Bryansk Region from the village Kostenichi (Fedotov, 2004; Bulokhov et al., 2016) as if it had previously been reported by Bosek (1975, 1982), which in fact is not the case. Thus, the original source of this information is unclear.

The boundary between Pochep District and Vygonichi District, near the settlement of Krasnyi Rog. «Krasnoy Rog, Herb. Fischer» (LE 01107803!, *C.m.*); «in sylva prope Krasnoy Rog, Herb. Fischer» (LE 01107804!, *C.v.*); «Krasnoy Rog, LP[?], Herb. Fischer» (LE 01107805!, *C.m.*, and LE 01107806!, *C.v.*); «In Ucrainia versus limites prov. Orel, prope pag. Krasnoi Rog, 1833, acc. a D. Fischer» (LE 01107818!, *C.v.*); «gub. Tschernigow, in sylvis pr. pag. Krasnoj Rog» (LE 01107809!, *C.m.*); «Tschernigow, Oeconomiae Krasnoiroch, ex itinere 1845» (LE 01107819!, *C.m.*). These specimens may be, at least partially, originally collected by F. Ruprecht. The species was numerously reported in the literature from this locality (Ruprecht, 1866; Zinger, 1886; Schmalhausen, 1897; Khitrovo, 1910; Averyanov, 1999; 2000; Fedotov, 2004; Bulokhov et al., 2016). Averyanov (1999) mistakenly believed this place to be the territory of the present-day Ukraine and supposed the specimens to have originated from cultivation. According to Khitrovo (1910), the locality near Krasnyi Rog in the older scheme of administrative division belonged to the former Trubchevsk County of the Orel Province. However, the village itself was situated within Mglin County of the Chernigov Province, near its boundary with the Trubchevsk County. Therefore, older reports from «Mglin County» (Schmalhausen, 1897; Khitrovo, 1910; Mayevskiy, 1941) as well as from «Mglin District» (Bosek, 1975; Bulokhov & Velichkin, 1998) may also refer to the same locality.

Pogar District. There is a set of very old collections of both *C. macranthos* and *C.* × *ventricosum* from the surroundings of the village Rogovichi: «Tschernigow Gub., Starodub County, near Rogovichev Khutor, in the forest, early May, Rogowitsch» (LE 01107807!, *C.m.*; LE 01107808!, *C.v.*); «Tschernigow Gub., Starodub County, near Rogovichev Khutor, in oak forests, 05.1847, Rogowitsch» (LE 01107817!, *C.m.*; LE 01107821!, LE 01107822!, *C.v.*); «Tschernigow Gub., Starodub County, near Rogovichev Khutor, in oak forests, 05.1844, A. Rogowitsch» (LE 01107816!, *C.m.*); «Tschernig. Gub., ad loco humido, 05.1842, Rogowitsch, [?herb.] Schirmer» (LE 01107820!, *C.v.*). The species was also numerously reported in the literature from this locality (Rogowitsch, 1855, 1869; Montrezor, 1881, 1886; Schmalhausen, 1897; Khitrovo, 1910; Averyanov, 1999, 2000; Fedotov, 2004; Bulokhov et al., 2016). Averyanov (1999, 2000) mistakenly believed this place to be the territory of the present-day Ukraine and supposed the origin of the specimens from cultivation.

Starodub District. Reports from the Starodub District without detailed localities (Bosek 1975; Bulokhov & Velichkin, 1998) are most likely based on the older reports from the Starodub County (Mayevskiy, 1933, 1941, 1954, 1964, 2006, 2014), where the village of Rogovichi was situated. Currently, it belongs to the Pogar District.

Bryansk District. There is one old herbarium specimen: «Orel Province, Bryansk County, a pine forest near Bryansk, 1903, N 1322» (MW 295229!, *C.m.*).

Navlya District. All recent and presently known localities belong here. But only hybrids *C.* × *ventricosum* have been confirmed. In the last 20 years, four localities were recorded, all belonging to a rather limited area in the Gavanskoye (formerly Saltanovskoye) Forestry at several kilometres from the village Prolysovo: in the forestry quarter 28 and quarter 29 in 2001 and 2002 (Fedotov & Evstigneev, 2003), and two localities in forestry quarter 39 in 2007 and 2010 (Bulokhov et al., 2016), the latter being extant in 2021 (authors' unpublished data). The older reports from this area («near Prolysovo») (Khitrovo, 1910) and «2 km south from Prolysovo» (Tikhomirov & Kharitontsev, 1984) cannot be confidentially attributed to any of the above-mentioned localities and may also represent different localities, which are now lost. Five herbarium specimens are known from the

Navlya District: «near the village of Prolysovo, a mixed forest, 2000» (BRSU VP3021!, *C.v.*); «25 from BAM, a pine woodland, 05.06.2001, 05.06.2001, 12.06.2001, Yu.P. Fedotov, N 352, N 353, N 344» (Herbarium of the Bryansk Forest State Nature Reserve!, *C.v.*, three specimens); «2 km south from the village Prolysovo, wet spruce forest, 30.05.1978, B.S. Kharitontsev» (MW 295228!, *C.v.*). It should be noted that the collector of the latter specimen, Boris Kharitontsev, is a person who is known in the Russian botanical society for his recently published contributions characterised by «zero or even negative scientific value» (Geltman & Matveeva, 2018), leaving doubts about his other research as well. However, there is no criticism of his previous floristic studies at the time of his PhD Thesis based on the material from the Bryansk Region.

Sevskiy District. «Orel Province, Pod'yevotskaya Datscha, 1885» (YALT!, *C.v.*). This collection has not been consulted for years and never taken into account before.

Komarichi District. «Orel Province, Sevskiy County, 285 forest quarter of the Komaritskoye Forestry of the Grand Duke Mikhail Aleksandrovich» (Khitrovo, 1910). The exact location of this place is unknown. It might be the same place as the previously mentioned one in the Sevskiy District. It may also belong to the bordering parts of the Brasovo District.

Brasovo District. It was reported by Bulokhov & Velichkin (1998), possibly after the locality in the former Komaritskoye Forestry. In fact, it most likely belongs to the Komarichi District (see above).

Cypripedium macranthos and C. × ventricosum localities in Ukraine and Belarus

Cypripedium macranthos was reported from the present-day territory of Ukraine in several literature sources (Smolyaninova, 1976; Borodin, 1984) but without detailed localities. Probably, the primary sources were publications by Kleopov (1933) and Bordzilovski (1950). In these sources, an assumption about further possible finding of this species in the Chernigov Region of Ukraine was expressed, taking into account the neighbouring localities in the Bryansk Region of Russia. The historical localities in the former Chernigov Province near the villages Krasnyi Rog and Rogovichi may also have been taken into account by Kleopov (1933) and Bordzilovski (1950). However, both villages according to the modern administrative division belong to the Bryansk Region of Russia, unlike the major part of the former Chernigov Province which is in present-day Ukraine.

There are also two herbarium specimens (probably 150–200 years old), which might previously have been interpreted as collected in the Ukraine, which can hardly be the case. One is «Rossia minor, herb. Fleischer, N 3044.7» (LE 01107813!, *C.v.*). Here, the toponym «Rossia minor» («Little Russia») may refer not only to Ukraine, but also to the bordering parts of the Bryansk Region and some other Russian regions. Another doubtful specimen «in montosis ad Catherinopolin haud vulgaris» (LE 01107810!, *C.m.*) was unlikely collected near the town of Catherinopol (now it is a village in the Cherkassy Region of Ukraine) because it is ca. 500 km south-south-west from the nearest confirmed localities. Most possibly, it was collected near the city of Yekaterinburg (Ural Mountains), where *C. macranthos* may be rather common, as it is given on the label. The mistake may be derived from the similarity of the toponymical names.

Later, Protopopova (1987) did not provide any reports of this taxon from Ukraine. The most recent checklist of the Ukrainian flora (Mosyakin & Fedoronchuk, 1999) claims that the records of this species need confirmation. Averyanov (1999, 2000) mentions two herbarium specimens from Ukraine that probably originated from cultivated or introduced plants. But both, collected near Krasnyi Rog village and Rogovichi village, in fact belong to the present-days territory of surroundings of the Bryansk Region, Russia.

However, none of the contributors cited above were aware of the fact that this species was indeed reported from Ukraine ca. 100 km west from the border with Russia by Sobko (1989): «in Ukraine, the only locality is known near the village Kachanovka, Ichnya District, Chernigov Region, in an oak forest». Sobko (1989) additionally left us a short description of the vegetation cover in this locality, and the information that the population included 27 young plants, but no generative individuals, possibly because flowering individuals were transplanted by local people. One plant flowered subsequently in culture. Also Sobko (1989) stated that the plants might have originated from culture, as the author had information that *C. macranthos* was indeed cultivated in one arboretum not far from the lo-

cality. In the later accounts of Ukrainian flora, this information has never been repeated again, including the pinpointed review of *Cypripedium* of Ukraine (Reshetiuk, 2003), led by V.G. Sobko. This fact is explained by V.G. Sobko's colleagues in the way that he had got convinced about the origin of these plants from cultivation (Irina Timchenko, Sergey Mosyakin, pers. comm.).

The interpretation of this locality is very controversial indeed. The assumption of Sobko (1989) that the species is a residue of cultivation seems doubtful, because this species has never been reported as such. According to our personal experience, as soon as the plants are abandoned, they disappear rather quickly without proper management. Several other alternatives seem to be possible. One is that the plants may have been mixed up in the field with *C. calceolus*, because no generative individuals have been observed, which is important for correct determination. Later, during cultivation, plants may have been mixed up with *C. macranthos* individuals originating in culture from a different source. In addition, any other type of mistake may have occurred, making Sobko'data (1989) to be incorrect. Last but not least, it cannot be discarded that in surrounding Russia, at a distance of ca. 180 km, there is an area with *C. macranthos* / *C.* × *ventricosum* localities. Therefore, plants observed by V.G. Sobko may also be native, thus representing part of their continuous natural distribution. However, the latter assumption is the least realistic, because the area around the village Kachanovka is very densely populated, and no primary type of forest vegetation can be present there, whereas, in adjacent Russia, all localities are always connected with problematically accessible localities and native forest remnants.

Cypripedium × *ventricosum* was reported in the literature for Ukraine as a possible finding in view of the existing locality in the former Starodubsk County, which is referable to the present-day Bryansk Region of Russia (Kleopov, 1933; Bordzilovski, 1950). Then, it was reported by Smolyaninova (1976) for Ukraine in general, but later it was reasonably questioned again by Mosyakin & Fedoronchuk (1999) and Averyanov (1999, 2000). In fact, the only possible, but very unlikely, finding of this hybrid in Ukraine is the specimen mentioned above (LE 01107813!) and data previously discussed by Sobko (1989).

In Belarus, neither *C. macranthos*, nor *C.* × *ventricosum* were ever reported in any regional literature. The indication of *C. macranthos* by Averyanov (1999, 2000) in Belarus is definitely a mistake.

Geography of the western portion of distribution range of Cypripedium macranthos and C.* × *ventricosum

Summarising all existing literature and herbarium sources, in European Russia, 38 localities of *C. macranthos* and *C.* × *ventricosum* in 16 of 44 regions have been reported so far (Table). Several localities concentrating near the village Prolysovo are formally treated in the Table as one. Of these 38 localities, 16 are treated as incorrect for various reasons, and in five regions (Republic of Chechnya, Republic of Mari El, Ulyanovsk Region, Penza Region, Kursk Region) only incorrect reports exist, which means that *C. macranthos* and (or) *C.* × *ventricosum* should not be included in corresponding local flora's accounts. Ten localities are treated as doubtful for various reasons, providing only doubtful information for six regions (Vologda Region, Yaroslavl Region, Republic of Komi, Republic of Udmurtia, Nizhniy Novgorod Region, Voronezh / Lipetsk Regions). Twelve localities are treated as fully reliable; ten of them are confirmed by herbarium specimens.

The geographic position of *C. macranthos* and *C.* × *ventricosum* localities in Eastern Europe is shown in Fig. 1. All localities may be classified in four groups according to geographic principle, as follows:

1) The localities in the River Volga basin, adjacent to the main distribution range of *C. macranthos* in the Ural Mountains, representing part of continuous species distribution. It is the only group, which was recognised as doubtless by Averyanov (1999, 2000).

2) The localities in the west of European Russia and in Ukraine, centered in the Bryansk Region of Russia, with a solitary unconfirmed locality in adjacent Ukraine. This portion of species' range is currently isolated from the main distribution range by a gap of ca. 800 km and makes an impression of a relict part of the distribution, a feature already noted by Khitrovo (1910). In this area, only localities in the Navlya District of the Bryansk Region seem to be still extant. In the last 100 years, only *C.* × *ventricosum* was recorded in this part of the species range. The supposition by Averyanov (1999, 2000), that this portion of distribution had been reported by mistake, proved to be incorrect.

Table. The number of incorrect, unconfirmed and unreliable localities of *Cypripedium macranthos* (*C.m.*) and *C.* × *ventricosum* (*C.v.*) in Eastern Europe

No.	**Country**, Region	Incorrect	Unconfirmed	Reliable
I.	**Ukraine**	**2**	**1**	–
II.	**Belarus**	**1**	–	–
III.	**Russia (European part)**	**16**	**10**	**12**
1	Republic of Chechnya	1	–	–
2	Vologda Region	–	1	–
3	Republic of Komi	2	1	–
4	Yaroslavl Region	–	1	–
5	Republic of Udmurtia	–	1	–
6	Republic of Tatarstan	2	–	2
7	Republic of Chuvashia	3	1	1
8	Nizhniy Novgorod Region	–	1	–
9	Samara Region	–	1	1
10	Ulyanovsk Region	1	–	–
11	Penza Region	1	–	–
12	Republic of Mari El	1	–	–
13	Orel Region	–	1	2
14	Belgorod Region	–	–	1
15	Kursk Region	1	–	–
16	Voronezh / Lipetsk Regions	–	1	–
17	Bryansk Region	4	1	5

3) Five scattered localities in the north of European Russia (three localities in the Republic of Komi, one in the Vologda Region, and one in the Yaroslavl Region), representing either evident mistakes, or unconfirmed data. This is a doubtful part of the species distribution.

4) The locality in the Caucasus, which is a certain mistake. This has been discussed with full details in the list of localities above.

Habitats of Cypripedium macranthos and C. × ventricosum in Eastern Europe

In the basin of the River Volga, *C. macranthos* occurs almost exclusively at the chalk or limestone outcrops on the slopes, covered with pine forests. These slopes are typically associated with the River Volga valley and its major tributaries of the River Kama and the River Sura, more rarely with smaller rivers such as at the locality near the city of Kazan. Such habitats represent a rare and rather specific type of plant communities, interpreted by Litvinov (1927) as the «mountain type» of pine forests, which occurs in the plain in scattered localities along the river valleys. The depletion of this forest type leads to the subsequent extinction of *C. macranthos.*

River valleys may not only provide specific habitat type, but may also indicate the main dispersal route of *C. macranthos*. The River Kama, as well as many other major left-bank tributaries of the River Volga, have their source in the Ural Mountains, where *C. macranthos* persists up to the present days in many localities (Knyasev et al., 2000a,b).

The isolated group of localities, centered in the Bryansk Region, is associated with pine forests, or oak forests, as well as with the variety of intermediate forest types. Khitrovo (1910), who was probably better informed than anyone else about *C. macranthos* in this area, characterised the habitats as follows: «places intermediate between those dominated by *Pinus*, and *Quercus*, i.e. where the soil is already sandy but not yet typical for *Pinus* forests». It is still unclear whether the habitat variety correlates with taxonomy, i.e. with specific requirements of hybrid and non-hybrid plants. No association with major rivers can be traced in this area. It is also typical that the plants were usually found in the least accessible localities in the forest remnants, thus giving an impression that the plants are connected with the primary vegetation. The localities, which presently persist, are situated in an extension of the widely known forest massifs called «Nerusso-Desnyanskoye Polesye», with its weakly disturbed forests protected in the Bryansk Forest State Nature Reserve. A large gap in the distribution of *C. macranthos* in European Russia may be connected with the rareness of appropriate habitats.

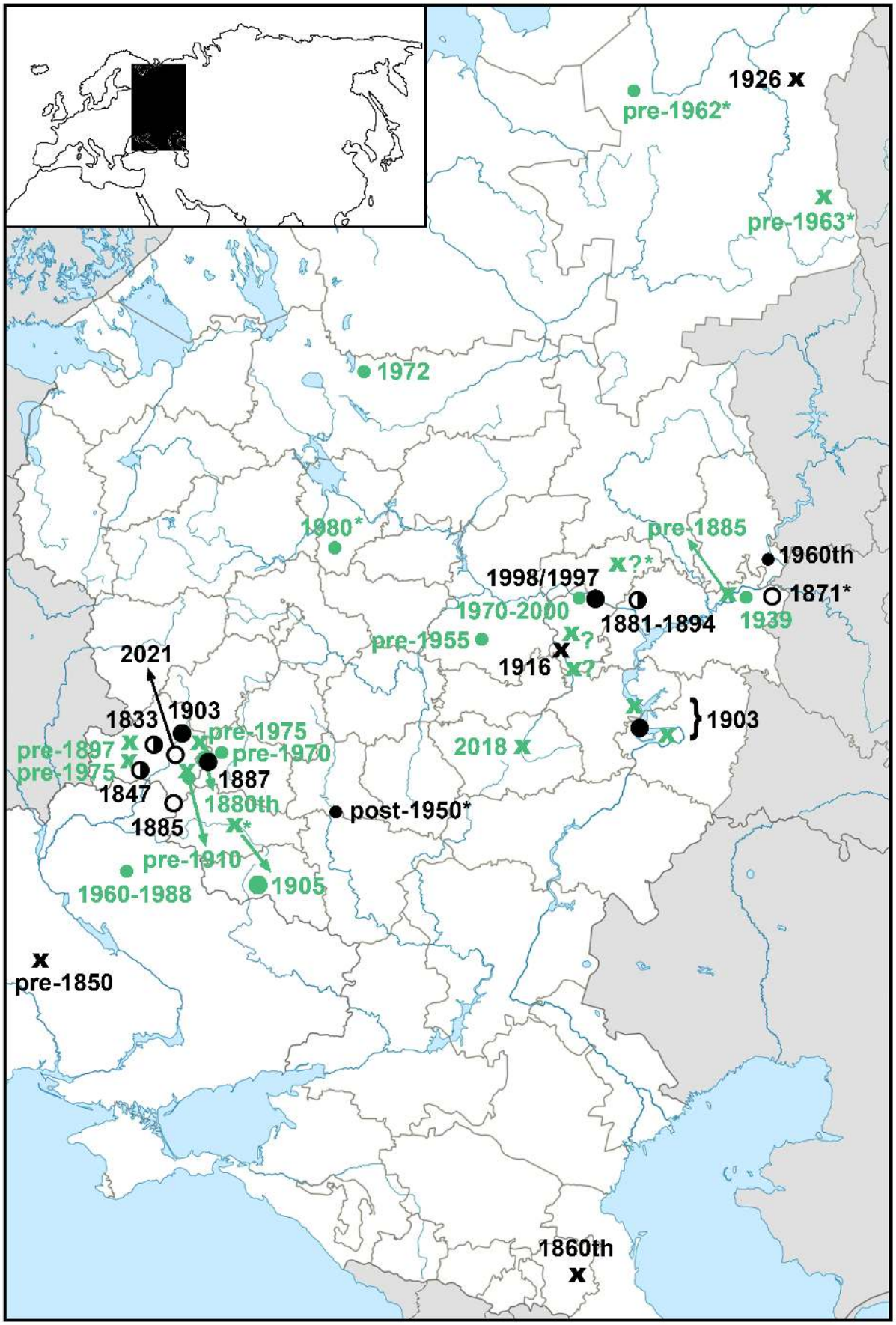


Fig. 1. Distribution of *Cypripedium macranthos* (shaded circles) and *C.* × *ventricosum* (empty circles) in European Russia. Half-shaded circles stand for the situations where both *Cypripedium macranthos* and *C.* × *ventricosum* were registered. Black symbols indicate localities confirmed by herbarium specimens. Green symbols show other types of data. Symbol «×» denotes incorrect (false) localities. Small symbols refer to doubtful localities and large symbols to the confirmed localities. The asterisks (*) denote vague localities.

Evidence of wide introgressive hybridisation between C. calceolus and C. macranthos in Eastern Europe

There is a self-evident problem of distinguishing between *C. macranthos* and *C.* × *ventricosum* when the information about localities is not confirmed by herbarium specimens, which is the case for some records in Eastern Europe. Moreover, herbarium specimens may be not enough for final conclusions either when only a part of existing taxonomic diversity has been collected. The general distribution of *C.* × *ventricosum* is tightly associated with the area where both parental species co-occur, but it is more common in the Ural Mountains and Primorsky Krai of Russia (Knyasev et al., 2000a,b).

In localities within the River Volga basin, the existing data show the predominance of *C. macranthos*, similar to the main Asiatic portion of the species distribution. Of five localities, which can be checked taxonomically by herbarium specimens, there are hybrids in only one locality (Menzelinsk County), non-hybrid plants in three localities (Urakovo, Rustovskiye Klyuchi, Sarapul), while both hybrid and non-hybrid plants have been recorded only in one locality (Semiozernaya Pustyn'). Previously, hybrids were noted in the literature either provisionally (Bakin et al., 2000) or without a reference to any particular localities (Averyanov, 1999, 2000; Mayevskiy, 2006, 2014). In the Ulyanovsk Region, information about hybrids (Mayevskiy, 1917, 1933, 1941, 1954, 1964, 2006, 2014; Rakov et al., 2014) is incorrect, being based on misinterpretation of the finding in the Samara Region, near the former village Rustovskiye Klyuchi, where, in fact, no hybrids were recorded.

In the isolated group of localities, centered in the Bryansk Region, hybrids are more common than within the River Volga basin. Of six localities, which can be checked taxonomically by herbarium specimens, only hybrid specimens have been collected in two localities (Pod'yevotskaya Datscha and Prolysovo); in two localities, only non-hybrid individuals are known (Bryansk and Molodovoye); in two other localities (Krasnyi Rog and Rogovichi); both hybrid and non-hybrid individuals are at our disposal.

Thus, existing data give evidence of a wider introgression between *C. macranthos* and *C. calceolus* in Eastern Europe than reported previously. In this area, historical reports of *C.* × *ventricosum* are limited, being expressed by Khitrovo (1910) and then by Mayevskiy (1954, 1964, 2006, 2014). Khitrovo (1910) was the first who has noted that at least some plants do not represent typical *C. macranthos* plants by stating that «we were unable to collect enough material to recover the distribution of two varieties, established by Reichenbach: v. *vulgare* and v. *ventricosum*». At that time, the hybrid origin of *C.* × *ventricosum* was not universally accepted, and it was frequently treated as a variety of *C. macranthos.* The same taxonomic status was accepted by Nevski (1935) and even later (Smolyaninova, 1976, in subspecific rank), when the hybrid origin of *C.* × *ventricosum* became widely recognised. In more recent time, Averyanov (1999, 2000) noted the presence of hybrids in two localities (Krasnyi Rog and Rogowichi), but simultaneous presence of both hybrid and non-hybrid individuals was interpreted by him as an evidence of the origin of these specimens from culture.

The distribution of hybrid and non-hybrid plants over time indicates a progressive replacement of non-hybrid plants by hybrids. In the isolated group of localities centered in the Bryansk Region, the last non-hybrid *C. macranthos* was collected in 1903. The present-day field investigation of the largest population has confirmed that only hybrids are extant, with no signs of non-hybrid *C. macranthos* individuals.

Cypripedium × *ventricosum* is easily distinguishable from *C. macranthos* by several morphological features, which are intermediate between its parents. One feature is the sparsely pubescent ovary (Fig. 2D,E,F,G,H,I,J) that is similar to that of *C. calceolus*, but the latter has even stronger pubescence. In contrast, the ovary of *C. macranthos* is always completely glabrous. Another characteristic feature is the narrowly ovate to broadly lanceolate shape of the median sepal, which is also intermediate between ovate to broadly ovate shape of *C. macranthos*, and lanceolate shape of *C. calceolus*. Then, hybrids are noticeable by the colour of the lip, which is not purely purple, but also has some visible yellowish colouration and (or) fragmentary whitish (Fig. 2B,C), but this cannot be examined on badly prepared or very old herbarium specimens. Lastly, *C.* × *ventricosum* is noticeable for its ability to form two-flowered inflorescences (Fig. 2A), whereas stems of *C. macranthos* always bear only one flower. The herbarium specimens and all the modern photographs from the Bryansk Region, which are in possession of the authors, web-published (Ueda, 2021a) or used in the Red Data Books of the Bryansk Region (Bulokhov et al., 2016) and Red Data Books of the Belgorod Region (Prisnyi, 2005), are clearly attributable to hybrids either by colour, or by two-flowered stems, or by pubescent ovaries, or by a combination of these features, with no noticeable signs of non-hybrid plants.

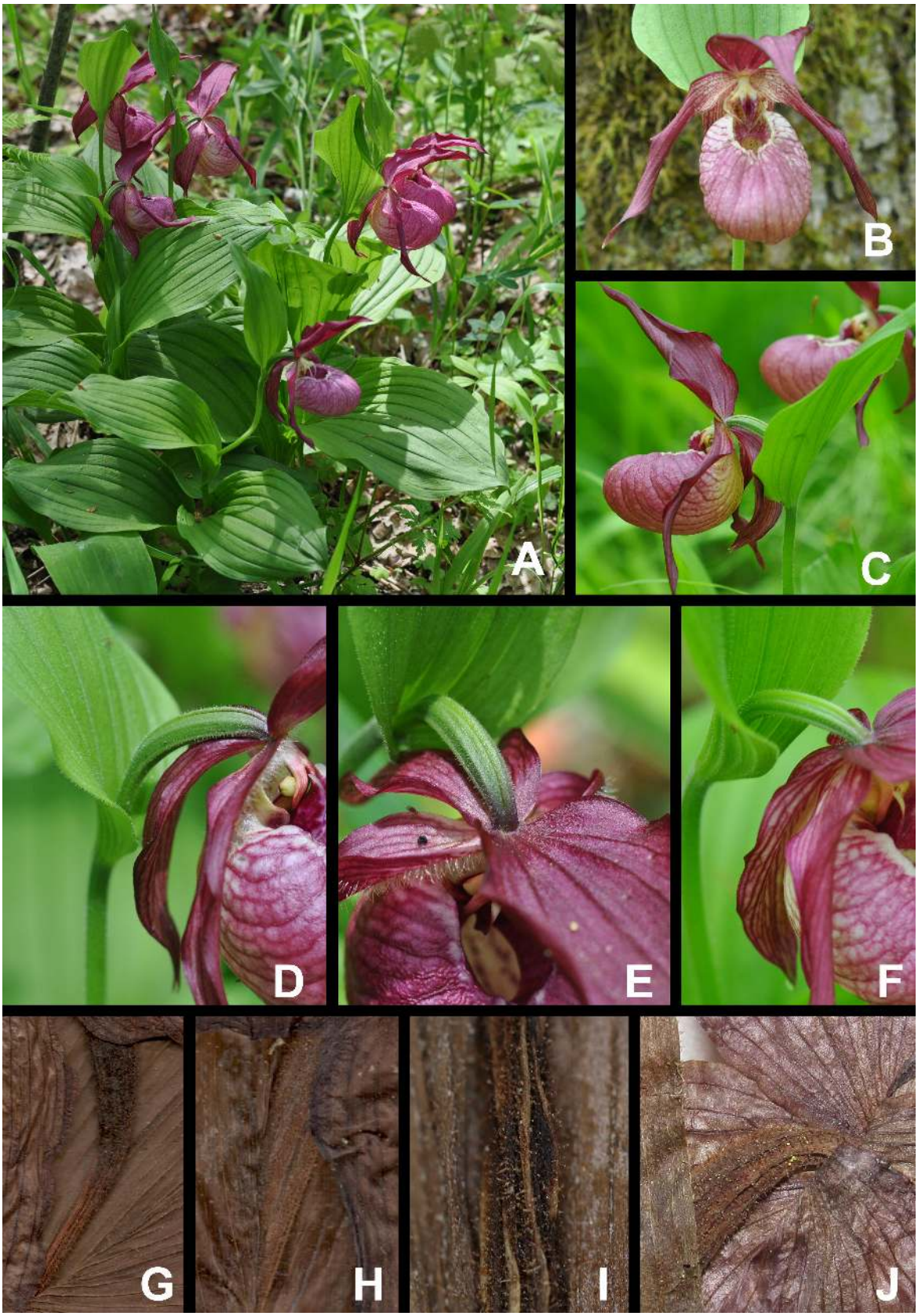


Fig. 2. Morphological characteristics of *Cypripedium* × *ventricosum* specimens in European Russia. Origin of specimens: Navlya District of the Bryansk Region (A, B, C, D, E, F, I, J); Pochep or Vygonichi District of the Bryansk Region (G); the former Menzelinsk County of the Republic of Tatarstan (G). Images display the following characters of *C.* × *ventricosum*: two-flowered inflorescences (A), whitish and yellowish colour on the lip (B, C), pubescent ovaries of the living plants (D, E, F) or herbarium specimens (G, H, I, J). The following herbarium specimens have been employed: LE 01107804 (G), LE 01107811 (H), herbarium of the Bryansk Forest Nature Reserve №353 (I), MW 295228 (J). All photographs are provided by the authors, except for photo «J», provided by Natalia Gamova on behalf of the staff of the Herbarium of the Moscow State University (MW).

Historically, co-occurrence of *C. macranthos / C. × ventricosum* and *C. calceolus* was reported in localities near the villages of Prolysovo and Molodovoye (Khitrovo, 1910). In the largest extant population near the village Prolysovo, there are *C. calceolus* plants growing side-by-side with *C. × ventricosum.* Obviously, such co-occurrence provides substantial possibilities for hybridisation, which has recently most likely led to the final elimination of *C. macranthos* in this part of its range by absorption from the more common *C. calceolus*. It cannot be excluded that introgression may continue further, resulting in the further gradual elimination of the *C. macranthos* genotype due to the pressure from the more numerous *C. calceolus*.

The new finding of a large introgressive zone may be interpreted as a confirmation of Averyanov's hypothesis that this hybrid is a stage of the speciation process leading to a new *bona fide* species of hybrid origin. Some advantage of hybrid individuals in contrast to non-hybrid plants may be supposed. Thus, hybrid individuals may benefit from the present-day ecological conditions of the area, resulting that they have outlived parental *C. macranthos*, occurring there in the past.

Decline in the number of localities of Cypripedium macranthos in European Russia

Cypripedium macranthos displays a negative change throughout its natural range in Russia, namely in the Far East, Siberia, the Urals, and European Russia, which has been ascertained by the analysis of the years of recording with the data adjustment relative to the intensity of botanical exploration in the respected time intervals (Petr G. Efimov, unpublished). In the westernmost portion of the species range within European Russia, the decrease in the number of *C. macranthos* localities is especially pronounced, and it is self-evident from the dates of recording. The current study shows that the only place, where non-hybrid plants are still extant in European Russia, is a population in the Republic of Chuvashia, near the village Urakovo. It was last re-visited by Margarita M. Gafurova (pers. comm.) in 2008. About 30 clones were found with ca. 200 generative shoots and ca. 100 vegetative ones. The prospects of the plant preservation were estimated to be high (Margarita M. Gafurova, pers. comm.) as they are confined to a hardly accessible place on the crumbled slope, but the plants undoubtedly deserve a special protection.

The hybrid plants are also currently present only at one place, near the village of Prolysovo in the Navlya District of the Bryansk Region, where several populations are known. In the Bryansk Region *C. macranthos / C. × ventricosum* has similarly undergone a severe decline, being originally recorded in 5–6 districts and now only present in one. The solitary survived populations represent a large contrast with the historic data, which tell us about very numerous plants: «according to the data from local people, it is not rare, and occurs in a large number» (Zinger, 1886); «this orchid[…] is so numerous that serves as a common source for bouquets on the Trinity day» (Khitrovo, 1910). In the vicinity of the village Prolysovo, four populations have been confirmed in the last 20 years; the populations were checked in 2001, 2002, 2007, and since 2010 up to the present, respectively. There were four stems (in 2001), 32 stems (in 2002), 49 stems (in 2007) and 310 stems (in 2010) (Bulokhov et al., 2016). In the latter population, the number of stems decreased to 178 in 2021 according to regular studies of the species dynamics conducted by the Bryansk State University. Besides Navlya District, records in other districts of the Bryansk Region date back to 1903 and earlier times, and thus they are more than 100 years old.

Remarks about the Cypripedium guttatum distribution near its western distributional limit

In Russia, the distribution of *C. guttatum* protrudes further to the west compared to *C. macranthos* (Averyanov, 1999, 2000; Bulokhov et al., 2016), which is confirmed by numerous localities between the Ural Mountains and the Bryansk Region. In total, in European Russia, *C. guttatum* is known as many as from 23 of 44 regions. In six regions, only a solitary locality is known.

Similarly to *C. macranthos*, the presence of *C. guttatum* in Ukraine is doubtful. In both editions of the «Flora of Ukrainian SSR» (Kleopov, 1933; Bordzilovski, 1950), an assumption about possible finding of this species in the Chernigov Region of Ukraine is expressed, taking into account the neighbouring locality in the Bryansk Region of Russia. Other sources (Protopopova, 1987; Sobko, 1989; Mosyakin & Fedoronchuk, 1999) completely omit this species, with an exception of Smolyaninova (1976), who reported it from Ukraine again, but gave no details. Similarly to *C. macranthos*, Averyanov (1999, 2000) expressed doubts about the presence of this spe-

cies in the Ukrainian flora. Herbarium specimens from Ukraine, mentioned by Averyanov (1999, 2000) from the villages of Rogowichi and Krasnyi Rog, do not belong to Ukraine, but to the Bryansk Region of Russia. Moreover, we have been unable to locate those specimens in herbarium LE. Therefore, it is possible that they were cited by mistake.

There are two other herbarium samples from Ukraine, but both are very doubtful. They are the following: «Khar'kov Province, herb. N.K. Sredinsky» (LE 1107800!); «in montosis umbrosis ad «Catherinopolin' et alibi haud vulgaris» (LE 1107799!). The former is questionable because it belongs to Sredinsky's herbarium, which is notable for many odd and unconfirmed collections, including collections of *Herminium monorchis* (L.) R.Br. and *Spiranthes spiralis* (L.) Chevall. from the Crimea, which have never been confirmed (Privalova & Prokudin, 1959; Efimov et al., 2018). The label of the latter specimen is the same that was discussed earlier, under the name of *C. macranthos*; most likely, it is a collection made in the Ural Mountains, near Yekaterinburg.

In Belarus, all main floristic sources (Nevski, 1949; Kozlovskaya, 1978; Lebed'ko, 2017) report *C. guttatum* only for Mohilev Region, with the reference to Cholovsky (1882) who obviously provides the original data. Cholovsky (1882) reported the finding of this species near the village of Polynovichi in the surroundings of Mohilev. No herbarium specimens are known. It should be noted that Cholovsky's reports are sometimes questionable (Dmitry V. Geltman, pers. comm.), which means that the historic presence of this species in Belarus is unconfirmed.

Conclusions

Assembling primary data is an important task to provide more correct distributional data for the conservationally important and protected plant species. In the studied case, such analysis allows us to substantially clarify the distribution of the studied *Cypripedium* species in Eastern Europe, to distinguish between incorrect, doubtful and true localities, and to estimate the amount of the *C. macranthos* introgression with *C. calceolus* in Eastern Europe. The temporal analysis of the data has made it possible to define localities where plants persist up to now. It also gives evidence of a previously wider distribution of *C. macranthos* along the western frontiers of Russia and possibly in Ukraine and Belarus, too. The study of this type can be recommended for other species, especially for those, which are simultaneously rare, decreasing, and legally protected.

Cypripedium macranthos should be excluded from floristic lists and documents that establish protection of plants in the Bryansk Region, while *C.* × *ventricosum* should be included instead. *Cypripedium* × *ventricosum* also represents a conservationally important part of the local biodiversity. Taking into account that it remains as a relict, it is quickly decreasing and is often collected by people as an ornamental plant, in the Bryansk Region, *C.* × *ventricosum* deserves to be protected at the «critically endangered» category, which is facilitated by its presence in the Red Data Book of the Russian Federation (Bardunov & Novikov, 2008).

At the same time, findings of new, previously unknown localities of the discussed taxa in Eastern Europe are possible. Further findings in the Republic of Tatarstan in the area adjacent to the Republic of Bashkortostan are especially awaited in view of the very close-set localities in Asiatic Russia, e.g. in the Republic of Bashkortostan (Ueda, 2021c). Further findings of original material in localities classified here under the category «unconfirmed» are of utmost importance. Simultaneously, more attention should be paid to the determination of *C. macranthos* / *C.* × *ventricosum* plants from European Russia both in herbaria and under natural conditions.

Acknowledgements

The study of Petr G. Efimov in 2020–2021 was supported by the Ministry of Education and Science of the Russian Federation, grant agreement №20-04-00561075-12-2021-1056 from 28.09.2021. The study of Aleksey V. Gornov was supported by the Ministry of Education and Science of the Russian Federation, grant agreement №121121600118-8. We sincere thank our colleagues Sergey L. Mosyakin and Irina Timchenko (both – M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, Ukraine) for providing valuable information about V.G. Sobko. Olga V. Biryukova (Lobachevsky State University of Nizhny Novgorod, Russia), Marina B. Fardeeva (Kazan Federal University, Russia), Margarita M. Gafurova (Chuvash State Museum, Russia), Lyudmila Kiseleva (Orel State University, Russia), Elena Parakhina (Peoples' Friendship University of Russia, Russia) and Andrey V. Shcherbakov (Moscow State University, Russia) are thanked for information about regional biodiversity and for access to some rare literature sources. We express special thanks to herbari-

um curators who provided information about herbarium specimens kept in various institutions, namely to Luisa Kadyrova (Kazan, Russia), Alexander Fateryga (Feodosia, Republic of Crimea), Natalia Gamova (Moscow, Russia), and Elena Kazmina (Voronezh, Russia).

References

Ammosov Yu.N., Belyaev V.A., Bromley G.F., Krivolutskaya G.O., Kupyanskaya A.N., Kurentsova G.E., Nechaev V.A. 1978. *A.I. Kurentsov, the scientist*. Tula: Priokskoe Publishers. 127 p. [In Russian]

Averyanov L. 1994. Orchids of the Caucasus. *Berichte aus den Arbeitskreisen Heimische Orchideen* 11(2): 4–45.

Averyanov L.V. 1999. Genus *Cypripedium* (Orchidaceae) in the Russia. *Turczaninowia* 2(2): 5–40. [In Russian]

Averyanov L.V. 2000. The genus *Cypripedium* (Orchidaceae) in Russia. *Lindleyana* 15(4): 197–221.

Averyanov L.V. 2006. Orchidaceae Juss. In: A.L. Takhtajan (Ed.): *Conspectus Florae Caucasi.* Vol. 2. Saint-Petersburg: Editio Universitatis Petropolitanae. P. 84–101. [In Russian]

Bakin O.V., Rogova T.V., Sitnikov A.P. 2000. *Vascular Plants of Tatarstan*. Kazan: Kazan State University. 496 p. [In Russian]

Baranova O.G. 2000. New and rare plants of the Viatka-Kama interfluve. *Botanicheskii Zhurnal* 85(9): 129–131. [In Russian]

Baranova O.G. 2006. The peculiarities of the Orchidaceae Juss. family species distribution in the Udmurt Republic and their protection. *Bulletin of Udmurt University* 3(10): 3–10. [In Russian]

Baranova O.G. (Ed.). 2012. *Red Data Book of the Udmurt Republic*. 2nd ed. Cheboksary: Perfectum. 458 p. [In Russian]

Baranova O.G., Adakhovskiy D.A., Borisovskiy A.G., Dedyukhin S.V., Zubtsovskiy N.E., Perevoshchikov A.A., Markova E.M., Rubtsova A.V., Tychinin V.A., Tyulkin Yu.A. 2011. *Rare and endangered plants and animals of the south part of Udmurtia and their protection: results of the research undertaken in 2005–2009.* Izhevsk: Udmurt State University. 272 p. [In Russian]

Baranova O.G., Ilminskikh N.G., Puzyrev A.N., Tuganaev V.V. 1992. *Udmurtia Flora Conspectus.* Izhevsk: Udmurt State University. 141 p. [In Russian]

Baranova O.G., Puzyrev A.N. 2012. *Conspectus Florae Provinciae Udmurtiensis (Plantae Vasculares).* Moscow; Izhevsk: Institute of Computer Research. 212 p. [In Russian]

Bardunov L.V., Novikov V.S. (Eds.). 2008. *Red Data Book of the Russian Federation (plants and fungi).* Moscow: KMK Scientific Press Ltd. 855 p. [In Russian]

Biryukova O.V., Vorotnikov V.P., Mininzon I.L. 2014. The Orchidaceae family in the flora of the Nizhni Novgorod Region. *Vestnik of Lobachevsky State University of Nizhni Novgorod* 3(3): 16–25. [In Russian]

Bolotova V.M., Dedov A.A., Lashchenkova A.N., Tolmachev A.I., Sholeninova T.P. 1962. *Manual of the vascular plants of the Republic of Komi*. Moscow; Leningrad: AS USSR. 359 p. [In Russian]

Bondartseva M.A., Prisnyi Yu.A. (Eds.). 2021. *Red Data Book of the Orel Region.* Orel: Papirus. 440 p. [In Russian]

Bordzilovski E.I. 1950. Orchidaceae Lindl. **In: M.I. Kotov**, A.I. Barbarich (Eds.): *Flora URSR.* 2nd ed. Vol. 3. Kiev: AS URSR. P. 312–401. [In Ukrainian]

Borodin A.M. (Ed.). 1984. *Red Data Book of the USSR.* 2nd ed. Moscow: Lesnaya promyshlennost. 480 p. [In Russian]

Bosek P.Z. 1975. *Plants of the Bryansk Region.* Bryansk: Priokskoye. 464 p. [In Russian]

Bosek P.Z. 1982. Plants. In: N.Z. Kharitonova, E.S. Murakhtanova (Eds.): *Rare and protected animals and plants of the Bryansk Region.* Bryansk: Bryansk Regional Publishing House. P. 133–205. [In Russian]

Bulokhov A.D., Panasenko N.N., Semenishchenkov Yu.A., Sitnikova E.F. (Eds.). 2016. *Red Data Book of the Bryansk Region.* 2nd ed. Bryansk: RIO BGU. 432 p. [In Russian]

Bulokhov A.D., Velichkin E.M. 1998. *A manual of plants of the southeast non-Chernozem Russia (Bryansk, Kaluga, Smolensk Regions).* 2nd ed. Bryansk: BGPU. 380 p. [In Russian]

Cholovsky K.A. 1882. *A review of the Flora of Mohilev Province.* Mohilev: Mohilev Province Administration Publishers. 188 p. [In Russian]

Claus C. 1851. *Localfloren der Wolgagegenden.* St. Petersburg: Buchdrukerei der Kaiserlichen Akademie der Wissenschaften. 324 p.

Dimitriev A.V. (Ed.). 2001. *Red Data Book of the Republic of Chuvashia.* Cheboksary: IPK Chuvashia. 275 p. [In Russian]

Efimov P.G., Gafurova M.M., Leostrin A.V., Melnikov D.G., Senator S.A., Fateryga A.V. 2018. New data on distribution of Orchidaceae species in several Regions of Russia. *Botanicheskii Zhurnal* 103(7): 923–930. DOI: 10.7868/S0006813618070062 [In Russian]

Efimov P.G. 2020. Orchids of Russia: annotated checklist and geographic distribution. *Nature Conservation Research* 5(Suppl.1): 1–18. DOI: 10.24189/ncr.2020.018

Efimova T.P. 1972. *A manual of the plants of Udmurtia.* Izhevsk: Udmurtia. 224 p. [In Russian]

Fardeeva M.B. 2006. Ecological analysis of the orchid flora of Tatarstan. In: L.A. Zhukova (Ed.): *Principles and methods in biodiversity conservation.* Yoshkar-Ola: Mari El State University. P. 51–53. [In Russian]

Fedotov Yu.P. (Ed.). 2004. *Red Data Book of the Bryansk Region. Plants. Fungi.* Bryansk: Chitay-Gorod. 272 p. [In Russian]

Fedotov Yu.P., Evstigneev O.I. 2003. Records of rare species of orchids (Orchidaceae) in Bryansk Region. *Botanicheskii Zhurnal* 88(10): 118–121. [In Russian]

Gafurova M.M. 2014. *Vascular plants of Chuvash Republic. Vol. 3 of the Flora of the Volga River Basin*. Togliatti: Kassandra. 333 p. [In Russian]

Gafurova M.M. (Ed.). 2019. *Red Data Book of the Republic of Chuvashia. Vol. 1, part 1*. 2nd ed. Moscow: Buki Vedi. 332 p. [In Russian]

Geltman D.V., Matveeva N.V. 2018. B.S. Kharitontsev Features of the genesis of phytostroma of Russia (ecological aspect): a monograph. Tobolsk: the Division of the Tyumen State University in Tobolsk,

2015. 161 p. B. S. Kharitontsev. Floristic pressure in phytostroma of Siberia: A monograph. Tobolsk: the Division of the Tyumen State University in Tobolsk, 2016. 186 p. *Botanicheskii Zhurnal* 103(2): 271–277. [In Russian]

Goworuchin W.S. 1937. *Flora Medio, Boreali et Polari Uralensis.* Sverdlovsk: Sverdlovsk Regional Publishing House. 536 p. [In Russian]

Grossheim A.A. 1940. *Flora of Caucasus. Vol. 2*. 2nd ed. Baku: Azerbaijanian Branch AS USSR. 284 p. [In Russian]

Ivanov A.L. 2019. *Conspectus florae Caucasi Rossicae (plantae vasculares).* Stavropol: SKFU. 341 p. [In Russian]

Ivanov A.L., Kovaleva O.A. 2005. *Orchids of the North Caucasus.* Stavropol: SKFU. 122 p. [In Russian]

Jakubska-Busse A., Tsiftsis S., Śliwiński M., Křenová Z., Djordjević V., Steiu C., Kolanowska M., Efimov P., Hennigs S., Lustyk P., Kreutz K. 2021. How to protect natural habitats of rare terrestrial orchids effectively: a comparative case study of *Cypripedium calceolus* in different geographical regions of Europe. *Plants* 10: 404. DOI: 10.3390/plants10020404

Khitrovo V.N. 1910. Critical notes on the Flora of the Orel Province. IV. *Proceedings of the Society for the study of the nature of the Orel Province* 2: 157–185. [In Russian]

Khitrovo V.N. 1923. *Account of the Flora of the Orel Province.* A manuscript kept in the Saint-Petersburg Branch of the Archive of the Academy of Sciences. 114 p. [In Russian]

Kiseleva L.L., Parakhina E.A., Shcherbakov A.V. 2021. *Checklist of vascular plants of the Orel Region.* Moscow: Galleya-Print. 78 p. [In Russian]

Kleopov Yu.P. 1933. Orchidaceae. In: M. Lyaskivskiy (Ed.): *Flora URSR.* Part 1. Kiev: Kolkhoz and Sovkhoz Literature State Publishers. P. 327–344. [In Ukrainian]

Knyasev M.S., Kulikov P.V., Knyazeva O.I., Semerikov V.L. 2000a. Interspecific hybridization in Eurasian species of *Cypripedium* (Orchidaceae), and the taxonomic status of *C. ventricosum*. *Botanicheskii Zhurnal* 85(5): 94–102. [In Russian]

Knyasev M.S., Kulikow P.V., Knyaseva O.I., Semerikov V.L. 2000b. Interspecific hybridization in Northern Eurasian *Cypripedium*: morphometric and genetic evidence of hybrid origin of *C. ventricosum*. *Lindleyana* 15(1): 10–20.

Konechnaya G.Yu., Suslova T.A. (Eds.). 2004. *Red Data Book of the Vologda Region*. Vol. 2. Vologda: Vologda State University and Rus' Press. 360 p. [In Russian]

Kozlovskaya N.V. 1978. *Flora of Belarus, rules of its formation, scientific basis for its use and protection.* Minsk: Nauka i Tekhnika. 128 p. [In Russian]

Kryshtofovich A.N. 1929. Orchidaceae. In: B.A. Fedtschenko (Ed.): *Flora Rossiae Austro-Orientalis.* Fasc. 3. Leningrad: Main Botanical Garden. P. 414–436. [In Russian]

Krylov P.N. 1885. Materialien zur flora des gouvernements Wjatka. *Proceedings of the Society of Naturalist at the Kazan' Imperial University* 14(1): 1–131. [In Russian]

Kulikov P.V., Filippov E.G. 2011. Short-spurred fragrant Orchid (*Gymnadenia odoratissima* (L.) Rich.) in Russia. In: I.I. Shamrov (Ed.): *Protection and cultivation of orchids*. Moscow: Moscow: KMK Scientific Press Ltd. P. 266–271. [In Russian]

Lebed'ko V.N. 2017. Orchidaceae Juss. In: V.I. Parfenov (Ed.): *Flora of Belarus.* Minsk: Belaruskaya Nauka. P. 232–310. [In Russian]

Lipschitz S. 1952. *Botanicorum Rossicorum Lexicon Biographo-Bibliographicum.* Vol. 5. Moscow: Editio Societatis Naturae Curiosum Mosquensis. 617 p. [In Russian]

Litvinov D.I. 1927. *On some botanical-geographical proportions in our flora.* Leningrad. 15 p. [In Russian]

Maltsev A.N. 1907. A review of the vegetation of Korocha County of Kursk Province. *Protocols of the Society of Naturalists at the Imperial Yur'yev University* 16(1): 1–56. [In Russian]

Marakaev O.A. 2015. *Orchids of Yaroslavl Region: a photoatlas*. Yaroslavl: Yaroslavl State University. 50 p. [In Russian]

Markov M.V. 1939. Wald und Steppe in Bedingungen des Sakamjas. II. Die Nadelwälder. *Scientific Notes from the Kazan' State University* 99(1–1): 67–131. [In Russian]

Martynenko V.A. 1976. Orchidaceae Juss. In: A.I. Tolmatchev (Ed.): *Flora regionis Boreali-Orientalis territoriae Europaeae URSS.* Vol. 2. Leninopoli: Nauka. P. 118–133. [In Russian]

Mayevskiy P.F. 1917. *Flora of the Middle European Russia.* 5th ed. Moscow: M. & S. Sabashnikovy. 909 p. [In Russian]

Mayevskiy P.F. 1933. *Flora of the Middle European Russia.* 6th ed. Moscow & Leningrad: Sel'hozgiz. 748 p. [In Russian]

Mayevskiy P.F. 1941. *Flora of the Middle European USSR.* 7th ed. Moscow & Leningrad: Sel'hozgiz. 824 p. [In Russian]

Mayevskiy P.F. 1954. *Flora of the Middle European USSR.* 8th ed. Moscow & Leningrad: State Agricultural Literature Publishing House. 910 p. [In Russian]

Mayevskiy P.F. 1964. *Flora of the Middle European USSR.* 9th ed. Leningrad: Kolos. 880 p. [In Russian]

Mayevskiy P.F. 2006. *Flora of the Middle European Russia.* 10th ed. Moscow: Moscow: KMK Scientific Press Ltd. 600 p. [In Russian]

Mayevskiy P.F. 2014. *Flora of the Middle European Russia.* 11th ed. Moscow: KMK Scientific Press Ltd. 635 p. [In Russian]

Montrezor V. 1881. *A review of the most beautiful plants in the flora of Kiev Academic District: Kiev, Podol'sk, Volhyn', Chernigov and Poltava Provinces.* Kiev: Kiev Society of Horticulturalists. 49 p. [In Russian]

Montrezor V. 1886. A review of the plants in the Flora of Kiyev Academic District: Kiev, Podol'sk, Volhyn', Chernigov and Poltava Provinces. *Notes of the Kiev Society of Naturalists* 7(1): 1–144. [In Russian]

Mosyakin S.L., Fedoronchuk N.M. 1999. *Vascular plants of Ukraine: A nomenclatural checklist*. Kiev:

M.G. Kholodny Institute of Botany. 345 p. DOI: 10.13140/2.1.2985.0409

Nazirov A.A. (Ed.). 2016. *Red Data Book of the Republic of Tatarstan.* 3rd ed. Kazan: Idel-Press. 760 p.

Nevski S.A. 1935. Orchidaceae Lindl. In: V.L. Komarov (Ed.): *Flora URSS.* Vol. 4. Leningrad: Editio Academiae Scientiarum URSS. P. 589–730, 750–754. [In Russian]

Nevski S.A. 1949. Orchidaceae Lindl. In: B.K. Shishkin (Ed.): *Flora of BSSR.* Vol. 1. Moscow: State Agricultural Literature Publishing House. P. 377–414. [In Russian]

Nyankovskiy M.A. (Ed.). 2015. *Red Data Book of the Yaroslavl Region.* Yaroslavl: Akademia 76. 472 p. [In Russian]

Okhapkin A.G. (Ed.). 2005. *Red Data Book of the Nizhniy Novgorod Region*. Vol. 2. Nizhniy Novgorod: Committee for Nature Conservation and Land-Use Management of the Nizhniy Novgorod Region. 328 p. [In Russian]

Protopopova V.V. 1987. Orchidaceae. In: Yu.N. Prokudin (Ed.): *Manual of the Higher Plants of Ukraine.* Kiev: Naukova Dumka. P. 405–412. [In Russian]

Perfiljev I.A. 1934. *Flora of the Severnyi Krai.* Part 1. Arkhangelsk: Sevkraigiz. 160 p. [In Russian]

Plaksina T.I. 2001. *Conspectus of the flora of the Volga-Ural Region.* Samara: Samara State University. 388 p. [In Russian]

Prisnyi A.V. (Ed.). 2005. *Red Data Book of the Belgorod Region*. Belgorod: Ecological Fund of the Belgorod Region. 532 p. [In Russian]

Privalova L.A., Prokudin Yu.N. 1959. Addenda et corrigenda ad vol. I «Florae Tauricae». *Transactions of the State Nikitskiy Botanical Garden* 31: 5–127. [In Russian]

Rakov N.S., Saksonov S.V., Senator S.A., Vasjukov V.M. 2014. *Vascular plants of the Ulyanovsk Region. Vol. 2 of the Flora of the Volga River Basin*. Togliatti: Kassandra. 295 p. [In Russian]

Rännbäck L.M. 2007. *Propagation, cultivation and breeding of terrestrial temperate orchids, with focus on Cypripedium spp.* Bachelor project in the Danish-Swedish Horticulture programme. Alnarp: SLU. 50 p.

Reshetiuk O.W. 2003. *The genus Cypripedium L. (Orchidaceae Juss.) in Ukraine (classification, horology, phytocenology and its species protection ex situ and in situ)*. PhD Thesis. Kyiv: M.M. Gryshko National Botanical Gardens, National Academy of Sciences of Ukraine. 20 p. [In Ukrainian]

Rogowitsch A.S. 1855. A review of vascular and semivascular plants in the flora of Kiev, Chernigov and Poltava. In: *Natural History of the provinces of Kiev Academic District*. Kiev. 146 p. [In Russian]

Rogowitsch A.S. 1869. *A review of vascular and higher cryptogamic plants in the flora of the Provinces of the Kiev Academic District: Volhyn', Podol'sk, Kiev, Chernigov and Poltava.* Kiev. 308 p. [In Russian]

Ruprecht F. 1866. *Geobotanical studies of Chernozem.* Saint-Petersburg: Imperial Academy of Sciences. 131 p. [In Russian]

Saksonov S.V., Senator S.A. 2012. *Guide to the Samara flora 1851–2011. Vol. 1 of the Flora of the Volga River Basin*. Togliatti: Kassandra. 511 p. [In Russian]

Saksonov S.V., Koneva N.V. 2006. The abstract of Orchidaceae family the Samara Area. *Bulletin of Udmurt University* 10: 43–50. [In Russian]

Schmalhausen I. 1897. *Flora of the Middle and South Russia, Crimea and North Caucasus.* Vol. 2. Kiev: I.N. Kushnerev i Ko. 752 p. [In Russian]

Shchepovskikh A.I. (Ed.). 1995. *Red Data Book of the Republic of Tatarstan.* Kasan: Priroda; Star. 454 p. [In Russian]

Shchepovskikh A.I. (Ed.). 2006. *Red Data Book of the Republic of Tatarstan.* 2nd ed. Kasan: Idel-Press. 832 p. [In Russian]

Smirnov A.G. 1979. Orchidaceae. In: M.V. Markov (Ed.): *A manual of plants of the Tatar Soviet Republic.* Kazan: Kazan State University. P. 108–115. [In Russian]

Smirnov V. 1904. Zur Flora des Gouv. Simbirsk. *Supplement to the Protocols of the Proceedings of the Society of Naturalist at the Kazan' Imperial University* 231: 1–24. [In Russian]

Smolyaninova L.A. 1976. Orchidaceae Juss. In: A.A. Fedorov (Ed.): *Flora Partis Europaeae URSS.* Vol. 2. Leningrad: Nauka. P. 10–59. [In Russian]

Sobko V.G. 1989. *Orchids of Ukraine.* Kiev: Naukova Dumka. 190 p. [In Ukrainian]

Sobolev N.A., Belonovskaya E.A. (Eds.). 2013. *Emerald Data Book of the Russian Federation. Conservationally Important Protected Areas of European Russia and their elucidation.* Part 1. Moscow: Institute of Geography. 308 p. [In Russian]

Thiers B.M. 2022. *Index Herbariorum.* Available from http://sweetgum.nybg.org/science/ih/

Tikhomirov V.N. (Ed.). 1986. *A manual of the flora of the Yaroslavl Region*. Yaroslavl: Verkhnyaya Volga. 182 p.

Tikhomirov V.N., Kharitontsev B.S. 1984. New data about the flora of the left-bank of Desna River within the Bryansk Region. *Biological Sciences* 8(248): 73–76. [In Russian]

Ueda K. (Ed.). 2021a. *Cypripedium macranthos*. In: *iNaturalist: A community for Naturalists.* Available from https://www.inaturalist.org/photos/135232996

Ueda K. (Ed.). 2021b. *Cypripedium macranthos*. In: *iNaturalist: A community for Naturalists.* Available from https://www.inaturalist.org/observations/20414490

Ueda K. (Ed.). 2021c. *Cypripedium macranthos*. In: *iNaturalist: A community for Naturalists.* Available from https://www.inaturalist.org/photos/32036217

Vakhrameeva M.G., Varlygina T.I., Tatarenko I.V. 2014. *Orchids of Russia (biology, ecology and protection).* Moscow: KMK Scientific Press Ltd. 437 p. [In Russian]

Wirzen J.E.A. 1839. *De geographica plantarum per partem provinciae Casanensis distributione.* Helsingforsiae: Frenckelliana. 130 p.

Yudin U.P. 1963. Relict flora of the limestone outcrops of the North-East of the European part of the USSR. In: V.N. Sukaczev (Ed.): *Materials on the history of the flora and vegetation of the USSR.* Fasc. 4. Moscow; Leningrad: AS USSR. P. 493–587. [In Russian]

Zinger V.Ya. 1886. *A Compendium of the Middle Russian Flora.* Moscow: M. Katkov. 520 p. [In Russian]

Appendix. Herbarium collections used in the present study. Data about herbarium collections with acronyms is presented predominantly according to *Index Herbariorum* (Thiers, 2022, with corrections)

Herbarium acronym	Herbarium's location	Institution
AA*	Almaty	Institute of Botany and Phytointroduction
ALTB	Barnaul	Altai State University
CHPU	Chelyabinsk	Chelyabinsk State Pedagogical University
CNR	Alushta, Crimea	Crimean Natural Reserve
CSAU	Simferopol	V.I. Vernadsky Crimean Federal University
CSR	Maikop	Caucasus State Nature Biosphere Reserve
CSUH	Chelyabinsk	Chelyabinsk State University
DAG	Makhachkala	Mountain Botanical Garden of the Dagestan Scientific Centre
GARIN	Borok, Yaroslavl Region	I.N. Garin Society for Study of the Flora of the Yaroslavl Oblast
H*	Helsinki	University of Helsinki
HERZ	Saint-Petersburg	Alexander Herzen Pedagogical University
HGU	Abakan	N.F. Katanov Khakass State University
IBIW	Borok, Yaroslavl Region	Papanin Institute for Biology of Inland Waters
IRK	Irkutsk	Siberian Institute of Plant Physiology and Biochemistry
IRKU	Irkutsk	Irkutsk State University
KAND	Kandalaksha, Murmansk Region	Kandalaksha State Nature Reserve
KAZ	Kazan	Kazan State University
KBAI	Krasnodar	Kuban Agricultural University
KBHG	Nalchik	H.M. Berbekov Kabardin-Balkar University
KFTA	Saint-Petersburg	Saint Petersburg S.M. Kirov Forestry Academy
KHA*	Khabarovsk	Institute for Water and Ecology Problems
KLGU	Kaliningrad	Immanuel Kant Baltic Federal University
KPABG	Apatity, Murmansk Region	Polar-Alpine Botanical Garden-Institute
KRAS	Krasnoyarsk	Krasnoyarsk State Pedagogical University
KRF	Krasnoyarsk	V.N. Sukachev Institute of Forest and Wood
KRM	Krasnoyarsk	Krasnoyarsk Regional Museum
KRSU	Krasnoyarsk	Siberian Federal University
KULPOL	Tula	State Museum-Reserve «Kulikovo Field»
KUZ	Kemerovo	Institute of Human Ecology
KW*	Kiev	M.G. Kholodny Institute of Botany
LE	Saint-Petersburg	Komarov Botanical Institute
LECB	Saint-Petersburg	Saint-Petersburg University (Department of Botany)
LENUD	Makhachkala	Dagestan State University
MAG	Magadan	Institute of the Biological Problems of the North
MHA	Moscow	Main Botanical Garden
MOSP	Moscow	Moscow State Pedagogical University
MW	Moscow	Moscow State University
NNSU	Nizhniy Novgorod	Lobachevsky State Nizhny Novgorod University
NS	Novosibirsk	Central Siberian Botanical Garden (I.M. Krasnoborov Herbarium)
NSK	Novosibirsk	Central Siberian Botanical Garden (M.G. Popov Herbarium)
ORIS	Orenburg	Institute of Steppe

Herbarium acronym	Herbarium's location	Institution
PERM	Perm	Perm State University
PHEO	Kurortnoye, Crimea	T.I. Vyasemsky Karadag Scientific Station
PKM	Penza	Penza State University
PSK	Pskov	Pskov State University
PTZ	Petrozavodsk	Karelian Research Centre
PVB	Togliatti	Institute of Ecology of the Volga River Basin
SAKH	Yuzhno-Sakhalinsk	Sakhalin Botanical Garden
SARAT	Saratov	Saratov State University
SASY	Yakutsk	Institute for Biological Problems of Cryolithozone
SIMF	Simferopol	Taurida National University
SPI	Stavropol	Stavropol State University
SVER	Yekaterinburg	Institute of Plant and Animal Ecology
SYKO	Syktyvkar	Komi Scientific Centre
TK	Tomsk	Tomsk State University
TKM	Tula	Historical, Regional and Art Museum
TUL	Tula	Tula State Lev Tolstoy Pedagogical University
TULGU	Tula	Tula State University
TVBG	Tver	Tver State University (Botanical Garden)
UDU*	Izhevsk	Udmurt State University
UFA	Ufa	Ufa Scientific Centre
UUH	Ulan-Ude	Institute of General and Experimental Biology
VBGI	Vladivostok	Botanical Garden-Institute
VLA	Vladivostok	Federal Scientific Center of the East Asia Terrestrial Biodiversity
VOR	Voronezh	Voronezh State University
WIR	Saint-Petersburg	N.I. Vavilov Institute of Plant Genetic Resources
YALT	Yalta	The State Nikita Botanical Gardens
–	Andreapol, Tver Region	Andreapol Regional Museum
–	Arkhangelsk	Lomonosov Northern (Arctic) Federal University
–	Cheboksary	Chuvash National Museum
–	Elizovo, Kamchatsky Krai	Kronotsky State Nature Reserve
–	Gremyachinsk, Permsky Krai	Basegi State Nature Reserve
–	Kirov	Vyatka State University
–	Krasnoyarsk	Stolby National Park
–	Moscow	K.A. Timiryazev State Biological Museum
–	Novoalekseevka, Yaroslavl Region	Svyato-Alekseevskaya Pustyn' Monastery
–	Saint-Petersburg	«Krestovskiy Ostrov» Centre for Ecology and Biology
–	Saint-Petersburg	Saint-Petersburg University (Department of Geobotany)
–	Tver	Tver State Museum
–	Tver	Tver State University (Department of Botany)
–	Velikiy Novgorod	Novgorod State University
–	Vladivostok	Elyakov Pacific Institute of Bioorganic Chemistry
–	Zapovednyi, Tver Region	Central Forest State Nature Reserve

Note: asterisks denote partly studied collections.

ОСТАТОЧНЫЕ ПОПУЛЯЦИИ *CYPRIPEDIUM MACRANTHOS* (ORCHIDACEAE) В ВОСТОЧНОЙ ЕВРОПЕ: СВИДЕТЕЛЬСТВА ПОЧТИ ПОЛНОГО ИСЧЕЗНОВЕНИЯ НА ФОНЕ ШИРОКО РАСПРОСТРАНЕННОЙ ИНТРОГРЕССИИ С *CYPRIPEDIUM CALCEOLUS*

П. Г. Ефимов[1,*], Н. Н. Панасенко[2], А. В. Горнов[3]

[1]*Ботанический институт имени В.Л Комарова РАН, Россия*
**e-mail: efimov@binran.ru*
[2]*Брянский государственный университет, Россия*
[3]*Центр по проблемам экологии и продуктивности лесов РАН, Россия*

Распространение видов *Cypripedium macranthos* и *C.* × *ventricosum* в Восточной Европе трактуется в литературе противоречиво. В то же время, виды рода *Cypripedium* являются угрожаемыми видами с высокой природоохранной значимостью, и точное знание их распространения критически важно для расстановки приоритетов в природоохранных мероприятиях. В настоящей статье была собрана первичная информация о местонахождениях *C. macranthos* и *C.* × *ventricosum* в Восточной Европе благодаря обращению к исходным источникам информации, в первую очередь к старому гербарию и литературе. В результате проведенной оценки 19 местонахождений оценены как ошибочные, 11 – как сомнительные, и только 12 местонахождений признаны достоверными. Подтверждено отсутствие *C. macranthos* и *C.* × *ventricosum* в исторической перспективе на территории Республик Чечня и Марий Эл, Ульяновской и Курской областей, в то время как наличие вида в Вологодской области, Республиках Коми и Удмуртия, Ярославской, Нижегородской и Воронежской/Липецкой областях требует подтверждения. Найдены гербарные образцы, документирующие произрастание *C. **macranthos*** в Самарской области, на основании которых ранее вид ошибочно приводился для Ульяновской области. Проблема присутствия *C. macranthos* или *C.* × *ventricosum* на Украине обсуждается ввиду сведений, опубликованных В.Г. Собко в 1989 г. Подтверждено резкое сокращение числа местонахождений вида в Европейской России. Единственное известное сохранившееся местонахождение *C. macranthos* находится в Республике Чувашия, а *C.* × *ventricosum* – в Брянской области (несколько близко расположенных популяций). Масштабы гибридизации между *C. macranthos* и *C. calceolus* в Европейской России ранее недооценивались. Так, в Брянской области и сопредельных регионах после 1903 г. отмечались только гибридные особи. Это обстоятельство определяет необходимость соответствующих корректировок во флористических данных и в документах, определяющих локальную охрану биоразнообразия сосудистых растений.

Ключевые слова: венерин башмачок, гибридизация, изменение состава флоры, охрана растений, реликтовые элементы, старые находки, угрожаемые сосудистые растения, флора России