



Article Genetic Diversity of Oxytropis Species from the Center of the Genus Origin: Insight from Molecular Studies

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Abstract: The genus *Oxytropis* (Fabaceae) was formed from the ancient species of *Astragalus* presumably approximately 5.6 Ma ago in Southern Siberia. Our study summarized data on the genetic diversity of 69 populations of 31 *Oxytropis* species in the center of origin of the genus based on the sequencing of plastid genome markers. Most of the populations (82.6%) are characterized by high gene diversity (0.600–1.000), which indicates a relatively stable state. Phylogenetic relationships between most *Oxytropis* species remain unresolved. Three genetic complexes and four phyletic lineages have been identified. Some species form weakly differentiated complexes, which is probably caused by their relatively recent divergence and the demography processes, as well as interspecific hybridization and polyploidy characteristic of *Oxytropis* species.

Keywords: Oxytropis; Fabaceae; genetic diversity; phylogenetic relationships; cpDNA



Citation: Sandanov, D.V.; Kholina, A.B.; Kozyrenko, M.M.; Artyukova, E.V.; Wang, Z. Genetic Diversity of *Oxytropis* Species from the Center of the Genus Origin: Insight from Molecular Studies. *Diversity* **2023**, *15*, 244. https://doi.org/10.3390/ d15020244

Academic Editor: Michael Wink

Received: 11 November 2022 Revised: 11 January 2023 Accepted: 6 February 2023 Published: 9 February 2023



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1. Introduction

Genus Oxytropis DC is one of the largest and most polymorphic genera of the family Fabaceae. According to different authors, it includes from 310 [1] to 450 species [2]. This is a predominantly Asian genus. Its range covers mainly North and Central Asia. The genus Oxytropis was supposedly formed about 5.6 million years ago at the Miocene–Pliocene boundary during the evolution of ancient species of the genus Astragalus L. in South Siberia [3,4]. The predominant life form of *Oxytropis* species is herbaceous perennials, inhabitants of mountain, steppe, meadow, forest-steppe, and forest communities. Some species form phytocenoses, e.g., O. lanata. Psammophytic oxytrope phytocenoses serve as habitats for many relict and endemic species, the existence of which directly depends on the state of the dominant species [5,6]. Many Oxytropis species are attractive as ornamental plants with a long flowering period, some species are valuable sources of vegetable protein for animals [7], but the most important and significant are the species with medicinal properties that are used in Tibetan, Mongolian, and Chinese medicine as hemostatic, diuretic, cardiovascular, anti-inflammatory, and antipyretic agents [8,9]. A wide range of medicinal properties of Oxytropis species is due to the diversity and complexity of chemicals. The main active substances are flavonoids, phenolcarboxylic acids, coumarins, alkaloids, and saponins [8–11]. The prospect of using such species as sources for the creation of medicines is obvious.

On the whole, 119 species and nine subspecies of *Oxytropis* were found in the Siberian flora in five subgenera and 16 sections [12]. The place of origin of the genus, the South Siberian mountainous region, is located between 49 and 56° north latitude and covers the Kuznetsk Alatau, Gorny Altai (including its Mongolian and Kazakh parts), Khangai, the Western and Eastern Sayan Mountains, the Western and Eastern Tannu-Ola, and the Baikal ridges of the southern framing of Lake Baikal (Primorsky and Khamar-Daban)

and Southwestern Transbaikalia [13]. This is a complex tectonic structure, where tectonic activity still continues. The modern relief of this area is characterized by a variety of forms, from foothill depressions to mountain plateaus and high mountain ranges, between which there are more or less large basins, the flora of which forms "steppe islands". Due to the isolation of these "islands" and the diversity of ecological and cenotic conditions in them, microevolutionary processes are intensively going on here. The main foci of species diversity are located in the place of origin of the genus Oxytropis: 69 species in the mountains of Southern Siberia, 39 of them in Altai, 34 each in the mountain floras of Tuva and Baikal Siberia [14]. The steppe flora of Southern Siberia mountains includes 59 species of *Oxytropis*, among them 17 species are found only in the steppes and are not part of the mountain floras of Southern Siberia [13]. The speciation within the genus occurs on the basis of hybridization and polyploidization. Polyploidy is widespread among Oxytropis species (basic number x = 8), especially in highland species, for which chromosome numbers 2n = 16, 32, 48, 64, 96 are known [15]. For Southern Siberia, a large number of hybrid forms are described, not fully formed taxa, whose species status is disputable [15]. The study of the genetic resources of Oxytropis species is relevant both for the conservation of the biodiversity of the flora of Southern Siberia, and for solving controversial taxonomic issues, as well as for studying the phylogeography and phylogeny of the genus as a whole.

In recent decades, much research has been conducted on plant barcoding using DNA sequences [16–18]. Chloroplast DNA has been extensively used to investigate phylogenetic relationships in plants [19]. Sequences of many cpDNA noncoding regions, including introns and intergenic spacers, have been used to assess interspecific relationships and suggested as molecular markers for species identification [20]. The intergenic spacers *psbA-trnH*, *trnL-trnF*, and *trnS-trnG* of cpDNA have proven to be useful as phylogenetic markers in the genus *Oxytropis* [4,21–29].

The aims of the present research are as follows: (1) to evaluate the genetic diversity of the populations of *Oxytropis* species from the center of the genus origin using intergenic spacers *psbA-trnH*, *trnL-trnF*, and *trnS-trnG* cpDNA; (2) to study the phylogenetic relationships of the *Oxytropis* species within Southern Siberia; (3) to determine a possible number of putative chloroplast lineages.

2. Materials and Methods

2.1. Taxon Sampling, DNA Extraction, and Sequencing

In this paper, we summarized the data of our previous studies [22–29] and new data obtained. A total of 621 plants of 69 populations of 31 *Oxytropis* species belonging to eight sections of three subgenera were sampled in four regions of Southern Siberia (Altai, Buryatia, Irkutsk Region, and Transbaikalia) and adjacent territories of Northeastern Mongolia to study cpDNA polymorphism (Figure 1). The complete specimen list, including the sampling localities, sample size, geographic coordinates, and codes for each population, is given in Table 1. The names of species, sections, and subgenera are accepted according to Malyshev [15]. The distribution of *Oxytropis* species in Asian Russia was analyzed using open-access data [30]. Additionally, species distribution data for Mongolia were considered [31].

All collected species were approved with herbarium specimens presented in the main Russian herbaria (LE, MW, UUH). All specimens used for DNA extraction are deposited at the Federal Scientific Centre of the East Asia Terrestrial Biodiversity, Far Eastern Branch of the Russian Academy of Sciences, Vladivostok, Russia.

To evaluate similarities and differences between *Oxytropis* species, 53 morphological traits have been analyzed. They include plant growth form, type of hairs on the plant, length of floral shoots, inflorescence type, form of stipules, leaves and leaflets, shape of calyx and length of its sepals, corolla color, length of standard and tip of keel, shape and type of legumes. Characteristic features are marked by unity (1), and non-characteristic, by zero (0). Sometimes transition features are marked positively (1) in both alternative states, but when the basic data are absent or unclear, they are marked by 0 in both alternative

states. Conformal features are not taken into account, if they invariably accompany other recorded parameters. The set of morphological traits was similar as in the previous study [2]. Data were estimated by cluster analysis using weighted pair-group average, taking into account relative Levenshtein's edit distance (normalized to theoretical maximum equal to number of traits) between qualitative morphological traits [32,33]. Basic matrices and dissimilarity matrices were calculated using the IBIS program [34,35]. Agglomerative hierarchical clustering (WPGMA) was performed in Statsoft Statistica 12.0.



Figure 1. Map of sample sites for natural populations of *Oxytropis* species from Southern Siberia (69 population, light brown circles). Population codes as in Table 1.

Total DNA was extracted from dried leaves. The extraction buffer contained 100 mM Tris-HCl (pH 8.0), 0.7 M NaCl, 40 mM EDTA, 1% CTAB (hexadecyltrimethylammonium bromide), and 10 mL/L β -mercaptoethanol. The extract was incubated at 65 °C for 40 min. The DNA was deproteinized with chloroform: octanol (24:1) and precipitated with equal volume of isopropanol in the presence of 0.3 M sodium acetate. DNA pellets were washed with 75% ethanol and dissolved in the buffer containing 10 mM Tris-HCl (pH 8.0) and 1 mM EDTA. Amplification of the *psbA-trnH*, *trnL-trnF*, and *trnS-trnG* intergenic spacer regions of cpDNA was performed with the use of universal primers, reaction conditions, and temperature regimes recommended for these regions [19,41]. Forward and reverse sequences for each region were determined on a genetic analyzer ABI 3500 (Applied Biosystems, Bedford, MA, USA) at the Joint Center of Biotechnology and Gene Engineering, the Federal Scientific Center of the East Asia Terrestrial Biodiversity (Vladivostok, Russia), and assembled using the Staden Package, version 1.5 [42]. The sequences of haplotypes of the intergenic spacers were deposited in the European Nucleotide Archive database. The accession numbers for all the sequences used are listed in Table 1.

2.2. Sequence Alignment and Phylogenetic Analyses

The sequences of each cpDNA region were aligned manually in SeaView v. 4.7 [43] using the CLUSTAL algorithm, manually edited when necessary, and concatenated for each specimen. We included indels and length variation in mononucleotide and dinucleotide repeats in the dataset because repeatability tests allowed us to exclude PCR errors. The haplotypes were identified based on combined DNA sequences using DnaSP v. 5.0 [44]. Haplotype (*h*) and nucleotide (π) diversity of populations (for populations with four or more samples) were calculated in Arlequin v. 3.5 software package [45].

The Location of the Population (No. of Samples)LongitudeFopulation CodeHaplotype DiversityNucleotide DiversityPsha-TmihTmil-TmifTmis-TmigSubgenus Tragacanthioxytropis Vass. Section Hystrix Bunge 0. tragacanthioxides Fisch. ex DC. [26], 2n = 16, 32 [15]49.51°, 88.66°TRA10.867 (0.107)0.0048 (0.0027)1. Russia, Altai Mis., Ucko Plateau, Zhumaly River (10)50.10°, 88.38°TRA20.700 (0.218)0.0008 (0.0006)MW172222-MW172234MW177548-MW1775603. Mongolia, Central Aimag, near the Ondorshireet sum (5)47.55°, 105.11°TRA30.800 (0.161)0.0017 (0.0012)LR898256-LR898269LR898302-LR898315LR898413-LR8984126Subgenus Phacoxytropis Bunge Section Janthina Bunge O. certlaa (Pal), DC. [26], 2n = 32 [36]51.87°, 108.24°COE10.900 (0.161)0.0017 (0.0012)LR898256-LR898269LR898302-LR898315LR898413-LR89841262. Russia, Irkutsk Region, near the village Zaignevo (5)51.87°, 106.85°COE20.970 (0.044)0.0046 (0.0025)LR898271, LR898279,LR898317, LR898318,LR898413-LR8984261. Mongolia, Central Aimag, near the Argalant sum (5)47.77°, 105.90°FIL21.000 (0.126)0.0048 (0.0031)LR898271, LR898272, LR898321, LR898318,LR898422, LR898429,2. Mongolia, Eastern Aimag, near the Gurvanzagal sum (9)49.27°, 114.71°FIL40.722 (0.159)0.0012 (0.0008)LR898271, LR898272, LR898321, LR898321, LR898432, LR898434,1. Russia, Buryatia, the village Orongoy (6)51.55°, 107.03°GLA10.333 (0.215)0.0001 (0.0002)LR898299, LR898300LR898435, LR898	Subgenus, Section, Species [Reference], 2n [Reference],	Latitude,	Demulation Code	Genetic Diversity (SD)		Genbank Accession Numbers		
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1. Russia, Buryatia, the village Orongoy (6) 51.55°, 107.03° GLA1 0.333 (0.215) 0.0001 (0.0002) LR898299, LR898300 LR898345, LR898346 LR898456, LR898457 Subgenus Oxytropis ex genere Oxytropis DC. Section Orobia Bunge 0.adamsiana (Trautv.) Jurtzev [29], 2n = 32 [15] 1. Russia, Buryatia, the village Uakit (10) 55.57°, 113.61° ADAM5 0.956 (0.059) 0.0047 (0.0027) OV260617-OV260624 OV260717-OV260724 OV260806-OV260813 0. popoviana Peschkova, 2n = 16, 32 [36] 51.28° 106 25° FOPOV 0.800 (0.164) 0.0007 (0.0027) OV567420 ON567421 OV567410 ON567421 OV567410 ON567421 ON567410 ON567421	O_{alabra} (Lam) DC [26] 2n = 16 [15]					ER090201 ER090209	ER090327 ER090329	E1090450 E1090440
In National, Darly data, late Hange Colorigy (6) 01.00 (10.000 Colority) 0	1 Russia Burvatia the village Orongov (6)	51 55° 107 03°	GLA1	0 333 (0 215)	0.0001 (0.0002)	LR898299 LR898300	I R898345 I R898346	I R898456 I R898457
Subgenus Oxytropis ex genere Oxytropis DC. Section Orobia Bunge O. adamsiana (Trautv.) Jurtzev [29], 2n = 32 [15] 1. Russia, Buryatia, the village Uakit (10) 55.57°, 113.61° ADAM5 0.956 (0.059) 0.0047 (0.0027) OV260617-OV260624 OV260717-OV260724 OV260806-OV260813 0. popoviana Peschkova, 2n = 16, 32 [36] E1 28° 106 25° 1. Russia, Buryatia, the village Restrict (5) E1 28° 106 25°	1. Russia, Buryana, ine vinage orongoy (b)	51.55 , 107.05	GL/II	0.555 (0.215)	0.0001 (0.0002)	ER070277, ER070300	Екоуозна, Екоуозна	ER030430, ER030437
O. adamsiana (Trautv.) Jurtzev [29], $2n = 32$ [15] 1. Russia, Buryatia, the village Uakit (10) 55.57° , 113.61° ADAM5 0.956 (0.059) 0. oppoviana Peschkova, $2n = 16$, 32 [36] 1. Russia, Buryatia, the village Uakit (10) 51.57° , 113.61° ADAM5 0.956 (0.059) 0.0047 (0.0027) OV260617-OV260624 OV260717-OV260724 OV260806-OV260813 O. popoviana Peschkova, $2n = 16$, 32 [36] Entropy of the prime the prima the prima the prima the prime the prime the prime the prime th	Subgenus Oxytropis ex genere Oxytropis DC. Section Orobia Bunge							
1. Russia, Buryatia, the village Uakit (10) 55.57°, 113.61° ADAM5 0.956 (0.059) 0.0047 (0.0027) OV260717-OV260624 OV260717-OV260724 OV260806-OV260813 0. popoviana Peschkova, 2n = 16, 32 [36] 51.28° 106.25° POPOV 0.800 (0.164) 0.0007 (0.0027) OVE60717-OV260724 OVE60717-OV260724 OVE6070724 OVE60806-OVE60813	<i>O. adamsiana</i> (Trautv.) Jurtzev [29], 2n = 32 [15]							
O. popoviana Peschkova, $2n = 16, 32$ [36] 1. Burgia Burgatia the village Barghy (5) (262)	1. Russia, Buryatia, the village Uakit (10)	55.57°, 113.61°	ADAM5	0.956 (0.059)	0.0047 (0.0027)	OV260617-OV260624	OV260717-OV260724	OV260806-OV260813
1 Durate the village Density (5) E1 200 10(250 DODOV 0.000 (0.1(4)) 0.0000 (0.0007) ONE(7420 ONE(740 ONE(740)	<i>O. popoviana</i> Peschkova, 2n = 16, 32 [36]							
1. Kussia, duryana, me vinage daraty (5) 51.26°, 100.35° FOFOV 0.800 (0.104) 0.0009 (0.0007) ON507429-ON507431 ON567410-ON567412 ON567391-ON567393	1. Russia, Buryatia, the village Baraty (5)	51.28°, 106.35°	POPOV	0.800 (0.164)	0.0009 (0.0007)	ON567429-ON567431	ON567410-ON567412	ON567391-ON567393
O. recognita Bunge, $2n = 32$ [15]	O. recognita Bunge, $2n = 32$ [15]							
1. Russia, Altai Mts., Jazator River (10) 49.63°, 87.87° REC1 0.822 (0.097) 0.0059 (0.0033) ONE67432_ONE67433_ONE67433_ONE67434_ONE67405_	1. Russia, Altai Mts., Jazator River (10)	49.63°, 87.87°	REC1	0.822 (0.097)	0.0059 (0.0033)	ONI567432-ONI567443	ONI567413-ONI567424	ON567394-ON567405
2. Russia, Altai Mts., Ukok Plateau (8) 49.50°, 88.13° REC2 1.000 (0.062) 0.0020 (0.0013)	2. Russia, Altai Mts., Ukok Plateau (8)	49.50°, 88.13°	REC2	1.000 (0.062)	0.0020 (0.0013)	01130/432-01130/443	011307413-011307424	011307394-011307403
<i>O. sordida</i> (Willd.) Pers. [25], 2n = 48, 64 [15]	<i>O. sordida</i> (Willd.) Pers. [25], 2n = 48, 64 [15]							
1. Russia, Buryatia, the village Ina (8) 53.73°, 110.25° SORD 0.786 (0.151) 0.0008 (0.0005) LS991870-LS991874 LS991896-LS991900 LS991922-LS991926	1. Russia, Buryatia, the village Ina (8)	53.73°, 110.25°	SORD	0.786 (0.151)	0.0008 (0.0005)	LS991870-LS991874	LS991896-LS991900	LS991922-LS991926
O. strobilacea Bunge [29], 2n = 16, 32, 48, 64 [15]	O. strobilacea Bunge [29], 2n = 16, 32, 48, 64 [15]		6 77 74		2 2222 (2 222 =)			
1. Russia, Buryata, the village Zagraevo (5) 51.88°, 108.25° 51R1 0.800 (0.164) 0.0009 (0.0007)	1. Russia, Buryatia, the village Zaigraevo (5)	51.88°, 108.25°	STRI	0.800 (0.164)	0.0009 (0.0007)			
2. Russia, Buryata, the village Komsomol skoe (10) 52.46° , 111.0° $SIR2$ 0.867 (0.107) 0.0016 (0.0010)	2. Russia, Buryatia, the village Komsomol'skoe (10)	52.48°, 111.09°	STR2	0.867 (0.107)	0.0016 (0.0010)			
3. Russia, Buryana, the Village Matsk (15) 54.61^{-} , 110.78^{-} $51R3^{-}$ 0.992^{-} (0.040) 0.032^{-} (0.01018) $OV2605/9-OV260/05,$ $OV26079-OV260/05,$ $OV26079-OV260/05,$ $OV26079-OV26079-0$	3. Russia, Buryatia, the village Maisk (15)	54.61°, 110.78°	SIK3	0.952 (0.040)	0.0032 (0.0018)	0V260579-0V260605,	OV260679-OV260705,	OV260768-OV260794,
4. Russia, Duryata, tract Oksnat (5) 53.20°, 111.45° 51R4 1.000 (0.127) 0.0042 (0.0027) OV260608-OV260614 OV260/08-OV260/14 OV260/9/-OV260803	4. Russia, buryana, tract Uksnaki (5)	55.20°, 111.45°	SIK4	1.000 (0.127)	0.0042 (0.0027)	OV260608-OV260614	OV260708-OV260714	0V260797-0V260803
5. Kussia, buryata, the village fory (b) 51.76 , 102.95 51.55 0.600 (0.215) 0.0015 (0.0005)	5. Russia, buryatia, the village Tory (6)	$51.76^{\circ}, 102.95^{\circ}$	51K3 6TD7	0.600 (0.215)	0.0013 (0.0009)			
0. Russia, bulyada, de vinage zurewundo (11) 51.75, 102.67 51R7 0.794 (0.051) 0.0025 (0.0015)	O subvitica (Poll.) DC [22] $2n = 16.32$ [15]	51.75 , 102.87	5117	0.904 (0.031)	0.0023 (0.0013)			
0. sylumina (1 al.) Do. [22], 211 - 10, 02 [12] 1 Russia Buryata the village Idius (12) 52 12° 109 13° SYLVAT 0.818 (0.084) 0.0006 IT856560-IT856562 IT856573-IT856573 IT856576-IT856578	1 Russia Burvatia the village Udinsk (12)	52 12° 109 13°	SYI VAT	0.818 (0.084)	0 0008 (0 0006)	I T856560-I T856562	I T856573-I T856575	I T856586-I T856588
Saction Variale Bunes	Section Xerohia Bunge	52.12,107.15	012011	0.010 (0.004)	0.0000 (0.0000)	E1050500 E1050502	E1050575 E1050575	E1050500 E1050500
$O_{cases into strikes}$ (Pa) Pers [27] 2n = 48 [37] 64 [15]	$O_{caesnitosa}$ (Pall) Pers [27] $2n = 48$ [37] 64 [15]							
1. Russia. Buryatia near the village Novoselenginsk (11) $51.08^{\circ}.106.60^{\circ}$ CAE1 $0.327(0.153)$ $0.0001(0.0001)$	1. Russia, Burvatia, near the village Novoselenginsk (11)	51.08°, 106.60°	CAE1	0.327 (0.153)	0.0001 (0.0001)			
2. Russia, Buryatia, near the village Dyrestuy (9) 50.64° , 106.01° CAE2 $0.000(0.000)$ $0.0000(0.0000)$	2. Russia, Burvatia, near the village Dyrestuy (9)	50.64°, 106.01°	CAE2	0.000 (0.000)	0.0000 (0.0000)			
3. Russia, Transbaikalia, near the village Kusocha (5) 50.69°, 115.70° CAE3 0.700 (0.218) 0.0030 (0.0020) LR861115-LR861122 LR828424-LR828431 LR828468-LR828475	3. Russia, Transbaikalia, near the village Kusocha (5)	50.69°, 115.70°	CAE3	0.700 (0.218)	0.0030 (0.0020)	LR861115-LR861122	LR828424-LR828431	LR828468-LR828475
4. Russia, Transbaikalia, near the village Tsugol (5) 51.02°, 115.60° CAE4 0.700 (0.218) 0.0017 (0.0012)	4. Russia, Transbaikalia, near the village Tsugol (5)	51.02°, 115.60°	CAE4	0.700 (0.218)	0.0017 (0.0012)			
O. $eriocarpa$ Bunge [27], $2n = 16$ [15], $24 + 2-3B$ [38]	<i>O. eriocarpa</i> Bunge [27], 2n = 16 [15], 24 + 2–3B [38]			. ,				
1. Russia, Altai Mts., Ukok Plateau, Zhumaly River (7) 49.29°, 88.07° ERI1 0.893 (0.111) 0.0090 (0.0051) LR861754-LR861759 LR861767 LR861767 LR861770-LR861775	1. Russia, Altai Mts., Ukok Plateau, Zhumaly River (7)	49.29°, 88.07°	ERI1	0.893 (0.111)	0.0090 (0.0051)	LR861754-LR861759	LR861762-LR861767	LR861770-LR861775
O. grandiflora (Pall.) DC. [27], 2n = 48 [39]	<i>O. grandiflora</i> (Pall.) DC. [27], 2n = 48 [39]							
1. Russia, Transbaikalia, near the village Bytev (5) 50.17°, 113.11° GRA1 0.900 (0.161) 0.0046 (0.0029)	1. Russia, Transbaikalia, near the village Bytev (5)	50.17°, 113.11°	GRA1	0.900 (0.161)	0.0046 (0.0029)			
2. Mongolia, Dornod Province, near the Bayandun sum (7) 49.37°, 113.81° GRA2 0.857 (0.137) 0.0035 (0.0021) LR861123-LR861131 LR828432-LR828440 LR828476-LR828484	2. Mongolia, Dornod Province, near the Bayandun sum (7)	49.37°, 113.81°	GRA2	0.857 (0.137)	0.0035 (0.0021)	LR861123-LR861131	LR828432-LR828440	LR828476-LR828484
3. Mongolia, Dornod Province, near the Bayan-Uul sum (9) 49.01°, 112.45° GRA3 0.667 (0.132) 0.0043 (0.0024)	3. Mongolia, Dornod Province, near the Bayan-Uul sum (9)	49.01°, 112.45°	GRA3	0.667 (0.132)	0.0043 (0.0024)			

Table 1. Sampling site locations, sample size, codes, genetic diversity within populations of *Oxytropis* species, and GenBank accession numbers.

Table 1. Cont.

Subgenus, Section, Species [Reference], 2n [Reference], The Location of the Population (No. of Samples)	Latitude, Longitude	Population Code	Genetic Diversity (SD)		Genbank Accession Numbers		
			Haplotype Diversity	Nucleotide Diversity	Psba-Trnh	Trnl-Trnf	Trns-Trng
O. mixotriche Bunge [27], 2n—no data							
1. Russia, Buryatia, near the village Urzhil (5)	54.07°, 110.39°	MIX1	0.400 (0.237)	0.0002 (0.0002)			
2. Russia, Buryatia, near the village Suvo (7)	53.65°, 110.02°	MIX2	0.851 (0.137)	0.0053 (0.0031)	LR861724 -LR861733	LR861734 -LR861743	LR861744 -LR861753
3. Russia, Buryatia, near the village Mozhayka (5)	52.35°, 110.80°	MIX3	1.000 (0.126)	0.0019 (0.0013)			
<i>O. peschkovae</i> M. Pop. [27], 2n = 48 [37]							
1. Russia, Irkutsk Region, near the Gyzgi-Nur Lake (9)	52.91°, 106.63°	PES1	0.972 (0.064)	0.0082 (0.0046)	1 00/1/01 1 00/1701	L DOC1502 L DOC1512	1 00/1510 1 00/1500
2. Russia, Irkutsk Region, Olkhon Island, near the village	53.25°, 107.49°	PES2	0.345 (0.172)	0.0016 (0.0009)	LK861691-LK861/01	LK861/02-LK861/12	LK861/13-LK861/23
Knuznir (11)			~ /	× ,			
0. tripnylla (Pall.) DC. [27], 2n = 16 [36,40]	E4 4E0 110 4E0	77011	0.024 (0.057)	0.0010 (0.0011)			
1. Russia, Buryatia, near the village Sakhuli (12)	54.45°, 110.45°	TRII	0.924 (0.057)	0.0018 (0.0011)			
2. Russia, Buryatia, near the village Udinsk (6)	52.08°, 108.98°	1 RI2	0.800 (0.172)	0.0022 (0.0014)	LR861134-LR861149,	LR828443-LR828458,	LR828487-LR828502,
3. Russia, Buryatia, near the village Bagdarin (10)	54.44°, 113.22°	1813	0.844 (0.103)	0.0021 (0.0013)	LR861154-LR861158	LR828463-LR828467	LR828507-LR828511
4. Russia, Irkutsk Region, Begul Bay (6)	52.74°, 106.54°	TRI7	1.000 (0.096)	0.0025 (0.0016)			
Section Polyadena Bunge							
O. glandulosa Turcz. [23], $2n = 32$ [15]							
1. Russia, Buryatia, near the village Argada (10)	54.37°, 110.53°	KUR	0.911 (0.077)	0.0059 (0.0033)			
2. Russia, Buryatia, near the village Urzhil (14)	54.07°, 110.39°	BAR	0.703 (0.101)	0.0036 (0.0020)	I T732668-I T732678	I T732657-I T732667	I T732646-I T732656
Russia, Buryatia, near the village Shiringa (15)	52.67°, 111.72°	SHIR	0.133 (0.112)	0.0002 (0.0002)	L1752000-L1752070	E1752057-E1752007	E1752040-E1752050
Russia, Buryatia, near the village Garam (10)	52.55°, 111.48°	GAR	0.356 (0.159)	0.0006 (0.0004)			
O. microphylla (Pall.) DC. [28], 2n—no data							
 Russia, Irkutsk Region, near the village Ozera (9) 	52.68°, 106.42°	MICR1	0.000 (0.000)	0.0000 (0.0000)			
Russia, Irkutsk Region, near the Gyzgi-Nur Lake (6)	52.91°, 106.63°	MICR2	0.600 (0.215)	0.0007 (0.0005)	MN100088 MN100000	MN1200000 MN1200002	MNI200014 MNI200016
Russia, Irkutsk Region, near the Gurbi-Nur Lake (11)	52.89°, 106.60°	MICR3	0.182 (0.144)	0.0001 (0.0001)	10110133300-10110133330	WIN200000-WIN200003	WIN200014-WIN200010
Russia, Irkutsk Region, near the Namish-Nur Lake (11)	52.83°, 106.59°	MICR4	0.182 (0.144)	0.0001 (0.0001)			
<i>O. muricata</i> (Pall.) DC. [28], 2n = 16, 32 [15]							
 Russia, Irkutsk Region, near the Gyzgi-Nur Lake (9) 	52.91°, 106.63°	MUR1	0.417 (0.191)	0.0009 (0.0006)			
Russia, Irkutsk Region, near the village Sarma (8)	53.12°, 106.85°	MUR2	0.250 (0.180)	0.0007 (0.0005)	MN199983-MN199987	MN199996-MN200000	MN200009-MN200013
3. Russia, Irkutsk Region, near the Oto-Khushun Cape (13)	53.29°, 107.17°	MUR3	0.692 (0.075)	0.0014 (0.0008)			
O. pseudoglandulosa Gontsch. ex Grub. [28], 2n—no data							
1. Mongolia, near the Ulan-Bator (7)	48.03°, 106.79°	PSEGLA	0.809 (0.130)	0.0011 (0.0007)	MN199991-MN199994	MN200004-MN200007	MN200017-MN200020
<i>O. varlakovii</i> Serg. [22,28], 2n = 24 + 1B [40]							
 Russia, Transbaikalia, near the Nozhii Lake (5) 	50.80°, 114.83°	VARL	0.700 (0.218)	0.0003 (0.0003)	LT856563-LT856565	LT856576-LT856578	LT856589-LT856591
Section Leucopodia Bunge							
O. squammulosa DC., $2n = 16$ [38]							
1. Russia, Buryatia, Uda River (5)	52.05°, 108.85°	SQUAM	0.900 (0.161)	0.0022 (0.0015)	ON567444-ON567447	ON567425-ON567428	ON567406-ON567409
Section Verticillares DC.							
O. bargusinensis Peschkova [22], 2n—no data							
1. Russia, Buryatia, Alla River (15)	54.71°, 110.68°	BARKUR	0.762 (0.096)	0.0011 (0.0007)			
2. Russia, Burvatia, near the village Urzhil (15)	54.06°, 110.36°	BARBAR	0.895 (0.070)	0.0016 (0.0009)	L1856473-L1856488	L1856506-L1856521	L1856539-L1856554
O. gracillima Bunge [24], 2n—no data			~ /	× ,			
	12 020 105 000	CD L C	1 000 (0 10()		MH174938,		
1. Mongolia, Central Aimag, near the Argalant sum (5)	47.83°, 105.88°	GRAC	1.000 (0.126)	0.0042 (0.0027)	LT996058-LT996061	L1996062-L1996066	L1996067-L1996071
<i>O. interposita</i> Sipl. [22], $2n = 24$ [40]							
1. Russia, Burvatia, Alla River (14)	54.71°, 110.68°	INTKUR	0.769 (0.075)	0.0015 (0.0009)	LT856489-LT856493	LT856522-LT856526	LT856555-LT856559
O. lanata (Pall.) DC. $[24]$, $2n = 16 [15]$,,						
1. Russia, Burvatia, near the village Unegetei (20)	52.17°, 108.60°	LAN1	0.895 (0.051)	0.0010 (0.0006)			
2. Russia, Burvatia, near the village Urzhil (15)	54.07°, 110.39°	LAN2	0.895 (0.052)	0.0010 (0.0006)	LT994841-LT994858	LT994895-LT994912	LT994949-LT994966
3. Mongolia, Central Aimag, near the Argalant sum (5)	47.83°, 105.88°	LAN3	0.900 (0.161)	0.0017 (0.0012)			

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Tabl	e I.	Cont

Subgenus, Section, Species [Reference], 2n [Reference],	Latitude, Longitude	Population Code	Genetic Diversity (SD)		Genbank Accession Numbers		
The Location of the Population (No. of Samples)			Haplotype Diversity	Nucleotide Diversity	Psba-Trnh	Trnl-Trnf	Trns-Trng
<i>O. myriophylla</i> (Pall.) DC [24], 2n = 16 [15]							
1. Russia, Transbaikalia, near the village Tsugol (5)	51.02°, 115.59°	MYR1	0.700 (0.218)	0.0003 (0.0003)			
Russia, Buryatia, near the village Udinsk (21)	52.11°, 109.13°	MYR2	0.767 (0.057)	0.0007 (0.0005)	LT994859-LT994866	LT994913-LT994920	LT996002-LT996009
3. Russia, Buryatia, the village Komsomol'skoe (8)	52.48°, 111.09°	MYR3	0.821 (0.101)	0.0008 (0.0005)			
O. $oxyphylla$ (Pall.) DC. [24], $2n = 16$ [15]							
1. Russia, Transbaikalia, near the Nozhii Lake (5)	50.77°, 114.79°	OXY1	0.900 (0.161)	0.0007 (0.0005)			
Russia, Buryatia, near the village Novoselenginsk (16)	51.07°, 106.60°	OXY2	0.958 (0.036)	0.0023 (0.0013)	1 200 49/ 7 1 200 490 1	1 7004021 1 7004045	1 200/010 1 200/024
3. Russia, Buryatia, the village Komsomol'skoe (8)	52.48°, 111.09°	OXY3	0.964 (0.077)	0.0045 (0.0026)	L1994867-L1994891	L1994921-L1994945	L1996010-L1996034
4. Mongolia, Bulgan Aimag, near the Rashaant sum (4)	47.41°, 103.66°	OXY4	1.000 (0.177)	0.0042 (0.0029)			
<i>O. selengensis</i> Bunge [24], 2n = 32 [15]							
1 Russia Burwatia poar the village Unegotei (18)	52 17° 108 60°	SEI	0.634 (0.127)	0,0009 (0,0006)	MH174937,	I T006045-I T006051	1 T006038-1 T006044
1. Russia, buryana, near the vinage Onegeter (10)	52.17,100.00	JEL	0.034 (0.127)	0.0009 (0.0000)	LT996052-LT996057	L1990045-L1990051	E1990030-E1990044
<i>O. stukovii</i> Palibin [24], 2n = 16 [40]							
 Russia, Transbaikalia, near the Nozhii Lake (4) 	50.81°, 114.84°	STUK1	0.833 (0.222)	0.0005 (0.0005)	1 7004807 1 7004804	1 T004046 1 T004048	1 T006025 1 T006027
Russia, Transbaikalia, near the Kunkur Lake (10)	50.71°, 114.89°	STUK2	0.711 (0.117)	0.0004 (0.0003)	L1994092-L1994094	L1994940-L1994940	L1990033-L1990037
O. tompudae M. Pop. [22], 2n—no data							
1. Russia, Buryatia, the village Maisk (8)	54.60°, 110.78°	TOMP	0.893 (0.111)	0.0026 (0.0016)	LT856566-LT856571	LT856579-LT856584	LT856592-LT856597

SD-standard deviations. The bold font has shown the genetic diversity and accession numbers in this study.

To reconstruct the phylogenetic relationships of haplotypes, we excluded length variation of mononucleotide and dinucleotide repeats in the dataset. A network of haplotypes was constructed using Network, version 5.0.1.1 [46], treating each deletion/insertion, regardless of size, as a single mutational event and using the MJ algorithm with default settings. Phylogenetic analyses of haplotypes were conducted using the ML, MP, and NJ methods as implemented in PAUP v. 4.0b10 [47]. Optimal trees were found using a heuristic search with TBR branch swapping and the MulTrees option in effect. For the ML analysis, the GTR + G + I model was selected according to the Akaike information criterion (AIC) using Modeltest v. 3.6 [48]. ML heuristic searches were performed using the resulting model settings, 100 replicates of random sequence addition, TBR branch swapping and MULTrees option on. The robustness of nodes in ML, NJ, and MP trees was tested using bootstrap with 1000 replicates (bootstrap percentage, BP). BP < 50% were not taken into account. *Astragalus davuricus* (Pall.) DC. from genus *Astragalus* L. (accession numbers in GenBank LM653198, LM653161, and LM653235) [49] was used as outgroup.

3. Results

The dendrogram reflects the measure of morphological differences between separate species and sections of *Oxytropis*. Studied species on the dendrogram are divided into seven branches separated by a linkage distance at 0.09 (Figure 2). Species from sections *Hystrix, Janthina,* and *Polyadena* are well distinguished (branches I, III, and VII, respectively). Joining of *O. interposita* at the branch VII and close presenting of *O. stukovii* at the branch VI showed morphological similarities of this species with section *Polyadena*. Branch II was represented by species of section *Xerobia* and *O. squammulosa* from the section *Leucopodia*. Representatives of section *Verticillares* mostly formed branch IV and include two species from section *Orobia* (*O. adamsiana* and *O. sylvatica*). The neighbor branch V has only species from section *Orobia* (*O. recognita, O. sordida,* and *O. strobilacea*).

Among the 620 specimens of 31 *Oxytropis* species, 101 haplotypes (H1–H101) were identified on the basis of polymorphic sites detected across 2576 aligned positions of three cpDNA regions. Eighty-one nucleotide substitutions were identified, of which 63 sites were parsimony informative. Fourteen of 101 haplotypes (H7, H16, H18, H25–H29, H32, H47, H52, H70, H73, and H89) were shared by several species of either the same section or different sections (Figure 3). The species-specific molecular markers were revealed only for *O. microphylla*, *O. gracillima*, and *O. lanata*.

Data on the genetic diversity of *Oxytropis* species from Southern Siberia are presented in Table 1. Only two populations (CAE2 *O. caespitosa* and MICR1 *O. microphylla*) of 69 populations studied were monomorphic. Low and medium levels of haplotype diversity (*h* varies from 0.133 to 0.417) were found for 10 populations (14.5%). A high level of haplotype diversity (*h* varies from 0.600 to 1.000) was found for 57 populations (82.6%). Concerning nucleotide diversity, a low level (π varies from 0.0001 to 0.0032) was determined for 50 populations (72.5%), while moderate and high levels (π varies from 0.0035 to 0.0090) were determined for 17 populations (24.6%). A high level for both parameters was found for 14 populations (20.3%), whereas a low level for both parameters was found for eight populations (11.6%). A combination of a high level of haplotype diversity and a low level of nucleotide diversity was determined for 39 populations (56.5%).

The relationships between haplotypes found in representatives of *Oxytropis* species from Southern Siberia are shown in Figure 3. Haplotype H101 of *O. glabra* sect. *Mesogaea* of the subg. *Phacoxytropis* was separated by 34 mutational steps from haplotype undetected in our study or an extinct ancestral one closely related to other *Oxytropis* haplotypes that formed three haplogroups (A, B, and C). These haplogroups contain loop structures between many haplotypes and are genetic complexes that include haplotypes of several species from different sections. Haplogroup A includes haplotypes of five *Xerobia* species and one *Orobia* species of the subg. *Oxytropis*, and haplotypes of *O. tragacanthoides* sect. *Hystrix* subg. *Tragacanthoxytropis*. Haplogroup B includes haplotypes of species from all five sections studied of the subg. *Oxytropis* as well as haplotypes of *O. tragacanthoides*. Haplogroup C includes haplotypes of the subg. *Oxytropis* only and specifically haplotypes of six *Verticillares* species and three *Orobia* species (Figure 3). Thus, haplotypes of *Orobia* species were present in all three haplogroups. Haplotypes of *O. tragacanthoides*, *O. grandiflora*, *O. eriocarpa*, and *O. peschkovae* were present in haplogroups A and B, and haplotypes of *O. strobilacea* were present in haplogroups B and C. Haplotypes of *Polyadena* species were present in haplogroup B. In addition, all haplotypes of *O. coerulea* and *O. filiformis* sect. *Janthina* subg. *Phacoxytropis* were found to form a single branch b1 that connected via unsampled or extinct haplotype to haplotypes of the haplogroup B (Figure 3). Haplotypes of *O. microphylla* sect. *Polyadena* formed another distinct branch b2 connected with the haplogroup B. Haplotypes of *O. lanata* and *O. gracillima* sect *Verticillares* were grouped into separate branches according to their species affiliation (c1 and c2, respectively) that connected with the haplogroup C. Loop structures between many haplotypes point to homoplasy, which hampers the identification of genetic relationships between them.



Figure 2. WPGMA similarity dendrogram of 31 *Oxytropis* species based of relative Levenshtein edit distance.



Figure 3. Median-joining network inferred from combined sequences of the *psbA-trnH*, *trnL-trnF*, and *trnS-trnG* regions showing the relationships among cpDNA haplotypes (H1–H101) of 31 *Oxytropis* species from Southern Siberia. Each circle represents the haplotype; the size of the circles reflects the frequency of occurrence of haplotype. The colors of circles indicate the affiliation of haplotype to certain species. Black small circles indicate the median vectors; thin bars indicate the mutational events; white thick bars indicate the indels; dashed lines are circled haplogroups A, B, C; thin lines are circled separate branches b1, b2, c1, and c2.

Phylogenetic analyses of 101 haplotypes of the species from *Tragacanthoxytropis*, *Phacoxytropis*, and *Oxytropis* subgenera supported the monophyly of the genus *Oxytropis*. Topology of ML tree shown in Figure 4 is similar to those of the MP and NJ trees with few differences in statistical supports of some nodes. All *Oxytropis* species except *O. glabra* formed a cluster with a high degree of support (BP 99, 100, and 97% for MP, NJ, and ML analyses, respectively). However, resolution within this cluster was poor, and only a few small groups have significant bootstrap support. Haplotypes of all species of sect. *Verticillares* (except *O. interposita*) are clustered together with low support only in MP and ML analyses. Within this clade, all haplotypes of *O. gracillima* form a distinct but weakly supported group (BP 61, 51, and 64%), and all haplotypes of *O. lanata* form a distinct group with a high degree of support (BP 88, 85, and 86%). The remaining *Verticillares* species are either unresolved or intermixed with each other or with the representatives of sect. *Orobia* in weakly supported subclades.



Figure 4. Maximum-likelihood topology obtained from the combined *psbA-trnH*, *trnL-trnF*, and *trnS-trnG* dataset and generated by PAUP under the GTR + I + G model showing branch lengths (–ln likelihood = 4997.50) for 69 populations of 31 *Oxytropis* species from Southern Siberia and *Astragalus davuricus* (accession numbers in GenBank LM653198, LM653161, and LM653235) as outgroup species. The numbers at nodes indicate bootstrap values (BI > 50%) for MP/NJ/ML analyses, respectively. The scale bar denotes the number of substitutions per site.

4. Discussion

4.1. Morphological Differences among Oxytropis Species

Species of well distinguished sections within genus *Oxytropis* were characterized by peculiar morphological features. Section Hystrix of subgenus Tragacanthoxytropis Vass. included shrubs and dwarf shrubs with membraneous legumes and hard leaf petioles which are presented on the plants after leaf fall. Section Janthina presented by tiny plants with opposite linear leaflets (usually 6–20 pairs) and small flowers (8–15 mm long) with bell calyx. Legumes are ovoid and unilocular [15]. All haplotypes of species from section *Janthina* were separate and form a single branch b1 (Figure 3). Representatives of section Polyadena are rosette plants with whorled leaflets and warty glands on legumes, leaves, stipules, and on calyx. The presence of *O. interposita* in the branch VII and close position of O. stukovii on the dendrogram (Figure 2) showed their morphological similarities and recently both species on the base of critical analysis included to the section *Polyadena* [50]. The haplotype of *O. interposita* is well presented in the haplogroup B in close relation with other species of section *Polyadena*, while the haploptype of *O stukovii* was found within another haplogroup C (Figure 3). The single species O. squammulosa representing monotypic section Leucopodia included branch II on the dendrogram with species from section Xerobia (Figure 2). Close morphological similarities of both sections have been previously discussed [2]. On the other hand, analysis of cpDNA haplotypes and position on ML tree revealed close relationships of O. squammulosa with species of section Polyadena (Figures 3 and 4).

4.2. Genetic Diversity of the Populations of Oxytropis Species

Genetic diversity, which is the product of the long-term evolution of species, is caused by many factors and is one of the prerequisites for adaptation and survival of species. The higher the level of genetic diversity of a species, the easier it is to adapt to changing environments. Our results of studying the genetic diversity of 69 populations of 31 Oxytropis species showed that the minimum values of haplotype diversity (0.133-0.182) were determined only in three populations of two species, O. glandulosa and O. microphylla, and two populations were monomorphic (Table 1). These populations are small and isolated [51,52], and gene flow from nearest related populations is limited due to physical barriers. Such isolated populations were apt to suffer from genetic drift that may have contributed to the lack of genetic diversity. Comparisons of the variability of *Oxytropis* species of sect. Verticillares, Polyadena, and Xerobia from Southern Siberia with the data for Oxytropis species of sect. Orobia, Arctobia, and Gloeocephala from Northeast Asia showed that the populations of species of the last sections inhabiting higher latitudes than the southern-Siberian species, or arctic latitudes, were characterized by lower levels of genetic diversity or were monomorphic [53]. The low level of genetic diversity or lack of it, combined with the high levels of population differentiation, may also be due to their small population sizes and high degrees of spatial isolation, suggesting low gene flow between populations over an extended period.

The most populations of *Oxytropis* species from Southern Siberia were characterized by a high level of genetic diversity. For example, maximum values of haplotype diversity (0.893–1.000) were revealed in the 25 populations of 16 species of the 31 studied (Table 1). As a rule, high genetic diversity is typical for polymorphic species with a wide range, such as *O. strobilacea* and *O. oxyphylla* (Figure 5). However, we did not find any evidence of genetic diversity loss, even for endemic species with the narrowest distributions (*O. triphylla*, *O. bargusinensis*, and *O. interposita*) (Figure 6). Our results are probably an exception to the statement that endemic species are characterized by low genetic diversity [54,55], so it can be assumed that other factors different from geographic range may influence genetic variability.



Figure 5. Distribution of Oxytropis strobilacea and Oxytropis oxyphylla.



Figure 6. Distribution of three Oxytropis species endemic to Baikal Siberia.

Studies of the genetic variability of plant species have shown that the level of genetic diversity is influenced by a number of factors, such as mating systems, life history features, chromosomal variability, population distribution, as well as ecological factors [54–56]. Modern reviews, which evaluated the effects of life-history traits and environmental factors on the genetic diversity of plants [57–60], including the studies based on chloroplast genetic variation [57,58,60], also show that population genetic diversity depends on species-specific life-history traits, population dynamics, past climatic and demographic events, topography, and biogeography. In part, the number of haplotypes was influenced by the type of geographic distribution, while haplotype diversity was affected by the type of flower

(monoecious, or dioecious), and the plant species most closely related phylogenetically have similar levels of genetic diversity [57].

The high level of genetic diversity within populations Oxytropis species from Southern Siberia studied is typical for the predominantly insect-pollinated species with the outcrossing breeding system and high longevity. Similarly high levels of chloroplast gene diversity were found in the populations of other legume species with similar life-history traits and mating systems (long-lived, insect-pollinated perennials that reproduce by outcrossing), such as Astragalus onobrychis L. (in diploid relict populations h varied from 0.833 to 1.000) [61], Sophora *microphylla* Aiton ($h = 0.812 \pm 0.019$), and *S. tetraptera* J.S. Mill. ($h = 0.931 \pm 0.015$) [62], as well *Oxytropis diversifolia* E. Peter ($h = 0.880 \pm 0.074$) [63]. It seems likely that these peculiarities of breeding system are the most important source for the maintenance of the variability reserve for Oxytropis species with low-level gene diversity. As for the relict species studied, which include O. tragacanthoides sect. Hystrix, O. eriocarpa, and narrow endemic O. triphylla (both ones belong to sect. Xerobia), the high genetic variability in these species should largely be attributed to its antiquity, in addition to the longevity and outcrossing. It is assumed that the ancestors of the sect. *Hystrix* and *Xerobia* were widely distributed in Southern Siberia in the past [13]. Probably, the populations of O. tragacanthoides, O. eriocarpa, and O. triphylla were stable for a long time, and ancestral genetic variation was maintained. Similar patterns of genetic diversity based on cpDNA data were also noted for other long-lived relict species: Linum flavum L. [64], an above-mentioned Astragalus onobrychis [61], some Chamaesium species [65].

Other factors that significantly affect the level of genetic variability are the topography of the region and the ecological specialization of species. A number of studies of the phylogeny and phylogeography of species which inhabited topographically complex areas [58,60,65,66] showed that topography plays a key role in maintaining genetic diversity and diversification. The territory of Southern Siberia includes high mountains, foothill depressions, deep valleys, and plateaus [13], and is just such a complex heterogeneous landscape with high microhabitat variation. It is supposed that the maintenance of high genetic diversity in these microhabitats could be associated with the survival and diversification of species, and that populations in topographically complex landscapes should be more resistant and resilient to climate change [58]. The mountainous relief of Southern Siberia, including territories surrounding Lake Baikal, creates a mosaic of microclimates, as well a long-term isolation of individual steppe habitats confined to the southern slopes or bottoms of the basins. These circumstances favor the formation of new species or the preservation of relicts of different ages [13,67].

According to ecological requirements, many Oxytropis species from Southern Siberia are highly specialized, as a rule, including xerophytes, petrophytes, and psammophytes. All these species are photophilous, often grow on talus, on gravel, rocky and sandy substrates, including along the banks of rivers and lakes [7,12,14,15]. The effects of ecological factors (especially climatic and edaphic factors) were estimated for rare Astragalus species [68], a sister group for genus Oxytropis. According to the authors, the revealed relatively high level of genetic diversity in rare Astragalus taxa is due to two main reasons: (1) aspects of seed biology (maintenance a healthy seed bank), (2) spatial climatic and soil variability shaping local adaptations. This combination (and possibly interaction) of demographic and ecological forces may also have implications for the Siberian Oxytropis species. The importance of local environmental heterogeneity and habitat specialization in keeping multiple putative adaptations and generating genetic diversity was also shown for other plant species [69,70]. Interesting information about the role of environmental factors was obtained during the study of the diversity and diversification of species of the Eastern Mediterranean genus *Ricotia* [71]. In the absence of large glaciations, taxa indigenous to the southern Mediterranean region could survive climatic fluctuations of the Quaternary via short distance shifts to more favorable habitats. Authors supposed that the main factor promoting diversification in this region seems to be long-term ecological adaptation and specialization, and not large-scale events, such as contraction-expansion in and out of glacial refugia [71]. It can be supposed that for *Oxytropis* species from Southern Siberia, the territory of which was not subjected to large-scale glaciations [13], local environmental dynamics and ecological specialization could also contribute to the diversification and radiation processes. Furthermore, it can be assumed that heterogeneous environments in the center of origin of the genus *Oxytropis* provide the climatic and edaphic optimum for the studied species.

Another major reason for the high genetic variability in *Oxytropis* species is polyploidy. It is widely acknowledged that polyploidy has made a major contribution to plant diversification, as well to an increase in genetic variability and the adaptive capacity of species [72–74]. Polyploidy is common in the genus [15,75], with the incidence of polyploidy in *Oxytropis* reaching 58% [76]. Arctic species of the biggest section *Orobia* usually characterized by polyploidy and hybridogenesis. That is why high chromosome ploidity within these species reflects their secondary origin [77].

Chromosome numbers are known for 25 out of 31 *Oxytropis* species studied (Table 1), among which only eight species are diploid. Seventeen species are polyploids or have a variable number of chromosomes (2n): 16 and 32; 16, 32, 48 and 64; 48 and 64. It is clear that the genetic polymorphism in a number of species is partly due to their polyploid origin, both through autopolyploidization and allopolyploidization. Related to these processes are the issues of hybridization, which is also regarded as a relevant process generating diversity in plants. Hybridization and introgression have been considered to be common in the evolution of *Oxytropis* [15], but this will be discussed in the next section.

Thus, the high level of chloroplast gene diversity found for the most of studied *Oxytropis* species from Southern Siberia is determined by the interaction of a wide variety of factors, including range size, topography, local climatic and environmental conditions, habitat specialization, species characteristics, and ploidy levels, as well as genetic and demographic processes in populations.

4.3. Phylogenetic Relationships of Oxytropis Species within Southern Siberia

According to the results of cpDNA variability, it was found that the most of Oxytropis species from Southern Siberia are highly mixed (Figures 3 and 4), and phylogenetic relationships between most taxa remain unresolved. The distribution of haplotypes both in the median network and in the ML tree does neither correspond to the division of the genus into sections nor to the population and species affiliation. The exception is four phyletic lineages (Figure 3) corresponding to the sectional (b1) and species (b2, c1, c2) affiliation. The combining of all haplotypes of O. coerulea and O. filiformis sect. Janthina into one phylogroup (Figures 3 and 4) indicates close genetic proximity of these two species. The remaining three phyletic lineages correspond to the three species, O. microphylla sect. Polyadena (b2), and O. lanata (c1) and O. gracillima (c2) sect Verticillares. All of them are inhabitants of the sandy banks of rivers and lakes [12,15,78]. Earlier, it was noted [77] that one of the ecological bases of evolutionary changes in the genus *Oxytropis* is the colonization of loose sandy substrates. In this case, it is ecological specialization that probably led to the appearance of separate phyletic lineages. In addition, O. lanata and O. gracillima differ morphologically both from each other and from other species of the section: O. lanata belongs to the monotypic subsection Lanatae, O. gracillima belongs to the subsection Gobicola.

All the rest of the species are genetically admixed, although they are morphologically and ecologically differentiated. It is noteworthy that haplotypes of *Orobia* species were present in all three haplogroups (Figure 3). Section *Orobia*, with its huge disjunctive Eurasian-American range, is the largest and one of the most ancient sections of the genus [3,15]. Earlier, based on the morphological traits and ecological specialization of the species, it was shown that the sections *Verticillares, Polyadena*, and *Xerobia* are derivatives from the section *Orobia* [3,74]. Probably, the presence of species of the section *Orobia* in all identified haplogroups may be due to the fact that this section is ancestral to the other sections. The closeness of sections *Orobia, Polyadena*, and *Verticillares* was also shown based on phenetic analysis. At the same time, the section *Xerobia* was distant from this group [2]. Separation of last section may be due to the narrow confinement of the species of this section to cryoxerophytic conditions

of mountain-steppe territories and specific adaptive traits of their morphotype [79]. In our study, most of the species of the section *Xerobia* also took a separate position (haplogroup A, Figure 3), possibly caused by ecological specialization. In addition, the rather separate position of all species of the section *Verticillares* formed haplogroup C and a weak-supported clade on the ML tree (Figures 2 and 3). The only exception is *O. interposita* sect *Verticillares*, whose taxonomic position is controversial: according to Malyshev [15], *O. interposita* is a mutant, and based on our cpDNA data, the species is genetically close to the section *Polyadena* [23,28].

Fourteen of 101 haplotypes identified for 620 samples of 31 Oxytropis species from Southern Siberia were shared by several species of the same section or by species of different sections (Figure 3). Chloroplast sharing between species has been reported for a number of species complexes or for closely related species [62,80-82]. Haplotype sharing can be explained by several reasons, including preserved ancestral polymorphism, incomplete lineage sorting, homoplasy, and introgressive hybridization caused by genetic exchange after secondary contact between previously isolated species, or a combination of several causes [62,80-82]. As for the five shared haplotypes (H25-H29) identified in populations of different species (Figure 3), the spatial distribution of these populations in the sympatric region suggests potential hybridization. The genus Oxytropis is one of the genera with a high frequency of natural hybridization [15]. Our study included six Oxytropis species of hybrid origin (O. bargusinensis, O. microphylla, O. mixotriche, O. peschkovae, O. selengensis, O. tompudae), as well as nine species capable of hybridization, i.e., easily interbreed with other species [15]. Apparently, the reproductive barriers between Oxytropis species are rather weak, which makes possible intensive hybridization between different species or their chromosome races. In addition, the sympatric region with populations having haplotypes H25-H29 belongs to the territory of Baikal Siberia, located at the juncture of three floral regions. In this area, natural hybridization of plants is widespread and often considered as a phenomenon affecting not separate species, including Oxytropis species, but entire plant formations [83]. The remaining shared haplotypes had a disjunctive distribution and were found in spatially isolated populations separated by numerous physical barriers. In this case, ancestral polymorphism and incomplete lineage sorting would explain the presence of shared cpDNA haplotypes. Thus, it can be assumed that both retained ancestral polymorphism and introgression have played roles in the existence of shared haplotypes among Oxytropis species.

The three haplogroups identified in this study reflect the presence of three genetic complexes in the genus Oxytropis on the territory of Southern Siberia, among which one is more isolated (haplogroup A) and the other two (haplogroups B and C) are more closely related. Within each complex, closely related relationships between species and a mixed distribution of haplotypes that did not correspond to either population or taxonomic affiliation were found. The revealed genetic similarity with clear morphological differences is typical of the taxa that have a common origin and have recently undergone rapid adaptive radiation followed by incomplete lineage sorting. Rapid adaptive radiation was shown for the Oxytropis species [4], as well as for the other genera of the family Fabaceae, including Sophora [62], Pultenaea [84], Lupinus [85], Astragalus [68,86], and the species of Indigofera bungeana complex [87]. Rapid radiation may be accompanied by rapid isolation for several species, e.g., for the species of Indigofera bungeana complex [87]. On the other hand, a certain contribution to the complex relationships between the Oxytropis species could be made by hybridization between the incompletely specialized taxa after rapid radiation, which took place at the early stages of the evolution of the genus, but before the divergence of genealogical lineages, as was shown for the *Pultenaea* species [84]. Indirect evidence of rapid radiation and expansion of a number of South-Siberian Oxytropis species is the presence of star-like structures in the haplotype network (Figure 3). Haplogroups B and C contain some star-like structures with one of the shared haplotypes in the center, which are connected to nearest haplotypes through a single mutational step. For example, haplogroup C has a well-defined star-like structure with a shared haplotype H73 in the center (Figure 3). Another signal of expansion is a combination of high haplotype diversity

with low nucleotide diversity, which was determined for more than half of the populations studied (56.5%). The interaction of processes of rapid adaptive radiation and introgression (the last is often complicated by following polyploidization) leads to the reticular evolution of *Oxytropis* species in the center of origin of the genus, which is characteristic for the genus *Oxytropis* at the whole [15], as well as for the closely related genus *Astragalus* [88].

In addition, our results shed light on the taxonomic position of *O. squammulosa* of the sect. *Leucopodia*. This monotypic section is morphologically close to the sect. *Xerobia* [2,89], and, according to Wang, should be merged with sect. *Xerobia* [90]. According to the results of studying the micromorphological traits of *Oxytropis* leaf epidermis [90], *O. squammulosa* did not group together with *O. ciliata* sect. *Xerobia* but was close to the group including *O. muricata* sect. *Polyadena* [90]. These authors concluded that the sect. *Leucopodia* is an independent section [90]. Our results also indicate the closeness of *O. squammulosa* to the species of sect. *Polyadena*. Thus, the haplotypes of *O. squammulosa* and of the species of sect. *Polyadena* together belong to haplogroup B (Figure 3), and on the ML tree *O. squammulosa* and *O. glandulosa* sect. *Polyadena* form a distinct branch with moderate support (Figure 4). At the same time, the absence of shared haplotypes for *O. squammulosa* haplotypes (Figures 3 and 4) confirm the interpretation of the sect. *Leucopodia* as an independent section.

5. Conclusions

Based on cpDNA sequences, the present study reveals the pattern of the genetic diversity and complex phylogenetic relationships of *Oxytropis* species in the center of genus origin. The high level of gene diversity found in most of the populations is shaped by an interplay between numerous factors, among which probably the most important are heterogeneous environmental conditions, life-history traits of species, and their ecological specialization. Phylogenetic relationships between most *Oxytropis* species remain unresolved. Three genetic complexes and four phyletic lineages have been identified. A high level of similarity of the plastid genomes of most *Oxytropis* species can be considered as an indication of their relatively recent divergence from a common ancestor, rapid radiation, a high level of interspecific hybridization, and the reticulate pattern of evolution typical of the genus.

Author Contributions: Conceptualization, D.V.S. and A.B.K.; methodology, D.V.S., A.B.K., M.M.K. and E.V.A.; validation, D.V.S. and A.B.K.; formal analysis, D.V.S., A.B.K., M.M.K. and E.V.A.; investigation, D.V.S., A.B.K., M.M.K. and E.V.A.; data curation, A.B.K.; writing—original draft preparation, A.B.K.; writing—review and editing, D.V.S., A.B.K., M.M.K., E.V.A. and Z.W.; visualization, D.V.S. and A.B.K.; supervision, D.V.S.; project administration, D.V.S. and A.B.K.; funding acquisition, D.V.S. and A.B.K. All authors have read and agreed to the published version of the manuscript.

Funding: This work was supported by the Russian Foundation for Basic Research (Grant No. 16-04-01399-a) and was partially supported by the Russian Federal budget (Project Number 121030900138-8, D.V.S.).

Institutional Review Board Statement: Not applicable.

Data Availability Statement: Original sequence data are available at GenBank (http://www.ncbi. nlm.nih.gov/genbank, accessed on 25 July 2022) by their accession numbers presented in Table 1.

Conflicts of Interest: The authors declare no conflict of interest.

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