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On species status of *Carex sordida* (Cyperaceae)

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Summary. This article deals with the problem of species independence of *Carex sordida*. Closely related species of the sect. *Carex*, *C. sordida*, *C. atherodes*, and *C. drymophila*, were analyzed based on material from Asian Russia. Based on morphological characteristics, it was suggested that *C. sordida* is more closely related to *C. atherodes* than to *C. drymophila*. Molecular analysis using the *matK* plastid gene and the ITS2 and ETS nuclear ribosomal spacers confirmed that *C. sordida* is a distinct species closely related to *C. atherodes*. Several specimens of hybrid origin among the studied species were found. During the revision of herbarium samples, several new localities of *C. sordida* were identified, which significantly expanded its range to the west. In this study, for the first time, distribution maps of *C. sordida*, *C. drymophila*, and *C. atherodes* in the Asian part of Russia were published.

О видовой самостоятельности *Carex sordida* (Cyperaceae)

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Ключевые слова: Азиатская Россия, новые местонахождения, филогения, *Carex*, ETS, ITS2, *matK*.

Аннотация. В данной статье рассматривается проблема видовой самостоятельности *Carex sordida*. Проанализированы близкородственные виды *C. sordida*, *C. atherodes* и *C. drymophila* из Азиатской России. Основываясь на морфологических характеристиках, выдвинуто предположение, что *C. sordida* более тесно связан с *C. atherodes*, чем с *C. drymophila*. Молекулярный анализ с использованием пластидного гена *matK* и ядерных рибосомальных спейсеров ITS2 и ETS подтвердил, что *C. sordida* является отдельным видом, близким к *C. atherodes*. Между изученными видами также было обнаружено несколько экземпляров гибридного происхождения. В ходе пересмотра гербарных коллекций выявлено несколько новых местонахождений *C. sordida*, значительно расширивших его ареал на запад. В данном исследовании приводятся карты распространения *C. sordida*, *C. drymophila* и *C. atherodes* в Азиатской части России.

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Introduction

The genus *Carex* L. is one of the biggest and widespread genera of the world flora. It includes over 2000 species (Reznicek, 1990; Egorova, 1999; Roalson et al., 2021). The sect. *Carex* contains about 30 species, mainly from the temperate and parts of the subtropical belts of the northern Hemisphere, as well as several species from South America (Egorova, 1999). Species of this section live on the plains and in forest belts of mountains on moderately humid places and swamps.

Three closely related species within the sect. *Carex*, *C. atherodes* Spreng., *C. drymophila* Turcz. ex Steud., and *C. sordida* Van Heurck et Müll. Arg., present a taxonomically challenging group with unclear phylogenetic relationships.

Carex sordida was described in 1870 from the collections of Chamisso from the Kamchatka Peninsula (Van Heurck, 1870). G. Kükenthal (1899: 94) described plants of the species from the basin of the Amur River (the Russian Far East) as *C. amurensis*. Later, he referred to the name *C. sordida* as a "species unknown to me" ("*species mihi ignotae*") (Kükenthal, 1909). In the "Flora of the USSR" (Kreczetowicz, 1935) the name *C. sordida* was also placed among "the species of unknown placement". However, in 1939 V. I. Kreczetowicz changed the names of many herbarium specimens in LE that he earlier identified as *C. drymophila* and *C. amurensis* (LE!), to "*C. sordida*".

For a long time, *C. sordida* was believed to be restricted to the Kamchatka Peninsula and the Far East of Eurasia, and to be absent from Siberia. T. V. Egorova (1979) examined the morphology of the species *C. amurensis* and *C. akanensis* Franch. and considered them to be synonyms of *C. sordida*. She also significantly expanded the range of *C. sordida*, which is currently believed to grow in larch forests, floodplain scrublands, on wet meadows, and along the banks of rivers and creeks, in Russia (Eastern Siberia and the Far East), eastern Mongolia, northeastern China, Japan (the Hokkaido Island), and the Korean Peninsula (Egorova, 1999; Hoshino et al., 2011).

However, many researchers did not accept *C. sordida* as a separate species. In the "Flora of Siberia", L. I. Malyschev (1990) identified Siberian plants with the habitus of *C. sordida* as *C. drymophila.* V. N. Voroshilov (1982, 1985), a specialist on the flora of the Russian Far East, also did not recognize *C. sordida* as a distinct species, considering it a synonym of the variety of *C. drymophyla* Turcz. ex Steud. var. *akanensis* (Franch.) Kük. The name *C. drymophila* was initially mentioned by N. S. Turczaninow (1838) as "*nomen nudum*". Later, E. G. Steudel (1855) validly published the name *C. drymophila*. This species is present in Russia, eastern Mongolia, northeastern China, the Korean Peninsula, and northern Vietnam (Egorova, 1999).

Carex atherodes was described from Canada (Sprengel, 1826). Its distribution includes Sweden, Finland, Belarus, Latvia, Estonia, Bosnia and Herzegovina, Germany, Poland, Ukraine, northeastern Turkey, Georgia, Armenia, Russia, Kazakhstan, Mongolia, China, Canada, and the USA (Egorova, 1999; Jiménez-Mejías et al., 2012; Koopman, Więcław, 2018).

The main objectives of this study were to find out if *C. sordida* is indeed a separate species using morphological and molecular characters and to clarify the distribution of *C. sordida* in Russia. To detect phylogenetic relationships among *C. drymophila*, *C. atherodes*, and *C. sordida*, we used plastid (*matK*) and nuclear ribosomal (ETS, ITS2) sequences (Jiménez-Mejías et al., 2016a).

Materials and Methods

In this study we examined herbarium collections of *C. sordida*, *C. drymophila*, and *C. atherodes* specimens stored in Herbaria P, LE, MW, TK, NS and NSK, as well as our own collections. Selected specimens were used for DNA extraction and sequencing of plastid and nuclear loci. Species identification and morphological analysis were based on the studies of V. I. Kreczetowicz (1935), L. I. Malyschev (1990), and T. V. Egorova (1979, 1999). For molecular analysis, we used herbarium specimens from the NSK Herbarium, as well as our own collections (Table 1, Fig. 1).

A total of six specimens was taken for *C. sordida*; ten for *C. drymophila*; and eight for *C. atherodes*. Another six specimens were demonstrated to be of intermediate position between these species.

DNA was extracted using the CTAB method (Clarke, 2009) with modifications. Dried leaves (100–500 mg) were ground in a mortar with sterile sand. The resulting powder was incubated in 1 ml of CTAB buffer (3% CTAB, 1.4 M NaCl, 30 mM Tris-HCl pH 8.0, 2 mM EDTA) for 4 h at 65 °C. Afterwards, 1 ml of chloroform was added, and the tube was centrifuged for 5 min at 16 000 g. An equal volume of isopropanol was added to the supernatant;

the tube was incubated for 5 min and centrifuged for 10 min at 16 000 g. The resulting pellet was dissolved in distilled water and purified on BioSilica columns (Russia) to remove residual polyphenols interfering with PCR reactions.

Table 1

Herbarium specimens taken for molecular analysis

№	**ID**	**Sampling locality**	**Collection date**	**Collectors**
		Carex atherodes		
1	C330	Republic of Altai, Ust-Kan dis., near v. Tyudrala, basin of r. Charysh, 51°00'19.2"N, 84°27'30.9"E	09 VII 2009	I. N. Shekhovtsova
2	C168	Novosibirsk Region, Toguchin dis., Osinovy ridge, 6 km from Peredovoye v. on the road to Taradanovka v., r. Krivoy Ichok	14 VII 1979	N. N. Lashchinskiy
3	C169	Novosibirsk Region, Toguchin dis., Osinovy ridge, 6 km from Peredovoye v. on the road to Taradanovka v., r. Krivoy Ichok	14 VII1979	N. N. Lashchinskiy
4	C170	Krasnoyarsk Territory, Sharypovo dis., near Beresh v., valley of r. Poperechka	9 VIII 1974	V. I. Valutskiy, V. Kaplin
5	C326	Republic of Buryatia, Tunkinsky dis., near Khoito-Gol v., sedge swamp, elev. 971 m, 51°40'16.3"N, 101°31'26.5"E, № 14	14 VIII 2007	I. N. Shekhovtsova, A. A. Petruk
6	C328	Republic of Buryatia, Tunkinsky dis., Tunkin valley, near Ulbugai v., sedge swamp, elev. 719 m, № 8, 51°48'53.3"N, 102°19'51.4"E	12 VIII 2007	I. N. Shekhovtsova, A. A. Petruk
7	C325	Republic of Buryatia, Zakamensky dis., near Bayangol t., right bank of Sangina r., swamp, elev. 1140 m, 50°48'23.20"N, 103°45'37.5"E, № 21a	16 VIII 2007	I. N. Shekhovtsova
8	C329	Republic of Buryatia, Dzhidinsky dis., near v. Khuldata, along the bank, elev. 747 m, № 30, 50°30'03.83"N, 104°42'30.7"E	24 VII 2009	I. N. Shekhovtsova
9	C327	Republic of Buryatia, Severo-Baykalsky dis., near Zarechnoye v., № 413, loc. 19	5 VII 2010	A. V. Verkhozina
10	C248	Republic of Sakha (Yakutia), Aldansky reg., near Verkhnyaya Amga v., left bank of r. Amga, № 4046	14 VIII 1982	K. Bolotnikov
11	C171	Republic of Sakha (Yakutia), Olyokminsky dis., near Chapaevo v., 6 km from the right bank of r. Lena, a lake under mountain top, № 744	9 VIII 1979	M. M. Ivanova
		C. drymophila		
1	C161	Irkutsk Region, Kazachinsko-Lensky dis., Baikal lake, Baikal ridge, r. Kurkula, middle part of forest belt	8 VII 1967	T. V. Egorova
2	C322	Irkutsk Region, Mamsko-Chuysky dis., near Lugovsky t., an island on r. Mama, elev. 240 m, № 1058,	30 VII 1977	M. M. Ivanova, A. Solovyev
3	C321	Irkutsk Region, Mamsko-Chuysky dis., left bank of r. Mama near Polyanovka v., 15 km upstream of Lugovsky t., № 1602	11 VIII 1977	M. M. Ivanova
4	C323	Republic of Buryatia, Severo-Baykalsky dis., Upper Angara valley, near Uoyan t., right bank of r. Upper Angara, № 2440	14 VIII 1976	M. M. Ivanova
5	C320	Irkutsk Region, Bodaibo dis., Vitim Natural Reserve, r. Vitim near the mouth of r. Amalyk, №221	21 VI 1983	E. V. Chechyotkin
6	C318	Irkutsk Region, Bodaibo dis., Vitim Natural Reserve, bank of r. Amalyk, № 247	8 VIII 1988	L. G. Chechyotkina
7	C351	Republic of Sakha (Yakutia), Aldansky reg., valley of r. Yakokut, along the road to Tommot t.	17 VII 1957	Karavaev
8	C165	Republic of Sakha (Yakutia), Zhigansky dis., valley of r. Urunky, swamp	03 VIII 1985	P. Gogoleva
9	C166	Republic of Sakha (Yakutia), Tomponsky dis., 13 km from Nezhdanensky t. along r. Tyra	04 VIII 1984	E. Rybinskaya
10	C231	Khabarovsk Territory, Verkhnebureinsky dis., near Sofiisk t., floodplain of r. Olga, first floodplain terrace	10 VII 1977	A. A. Nechaev

Table 1 (continued)

		C. sordida		
1	C163	Republic of Buryatia, Severo-Baykalsky dis., Upper Angara valley, near Uoyan t., mouth of r. Gonkuli, left tributary of r. Upper Angara, № 2064	19 VIII 1976	M. M. Ivanova
2	C334	Magadan Region, Olsky dis., near Gadlya t.	24 VII 2008	S. V. Ovchinnikova, I. V. Khan, D. S. Lysenko, A. Yu. Ovchinnikov
3	C224	Sakhalin Region, Sakhalin isl., Nogliki dis., upper reaches of r. Daga, floodplain	01 VII 1972	Sokolova, Stovbyr
4	C233	Khabarovsk Territory, Verkhnebureinsky dis., 35 km east of Sofiisk t., basin of r. Silichi, upper reaches of a stream, pass through Sikhote-Alin ridge towards r. Silichi, elev. 1100 m	17 VIII 1978	A. A. Nechaev, A. A. Terlezky, N. V. Frizen
5	C234	Primorsky Territory, Ussuri dis., near Gornotayozhnaya station of the Far Eastern Branch of the Russian Academy of Sciences	26 VII 2001	K. S. Baikov
6	C229	Kamchatka Territory, Elizovo dis., near Elizovo t.	20 VI 1978	A. E. Kozhevnikov
		Hybrid specimens		
1	C162	Irkutsk Region, Bodaibo dis., 28 km upstream of Bodaibo t., left bank of r. Bodaibo, sandy precipice of river terrace, № 631	06 VII 1978	M. M. Ivanova, G. Moskvitina
2	C327	Republic of Buryatia, Severo-Baykalsky dis., near Zarechnoye v., № 413, location 19	5 VII 2010	A. V. Verkhozina
3	C159	Krasnoyarsk Territory, near v. Timba, left bank of r. Podkamennaya Tunguska, floodplain meadow in the mouth of r. Nemba, № 345	8 VII 1980	N. K. Arslanova, N. M. Bolshakov
4	C317	Trans-Baikal Territory, Mogochinsky dis., Ksenyevka station, r. Cherny Uryum	11 VIII 1953	G. A. Peshkova, B. M. Kh.
6	C335	Magadan Region, Olsky dis., basin of r. Oksa, wet soil along the river bank, № 6	25–26 VII 2008	S. V. Ovchinnikova, I. V. Khan, D. S. Lysenko, A. Yu. Ovchinnikov

Note: № refers to Fig. 1; ID – specimen ID; dis. – district; r. – river; isl. – island; t. – town; v. – village; h – height above sea level.

DNA amplifications were performed using commercial PCR mix (Biolabmix, Russia). A fragment of the plastid *matK* gene was amplified using universal primers matK-1 (5′-TTCAA-ATCCT-TCAAT-GCTGG-3′) and matK-3 (5′-TGAGA-GGAAG-GACTG-GAACT-AA-3′) from Shekhovtsov et al. (2012). For the external transcribed spacer (ETS), the universal primers ETS-1F (5′-CTGTG-GCGTC-GCATG-AGTTG-3′) and 18S-R (5′-AGACA-AGCAT-ATGAC-TACTG-GCAGG-3′) from Starr et al. (2003) were used. The complete internal transcribed spacer 2 (ITS2) with flanking sequences were amplified using primers CITS2-F2 (5′-CAACG-GATAT-CTCGG-CTCTC-3′) and CITS2-R2 (5′-GATTC-GCTCG-CCGTT-ACTAT-3′) from Shekhovtsov et al. (2012).

All DNA fragments were sequenced in two directions with the same primers. DNA chromatograms were edited using Chromas v.2.6.6 (Technelysium Pty Ltd). The obtained sequences were deposited in Genbank under accession nos. MW465549–MW465638.

Phylogenetic trees were constructed for single loci, as well as for the concatenated dataset using MEGA X (Kumar et al., 2018). For the Maximum Parsimony (MP) algorithm, the Subtree-pruning-regraphing search was performed. For Maximum Likelihood (ML), the GTR+I+G model was applied. For both algorithms 1000 bootstrap replicates were performed.

Results

Morphological characteristics

In *C. drymophila*, leaf sheaths are always glabrous at the mouth, in contrast to *C. sordida*; utricle (Jiménez-Mejías et al., 2016b) beaks smooth or with solitary bristles. And the main distinctions, to our

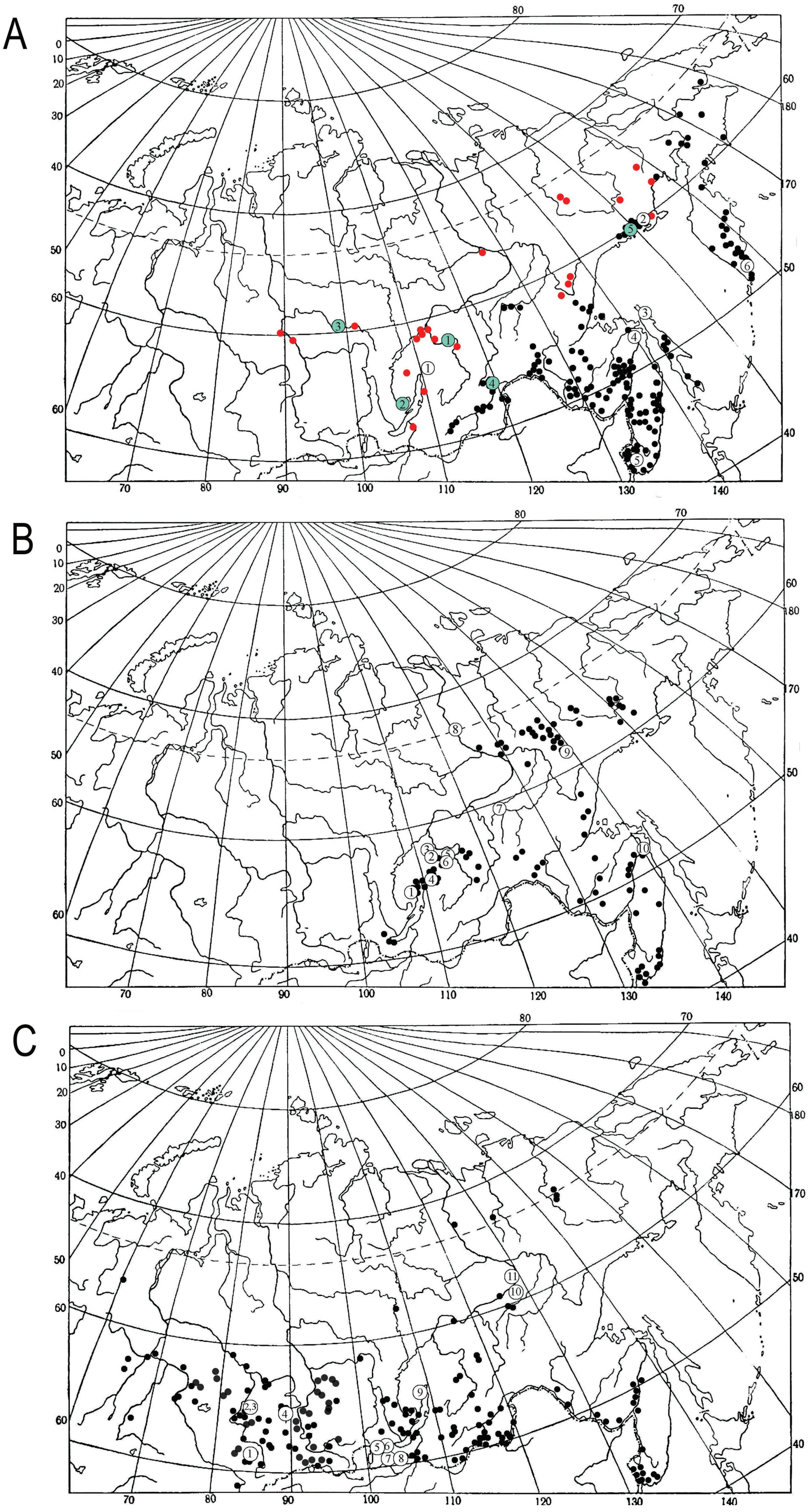

Fig. 1. Geographical distribution of the studied species: A – *Carex sordida*; B – *C. drymophila*; C – *C. atherodes*. Dots – studied herbarium specimens; circles with numbers – the specimens taken for molecular analysis. A: red dots indicate newly found locations for *C. sordida*; green circles with numbers denote specimens of putative hybrid origin.

opinion, are the size and form of the utricle and the length of the beak teeth. In *C. sordida*, utricles are big, 6–(8)9 mm long and 2–3 mm wide, oblong ovoid, inflated in the lower part, with strong veins; beak with two teeth 1.5–2.5 mm long. Utricles in *C. drymophila* are ovoid and somewhat smaller ((4.5)5–7 mm long) with significantly smaller beaks (0.5–1.2 mm long), while in *C. atherodes* they are more similar in size and shape to *C. sordida* (Table 2; Fig. 2); the difference is that utricle beaks in *C. atherodes* have stiff awn-like teeth that are white or of the same color as the utricles.

Table 2

Morphological characters distinguishing *Carex sordida*, *C. atherodes*, and *C. drymophila*

Character	***C. sordida***	***C. drymophila***	***C. atherodes***
№ of male spikes	3–4(5)	2–3(4)	(2)3–5
№ of female spikes	(3)4–5	2–3(4)	(2)3–4
Utricle	glabrous or hairy	glabrous	glabrous or with few hairs
Utricle form	oblong ovoid	ovoid	oblong ovoid
Utricle length	6–8(9) mm	(4.5)5–7 mm	6–10 mm
Utricle beak	teeth long, broad, soft, reddish brown at the edges or, more rarely, same color as the utricle	teeth short, broad, soft, brown at the edges	teeth long, rigid, subulate, same color as the utricle
Utricle beak length	1.5–2.5 mm	0.5–1.2 mm	1–2.5(3) mm
Leaf sheath	hairy, at least at mouth	glabrous	hairy
Length of inflorescence bract sheath	2–7 cm	0–3 cm	1–3 cm
Leaf blade	glabrous or hairy	glabrous	glabrous or hairy

Geographic distribution

We studied herbarium specimens of *Carex sordida*, *C. drymophila*, and *C. atherodes* from Siberia and the Russian Far East (P, LE, MW, TK, NS, NSK) and found a set of new locations (shown by red dots in Fig. 1A) for *C. sordida* that significantly expand its range to the west, which now includes Krasnoyarsk Territory, Irkutsk Region, and Republic of Buryatia (Fig. 1A). The list of new locations includes: **Krasnoyarsk Territory:** "[*Evenkiysky district*], Taimba town, left bank of r. Podkamennaya Tunguska, mouth of r. Nemba. 08 VII 1980. № 345. N. Arslanova, N. Bolshakov" (NSK!); "Vanavara village, basin of the Podkamennaya Tunguska r. 19 VII 1974. S. Andrulaitis" (LE!); "[*Yeniseysky district*], Yartsevo village. 29 VII 1914 and Nazimovo village. 17 VII 1914. № 4534. Z. V. Evseeva" (LE!). **Irkutsk Region:** "[*Bodiabo district*], along the Vitim r., 65 km upstream of Bodaibo town. 1911. anonymous collector" (NSK!); "Bolshoy Severnyi town, 30 km upstream of Mama town along Vitim r., mouth of Takhtyga r. 09 VII 1977. № 184. M. Ivanova, Z. Starovoitova" (NSK!); "Ust-Chuya town. 31 VIII 1977. № 2304. M. Ivanova" (NSK!); "Vitim Natural reserve, Oron lake. 26 VII 1983. S. Ivanova, D. Saiganov" (NSK!); "[*Kazachinsky district*], Konets-Lug village. 05 VIII 1976. Zolotseva, Kornil'ev, Vodopianova" (NSK!). **Republic of Buryatia:** "[*Kabansky district*], mouth of Kabanya r. 22 IX 1940. L. Tyulina" (LE!); "[*Severo-Baykalsky district*], Uoyan town, mouth of r. Gonkuli, left tributary of r. Upper Angara. 19 VIII 1976. M. Ivanova" (NSK!); "lower reaches of r. Chaya, left tributary of r. Lena. 04 VIII 1967. A. V. Belov" (NSK!). **Trans-Baikal Territory**: "[*unknown district*], r. Bely Uryum. 06 VII 1908. I. Novopokrovskiy" (LE!); "[*Nerchinsko-Zavodsky district*], r. Cherny Uryum, Ust-Urov village. 21 VII 1960. L. I. Nomokonov, A. M. Zarubin" (NSK!); "[*Ulyotovsky district*], Deshulan, Chenguruk village, right floodplain terrace of r. Inogda. 05 VII 1963. A. M. Zarubin" (NSK!); "[*Mogochinsky district*], valley of r. Amazar. VII 1965. Larina" (NSK!); "valley of r. Shilka. 1859. Maximovich" (LE!).

We also constructed an updated map for *C. drymophila* and *C. atherodes* in Siberia and the Russian Far East based on the studied herbarium data (Fig. 1B, C).

We reidentified all specimens designated as *C. drymophila* Turcz. ex Steud. from the Kamchatka Peninsula from LE, MW, NS, and NSK, as well as those kindly provided to us by V. V. Yakubov from his personal collection, as *C. sordida*. We found no credible specimens of *C. drymophila* from Kamchatka, which confirms the opinion of T. V.

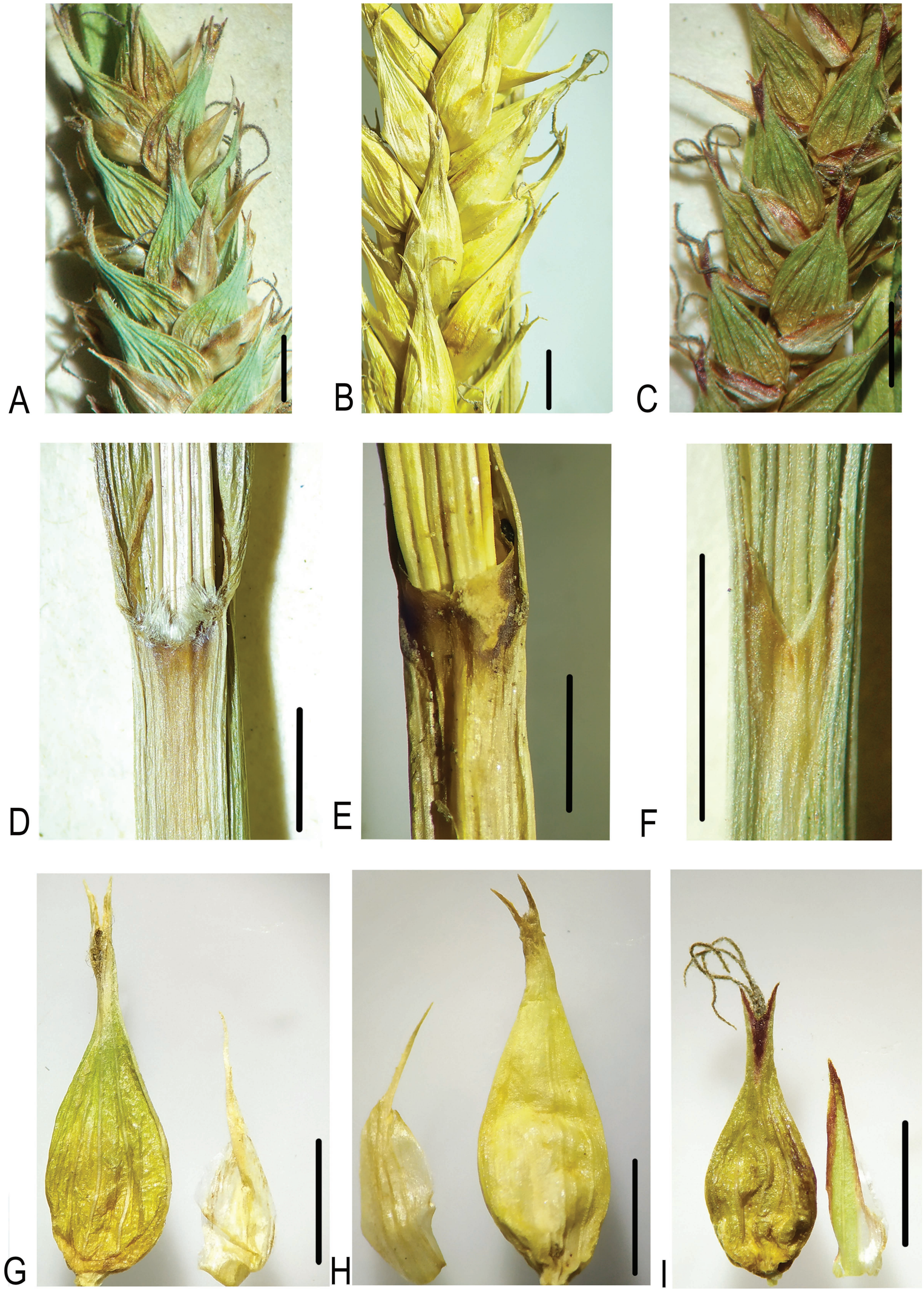

Fig. 2. Morphological distinctions among the studied species: *Carex sordida* (A, D, G), *C. atherodes* (B, E, H), *C. drymophila* (C, F, I). Scale bar – 2 mm.
A, B, C, pistillate spikes; D, E, F, leaf sheaths; G, H, J, utricles and pistillate glumes.

Egorova (1999) that this species is absent from the Peninsula. We should note that V. N. Voroshilov (1985) believed that the type variety of *C. drymophila* is present only on the mainland part of the Russian Far East, while in Kamchatka he recognized only *C. drymophila* var. *akanensis* (Franch.). Kük., which he synonymized with *C. sordida*.

According to T. V. Egorova (1979), one of the reasons of the frequent reports of *C. drymophila* from the Kamchatka Peninsula is the variation of pubescence in *C. sordida*: one can often find specimens with glabrous sheaths, with hairs only near its mouth, and with glabrous leaves and utricles. However, according to our observations, these specimens differ from *C. drymophila* in the utricle form, beak length, and sheath form (Fig. 2). The form and size of utricles are similar in *C. sordida* and *C. atherodes*, and the difference is that utricle beaks in the latter have stiff awn-like teeth that are white or of the same color as the utricles.

The specimen C248 from Yakutia (Aldan reg., near s. Verkhnyaya Amga, left bank of River Amga, 14 VIII 1982. № 4046. K. Bolotnikov (NSK!)) is given in "Flora Siberia" as the only finding of *C. kirganica* for this region (Malyschev, 1990). We re-identified it as *C. atherodes*, which was also confirmed by our molecular analysis. *C. kirganica*, thus, should be excluded from the list of *Carex* species of the flora of Yakutia.

Molecular phylogeny

For all specimens listed in Table 1, we sequenced a fragment of the plastid *matK* gene (591 bp), as well as ribosomal spacers ITS2 (438 bp) and ETS (593 bp). Based on nucleotide substitution patterns (Table 3), three groups corresponding to the studied species could be distinguished. However, six specimens contained several polymorphic positions that could be interpreted as signs of hybrid origin. These intermediate specimens disturbed the stability of the phylogenetic trees; once they were excluded, the three studied species formed monophyletic clades with high bootstrap support (Fig. 3). Phylogenetic analysis recovered *C. sordida* and *C. atherodes* as sister groups, while *C. drymophila* was a more distant relative.

Table 3

Nucleotide substitutions in the studied specimens

Specimen	**matk**				**ITS2**							**ETS**					
	169	**288**	**379**	**405**	**121**	**158**	**159**	**210**	**249**	**284**	**301**	**98**	**109**	**147**	**175**	**498**	**503**
								C. sordida									
C163, C229, C233	T	G	G	C	C	T	A	T	G	G	A	G	A	A	G	T	C
C224, C334	.	.	.	.	.	Y	.	.	.	.	.	.	.	.	.	.	.
C234	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.
								C. atherodes									
C168, C169	C	.	.	.	.	.	G	.	.	.	.	T	.	.	A	.	T
C170	C	.	.	.	Y	.	G	.	.	.	.	T	.	T	A	.	.
C171	C	.	.	.	Y	.	G	.	.	.	.	T	.	.	A	.	T
C248, C329	C	.	.	.	T	.	G	.	.	.	.	T	.	T	A	.	.
C326	C	.	.	.	Y	.	G	.	.	.	.	T	.	.	A	.	.
C328	C	.	.	.	T	.	G	.	.	S	.	T	.	T	A	.	.
								C. drymophila									
C161, C165, C166, C231, C318, C320, C321, C322, C323, C351	C	A	A	A	.	.	.	C	T	C	G	.	G	.	A	A	T
								hybrid specimens									
C162	.	.	.	.	.	.	.	C	T	C	G	.	G	.	A	.	T
C327	C	.	.	.	Y	.	G	.	.	.	.	.	.	.	A	.	Y
C159	.	.	.	.	.	C	R	.	.	.	.	K	.	.	R	.	Y
C317	.	.	.	.	.	.	R	.	.	.	R	.	R	.	R	.	Y
C335	.	.	.	.	.	.	.	.	.	.	.	.	R	.	.	.	Y

Note: Numbers denote positions within the respective sequences; specimen numbers refer to Table 1.

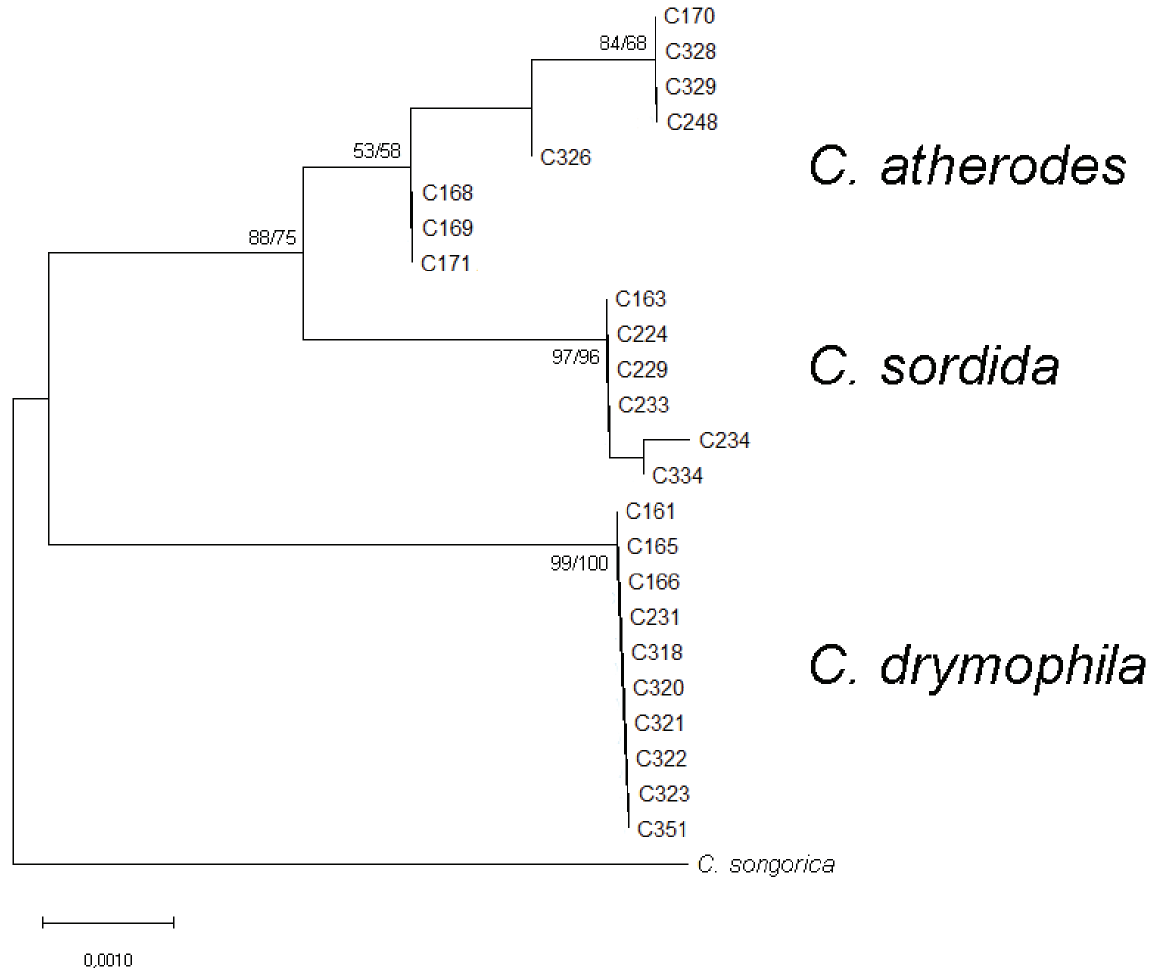

Fig. 3. Phylogenetic tree of the concatenated gene dataset constructed using the ML algorithm. Numbers near the nodes denote MP/ML bootstrap support. Scale bar indicates the expected number of substitutions per site.

Specimens of hybrid origin

Molecular analysis revealed several specimens with patterns of nucleotide variation intermediate between the studied species (Table 3, Fig. 4). The most probable explanation for at least some of them is their hybrid origin.

The specimen C162, which was identified by us as *C. sordida*, had the *matK* gene characteristic for *C. sordida*, and nuclear loci for *C. drymophila* (Table 3). This specimen had hairy leaf sheaths, which is characteristic for *C. sordida* (Fig. 5). However, its beaks were shorter than in *C. sordida*. This specimen was collected in the Irkutsk Region: “left bank of r. Vitim, 20 km upstream from Bodaibo city, on a sandy precipice of the river terrace. 06 VII 1978. № 631. M. Ivanova, G. Moskvitina” (NSK!).

Only three polymorphic sites in ITS2 and ETS sequences consistently differentiate between *C. sordida* and *C. atherodes* (Table 3). In four specimens (C159, C317, C327, C335), one to three of these sites contained degenerate positions that combined nucleotides from both species, as well as several other degenerate sites. Specimen C159 had degenerate positions in all three characteristic sites. It was similar to *C. atherodes* in utricle form and beak characters (stiff awn-like teeth of the same color as the utricle; Fig. 6). Hairs were present only on the upper edge of leaf sheaths. The form of the inflorescence bract sheath typical for *C. sordida*. Leaves glabrous.

In specimen C317, two of the three characteristic positions were degenerate. It was close to *C. atherodes* in overall habitus and in beak form (teeth soft and wide), but its female glumes had awns as in *C. atherodes*.

In specimen C335, only one characteristic site was degenerate, and its morphology was characteristic for *C. sordida*. Specimen C327 was the only one of these four that had the plastid DNA of *C. atherodes*, and most of its characteristic sites were characteristic for that species except one that was typical for *C. sordida*. The morphology of this specimen was also typical for *C. atherodes*.

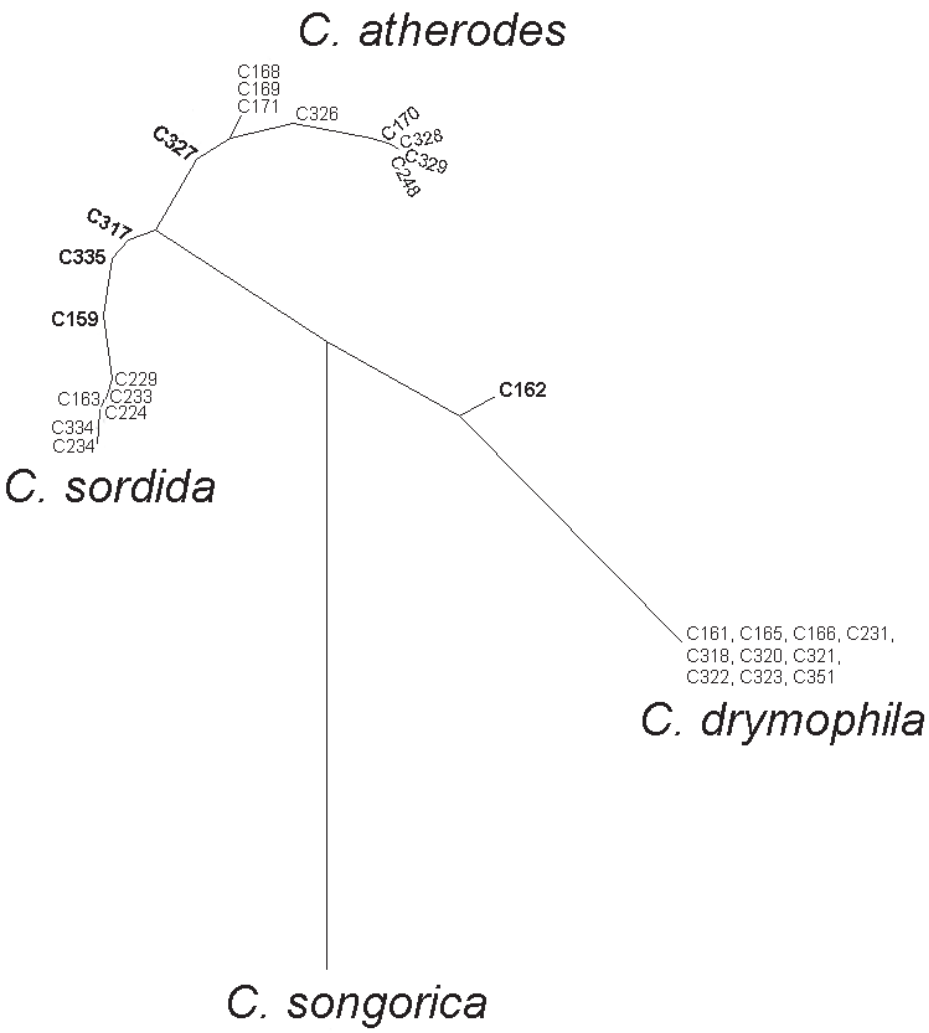

Fig. 4. Radiation phylogenetic tree constructed using the ML algorithm. Putative hybrids are indicated in bold.

Taxonomic treatment

C. sordida Van Heurck et Müll. Arg., 1870, in Van Heurck, Observ. Bot. 1: 33; Kük., 1909, in Engler Pflanzenreich 38: 480 (pro sp. ingot.); V. I. Krecz., 1935, in Fl. USSR 3: 462 (pro sp. obscure.); K. A. Sobolevskaya, 1965, in Fl. Krasn. Kr. 3: 114 (in adnot. *C. drymophila*); L. P. Sergievskaya, 1972, in Fl. Zabaik. 3: 111; T. V. Egorova, 1979, Novosti Sist. Vyssh. Rast. 16: 52; A. E. Kozhevn., 1988, in Sosud. Rast. Sovet. Dalnego Vostoka 3: 338; T. V. Egorova, 1999, Sedges (*Carex* L.) Russia and adjacent states: 163; Doronkin, 2003, in Fl. Sib. 14: 31; A. E. Kozhevn., 2006, in Fl. Ros. Dalnego Vostoka: 316.

On the protologue: "In Kamtschatka, Chamisso, in hb. Van Heurck, sub nomine schedulino hic admisso".

Holotype: [Russia] "Kamtschatka, Chamisso" (BR [BR0000080007753] (photo!) https://www.botanicalcollections.be/specimen/BR0000080007753).

= *Carex akanensis* Franch., 1895, Bull. Soc. Philom. Paris, sér. 8, 7: 51.

Lectotype (Shekhovtsova, designated here): [Japan] "Forêt d'Akan. 31 VII 1893. N 10659. [Faurie]" (P [P00281890] (photo!); iso – P [P00281891] (photo!), [P00284061] (photo!)).

= *Carex amurensis* Kük., 1899, Bot. Centralbl. 77: 94.

Lectotype (Egorova, 1999: 164): [Russia] "Amur, Bölör, in Laubwäldern, häufi. 1 VII 1855. Maximowicz" (LE! [LE 01006688]).

= *Carex amurensis* var. *abbreviata* Kük., 1899, Bot. Centralbl. 77: 95. ≡ *C. hirta* var. γ. Trevir., 1852, in Ledeb. Fl. Ross. 4: 319. ≡ *C. drymophila* var. *abbreviata* (Kük.) Ohwi, 1943, Acta Phytotax. Geobot. 12: 107; Dai et all., 2010, in Flora of China: 413.

Lectotype (Shekhovtsova, designated here): [Russia] "In umbrosis ad fl. Schilka. 1833. [Turczaninow]" (LE! [LE01006962]; iso – LE! [LE01006961], [LE01006960]).

Fig. 5. Morphology of the hybrid specimen C162. A – utricles; B – utricle and pistillate glume; C – habitus.

Fig. 6. Morphology of the hybrid specimen C159. A – utricles; B – utricle and pistillate glume; C – habitus.

C. atherodes Spreng., 1826, Syst. Veg. 3: 828; Malyschev, 1990, in Fl. Sib. 3: 120; A. E. Kozhevn., 1988, in Sosud. Rast. Sovet. Dalnego Vostoka 3: 342, p. p., excl. var. *vix-vaginata* (Kük.) A. E. Kozhevn.; T. V. Egorova, 1999, Sedges (*Carex* L.) Russia and adjacent states: 162; A. E. Kozhevn., 2006, in Fl. Ros. Dalnego Vostoka: 300. ≡ *C. aristata* R. Br. 1823, in Richards. App. VII Bot. in Franklin, Narr. Journey Polar Sea: 753, non Honck. 1792.

On the protologue: "Amer. arctic. (*C. aristata* R. Br.)".

Typus est typus *C. aristatae* R. Br. (Egorova, 1999: 162): [Canada] "Cumberland House, Dr. Richardson" (BM?; iso – NYBG [NY02236998] (photo!), [NY00025111] (photo!); HUH [HUH00027141] (photo!)).

= *C. orthostachys* C. A. Mey., 1833, in Ledeb. Fl. Alt. 4: 231.

Holotypus: [Kazakhstan] "In pratis humidis ad lacum Noor-Saisan. 13 V [1826]. N1465. [Meyer]. Hb. Meyer" (LE!).

A. E. Kozhevnikov (1988) recognized three varieties of *C. atherodes* for the flora of the Russian Far East.

He considered plants with sessile pistillate spikes, utricles 5–6 mm long, and with lowest bract usually sheathless, as *C. atherodes* var. *vix-vaginans* (Kük.) A. E. Kozhevn. The basionym for this combination is a variety proposed by G. Kükenthal (1911), *C. aristata* R. Br. subsp. *raddei* (Kük.) Kük. var. *vix-vaginans* Kük. Its syntypes are three specimens collected by I. V. Kuznetsov from Amgun (No. 158, 204, 409). We identified them as *C. kirganica* Kom., which accords with the opinion of V. I. Kreczetowicz (1935: 411), whose labels can be found on these specimens. We, thus, consider *C. atherodes* var. *vix-vaginans* (Kük.) A. E. Kozhevn. as a synonym of *C. kirganica*.

According to A. E. Kozhevnikov (1988, Fig. 101), it is *C. atherodes* var. *vix-vaginans* (Kük.) that is found in northern Sakhalin. We studied herbarium collections of LE, MW, NS, and NSK, and found no specimens of *C. atherodes* from Sakhalin; the specimens earlier designated as *C. atherodes* were reidentified as *C. sordida* by us.

Big plants with thickened sessile spikes and utricles about 10 mm long were isolated by A. E. Kozhevnikov into the variety *C. atherodes* var. *maxima* (Kük.) A. E. Kozhevn. (basionym: *C. trichocarpa* Muhl. ex Willd. var. *maxima* Kük.). We reviewed the specimens listed by G. Kükenthal in the protologue; in our opinion, they are identical to *C. atherodes.*

The third variety *C. atherodes* var. *orthostachys* (C. A. Mey) A. E. Kozhevn. was also synonymized with *C. atherodes* by T. V. Egorova (1999). Intraspecific diversity of *C. atherodes* requires further investigation using many specimens from throughout its distribution.

C. drymophila Turcz. ex Steud., 1855, Syn. Pl. Glum. 2: 238; Turcz., 1838, Bull. Soc. Nat. Moscou 11, 1: 104, nom. nud; V. I. Krecz., 1935, in Fl. USSR 3: 456, p. p., excl. pl. kamtsch.; A. E. Kozhevn., 1988, in Sosud. Rast. Sovet. Dalnego Vostoka 3: 339, p. p.; Malyschev, 1990, in Fl. Sib. 3: 121, p. p., excl. syn.; T. V. Egorova, 1999, Sedges (*Carex* L.) Russia and adjacent states: 164; A. E. Kozhevn., 2006, in Fl. Ros. Dalnego Vostoka: 303; Dai et all. 2010, in Flora of China: 416, p. p.

On the protologue: "Ad torrentem Chara-Murin Baikal".

Lectotype (Egorova, 1999: 164): [Russia] "Ad torrentem Chara-Murin. 1835. Turczaninov" (P [P00283539] (photo!); iso (5) – P [P00283526] (photo!); K [K000960629] (photo!); LE! [LE01006751], [LE01006752], [LE01006753]).

Discussion

Sedges are one of the most species-rich genera. Morphological distinctions among many of these species are elusive, which impedes both their identification and the reconstruction of phylogenetic relationships using morphological data alone (Jiménez-Mejías et al., 2016a). This is further complicated by the occurrence of intraspecific hybrids with intermediate habitus. These hybrids are often fertile or partially fertile (Cayouette, Catling, 1992; Egorova, 1999).

In this study, we analyzed three closely related and morphologically similar species of the sect. *Carex*: *C. sordida*, *C. atherodes*, and *C. drymophila*. Morphological analysis indicated that *C. sordida* is the sister group of *C. atherodes*, not of *C. drymophila* as believed earlier (Egorova, 1979, 1999). In *C. sordida* and *C. atherodes*, utricles and their beaks are similar in form and size. These two species are also similar in the presence of hairs on utricles and leaf sheaths. They differ by characters of beak teeth (stiff and awn-like in *C. atherodes*, of the same color as the utricle; soft and wide in *C. sordida*, reddish-brown along the edge). *C. drymophila* significantly differs from both species by the form of the utricles (Table 2) and the absence of hairs.

Our hypotheses were corroborated by molecular analysis. *C. sordida* formed a separate clade confirming that it is a separate species. Phylogenetic trees suggest that *C. sordida* is indeed a close relative of *C. atherodes* (Fig. 3).

C. sordida was long believed to be restricted to the Far East of Eurasia and absent from Siberia. T. V. Egorova expanded its range by listing new locations from East Siberia (the Aldan Highlands and the Chita Region) and the Far East. However, L. I. Malyshev (1990) again put *C. sordida* into synonymy to *C. drymophila* in the "Flora of Siberia". *C. sordida* was believed to be absent in certain floristic studies in East Siberia, e. g., "Check-list of the vascular flora of the Irkutsk Region" (Czepinoga et al., 2008), "Identification guide to the plants of Buryatia" (Anenkhonov et al., 2001). The interpretation of geographic ranges of these species was impeded by the fact that *C. sordida* is often confused with *C. atherodes* or *C. drymophila*. We re-examined herbarium material and found multiple cases of misidentified *C. sordida*. Some of these specimens were verified by DNA sequencing, when the state of the specimen allowed that. We could thus significantly expand the range of this species.

Study of herbarium material revealed several specimens that demonstrated intermediate morphology and thus could not be unambiguously identified. Molecular analysis also demonstrated that these specimens did not clearly belong to any of the studied species (Table 3). One of the specimens, C162, can be identified as a hybrid between *C. drymophila* and *C. sordida*: its nuclear DNA sequences belong to the former species, and the plastid ones, to the latter. Its morphology was closer to *C. sordida*, and we suggest it is a result of introgressive hybridization between these two species.

The other four specimens had degenerate positions in nuclear sites distinguishing *C. sordida* and *C. atherodes* (Table 3), so they occupied an intermediate position on phylogenetic trees (Fig. 4). Nuclear sequences of one of them (C159) were degenerate at all characteristic positions and, thus, might be an F1 hybrid. Sequences of another one (C317) were degenerate at two of the three positions. We should note that the studied loci, ITS2 and ETS, belong to the ribosomal cluster. Sequences within this cluster exist as hundreds of tandemly repeated copies in the nuclear genome, so degenerate positions represent the ratio of different copies in the cluster, not two alleles of one locus as is typical for most nuclear genes. The observed pattern may be interpreted either as the result of introgressive hybridization or as incomplete lineage sorting. The latter hypothesis seems less plausible for these specimens, because these two species appear to be sufficiently diverged (Fig. 3). Another two specimens, C327 and C335, had only one non-characteristic position and typical morphology for *C. atherodes* and *C. sordida*, respectively, so it is hard to infer definite conclusions about them.

Recurrent hybridization is a well-known phenomenon in *Carex* (Cayouette, Catling, 1992). Most of the reports of *Carex* hybrids were inferred based on morphological characters, but some were proven by experimental hybridization (Faulkner, 1973; Schmid, 1982; Whitkus, 1988) or molecular analysis (Korpelainen et al., 2010; Jiménez-Mejías et al., 2012; Pedersen et al., 2016; Nowak et al., 2020). It is believed that sympatric sedge species can maintain their integrity despite ongoing hybridization (Schmid et al., 2018), and our results corroborate this hypothesis: although all three studied species have overlapping ranges in Siberia and the Far East (Fig. 1) and can hybridize, they remain distinct in morphology and genetic content.

Conclusions

In this study, we have proved that *C. sordida* is a separate species that is more closely related to *C. atherodes* than to *C. drymophila* as believed earlier. Based on the studies of herbarium specimens, we created a map of its distribution in Asian Russia. We provide the first reports of *C. sordida* from certain regions of Russia (Krasnoyarsk Territory, Republic of Buryatia). Molecular analysis also revealed several cases of intraspecific hybridization between the studied species.

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