



Survey of the genus *Adoxa* (Viburnaceae) in Northeast Asia: taxonomical diversity and a new species

Marina N. Koldaeva

Marina N. Koldaeva *
e-mail: mnkoldaeva@mail.ru

Botanical Garden-Institute FEB RAS,
Vladivostok, Russia

* corresponding author

Manuscript received: 07.05.2026
Review completed: 24.08.2026
Accepted for publication: 05.09.2026
Published online: 18.09.2026

ABSTRACT

The article examines the species diversity and taxonomic position of known Adoxaceae (Viburnaceae) species. Currently, the genus *Adoxa* comprises 4 accepted species; the taxonomic status of 3 other species remains disputed. Based on comparative morphological analysis, a new species from Trans-Baikal Territory, *Adoxa itegriloba* sp. nov., has been identified, described, and illustrated. It is characterized by an entire or entire-lobed blade of stem and rosette leaves, with lobes remaining entire even when the rosette leaf blade is dissected or divided. The upper flower is tetramerous, with the formula $Ca(2)Co(4)A_4G(4)$; the lateral flower is pentamerous, with $Ca(3)Co(5)A_5G(5)$, similarly to *A. moschatellina*, but the stamens have entire (unsplit) filaments. The new species possibly originated through hybridization between the Holarctic *A. moschatellina* and the disjunctly distributed South Siberian–Far Eastern relict *A. orientalis*. The occurrence in Trans-Baikal Territory of *A. itegriloba* with its original leaf blade structure, along with the relict *A. orientalis* and the widely distributed *A. moschatellina*, allows the mountainous regions of the upper reaches of the Amur basin to be regarded as a secondary center of species diversity of the genus *Adoxa*.

Keywords: *Adoxa moschatellina*, *Adoxa orientalis*, morphology, origin, taxonomy

РЕЗЮМЕ

Колдаева М.Н. Обзор рода *Adoxa* (Viburnaceae) в северо-восточной Азии: таксономическое разнообразие и новый вид. Рассмотрено видовое разнообразие и таксономическое положение известных видов Adoxaceae (Viburnaceae). В настоящее время род *Adoxa* включает 4 вида; таксономический статус 3 других видов остается дискуссионным. На основании сравнительно-морфологического анализа с территории Забайкальского края выявлен, описан и проиллюстрирован новый вид *Adoxa itegriloba* sp. nov. Он характеризуется цельной или цельно-лопастной пластинкой стеблевых и розеточных листьев, при этом в случае рассеченной или раздельной пластинки розеточных листьев ее лопасти остаются цельными. Верхний цветок тетрамерный, с формулой $Ca(2)Co(4)A_4G(4)$; боковой цветок пентамерный, с формулой $Ca(3)Co(5)A_5G(5)$, как у *A. moschatellina*, однако тычинки имеют цельные (нерассеченные) нити. Предполагается, что новый вид мог возникнуть в результате гибридизации между гомарктическим *A. moschatellina* и дизъюнктивно распространенным южносибирско-дальневосточным реликтовым видом *A. orientalis*. Произрастание в Забайкальском крае *A. itegriloba* с оригинальным строением листовых пластинок наряду с реликтовым *A. orientalis* и широко распространенным *A. moschatellina* позволяет рассматривать горные районы верховий бассейна Амура в качестве вторичного центра видового разнообразия рода *Adoxa*.

Ключевые слова: *Adoxa moschatellina*, *A. orientalis*, Забайкальский край, морфология, происхождение, таксономия

The genus *Adoxa* L. (1753: 367) is distinguished by an unusual structure: the combination of alternate rosette leaves with opposite stem leaves; the tetramerous apical flower in the inflorescence and pentamerous lateral flowers, but with a 3-lobed calyx, which could be interpreted as bracts (Martinovsky 1931, Fukuoka 1974, Li & Ning 1987, Erbar 1994); the stamen filament divided into two branches, each with a separate anther; and the bases of the carpels fused, forming a semi-inferior ovary (Eriksson & Donoghue 1997). Owing to such a specific structure, the genus with the single species *A. moschatellina* L. (1753: 367) did not have a definite systematic position for a long time (Nepomnyashchaya 1984, Peruzzi & Passalacqua 2006).

The structural features of the generative organs served as a basis for placing it in a separate family, Adoxaceae E. Meyer (1839: 198). However, even after this, the systematic position of Adoxaceae long remained a subject of debate (Erdtman 1952, Takhtajan 1966, Cronquist 1968, Hutchinson 1969, Fukuoka 1974, Poddubnaya-Arnoldi 1982, Donoghue et al. 1992). The phylogenetic relationships of the family and the phylogeny of Adoxaceae were subsequently resolved on the basis of genetic and morphological data with sufficient reliability (Donoghue et al. 1992, Eriksson & Donoghue 1997, Liu et al. 2000, Donoghue et al. 2003, Zhang et al. 2003, Mao et al. 2005, Jacobs et al. 2010, Fan et al. 2018). As a result, the close relationships of Adoxaceae with

Sambucus L. (Linnaeus 1753:269) and *Viburnum* L. (Linnaeus 1753:267) from the family Caprifoliaceae Jussieu (Linnaeus 1789:210) were confirmed. All three taxa were placed in the family Adoxaceae, later given the priority name Viburnaceae Raf. (Rafinesque 1820:87) (APG IV 2016, Global Fl. 2018). In the phylogenetic tree, each taxon forms a monophyletic clade (Liu et al. 2000, Donoghue et al. 2001, Donoghue et al. 2003, Zhang et al. 2003, Mao et al. 2005, Jacobs et al. 2010, Fan et al. 2018).

Widespread in the Holarctic, *A. moschatellina* remained the only known species of both the genus and the family Adoxaceae for over two hundred years. Surveys of poorly studied regions of Asia in the 1980s revealed several new species of Adoxaceae. Hara (1981:271) described a montane species of *Adoxa*, *A. omeiensis* H. Hara, from the vicinity of Mount Omei, Sichuan Province (China), distinguished by a tripartite leaf blade and a racemose inflorescence with long pedicels, long-pointed corolla lobes, and T-shaped stamen filaments. Wu (1981:384) considered the distinctive features of the new species sufficient to place it in a separate genus, *Tetradoxa* C.Y. Wu. At the same time, another species of Adoxaceae, *Sinadoxia corydalisifolia* C.Y. Wu, Z.L. Wu et R.F. Huang (Wu et al. 1981:207), was described as a new genus from the highland Qinghai-Tibet Plateau (Qinghai Province, China). It was distinguished by pinnately dissected leaves with pinnately parted or pinnately lobed leaflets, elongated inflorescences consisting of several few-flowered cymes interruptedly positioned along the axis, and the distinctive structure of the calyx, corolla, and ovary (Wu et al. 1981). Both species have small ranges with a limited number of localities and are endangered (Liu et al. 2000, Wang et al. 2008, Qiner et al. 2011). In 1984, a new species of the genus *Adoxa* was described from Russia, *A. orientalis* Nepomnjasczaja (Nepomnyashchaya 1984a:260), which occurs in montane regions of the south of Eastern Siberia and the Far East (Russia) and in the Greater Khingan Mountains (northeast China). Subsequently, the genus was extended to include three more species closely related to *A. moschatellina*: *A. inodora* (Falc et C.B. Clarke) Nepomnjasczaja (Nepomnyashchaya 1987:89) from the Himalayas (Kashmir, India), *A. insularis* Nepomnjasczaja (Nepomnyashchaya 1985:524) occurring on the islands of Kunashir and Sakhalin, Russia and *A. xizangensis* G. Yao (Yao 1992:29) from the provinces of Sichuan and Yunnan, southwestern China. Some local morphotypes of the widely distributed *A. moschatellina* were also described as subspecies, varieties, or forms (*A. moschatellina* subsp. *cescae* Peruzzi et N.G. Passalacqua (Peruzzi & Passalacqua 2006:254) from southern Italy and *A. moschatellina* f. *japonica* H. Hara (Hara 1956, 1983:305) from the Japanese Islands).

Cytological studies of *Adoxa* s.l. have shown that all Adoxaceae species possess similar cytotypes with a unique combination of karyomorphological features and a base chromosome number of $n = 18$ (Hara 1962, Sokolovskaja 1966, Zhukova 1967, Packer 1968, Liang 1986, 1993a,b, Noguchi & Kawano 1974, Inaba et al. 1999, 2000, Probatova 2014), and that they form a natural group (Liu et al. 1999).

Within *Adoxa* s.l., Hara (1981) considered *A. omeiensis* (= *T. omeiensis* (H. Hara) C.Y. Wu, 1981:385) to be a spe-

cies with more primitively structured floral organs and an ancestral form of *A. moschatellina*. Wu (1981) shared this point of view. Nepomnyashchaya (1984b, 1987) proposed to consider *A. orientalis* as an ancestral form, a species with ancestral features in the floral structure: the 3-dimensionality of lateral flowers and the entire stamen filaments developing from a single primordium, like the split stamen filaments of *A. moschatellina* (Payer 1857, Roels & Smets 1994).✕

Molecular phylogenetic methods showed that *S. corydalisifolia* forms a basal branch of the Adoxaceae (*Adoxina* clade) (Liu et al. 2000, Donoghue et al. 2001, 2003, Mao et al. 2005). In the phylogenetic tree, *Tetradoxa* is combined into a single branch with *A. moschatellina* (Donoghue et al. 2001, 2003, Mao et al. 2005, Jacobs et al. 2010), which confirms the correctness of its initial placement in the genus *Adoxa* (Hara 1981, 1983). The divergence time between the genera *Adoxa* s.s. and *Sinadoxia*, as estimated by Mao et al. (2005), was about 2.3 Myr ago (from 2 to 4 Myr ago), and between *Adoxa* s.s. (*A. moschatellina*, *A. orientalis*) and *Tetradoxa*, only about 0.32 Myr ago (from 1.2 to 0.3 Myr ago), which fits into the late Tertiary to early-middle Quaternary period. According to the assumption of Mao et al. (2005), the divergence of the genera within Adoxaceae was caused primarily by allopatric differentiation.

The least studied part of the genus *Adoxa* is the species closely related to *A. moschatellina* that inhabit the Himalayas (*A. inodora*), southwestern China (*A. xizangensis*), and Asian Russia (*A. orientalis* and *A. insularis*). *Adoxa inodora*, elevated to the species level from a subspecies, is characterized by ternate leaves with 3-divided leaflets, usually a single stem leaf, a pentamerous apical flower ($\text{Ca}(3)\text{Co}(5)\text{A}_5\text{G}(4)$), hexamerous lateral flowers ($\text{Ca}(3)\text{Co}(6)\text{A}_6\text{G}(4-5)$), and by differences in chemical composition, manifested as the absence of the light musky odor characteristic of *A. moschatellina* (Nepomnyashchaya 1987). *Adoxa insularis*, unlike *A. moschatellina*, has pointed petals with an unbranched or weakly branched vein, pointed calyx lobes, and only 7–10 nectary glands located on the flat surface of the petal rather than in a pit (Nepomnyashchaya 1985, 1988, Popova 2000). *Adoxa xizangensis* differs from *A. moschatellina* by the curved or spirally twisted peduncle during flowering and fruiting, usually positioned under the leaves, and by the slightly narrower corolla lobes (Yao 1992, Hong & Boufford 2011). The stamen filaments of *A. insularis*, *A. inodora* and *A. xizangensis* are bipartite to the base. These species have not yet been studied by any of the molecular genetic and comparative morphological approaches. The karyotypes (Liang 1993a,b) and the structure and variability of floral morphology were described for *A. orientalis* (Nepomnyashchaya 1984b, Liang 1997), including those of plants collected in Heilongjiang Province (China). Molecular methods have shown that *A. orientalis*, although close to other representatives of the genus *Adoxa* s.s., is an independent species (Mao et al. 2005). However, in the Flora of China (Qiner et al. 2011, Hong & Boufford 2011), it is absent both as a separate species and among synonyms, and *A. inodora* is mentioned as a subspecies of *A. moschatellina*. The lack of detailed studies raises doubts

about the existence of these species as independent taxa or suggests uncertainty regarding their positions (Jacobs et al. 2010, Hong & Boufford 2011). All the above-listed species are poorly studied and, probably for this reason, are not accepted in the updated international POWO database (except for *A. xizangensis*) and are treated as synonyms of *A. moschatellina* (POWO 2025). Currently, all Adoxaceae species are combined into the genus *Adoxa*, which includes four species: *A. corydalifolia* (C.Y. Wu, Z.L. Wu et R.F. Huang) Christenhusz et Byng (2018:146), *A. moschatellina*, *A. omeiensis* and *A. xizangensis* (Christenhusz et al. 2018, POWO 2025).

Knowledge of the diversity of flowering plants on Earth increases annually, as researchers discover and describe an increasing number of species new to science (Christenhusz & Byng 2016). In the Trans-Baikal Territory, we identified a new species of the genus *Adoxa* with unusual features, such as nearly entire leaves, undivided filaments, and reddish fruit. The aim of the study was the description, illustration, and comparative morphological analysis of this new species.

MATERIAL AND METHODS

We analyzed the herbarium specimens of the genus *Adoxa* deposited at MHA, MW, LE, VLA, and VBG (acronyms according to Thiers 2025) (Appendix 1). We consulted various taxonomic and floristic literature, with particular emphasis on key publications (Hara 1981, Wu 1981, Nepomnyashchaya 1984a,b, 1985, 1987, 1988, Yao 1992, Hong & Boufford 2011, Popova 2020). We also viewed photographic images of *Adoxa* plants from different localities within the range available from public online resources such as Plantarium (URL: <http://www.plantarium.ru>) and iNaturalist (iNaturalist contributors 2025). For the comparative study of the morphology of the *Adoxa* species (*A. moschatellina*, *A. orientalis*, and newly founded species), we collected 10 to 20 live specimens per population. We analyzed the qualitative and quantitative characteristics of their underground and above-ground shoots, rosette and stem leaves, inflorescences, and flowers (Table 1). The morphology of the plants was examined under a Stemi 2000C stereomicroscope (Carl Zeiss, Germany) equipped with an AxioCam Icc 3 digital camera and using the AxioVision 4.8.2 software.

RESULTS

During expeditionary research conducted in the Trans-Baikal Territory in June 2025, a new species of the genus *Adoxa* was identified in the vicinity of the village of Ust-Narinzor, in the floodplain of the Kurlych River upstream of the village. An earlier herbarium collection of this species, originating from the floodplain of the Narinzor River in the vicinity of the same village (Chita Region, Sretensky District, floodplain of the Narinzor River north of the village of Ust-Narinzor; 6 July 1977; N.S. Alyanskaya, T.M. Sofeykova, and G.V. Porubinskaya), was discovered by us in the Herbarium of the Main Botanical Garden in Moscow (MHA). Owing to an erroneous identification, this specimen had been filed together with the collections of the genus *Chrysosplenium* L.

The new species of the genus *Adoxa* has a strong similarity in the structure of its underground shoots to *A. moschatellina*, which grows in the same ecotopes, and to *A. orientalis*, which is distributed in Trans-Baikal Territory, but differs from both species in a number of significant features in the morphology of its above-ground shoots (Table 1, Figs 1–4). The new species has a simple, weakly dissected rosette leaf blade (Figs 1–2, 3C, 4A–D) vs. heavily dissected leaf blades in *A. orientalis* (ternate) (Fig. 3D) and *A. moschatellina* (twice ternate) (Fig. 3A–B). The leaf blade of the new species is shallowly 3–5-lobed and, occasionally, ternately parted (more rarely, more deeply incised – also ternately parted). A single instance was noted of the formation of a lateral entire segment borne on a short petiole. The margins of the lobes and segments in the new species are shallowly wavy-lobed or entire. The leaf lobes in *A. orientalis* and *A. moschatellina* are lobed at the apex.

The base of the leaf blade in the new species is cordate, with overlapping margins, descending funnel-shaped onto the petiole (Fig. 4A–B); in juvenile specimens and in cauline leaves of adults, the base of the leaf is slightly notched (Fig. 4D). In *A. orientalis*, the base of the leaf segments is rounded-cuneate or rounded (Fig. 3D), while in *A. moschatellina*, the base of the leaf segments is usually cuneate or narrowly cuneate, varying to rounded.

Stem leaves in the new species are entire (Figs 1–2, 4E) (vs. trifoliate leaves in *A. orientalis* (Fig. 3D) and *A. moschatellina* (Fig. 3A–B)), with their segments having 2–3 lobes at the apex.

The new species is similar to *A. moschatellina* in the shape, number, and arrangement of corolla lobes and in the pedicel length (Fig. 3E–F), but differs by having entire, unsplit stamen filaments, similar to those of *A. orientalis* (Fig. 3F–G). However, the anther lobes in the new species are fused, not separate, unlike those in *A. orientalis*. Like *A. moschatellina*, the new species has pentamerous lateral flowers and a larger corolla with broader lobes compared to those in *A. orientalis*. The number of flowers per inflorescence in the new species and *A. moschatellina* is also smaller than in *A. orientalis*, and the inflorescence appears denser due to shorter pedicels (Table 1).

Taxonomy

The new taxon of the genus *Adoxa* possesses distinct diagnostic characters and warrants recognition as a distinct species. A description and illustrations of the new species from Trans-Baikal Territory, referred to as *A. integriloba*, are provided here.

***Adoxa integriloba* Koldaeva, sp. nov.** (Figs 1–4)

Diagnosis: The new species differs from all known species of the genus *Adoxa* mainly by its entire or entire-lobed leaf blade and, in the case of divided or dissected blade, by the lobes and segments remaining entire.

Holotype: RUSSIA. Trans-Baikal Territory, Sretensky District, environs of the village of Ust-Narinzor, floodplain of the Kurlych River. Floodplain forest, on rich drained soil. 14 VI 2025. M.N. Koldaeva (holotype TK-007170! (Fig. 1).

Paratype: RUSSIA. Chita Region, Sretensky District, floodplain of the Narinzor River (north of the village of

Table 2. Comparison of the main morphological characters in *Adoxa* species.

Character		<i>Adoxa moschatellina</i>	<i>Adoxa orientalis</i>	<i>Adoxa integriloba</i>
Caulis	length, cm	8–16	8–14	9–15
	at flowering	erect, inflorescence above leaves	erect, inflorescence above leaves	erect, inflorescence above leaves
	at fruiting	erect, drooping, or spirally twisted	spirally twisted	erect
Rosette leaves	leaf blade shape	twice ternate	ternate	simple, entire or lobed; less often tripartite or dissected
	leaf blade (leaflet)	broadly ovate, rounded or broadly obovate, 3-partite or 3-dissected, with tops of lobes lobed or serrate-lobed	obovate or broadly obovate, pinnately lobed above middle of leaflet, with upper lobe being the largest, entire or crenate-dentate	broadly ovate or rounded-broadly ovate, shallowly 3–5-lobed, less often 3-partite, occasionally 2–3-dissected
	leaf segment base	wedge-shaped or narrowly wedge-shaped, to rounded	rounded or rounded-wedge-shaped	cordate, with overlapping edges, funnelliform, decurrent onto petiole
	petiole length, cm	3–9	5–8	4–10
	petiolule length, cm	0.6–4.0	0.2–0.8	0.2–0.3 (if present)
Cauline leaves	number	2, opposite	2, opposite	2, opposite
	shape	3-dissected or ternate, with lobes and segments obovate, deeply lobed in upper part	3-dissected; segments narrowly obovate, shallowly 3-lobed at apex	broadly ovate, broadly oval, or slightly reniform
	petiole length, cm	0.5–2.8	0.7–2.1	0.6–2.5
Inflorescence	type	compact headlike cyme	lax headlike cyme	compact headlike cyme
	size (diameter), cm	0.7–0.9	0.55–0.72	0.7–0.75
	number of flowers	5	5–9	5
Flowers	peduncle length, mm	0.3–0.5	0.7–1.17	0.2–0.3
	size (diameter), cm	0.55–0.68	0.3–0.4	0.45–0.55
Flower formula	apical	Ca ₍₂₎ Co ₍₄₎ A ₄ G ₍₄₎	Ca ₍₂₎ Co ₍₄₎ A ₄ G ₍₄₎	Ca ₍₂₎ Co ₍₄₎ A ₄ G ₍₄₎
	lateral	Ca ₍₃₎ Co ₍₅₎ A ₅ G ₍₅₎	Ca ₍₃₎ Co ₍₆₎ A ₆ G ₍₃₎	Ca ₍₃₎ Co ₍₅₎ A ₅ G ₍₅₎
Corolla	shape	rotate	rotate, with lobes gently curved downward	rotate, with lobes directed slightly upward
	lobes	ovate or rounded-ovate, with apex rounded or acute	elliptic, with apex rounded	ovate, with apex acute
Stamens	filaments	split to base, V-shaped, widely diverging	entire	entire
	filament length, mm	0.5–0.7	0.52–0.78	0.44–0.53
	anther lobes	separate, free	separate, free	fused, partially fused, or free

Ust-Narinzor). 6 VII 1977. N.S. Alyanskaya, T.M. Sofeikova, G.V. Porubinskaya (paratype MHA 0382418!).

Description of a new species: Perennial herbaceous, juicy, glabrous, ephemeroïd plant. Underground shoots whitish, long, branching, consisting of thickened, short, 0.4–0.7 cm long and 0.3 cm thick rhizome parts with short internodes and 2–4 fleshy, protruding storage scales alternating with thin, long parts (stolons) with long internodes (up to 5.5 cm long). Basal leaves 1–3; petiole reddish, 4–10 cm long, narrowly alate. Blade 1.4–5 × 1.4–5.4 cm, broadly ovate or rounded-broadly ovate, shallowly 3–5-lobed, less often ternately divided, occasionally ternately dissected, with base cordate, often with overlapping edges, funnelliform, decurrent onto petiole, or sinuate (in juveniles). Folds between lobes cartilaginous. Lobe margins entire, wavy, smoothed, 3(5)-wavy-lobed or 3(5)-smoothed-lobed. Lobe tops rounded, slightly sinuate or slightly acuminate, with small triangular spine. Lobes of trifoliate leaf (if present)

on petiolules 0.2–0.3 cm long. Cauline leaves 2, opposite, slightly above midstem. Petioles 0.6–2.5 × 0.5–1.5 mm, broadened at base. Blade 0.9–2.4 × 1.0–3.5 cm, broadly ovate, broadly oval or slightly reniform, with base rounded or slightly sinuate, margin smoothly 3–5-wavy-lobed or almost entire. Caulis slightly reddish, erect, with apex slightly inclined, 9–12 cm long in flowering, 11–15 cm long in fruiting, 1.5–2.5 cm above the leaves. Inflorescence terminal, capitate cyme, ca. 0.8 cm in diameter, consisting of 5 flowers. Flowers ca. 5 mm in diameter, pedicels short, ca. 1 mm long. Calyx light green, teeth ovoid; corolla yellowish green, rotate, merging into short tube to 1/4–1/3 of its length at base. Corolla lobes ovate, acuminate. Filaments entire, 0.45–0.55 mm long; anthers light yellow, fused or separate. Ovary semi-inferior; styles ca. 0.6 mm long, deflecting to sides; stigmas capitate. Upper flower 2-dimensional, with calyx 2-lobed, corolla 4-lobed, stamens 4, styles (3)4; lateral flowers 5-dimensional, with calyx 3-lobed, corolla 5-lobed, stamens 5, and styles (4)5. Fruit juicy drupe,

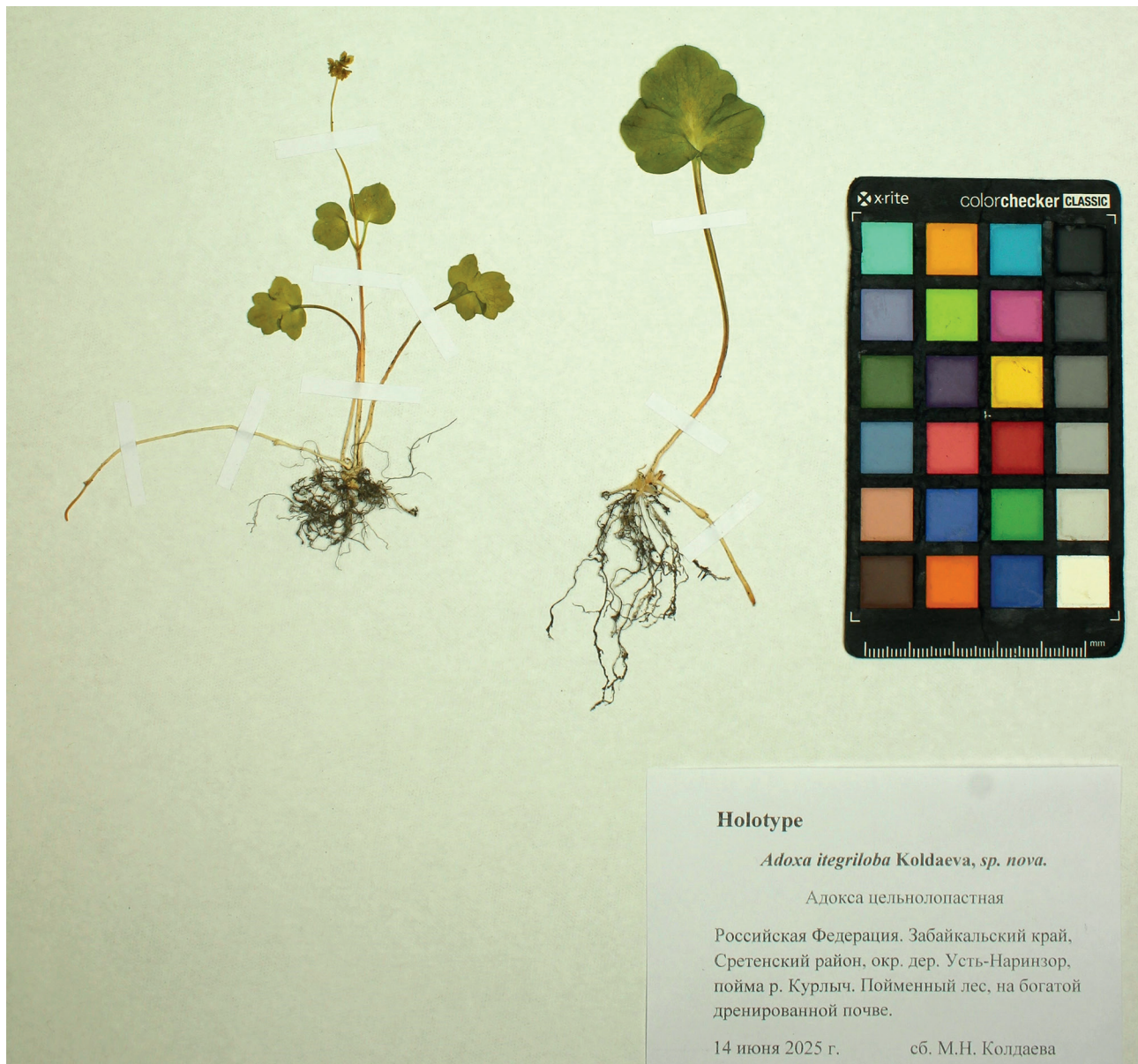


Figure 1 Holotype of *Adoxa integriloba* sp. nov. (TK-007170)

reddish (according to herbarium specimen). Seeds not seen.

Distribution: To date, the new species has been known only from the Kurlych River basin (Sretensky District, Trans-Baikal Territory) (Fig. 4). The absence of collections other than those listed above may indicate its local distribution and possible category as a rare species that needs protection.

Habitat: Unsoiled areas in floodplain forests; on moist, rich, drained soil; at an altitude of 515–530 m above sea level. The species is likely characterized by low competitive ability.

Phenology: This species has a short growing season and is ephemeroid. Its flowering season is in the second or third ten days of June; the fruiting season, in the second or third ten days of July. After fruiting, the above-ground shoots die off, and plants enter a dormant state.

Etymology: The species epithet indicates the main distinguishing feature: entire leaf blades or entire leaf lobes (or segments, if present).

Relationships: The species is closely related to *A. moschatellina*, to which it has a similarity in the structure of the perianth but differs by its unsplit stamen filaments and entire or entire-lobed stem and rosette leaves.

DISCUSSION

It is known that representatives of the genus *Adoxa* exhibit variability in floral structure, manifested as variation in the number of components (Nepomnyashchaya 1984b, Liang 1997). Particularly high variability has been reported for *A. moschatellina*, reaching 20 % in apical flowers and 36.1 % in lateral flowers (Liang 1997). The number of components in apical flowers of *T. omeiensis*, *S. corydalis* and *A. orientalis* is stable, whereas lateral flowers are variable in all of the above-listed species: in *T. omeiensis*, the variation is 5 %; in *A. orientalis* – 4 %; and in *S. corydalis* – 6.6 %. Variation is observed in the number of carpels, stamens, and corolla lobes, both increasing and decreasing, in different combinations. Moreover, the terminal flower in the inflorescence of *A. moschatellina* may have the same number of corolla lobes as the lateral flowers. The number of corolla lobes, as well as carpels and sometimes stamens, in *A. moschatellina* can be 6, which sometimes leads to mis-



Figure 2 Paratype of *Adoxa integriloba* sp. nov. (MHA 0382418)

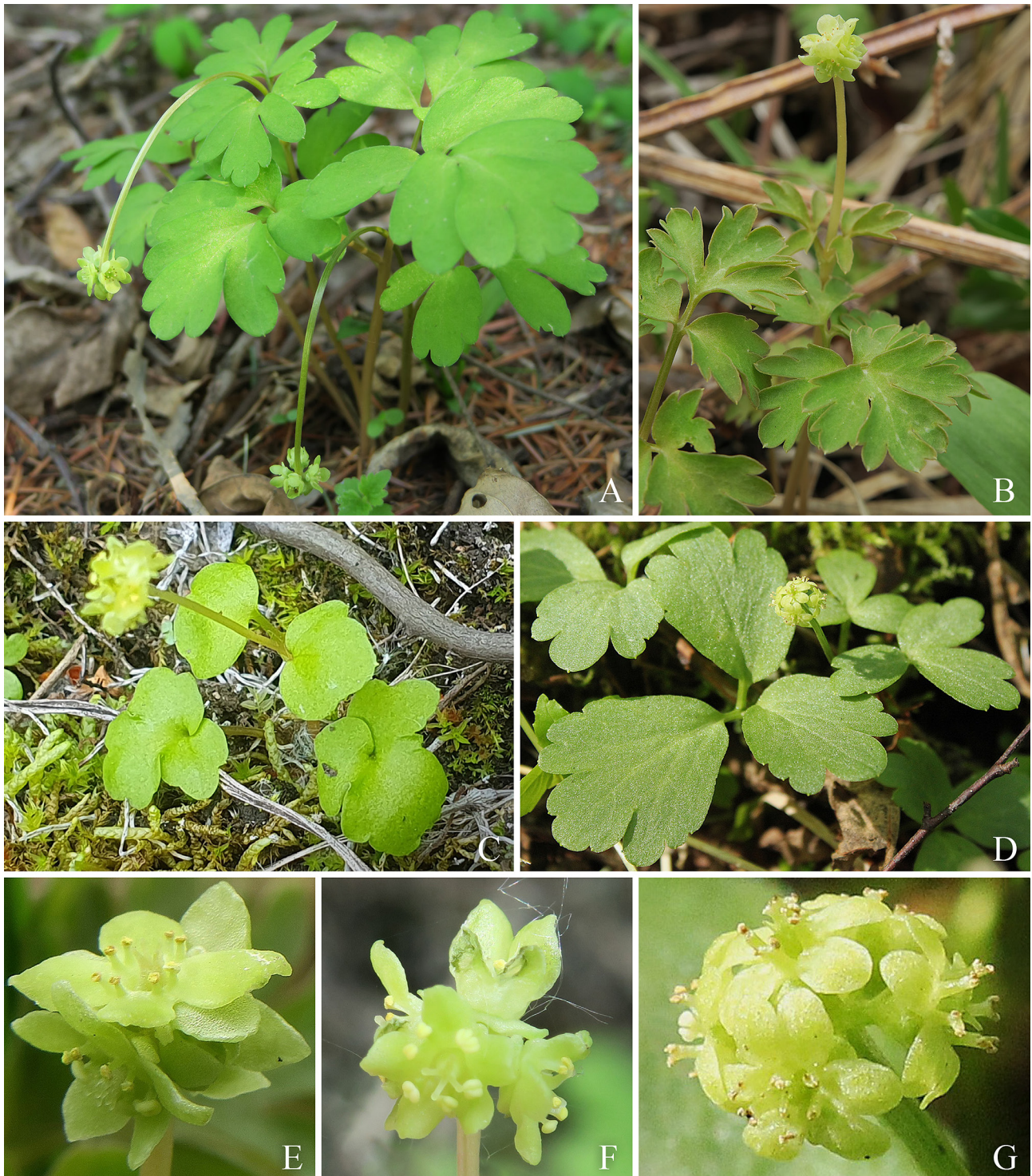


Figure 3 Morphology of *Adoxa* species. A–D – External view: A, B – *A. moschatellina* L., C – *A. integriloba* sp. nov., D – *A. orientalis* Nepomnjasczaja; E–G – Inflorescences: E – *A. moschatellina*, F – *A. integriloba*, G – *A. orientalis*

identification and the assignment of specimens with six-membered corollae to a different species, *A. orientalis*, despite the distinct morphology of the floral and leaf components.

The terminal flower of the new species *Adoxa* exhibits a dimerous calyx, a dimerous corolla composed of four petals fused into a short tube, four stamens, and four carpels ($\text{Ca}_{(2)}\text{Co}_{(4)}\text{A}_4\text{G}_{(4)}$). The lateral flower possesses a 3-merous calyx, a 5-merous corolla, five stamens, and five carpels

($\text{Ca}_{(3)}\text{Co}_{(5)}\text{A}_5\text{G}_{(5)}$). In the new species, we observed only minor variability, which was confined to the lateral flowers. We recorded individual cases of deviation from the basic formula, specifically either a reduction in the number of carpels in the lateral flower by one, or the bifurcation of the filament of one stamen down to its base, with each anther locule positioned separately on its own branch. Under normal conditions, the filament of the new species is entire. According to Popova (2020), the species diversity

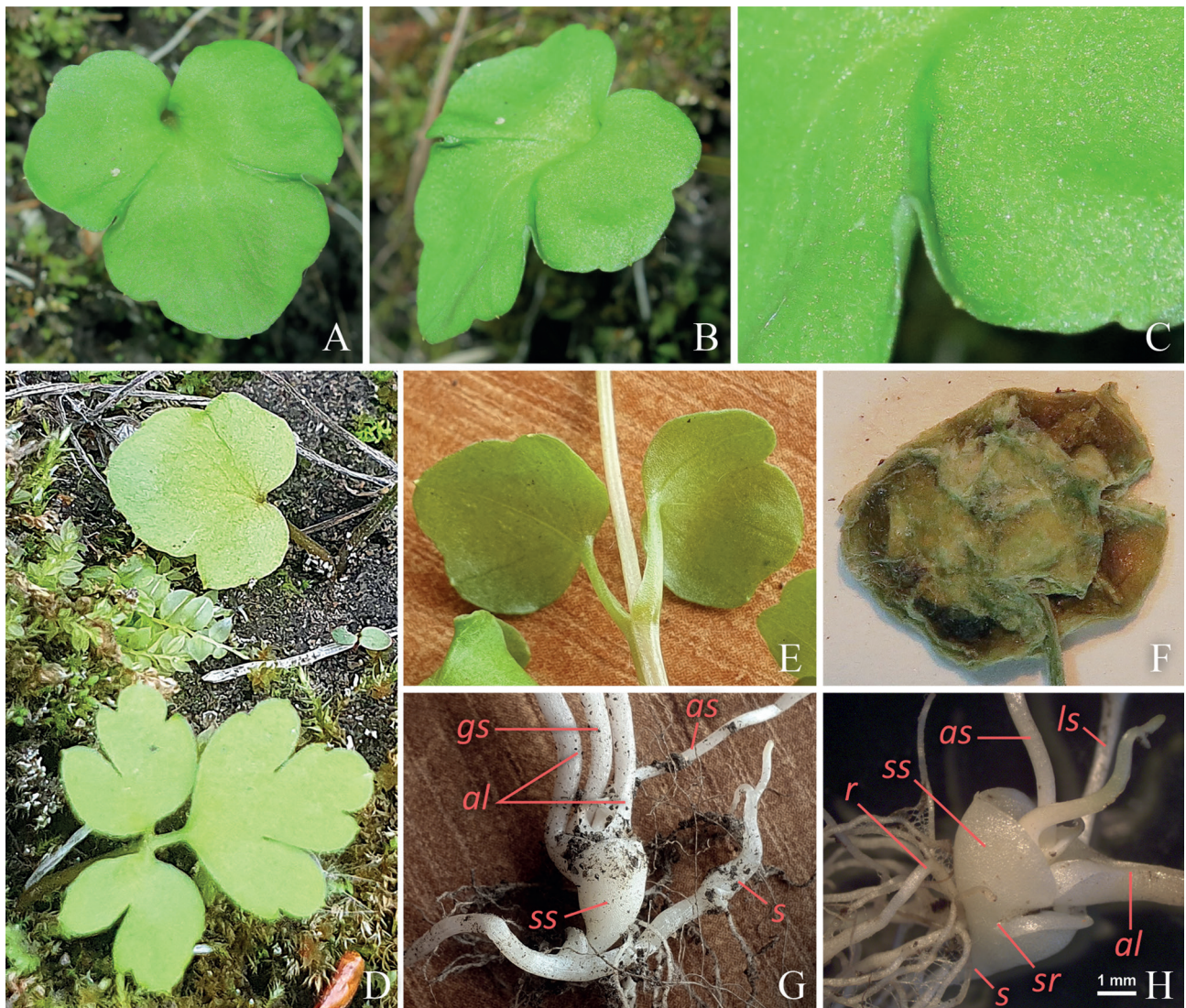


Figure 4 Morphology of *Adoxa integriloba* sp. nov. A, B – rosette leaf of an adult plant; C – leaf fold; D – leaf of a young vegetative plant of *A. integriloba* (upper) and *A. moschatellina* (lower); E – cauline leaves; F – fruit (from herbarium specimen); G, H – underground shoots. Legend: (al) base of petiole of rosette assimilating leaf; (gs) base of stem of generative shoot; (ss) storage scale; (r) abundantly branching root; (sr) short thickened rhizome; (s) underground stolon; (ls) lateral stolon; (as) axial stolon



Figure 5 Distribution of Asian species of the genus *Adoxa*: *A. integriloba* sp. nov. (yellow triangle); *A. orientalis* (pink circle); *A. omeiensis* (red triangle); *A. corydalisfolia* (green circle); *A. xizangensis* (blue square)

within *Adoxa* s.str. is largely associated with the evolutionary reduction of floral elements.

It may be assumed that the new species appeared through hybridization of one of the chromosome races known for *A. moschatellina* (Noguchi & Kawano 1974, Liang 1993a, Inaba et al. 2000), e.g., $2n = 54$, probably growing in this region, as well as in the south of Primorye Territory (Russia) (Inaba et al. 2000), and *A. orientalis*, whose origin is based on polyploidy ($2n = 108$) (Liang 1986, 1993a,b). The new species inherits the corolla shape and some instability in the number of floral components characteristic of *A. moschatellina*, but the entire stamen filaments are a feature probably inherited from *A. orientalis*. The leaf blade shape in the new species (entire or with entire lobes or segments and a smoothed, broadly wavy-lobed margin) is unique and is not found in any other *Adoxa* s.l. species. The

cartilaginous, darker green folds at the junctions of the lobes also appear unusual. This hypothesis, however, needs to be carefully verified.

Based on our hypothesis and taking into account the divergence time of the species in *Adoxa* s.l. (Mao et al. 2005), we may assume a relatively recent origin and phylogenetic youth of *Adoxa integriloba*.

CONCLUSIONS

According to Mao et al. (2005), the highland regions of southwestern China (Qinghai-Tibet Plateau) are the site of divergence of the genus and are likely the primary center of diversity of Adoxaceae species. The montane regions of southern Eastern Siberia can be considered a secondary center of diversity of Adoxaceae species. Here, we identified a new species of the genus *Adoxa*, *A. integriloba*, distinguished by the original structure of its leaf blades, in addition to the previously found *A. moschatellina*, a widespread Holarctic species, and *A. orientalis*, a southern Siberian–Far Eastern (Amur River basin) relict species with a disjunctive range. The collected specimens of the new species will serve as material for further study and clarification of its phylogenetic position among the species of the genus *Adoxa*. The new taxon of the genus *Adoxa* possesses distinct diagnostic characters and warrants recognition as a distinct species. A description and illustrations of the new species from Trans-Baikal Territory, referred to as *A. integriloba*, are provided here.

ACKNOWLEDGEMENTS

I am sincerely grateful to A.Y. Bochkarnikov, the head of the Ust-Narinzor Rural Settlement Administration, for his assistance in organizing the research. I thank the curators and the staff of the consulted herbaria for making specimens available for my study. The detailed study of the morphology of the new and related species was carried out using the equipment of the Center for Microscopy at the Botanical Garden-Institute FEB RAS (Vladivostok). This work was conducted within the framework of the project no. 122040800085-4.

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APPENDIX 1. Specimens of *Adoxa* studied.

***Adoxa integriloba*. RUSSIAN FEDERATION. TRANS-BAIKAL TERRITORY. Sretensky District:** floodplain of the Narinzor River, 6 July 1977, N. S. Alyanskaya, T. M. Sofeikova, G. V. Porubinskaya (MHA 0382418!); environs of Ust-Narinzor Village, floodplain of the Kurlych River, 14 June 2025, M. N. Koldaeva (TK-007170).

***Adoxa orientalis*. RUSSIAN FEDERATION. AMURSKAYA OBLAST. Zeysky Urban Okrug:** Zeya River Basin. Zeya-Pristan. Pikan Meteorological Station, 30 May 1912, A.I. Arkhangel'skaya (LE01043450!); Zeya State Nature Reserve, env. of Cordon "34 km", 53.98923° N, 127.07561° E, 17 June 2023, G.F. Darman (ABG167967!). **Selezmdzhinsky District:** env. of Stoiba Village, 12 August 1984, V.V. Yakubov (VLA, No. 258945!). **Skovorodinsky Municipal Okrug:** valley of Verkhnyaya Alma River, 0.2 km below the mouth of the Berezovyi stream, 53.91304° N, 123.81000° E, alt. 401 m, 27 May 2005, V.V. Shalygin (ABG134134!). **Tyndinsky Urban Okrug:** env. of Tynda (northern outskirts), 7 August 1986, A.E. Kozhennikov (VLA, No. 258993!, 258992!, 258991!). **PRIMORSKY KRAI. Pozharsky Municipal Okrug:** Bikin National Park, near the mouth of the Kilow River, 46.81301° N; 137.26987° E, 03 July 2019, E.A. Marchuk, M. N. Koldaeva, S.V. Nesterova, V.A. Kalinkina (VBG188559!, VBG188558!). **Terneysky Municipal Okrug:** upper reaches of the Samarga River, 1 km below the mouth of the Puhi River, 10 July 1982, I.B. Vyshin, A.E. Vrishch (VLA, No. 258887!). **KHABAROVSKY KRAI. Tuguro-Chumikansky District:** basin of Uda River, on the left bank of the Ugokhan River in its upper reaches, 31 May 1964, Yu.A. Doronina (VLA, No. 258995!).

***Adoxa moschatellina*. RUSSIAN FEDERATION. AMURSKAYA OBLAST. Arkharinsky Municipal Okrug:** env. of Malinovsky Island, left bank of the Bureya River, 49.75205° N, 129.85399° E, alt. 267 m, 17 May 2019, G.F. Darman, V.V. Semenka (ABG177634!); road to Arkhara, in the vicinity of the turnoff to Krasnaya Gorka, 49.40471° N, 129.96374° E, alt. 165 m, 1 June 2003, V.M. Starchenko, G.F. Darman (ABG153957!); Island near Kulustai Village, 49.73632° N, 129.84894° E, alt. 167 m, 24 May 2008, V.M. Starchenko, G.F. Darman (ABG195062!); Domikan Village, snake hill, 27 May 2013, V.M. Starchenko (ABG1537!); Gribovka Village, 15 May 1982, V.F. Goncharova (VLA, No. 258938!); env. of Kundur railway station, 19 May 1986, V.V. Yakubov (VLA, No. 258939!); Khingan State Nature Reserve, 26 km south of Uril railway station, 2 June 1985, E. Barannik (VLA, No. 258940!); Khingan State Nature Reserve, 20 km west of Kundur railway station, along the bank of Gryaznaya River, 21 May 1986, V.V. Yakubov (VLA, No. 258942!, No. 258941!); Khingan State Nature Reserve (8 km northwest of Kundur railway station), 25 June 1984, V.V. Yakubov, A.E. Vrishch (VLA, No. 258943!); Khingan State Nature Reserve (40 km west of Arkhara settlement), 16 June 1984, V.V. Yakubov, A.E. Vrishch (VLA, No. 258944!). **Blagoveshchensky Municipal Okrug:** Outskirts of Mikhailovka settlement, in the direction of Markovo settlement, 50.61355° N, 127.37726° E, alt. 345 m, 6 June 2007, V.M. Starchenko, G.F. Darman (ABG198338!); env. of the Verkhblagoveshchensk Village, 50.27804° N, 127.44148° E, alt. 143 m, 15 July 2008, E.Yu. Pikunov (ABG178793!); env. of the Grodekovo Village, 50.08988° N, 127.56989° E, alt. 213 m, 18 June 2003, V.M. Starchenko, G.F. Darman (ABG153956!); Verkhblagoveshchensk Village, 50.27322° N, 127.45884° E, alt. 214 m, 27 May 2005, G.F. Darman (ABG142323!). **Bureysky Municipal Okrug:** env. of the Malinovka Village, floodplain forest along the Bureya River, 49.75837° N, 129.82970° E, alt. 247 m, 31 May 2006, G.F. Darman, I.V. Kozyr (ABG182773!); env. of the Kulikovka Village, 50.11458° N, 130.10986° E, 29 May 2006, G.F. Darman, I.V. Kozyr (ABG182772!); the valley of the Obdergan River, 50.30385° N, 131.23141° E, 21 June 2006, G.F. Darman (ABG182771!); env. of the Domikan Village, the valley of the Bureya River, Pryamoy Island, 49.70251° N, 129.82124° E, 6 August 2013, V.M. Starchenko (ABG182581!); BPP "Irkun", 49.56216° N, 129.59530° E, alt. 131 m, 3 May 2007, G.F. Darman, M.G. Ivanchikova, I.V. Kozyr (ABG145652!); env. of the Bakhirevo Village, 50.03858° N, 129.99940° E, alt. 245 m, 5 May 2007, G.F. Darman, M.G. Ivanchikova, I.V. Kozyr (ABG145651!, ABG145651!); Paykanchik, River, 50.21226° N, 130.09988° E, alt. 245 m, 5 May 2007, G.F. Darman, M.G. Ivanchikova, I.V. Kozyr (ABG145650!); Irkun, Bureya River bank, 49.95314° N, 129.96448° E, alt. 351 m, 4 July 2004, V.M. Starchenko, G.F. Darman, I.G. Borisova (ABG140965!). **Ivanovsky Municipal Okrug:** env. of the Andreyevka Village, territory of the "Andreevskaya Grove", 50.27579° N, 128.28022° E, alt. 145 m, 1 July 1996, V.M. Starchenko, I.I. Shapoval (ABG196359!); Kharginsky Ridge, Mt. Zvezdnaya, 12 June 2011, E.Yu. Pikunov (ABG127877!); left bank of the Selezmdzha River near the Ekimchan Village, 6 July 1974, S.D. Shlotgauer (KHA06851!). **Konstantinovskiy Municipal District:** env. of Zolotonozhka, 49.83588° N, 128.36177° E, alt. 246 m, 24 June 2003, V.M. Starchenko, G.F. Darman (ABG153955!). **Selezmdzhinsky Municipal District:** Reservoir near the Big Karaurak River, 53.15551° N, 132.75176° E, alt. 257 m, 20 July 2008, V.M. Starchenko (ABG197946!). **Shimanovskiy Municipal Okrug:** Kumarsky Cliff, 50.27453° N, 127.43755° E, 29 July 2005, V.M. Starchenko, G.F. Darman (ABG142324!). **Skovorodinsky Municipal Okrug:** bank of Big Never River, 53.72439° N, 123.85645° E, alt. 359 m, 12 August 2004, V.M. Starchenko, G.F. Darman, I.G. Borisova (ABG140963!). **Tambovskiy Municipal Okrug:** Tambovka River south of Tambovka Village, 31 May 1981, V.A. Nedoluzhko, V.N. Starodubtsev (VBG1158448!). **Zeysky Municipal Okrug:** Mouth of the Pikan River, a left tributary of the Zeya River, 53.67753° N, 127.46020° E, alt. 359 m, 6 June 2002, V.V. Shalygin (ABG140966!); Bureya River, road along the Thalaya River, 49.47209° N, 130.15466° E, alt. 351 m, 1 July 2004, V.M. Starchenko, G.F. Darman, I.G. Borisova (ABG140964!); Zeya Nature Reserve, env. of the Teply cordon, 54.03526° N, 127.30944° E, alt. 367 m, 8 June 2011, T.N. Veklich (ABG132470!, ABG1539!, ABG1538!); island opposite the of Novoysoke Village, 17 June 2015, T.N. Veklich (ABG1536!); eastern part of the Tukuringa Ridge, northern shore of Teply Bay, 11 September 1977, L.A. Gubanov, V.S. Novikov (MW0136087!). **CHUKOTSKY AUTONOMOUS OKRUG. Anadyrsky district:** lower course of the Enmyvaam River, mouth of the Shustrai River, 7 July 1980, A.A. Korobkov, N.A. Sekretareva (VLA, No. 258960!); mouth of the Mecherev River, 6 July 1980, A. Polezhaev, A. Berketenko (VLA, No. 258962!, No. 258958!); mouth of the Eropol River, 1 August 1980, A. Berketenko (VLA, No. 258961!). **Bilibinsky district:** Anyui Highland, Leluveem River basin, upper course of the Left Yarakvaam River, 18 July 1965, B. Yurtsev (VLA, No. 258954!); Pogynedno Village, 9 August 1975, T.M. Koroleva, V.V. Petrovsky (VLA, No. 258953!); left bank of Bol. Anyuy River, Baimki River valley in the middle course, 9 July 1966, V.K. Bushanskaya, L.I. Maksimenko, B.A. Yurtsev (VLA, No. 258956!); env. of Bilibino Village, 29 June 1974, T.M. Koroleva (VLA, No. 258955!); ibid., 16 June 1988, E.V. Voronkova (VLA, No. 258957!). **Chaunsky district:** mouth of the Rauchua River, 6 km from the village, 1 July 1975, T.M. Koroleva, V.V. Petrovsky (VLA, No. 258959!). **KAMCHATSKY KRAI. Penzhinsky district:** env. of Manila Village, 15 June 1975, S. Kharkevich, T. Buch (VLA, No. 258963!, No. 258964!). **KHABAROVSKY KRAI. Ayano-Maisky district:** SW Mt. Palatka, spurs of Dzhangdzhur Range, 14 July 1978, T. Buch (VBG1158447!, ABG127924!); Southwestern spurs of the Dzhangdzhur ridge, Mt. Palatka (1222), 14 July 1978, G.F. Yashenkova (VBG1158446!, VBG1294314!); env. of Nelkan Village, right bank of the Maya River, 50 km above the Nelkan Village, 29 June 1978, S. Kharkevich, G. Yashenkova (VLA, No. 258932!); env. of Totta Village, Chelasin River, 6 June 1979, S. Kharkevich, T. Buch (VLA, No. 258934!, No. 258933!); southwestern shoulder of the Topko Mt. Range, 29 June 1979, S. Kharkevich, T. Buch (VLA, No. 258935!); Chelasin River, 1 km below the Totta Village, 22 June 1968, Yu.I. Manko, V.P. Voroshilov (VLA, No. 258931!); Ket-Kap Ridge, upper course of Jarmarka River, 29 June 1989, I.B. Vyshin, V.Yu. Barkalov, T.A. Bezdeleva (VLA, No. 258937!, No. 258936!); Tukchi River, mouth of Namgandwa River, 19 July 1970, Yu.I. Manko, V.P. Voroshilov (VLA, No. 258928!). **Bikinsky district:** Strelnikov Ridge, sources of the Right Samur River, 10 June 1999, I.V. Shibnera (VLA, No. 288437!). **Komsomolsky district:** Komsomolsky reserve, Pivan, floodplain of the Pionersky Spring, 25 May 1966, S.D. Shlotgauer (VLA, No. 258927!); Cordon Village, 10 June 1959, s.coll. (VLA, No. 258926!); Komsomolsky Reserve, lower course of the Gorin River, floodplain of Siutaru River, 10 June 1980, V. Van (VLA, No. 258925!); env. of Pivan Village, 19 May 1966, S. D. Shlotgauer (VLA, No. 258892!); Mt. Golaya (1737 m), 8 August 1983, I. Vyshin (VLA, No. 258891!, No. 258890!). **Kur-Urminsky district:** Yarp River basin, 50.28012° N, 134.70946° E, alt. 551 m, 10 August 2016, P.V. Krestov (VBG1161!). **Named Lazo district:** upper course of the Choir River, 22 July 1987, I.B. Vyshin, V.Yu. Barkalov (VLA, No. 258897!); river valley Chukhen - Right Ima - Sikhi - Kafeng, 18 August 1987, I.B. Vyshin, V.Yu. Barkalov (VLA, No. 258898!); Chukhen River valley (Khor River bas.) above the Tasi channel, 21 September 1987, I.B. Vyshin, V.Yu. Barkalov (VLA, No. 258900!, No. 258899!); lower course of the Khor River, 1 km below the mouth of the Chukhen River, 12 August 1987, I.B. Vyshin, V.Yu. Barkalov (VLA, No. 258901!, No. 258896!). **Nanaisky district:** peak "1790" on the watershed of the Chui - Anyui rivers, 10-17 July 1983,

S.S. Kharkevich, T.G. Butch, A.E. Vrishch, I.B. Vyshin (VLA, No. 258895!, No. 258894!, No. 258893!). **Okhotsky district:** right tributary of the Luktur River (south of the Urak River), 20 August 1973, *S.S. Kharkevich, T.G. Butch* (VLA, No. 258930!, No. 258929!). **Solnechny district:** 8 km southwest at Mountain Village, Miaochn Ridge, upper course of Left Silinka River, 30 July 2006, *V. Yu. Barkalov* (VBGI24339!). **Sovetsko-Gavansky district:** Tumnin River basin, Bolshoy Yan Ridge, Mt. Komandnaya, 25-31 August 1983, *I. Vyshin, A. Vrishch* (VLA, No. 258888!); Mt. Yako, on the watershed of the Anyui - Koppri rivers, 14-20 August 1983, *I. Vyshin, A. Vrishch* (VLA, No. 258889!). **Tuguro-Chumikansky district:** Taikan River, 12 August 1978, *V.P. Verkhobol* (VBGI158445!); Tugur River valley, 24 July 1969, *Smetova* (VLA, No. 258923!); Tyl River, 20 km from the mouth, 26 June 1961, *s.coll.* (MW0136086!). **Verkhnebureinsky district:** Badzhalsky Ridge, Yarp River valley 13 km below the confluence of the Left and Right Yarp River, 10 August 2016, *V.Yu. Barkalov* (VBGI158444!); 45 km east of the Sofiysk Village, 6 July 1978, *A.A. Nechaev* (VLA, No. 258924!). **MAGADANSKAYA OBLAST. Olsky Municipal Okrug:** Middle reaches of the Chelomdzha River, Chelomdzha station, 26 June 1986, *S.S. Romanovsky* (VBGI158449!); Ola settlement, 11 June 1976, *A.P. Khokhryakov* (VLA, No. 258949!); middle reaches of the Lev. Yana River, at the confluence of the Zverinogo Stream, 11 July 1982, *N.S. Pavlova* (VLA, No. 258950!); Yamskoye Forestry of the Magadan Nature Reserve, lower reaches of the Yama River 1 km upstream from the mouth of the Floskachan Stream, 1 August 1990, *V.V. Yakubov* (VLA, No. 258948!). **Srednekansky Municipal Okrug:** settlement Oroek, 24 June 1982, *O. Khokhryakova* (VLA, No. 258946!); Seymchanskoye Forestry of the Magadan Nature Reserve, Upper Cordon, 17 August 1990, *S. Kharkevich, T. Buch* (VLA, No. 258947!). **Tenkinsky Municipal Okrug:** 395 km of the Tenkinskaya Highway, Arga-Yuryakh River Valley, 21 August 1993, *N. Probatova, V. Seledets* (VLA, No. 258952!, No. 258951!). **PRIMORSKY KRAI. Anuchinsky Municipal Okrug:** Partizan Village, Sinanchinsky spring, 10 June 1971, *O. Zhurba, n. 144* (MW0136084!). **Artemovskiy Urban Okrug:** Muravyov-Amursky Peninsula, Muravynaya Bay, env. of Lake Cherepashye, 10 May 1999, *V.P. Verkhobol* (VBGI158402!, VBGI158395!). **Chuguevskiy Municipal Okrug:** Chuguevskaya scientific station, 28 August 1974, *T. Bezdeleva* (VLA, No. 258903!, No. 258902!); Mt. Sestra, 21 September 1983, *I. Vyshin* (VLA, No. 258856!). **Dalnogorsky Urban Okrug:** Sikhote-Alin Nature Reserve, Skalny cordon, Nevidimka River, 16 May 1998, *A.V. Belikov, A.V. Galanin* (VBGI158441!); env. of the Dalnegorsk, 24 May 1984, *Gular'yants* (VLA, No. 258858!). **Kavalersky Municipal Okrug:** Lipovy Spring Valley, 9 June 1974, *Komarova* (VLA, No. 258918!); env. of Kavalero Village, Dersu limestone mountain, 25 May 1978, *P.V. Seledets, N.S. Probatova* (VLA, No. 258916!). **Khankaisky Municipal Okrug:** Kamen-Rybolov Village, 22 May 1885, *N. Palchensky, 32* (MW0136079-1!). **Khasansky Municipal Okrug:** Furugelma Island, North Bay, 42.471033° N, 130.925683° E, alt. 18 m, 24 May 2023, *M.N. Koldaeva* (VBGI!); env. of the Mramorny Village, Mramorny Cape, 24 May 2001, *V.P. Verkhobol* (VBGI158429!); Posyet Bay, Krabbe Peninsula, coast of Novgorod Bay, 25 May 1998, *V.P. Verkhobol* (VBGI158428!); Kedrovaya Pad Nature Reserve, Kedrovaya River valley, below the base, 7 May 1977, *V.M. Uruson, V.A. Nedoluzhko* (VBGI158426!, VBGI158412!); Leopard's Land National Park, upper reaches of the Artillery Stream, 43.19717°N, 131.34577°E, alt. 175 m, 8 June 2017, *E.A. Pimenova, M.N. Koldaeva, V.A. Kalinkina, V.P. Verkhobol, E.A. Bisikalova* (VBGI35358!); *ibid.*, behind Barabash Village, 43.20215°N, 131.46792°E, alt. 52 m, 29 April 2016, *E.A. Pimenova, M.N. Koldaeva, S.V. Nesterova, V.A. Kalinkina, E.A. Petrunenko* (VBGI2227!); Ovchinnikovo Village, Barabashevka River valley, right shore, Kamenny Spring, 43.19962°N, 131.45774°E, alt. 56 m, 29 April 2016, *E.A. Pimenova, M.N. Koldaeva, S.V. Nesterova, V.A. Kalinkina, E.A. Petrunenko* (VBGI2226!); Kedrovaya Pad Nature Reserve, 11 May 1963, *T.I. Nechaeva* (VLA, No. 258866!); *ibid.*, the floodplain of the Kedrovka River, 20 May 1960, *P.G. Gorovoy* (VLA, No. 258917!); *ibid.*, near the Kedrovaya, 1 June 1963, *T.I. Nechaeva* (VLA, No. 258867!); *ibid.*, not far from Kedrovaya River for the 1st Gold Spring, 11 May 1963, *T.I. Nechaeva* (VLA, No. 258868!); *ibid.*, Kedrovaya River valley, middle course, 29 April 1977, *Zhukova* (VLA, No. 258885!; No. 258884!); Marine reserve in Peter the Great Bay, Durnovo Island, 26 April 1979, *L.M. Borzova, G.E. Kurentsona* (VLA, No. 258870!); *ibid.*, Gorshkova Bay, 18 May 1980, *Korkishko* (VLA, No. 258847!); *ibid.*, De-Livrona Island, 26 April 1979, *L.M. Borzova, G.E. Kurentsona* (VLA, No. 258863!); Telyakovskogo Bay, 17 May 1979, *T. Bezdeleva* (VLA, No. 258880!; No. 258879!); Popova Island, env. of Stark Strait, 8 May 1978, *P.V. Seledets, N.S. Probatova* (VLA, No. 258874!). **Khorolsky Municipal Okrug:** env. of the Novo-Devitsa Village, 10 August 1983, *V.A. Nedoluzhko* (VLA, No. 258857!). **Lazovskiy Municipal Okrug:** Kievka Village, 11 May 1961, *O. Forsb* (VBGI171624!); Lazovsky Nature Reserve, Koreyskaya Pad', 12 May 1983, *A.A. Taran* (VBGI171622!, VLA, No. 258860!; No. 258853!; No. 258852!); Petrov Island, 27 May 1982, *A.A. Taran* (VBGI171621!, VLA, No. 258849!); Uglovoy Spring Valley, 26 September 1998, *A.A. Taran* (VBGI171620!); Sudzukhinsky State Nature Reserve, cape Tumanny, 16 July 1944, *P. Zhudova, Pokrovskaya* (VLA); *ibid.*, Se-Chingou, 18 May 1965, *Valova* (VLA, No. 258864!); upper reaches of the Mal. Ifam River, 9 September 1944, *P. Zhudova, Pokrovskaya* (MW0136083!); northeastern slope of Tumannaya Hill, 16 May 1945, *P. Zhudova* (MW0136082!); Berezovy Spring, 10 km upstream of the Berezovy Village, 13 July 1946, *P. Zhudova, K. Kurkin* (MW0136081!). **Mikhailovskiy Municipal Okrug:** Pavlovsky Open Pit, 25 May 1979, *Ya. Lelikon, V. Nedoluzhko* (VLA, No. 258875!). **Nadezhdinsky Municipal Okrug:** Borisovskoye Plateau, upper reaches of the Nezhinka River, above the mouth, Razdolnensky Creek, 20 May 2014, *V.Yu. Barkalov, P.V. Kreston, M.N. Koldayeva, E.A. Pimenova, E.A. Petrunenko* (VBGI158424!, VBGI158423!); near the Baranovsky railway siding, basalt volcano on the right bank of the Razdolnaya River, 2 May 1973, *S.S. Kharkevich* (VLA, No. 258912!, No. 258911!); upper reaches of the Shufan, 19 May 1965, *Probatova, Kurentsona* (VLA, No. 258871!); the Shufan River valley near the Borisovka Village, 20 May 1965, *N.S. Probatova* (VLA, No. 258865!). **Nakhodkinsky Urban Okrug:** Nakhodka, env. of Avangard Village, 3 May 1989, *S. Kharkevich, T. Buch* (VLA, No. 258854!). **Olginsky Municipal Okrug:** "Call of the Tiger" national park, Milogradovka River, "Botanical Garden" section, 19 June 2012, *M.N. Koldaeva, V.A. Kalinkina, N.A. Tonkova, V.D. Nebaykin* (VBGI158438!, VBGI158437!, VBGI158436!). **Partizansky Urban Okrug:** Mt. Chitnza, 3 May 2008, *E.N. Roenko* (VBGI158433!, VBGI158434!); Mt. Olkhovaya, 43.30539°N, 133.66589°E, alt. 524 m, 2 July 2022, *S.V. Nesterova* (VBGI146054!, VBGI146053!). **Pogranichny Municipal Okrug:** 30 km north of the Rubinovka Village, 14 June 2006, *A.V. Galanin* (VBGI158425!). **Pozharsky Municipal Okrug:** Bikin National Park, Khomyakova tract, Khomyakova Creek, 46.63903° N, 137.09607° E, alt. 424 m, 29 June 2019, *E.A. Marchuk, M.N. Koldaeva, S.V. Nesterova, V.A. Kalinkina* (VBGI188622!); *ibid.*, Ulma base, island opposite the mouth of the Amba River, 46.69211° N, 135.70561° E, alt. 181 m, 24 June 2019, *E.A. Marchuk, M.N. Koldaeva, S.V. Nesterova, V.A. Kalinkina* (VBGI188617!, VBGI188616!); *ibid.*, cedar-broadleaf moist forest, 46.69537° N, 135.76976° E, alt. 295 m, 23 June 2019, *E.A. Marchuk, M.N. Koldaeva, S.V. Nesterova, V.A. Kalinkina* (VBGI188555!); *ibid.*, Bogoladza Ridge, upper reaches of Udachny Creek, 46.42184° N, 136.51419° E, alt. 970 m, 23 July 2021, *E.A. Marchuk, M.N. Koldaeva, V.A. Kalinkina* (VBGI123427!); Sikhote-Alin Ridge, Mt. Anik, upper reaches of Samsonov Creek, 47.25036° N, 137.05128° E, alt. 1401 m, 12 August 2022, *E.A. Marchuk, M.N. Koldaeva, V.A. Kalinkina* (VBGI145722!); *ibid.*, near the mouth of the Omorochka River, E. Kabanov's winter hut, 46.675874° N, 136.26195° E, alt. 264 m, 23 May 2022, *E.A. Marchuk, M.N. Koldaeva, V.A. Kalinkina* (VBGI135367!, VBGI135359!); Verkhne-Perevalskaya Sopka, 20 May 1982, *I.V. Shibaeva* (VBGI158435!); Bikin River basin, watershed of the Klyuchevaya – Plotnikova rivers, 4 July 1981, *I.B. Vyshin* (VLA, No. 301063!); Lauhe tract, 20 May 1978, *I.B. Vyshin* (VLA, No. 258873!). **Shkotovskiy Municipal Okrug:** Novonezhino Village, 9 May 1971, *V.P. Verkhobol* (VBGI158432!); Upper course of the Steklyanukha River, 30 May 1973, *V.P. Verkhobol* (VBGI158431!); env. of the Bolshekamensk Village, 29 April 1976, *O.N. Zhdanov* (VBGI158430!); upper course of the Artyomovka River, on the rocks, 28 May 2013, *L.A. Fedina* (VLA, 287894!); Ussuriysky Natural Reserve, Valley of Petrovsky Stream near cordon "Anikyna Pad", N 43°38'59", E 132°29'34", alt. 220 m, 13 May 2004, *A.E. Kozhennikov, Z.V. Kozhennikova, V.Yu. Barkalov* (VLA, No. 296547!); *ibid.*, Anikina Pad River valley, 10 May 1975, *T. Bezdeleva* (VLA, No. 258881!); Anisimovka Railway Station, shore of Smolny Spring, 8 May 1975, *Kozhennikov, Gorshkov* (VLA, No. 258850!); Suchansko-Daubikhinskoe plateau, 23 May 1970, *Tumanova* (VLA, No. 258861!). **Spassky Municipal Okrug:** Khankaysky State Nature Reserve, Rechnoy section, Vostochny cordon, 31 May 1993, *V.Yu. Barkalov* (VLA, No. 293444!, No. 293445!); *ibid.*, 26 April 1995, *V.Yu. Barkalov* (VLA, No. 292642!); *ibid.*, Zhuravliny section, 26 May 1993, *V.Yu. Barkalov* (VLA, No. 289093!, No. 289094!). **Terneysky Municipal Okrug:** Sikhote-Alin Nature Reserve, vicinity of Blagodatnoye cordon, 1 May 1998, *A.V. Galanin* (VBGI158440!); *ibid.*, Skalny cordon, Dzhygotovka River valley, 7 May 1998, *A.V. Galanin, A.V. Belikov* (VBGI158439!); the middle reaches of the Samarga River, the floodplain between the mouths of the Issimi and Dagda rivers, 30 May 1980, *I.B. Vyshin* (VLA, No. 258913!, No. 258905!); env. of the Peretychikha Village, the southern slope 5° opposite the village, 25 May 1980, *I.B. Vyshin* (VLA, No. 258915!, No. 258914!); Edinka River basin, the upper reaches of the Belochka Stream, the left tributary of the Biya Stream, 10 June 1980, *I.B. Vyshin* (VLA, No. 258919!); upper reaches of the Samarga River, the upper reaches of its left tributary, the Dagda River, 16 July 1980, *I.B. Vyshin, V.D. Nebaykin* (VLA, No. 258920!); mouth of the Edinka River, 150 m from the seashore, 28 May 1980, *I.B. Vyshin* (VLA, No. 258921!, No. 258922!); Sikhote-Alin Nature Reserve, Mt. Glukhomanka, 8 August 1984, *S.S. Kharkevich, T.G. Buch, I. Vyshin* (VLA, No. 258855!); Edinka River basin, Yaponskiy Spring, 20 km west of Peretychikha Village, 1 June 1979, *V.A. Nedoluzhko* (VLA, No. 258859!); watershed of the Paktu – Kadanau Rivers, Plateau Mount, 22 July 1982, *I.B. Vyshin, A.E. Vrishch* (VLA, No. 258886!); upper reaches of the Samarga River, 1 km below the mouth of the Puhi River, floodplain, 10 July 1982, *I.B. Vyshin, A.E. Vrishch* (VLA, No. 258878!). Sikhote-Alin Nature Reserve, Venera cordon, 23 June 2000, *A.V. Galanin, A.V. Belikov* (VBGI158443!). **Ussuriysky Urban Okrug:** Monakino Village, Leopard's Land National Park, Kamenisty stream, 43.58000°N, 131.35597°E, alt. 445 m, 8 June 2016, *E.A. Pimenova, V.Yu. Barkalov, M.N. Koldaeva, S.V. Nesterova, V.A. Kalinkina* (VBGI2230!); *ibid.*, 43.57740°N, 131.35419°E, alt. 470 m, 7 June 2016, *E.A. Pimenova, V.Yu. Barkalov, M.N. Koldaeva, S.V. Nesterova, V.A. Kalinkina* (VBGI2229!, VBGI2228!);

env. of Nikolsk-Ussuriysk, Krasnoyarskaya Sopka, 7 May 1919, *E. Alisova*, *I. Shishkin*, 4949 (VLA, No. 258872!); env. of the Kaymanovka Village, 13 May 1999, *T.A. Bezdeleva* (VBGI158419!; VBGI158413!); *ibid.*, 13 May 1999, *T.A. Bezdeleva*, *A.B. Bezdelev* (VBGI158415!; VBGI158414!); *ibid.*, 16 May 1980, *N. Potapova* (MW0136088!; MW0136089!); Ussuriysky Nature Reserve, Komarovka River valley, 19 May 1974, *T. Bezdeleva* (VLA, No. 258908!); *ibid.*, about 50 m from the Kamenka River, 16 May 1974, *T. Bezdeleva* (VLA, No. 258909!); *ibid.*, “Mironov Klyuch”, 14 May 1975, *V.N. Starodubtsev*, *N.N. Gurzenkov* (VLA, No. 258910!); Ussuriysky Nature Reserve, 20 May 1991, *T.A. Bezdeleva* (VBGI158417!); env. of the Ussuriysk, 27 April 1975, *V.A. Nedoluzhko* (VBGI158411!); Ussuri forestry, near the road to the Rakovka Village, 4 May 1977, *V.A. Nedoluzhko* (VBGI158410!); Ussuri forestry, 19 May 1979, *V.A. Nedoluzhko* (VBGI158409!); Suputinsky Reserve, 15 May 1973, *T. Bezdeleva* (VLA, No. 258906!); *ibid.*, 13 May 1973, *T. Bezdeleva* (VLA, No. 258907!); *ibid.*, right bank of the Suputinka River, 0.5 km above the base of the reserve, 29 June 1972, *I.B. Kosharovskaya* (MW0136085!); Suifunskaya Sopka, valley 95 ver., 19 May 1924, *E. Alisova*, *M. Ivanova* (VLA, No. 258851!). **Vladivostoksky Urban Okrug**: Muravyev-Amursky Peninsula, Malaya Pionerskaya River valley, 43.201767° N, 132.022407° E, 30 May 2025, *M.N. Koldaeva* (VBGI!); *ibid.*, territory of the Botanical Garden-Institute of the FEB RAS, 20 May 2026, *M.N. Koldaeva* (VBGI!); env. of Akademgorodok, 2 June 2000, *T.A. Bezdeleva* (VBGI158422!); Botanical Garden, 6 May 2002, *T.A. Bezdeleva* (VBGI158421!); *ibid.*, 9 June 2012, *T.A. Bezdeleva* (VBGI158420!); *ibid.*, 1 August 1995, *T.A. Bezdeleva* (VBGI158418!); *ibid.*, 27 May 2003, *T.A. Bezdeleva* (VBGI158416!); Rikorda Island, southern part, vicinity of the height “66.1 m”, undated, *V.A. Nedoluzhko* (VBGI158408!); env. of the Botanical Garden, 15 May 1979, *O.V. Khrapko* (VBGI158407!); Suburb Vladivostok, vicinity of Academic town, 18 May 1986, *T. Buch*, *S. Kharkevich* (VBGI158406!; ABGI27923!); biological station, 1 June 1966, *V.P. Verkholat* (VBGI158405!); env. of the Vladivostok City, “26 km”, 25 May 1965, *V.P. Verkholat* (VBGI158404!); forest area of the Botanical Garden, 1 May–31 May 1983, *V.A. Nedoluzhko* (VBGI158403!); Akademgorodok, 30 April 1998, *V.P. Verkholat* (VBGI158401!); Bogataya River basin, 14 May 1998, *V.P. Verkholat* (VBGI158400!); Bolshaya Sedanka River basin, 18 September 1992, *V.P. Verkholat* (VBGI158399!); Vtoraya Rechka River basin, 1 May 1998, *V.P. Verkholat* (VBGI158398!); Lyanchikha River valley, 17 May 1997, *V.P. Verkholat* (VBGI158397!); Vtoraya Rechka River basin, 9 May 1999, *V.P. Verkholat* (VBGI158396!); Botanical Garden of the Far Eastern Scientific Center of the USSR Academy of Sciences, 1 January 1983 – 31 December 1983, *V.A. Nedoluzhko* (VBGI158394!); Russky Island, northwestern part, Elena Island, 22 July 1999, *V.A. Nedoluzhko*, *N.I. Denisov* (VBGI158393!); Malaya Sedanka River valley, 20 May 1993, *V.P. Verkholat* (VBGI!); Chernaya Rechka River basin, 18 May 1997, *V.P. Verkholat* (VBGI158391!); BSI FEB RAS, forest area, northern slope, 15 May 2021, *S.V. Nesterova* (VBGI143811!); Sedankinskoye Reservoir, 24 May 2011, *A.B. Bezdelev* (VBGI23405!); Peschany Cape, 17 May 1964, *Stepanova* (VLA, No. 258869!); Okeanskaya station, Botanical Garden, 21 May 1971, *D.P. Vorobyov*, *T.I. Nechaeva* (VLA, No. 258848!); *ibid.*, 6 May 1970, *L. Slizik* (VLA, No. 258862!); cape Peschany, 25 June 1974, *S.S. Kharkevich* (VLA, No. 258877!; No. 258876!); Second Rechka valley, 18 May 1975, *N. Probatova*, *V. Seledets* (VLA, No. 258883!; No. 258882!); northern slope of the Bogataya Griva ridge, 29 June 1931, *s.coll.* (MW0136080!). **REPUBLIC OF BURYATIA. Dzhidinsky district**: middle course of the Verkhniy Khandagayta River, 2 km upstream of the mouth of the Zun-Dzhidata River, 23 July 2009, *L. Abramova*, *P. Volkova* (MW0136100!). **SAKHA REPUBLIC (YAKUTIA). Neryunginsky District**: Left bank of the Chulman River, 56.76128°N, 124.75002°E, alt. 456 m, 4 July 2006, *T.N. Bliznyuk*, *I.V. Kozyr* (ABGI 85151!). **Tomponsky District**: Verkhoyansk Mountains, upper course of the Seyule River (affluent of Tompo River), 4 July 1956, *V.I. Ivanova*, 53/5 (MW0136095!). **Ust-Yansky District**: Kular Village on the Yana River, 4 August 1971, *V.R. Filin* (MW0136094!). **SAKHALINSKAYA OBLAST. Dolinsky district**: Takae River, 3 km to the south from Dolinsk, 5 June 1949, *A. Tolmachev* (VLA, No. 258975!). **Makarovsky district**: along the right bank of the Makarov River, 1 km above the city of Makarov, 1 August 1986, *V.A. Nedoluzhko*, *V.N. Starodubtsev* (VBGI158455!). **Nevelsky district**: of the outskirts of the city of Nevelsk, 20 July 1986, *V. Starodubtsev*, *V. Nedoluzhko* (VBGI158454!); Moneron Island, 1 May 1973 – 31 May 1973, *V.A. Nechaev* (VBGI158453!); env. of the Pereputye Village, 28 May 1949, *A. Tolmachev* (VLA, No. 258974!); *ibid.*, 28 May 1949, *S. Kravchenko* (VLA, No. 258974!). **Smirnykhovskiy district**: Nabilsky Ridge, Mt. Balagan (1471.9 m), 25 July 1988, *I.B. Vyshin*, *V.Yu. Barkalov* (VLA, No. 258989!; No. 258988!); Nabilsky Ridge, mountain array of Mt. Vodorazdelnaya (1428.7 m) – Mt. Nevelskogo (1397.8 m), 17 July 1988, *I.B. Vyshin*, *V.Yu. Barkalov* (VLA, No. 258987!). **South Kuril Municipal District**: Kunashir Island, Cape Alyokhina, 11 August 1987, *N. Probatova*, *V. Seledets*, *E. Malakha* (VLA, No. 258965!); *ibid.*, Filatovka River valley, 10 August 1983, *V.Yu. Barkalov* (VLA, No. 258967!); *ibid.*, 3 km north of Alyokhino, 31 May 1979, *L.M. Alekseeva*, *N.N. Kornienko*, 6544 (VLA, No. 258968!); *ibid.*, Chetverikov Cape, near Sernovodsk, 7 August 1987, *N. Probatova*, *V. Seledets* (VLA, No. 258969!); *ibid.*, env. of the Kamyshevka River, north of Rogachev Cape, 20 June 1978, *L.M. Alekseeva*, 6247 (VLA, No. 258970!); Shikotan Island, 13 August 1968, *Vasilien*, *Rosenberg* (VLA, No. 258966!). **Yuzhno-Sakhalinsky Urban Okrug**: Natural monument “Yuzhno-Sakhalinsky mud volcano”, 47.07952°N, 142.58000°E, alt. 258 m, 23 August 2014, *A. Taran* (SAKH37433!); env. of the Novo-Alexandrovsky Village, 25 June 1952, *Stepanov* (VLA, No. 258972!); Susuya River basin, 47°2'N, 14 May 1948, *A. Tolmachev* (VLA, No. 258923!). **TRANS-BAIKAL TERRITORY. Baleytsky district**: env. of the N. Giryunino Village, 5 June 1962, *Shafiranov* (MW0136098!). **Kyrynsky district**: Sokhondinsky reserve, shore of Bukukun Lake, 30 June 2007, *E.N. Roenko* (VBGI158452!; VBGI158450!). **Mogochinsky district**: Razvalny Stream, 53.82639°N, 119.43306°E, alt. 792 m, 15 June 2021, *T.N. Veklich* (ABGI171286!). **Sretensky District**: environs of Ust-Narinzor Village, floodplain of the Kurlych River, 52.289442° N, 117.333047° E, 14 June 2025, *M.N. Koldaeva* (VBGI!).