Botanica Pacifica. 2023. 12(2):73–80 (This article belongs to the Special Issue dedicated to the memory of Alexey Shipunov)
DOI: 10.17581/bp.2023.12210

BIODIVERSITY STUDIES

Floristic survey of Karaginskii Island (southwest Bering Sea) revealed predictably high diversity of aquatic plants and unexpectedly overlooked terrestrial species

Maria O. Ivanova[1,2]*, Polina A. Volkova[1], Valentin V. Yakubov[3], Yury O. Kopylov-Guskov[2,4], Ivan A. Dadykin[2], Stepan V. Bakhmarin[2] & Alexander A. Bobrov[1]*

Maria O. Ivanova[1,2]*
e-mail: m.ivanova3105@gmail.com

Polina A. Volkova[1]
e-mail: polina.an.volkova@gmail.com

Valentin V. Yakubov[3]
e-mail: yakubov@biosoil.ru

Yury O. Kopylov-Guskov[2,4]
e-mail: yurez-kg@yandex.ru

Ivan A. Dadykin[2]
e-mail: ivan.dadykin@gmail.com

Stepan V. Bakhmarin[2]
e-mail: stepanbahmarin9647@gmail.com

Alexander A. Bobrov[1]*
e-mail: lsd@ibiw.yaroslavl.ru

[1] Papanin Institute for Biology of Inland Waters RAS, Borok, Russia

[2] Lomonosov Moscow State University, Moscow, Russia

[3] Federal Scientific Center of the East Asia Terrestrial Biodiversity FEB RAS, Vladivostok, Russia

[4] Shenzhen MSU-BIT University, Shenzhen, China

* corresponding authors

Manuscript received: 26.05.2023
Review completed: 03.10.2023
Accepted for publication: 15.10.2023
Published online: 17.10.2023

ABSTRACT

Given the high diversity of aquatic habitats with favorable microclimate, surprisingly low number of aquatic vascular species was reported from Karaginskii Island. Therefore, we conducted its extensive field inventory. Terrestrial and bog plant species were also registered on the island whenever possible to check for general completeness of floristic knowledge. We also performed preliminary survey of aquatic flora of adjacent mainland as a reference. We revealed 26 aquatic vascular taxa, new for the flora of Karaginskii Island among which 17 were new to the Karaginskii District. Ten of them were also found on the adjacent mainland; 6 taxa revealed only on the mainland were new for the Karaginskii District. We found 27 terrestrial and bog vascular species, new for the island flora (14 new for the Karaginskii District). The documented deficiency of data on northern Kamchatka (Koryakia) flora hampers informed protection of endangered species and prevents sound biogeographic zonation of Kamchatka.

Keywords: aquatic vascular plants, biodiversity, endangered species, Karaginskii Island, *Sparganium*

РЕЗЮМЕ

Иванова М.О., Волкова П.А., Якубов В.В., Копылов-Гуськов Ю.О., Дадыкин И.А., Бахмарин С.В., Бобров А.А. Флористическое исследование острова Карагинский (юго-запад Берингова моря) выявило ожидаемо высокое разнообразие водных растений и неожиданно пропущенные наземные виды. Несмотря на большое разнообразие водных местообитаний с благоприятным микроклиматом, судя по опубликованным данным, водная сосудистая флора острова Карагинский на удивление бедна. Чтобы проверить это, мы провели тщательные полевые исследования водной флоры острова. По возможности мы также регистрировали наземные и болотные растения на острове для проверки общей полноты флористических данных. Мы также провели предварительное обследование водной флоры ближайшей к острову части материка. Мы обнаружили 26 видов и гибридов водных сосудистых растений, новых для флоры острова Карагинский, из которых 17 оказались новыми для Карагинского района. Десять из них также были отмечены на материке; 6 таксонов, найденных только на материке, оказались новыми для Карагинского района. Мы нашли 27 наземных и болотных сосудистых видов, новых для острова (14 новых для Карагинского района). Продемонстрированная нами неполнота данных о флоре северной Камчатки (Корякии) затрудняет охрану редких видов и ставит под вопрос существующее биогеографическое районирование Камчатки.

Ключевые слова: биоразнообразие, водные сосудистые растения, остров Карагинский, охраняемые виды, *Sparganium*

Electronic Appendix: http://www.geobotanica.ru/bp/2023_12_02/BP_2023_12_2_ivanova_e_suppl.pdf

Recent studies of the aquatic flora of the Far East have shown that its richness is inhibited little by the harsh climate, but rather depends on habitat diversity and the presence of local refugia with favorable microclimate (Bobrov et al. 2021, 2023a, Volkova et al. 2022). In this regard, the low diversity of aquatic vascular plants noted for Karaginskii Island (Bering Sea, northeastern coast of the Kamchatka Peninsula: Barkalov et al. 1986) compared to the entire peninsula (Bobrov et al. 2014) or even to the oceanic Commander Islands (Volkova et al. 2016, 2018) is surprising.

The climate of Karaginskii Island is quite severe. The mean annual temperature is about -1°C, summer lasts only two months, and the average temperature of the warmest, August, is 12°C (Barkalov et al. 1986). Despite this, the island was not completely covered by ice in the Pleistocene (glacier occupied the highest mountains and upper parts of valleys: Kharkevich 1941). The island extends along the mainland for about 100 km, separated by about 50 km of the Litke Straight (Fig. 1). The island is divided into NE mountainous and SE lowland parts by a central mountain ridge with altitudes of 500–900 m (Fig. 2). Thus, the SE lowland, hosting extensive swamps with many hollows and lakes with different mineralization (Supplementary materials: Fig. S1, A), is protected from the cold oceanic influence by the central ridge. This lowland is cut through by numerous rivers, some of which (especially the Gnunvayam, Mamikinvayam, and Markelovskaya rivers) have broad valleys with oxbows (Supplementary materials: Figs S1, F–I). The lower parts of

© The Author(s). 2023 **Open Access** (CC) BY-NC license: https://creativecommons.org/licenses/by-nc/4.0/

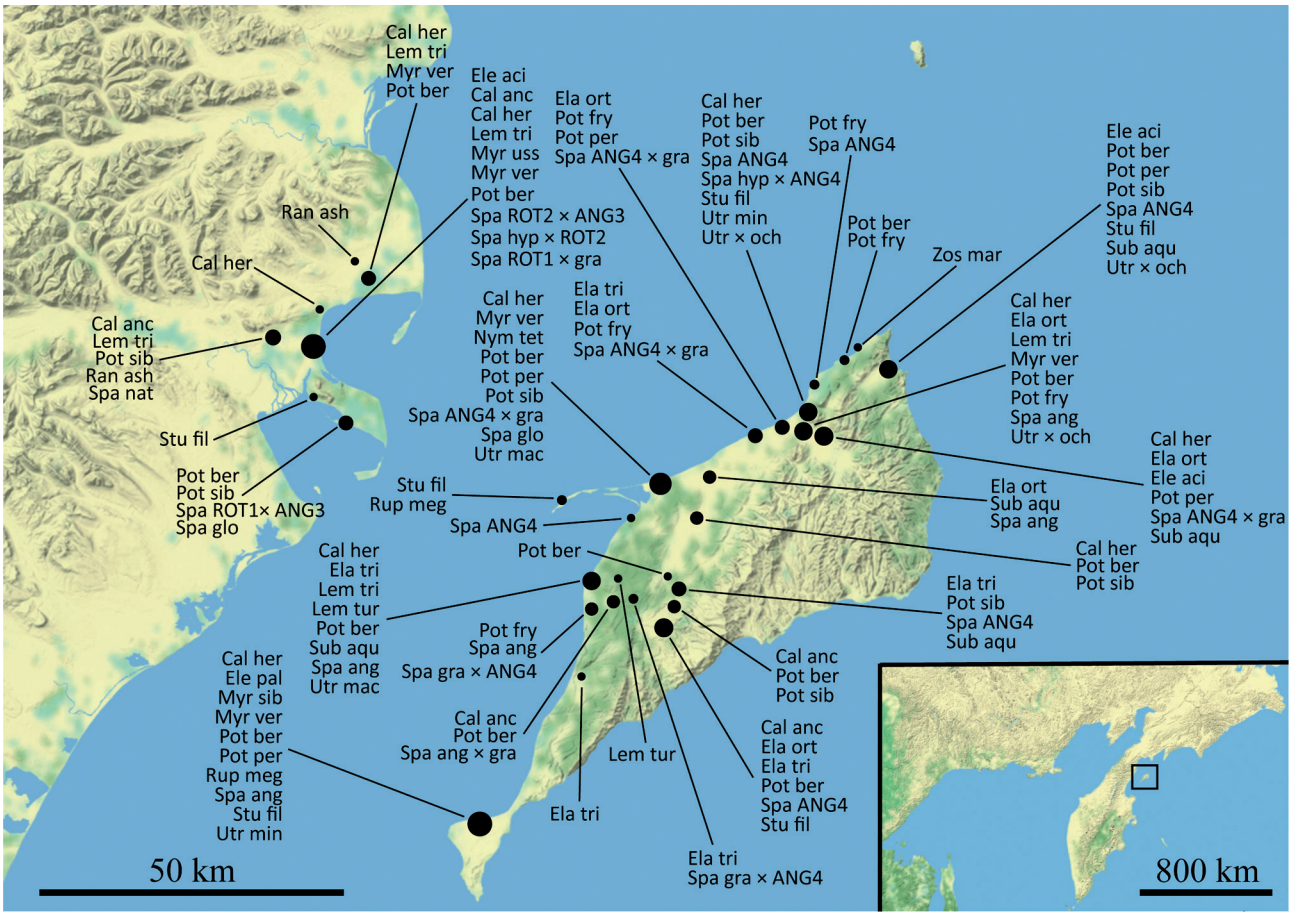

Figure 1 Aquatic flora novelties, revealed by us, in the Karaginskii Island and the adjacent mainland. All taxa names are abbreviated, localities are indicated by circles (with size proportional to a number of new taxa). Whenever possible, nuclear haplotypes (PHYC, following Bobrov et al. 2023b) are indicated with capital letters for *Sparganium angustifolium* Michx. and hybrids with it and with *S. rothertii* Tzvel. (maternal parent is indicated on the first place)

such valleys are characterized by an unusually favorable climate (as evidenced by the presence of alder trees) because they are protected from cold winds from all directions. Estuaries with adjacent coastal marshes are flooded during high tides, forming systems of reservoirs with a salinity gradient. The most prominent of these is the former estuary of the largest river, Mamikinvayam (connected with the sea by an artificial channel in 2018) and representing a lagoon bounded by a ca. 15 km long bar running into the sea. The second major system, Elnavan Lagoon, is located at the southeast extremity of the island and surrounded by numerous waterbodies on ancient marine terraces of different levels (Supplementary materials: Fig. S1, L).

Given the described high diversity of aquatic habitats with a favorable microclimate (Supplementary materials: Fig. S1), the poverty of aquatic vascular flora (13 species) reported for Karaginskii Island (Barkalov et al. 1986) likely reflects insufficient research work rather than the real situation. The flora of the island comprises 490 species (Barkalov et al. 1986) and should be generally well explored, since it has been studied both by single routes since the early 19th century (Voroshilov et al. 1971, Fig. 2) and by the description of four local floras in 1976 (Markelovskaya River basin and main ridge, including its SE macro-slope: Barkalov et al. 1986, Fig. 2). Thus, we assume that the aquatic component has been neglected to some extent in a rather systematic floristic study of the island, as in other regions of the Far East (e.g., Volkova et al. 2022).

To test this assumption, we conducted an extensive field inventory of aquatic vascular plants of Karaginskii Island. To test the overall completeness of floristic knowledge on the island, terrestrial and bog plant species were also recorded whenever possible. As a benchmark, we also conducted a preliminary survey of the aquatic flora of the adjacent mainland.

MATERIAL AND METHODS

Field studies were carried out in 2022 by P. Volkova, M. Ivanova, I. Dadykin and S. Bakhmarin on Karaginskii Island (the whole island was thoroughly explored, except for its southeast part which is poor with waterbodies: 13 July – 13 August, Fig. 2) and the adjacent mainland (vicinity of the Ossora settlement: Russia, Kamchatka Territory, Karaginskii District: 14–18 August, Fig. 1). Since the main object of our study was aquatic flora, the routes (Fig. 2) were associated with most of the island's waterbodies marked on detailed topographic maps or visible on publicly available satellite images. We estimated the frequency of occurrence of aquatic taxa with non-solitary locations on the island following the methodology of Bobrov et al. (2023a): rare (<30 % of the studied waterbodies), sporadically (30–60 %), frequently (>60 %). On Karaginskii Island, in addition to aquatic flora, we collected terrestrial and bog vascular plants whenever

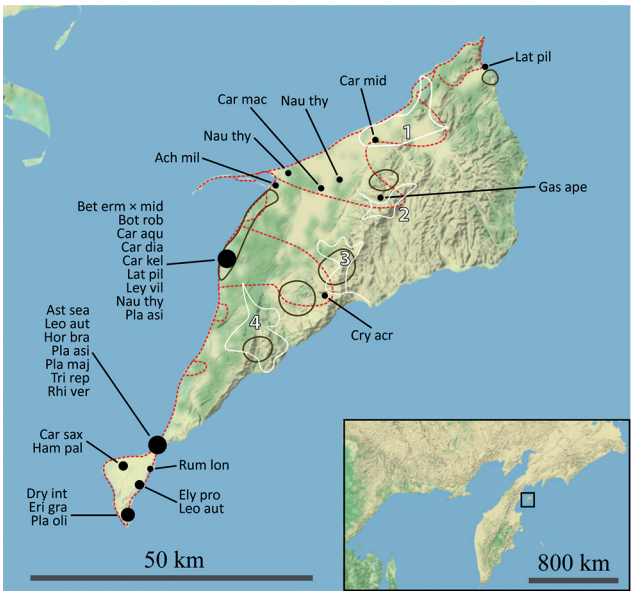

Figure 2 Terrestrial and bog novelties, revealed by us, and floristically explored areas of Karaginskii Island: our studies (tile red dash contours), borders of local floras (Barkalov et al., 1986): white contours (1 – Mt. Pereval, 2 – Mt. Tumannaya, 3 – Mt. Vysokaya, 4 – Markelovskaya River), earlier studies (Voroshilov et al. 1971: brown countours). All taxa names are abbreviated, localities are indicated by circles (with size proportional to a number of new taxa)

possible. All herbarium specimens below are deposited in IBIW (aquatic and bog plants) and MW (Seregin 2023; terrestrial plants). Accession numbers are given if they have already been attributed by the herbarium (scans of vouchered specimens can be obtained from the corresponding authors upon request). Aquatic and bog plants were identified by M. Ivanova and A. Bobrov, and Poaceae taxa were identified by Y. Kopylov-Guskov, *Carex* species by P. Jimenez-Mejias, and other terrestrial plants by V. Yakubov, unless otherwise noted. Identifications in the most important aquatic plant groups were confirmed by genetic analyses detailed for each genus elsewhere (*Callitriche*: Ivanova et al. (2022); *Lemna*: Braglia et al. (2021); *Myriophyllum*: Moody & Les (2007); *Potamogeton*: Bobrov et al. (2018); *Ranunculus* sect. *Batrachium*: Bobrov et al. (2022a); *Sparganium*: Bobrov et al. (2023b); *Stuckenia*: Fehrer et al. (2022)).

We compared our data on the flora of Karaginskii Island with the available information summarized by Barkalov et al. (1986). The general distribution of plants in Kamchatka Territory, unless otherwise indicated, is given from the following sources: Yakubov & Chernyagina (2004) – mainland; Mochalova & Yakubov (2004) – Commander Islands; Bobrov et al. (2014) – aquatic plants; Chernyagina & Devyatova (2018) – alien species. We used the following designations for districts of Kamchatka Territory: A – Aleutskii, B – Bystrinskii, E – Elizovo, K – Karaginskii, M – Milkovo, O – Olyutorskii, P – Penzhinskii, S – Sobolevo, T – Tigil, UB – Ust-Bolsheretsk, UK – Ust-Kamchatsk.

RESULTS

We obtained new data on the aquatic flora of Karaginskii Island and present below its annotated list of 32 species and three hybrids (herbarium labels are given in the Appendix 1). We report for the first time 26 aquatic taxa of the island (Fig. 1) and exclude from its flora four aquatic species (*Hippuris tetraphylla* L. f., *Potamogeton natans* L., *Sparganium gramineum* Georgi, *Utricularia vulgaris* L. – see below). We also identified 27 terrestrial and bog taxa new to Karaginskii Island (Fig. 2). Their exact locations with brief information on their distribution in Kamchatka Territory are given below. Most of the listed new species (17 aquatic and 14 terrestrial and bog species) were recorded for the first time not only for the island, but also for the whole Karaginskii District (marked with asterisks in the list below). Ten of these additions to the district flora were also recorded on the neighboring mainland, in the vicinity of Ossora settlement.

Additionally, we found six more aquatic taxa new for the Karaginskii District on the mainland (the herbarium labels are cited in Supplementary materials: Appendix 1). *Myriophyllum ussuriense* (Regel) Maxim., which is listed in Red Book of Kamchatka Territory (Chernyagina 2018) as rare, was known only from B and E, while *Ranunculus ashibetsuensis* Wiegleb was reported from almost all the districts (Bobrov et al. 2014, Volkova et al. 2016). Four *Sparganium* taxa were documented by genetic analysis (Bobrov et al. 2023b). Namely, *S. natans* L. was previously known only from several localities in Elizovo District. The rarest hybrid between S. *angustifolium* Michx. and S. *rothertii* Tzvel. (*S.* × *komandorense* A.A. Bobrov, Volkova, Mochalova et Chemeris) was previously observed in only two localities in Kamchatka Territory (lower Semyachik River and Bering Island), whereas hybrids of *S. rothertii* with *S. hyperboreum* Laest. (*S.* × *probatovae* Tzvel.) and *S. gramineum* (*S.* × *longifolium* Turcz. ex Ledeb.) are scattered in eastern East Siberia and the Russian Far East (Bobrov et al. 2023b).

Annotated list of aquatic vascular plants of Karaginskii Island

Cruciferae

****Subularia aquatica*** L. Frequently through the island, lakes. It was previously known from B, E, M, O, P, UB, UK and was also collected in the vicinities of Ossora village by O.A. Chernyagina and V.E. Kirichenko (Ossora village, lake, 07.09.2015; IBIW63987) and by us.

Cyperaceae

****Eleocharis acicularis*** (L.) Roem. et Schult. We found this species in two lakes in the northern part of the island. However, we suppose wider distribution of that species through the island. Also, we observed this species in the vicinities of Ossora village. This species was previously known from E and M.

Eleocharis palustris (L.) Roem. et Schult. We found the species only once on the southwest island extremity, but suppose its wider distribution through the island. This species was reported from all Kamchatka districts.

Elatinaceae

Elatine aff. ***triandra*** Schkuhr vel ***americana*** (Pursh) Arnott. Sporadically in the central part of the island, rare in tundra lakes in the NW and SW parts of the island. As in Magadan Region, the plants are morphologically close to *E. triandra* and *E. americana*, reported from the Russian Far East, including eastern Kamchatka (E, K: Bobrov et al. 2023a), but genetically are clearly differentiated from both of them (Ivanova, unpubl.). Taxonomical status of such plants from the northern Far East is to be clarified.

****Elatine orthosperma*** Düben. Sporadically in the northern half of the island. The species is included in the Red Book of Kamchatka Territory (Chernyagina 2018) as rare, being known only from three localities in Kamchatka in UK and E.

Haloragaceae

****Myriophyllum sibiricum*** Kom. We found it only in one lake in the southern part of the island. This species was previously known only from E and UK and was also collected in the vicinities of Ossora village by O.A. Chernyagina and V.E. Kirichenko (Ossora village, lake, 07.09.2015; IBIW63982) and by us.

****Myriophyllum verticillatum*** L. Rare, in lakes and oxbows; also observed in the vicinities of Ossora village. This species was previously known from B, E, M, UB, UK.

Isoëtaceae

Isoëtes asiatica (Makino) Makino. Frequently in different types of fresh waterbodies. The species was identified by sculpture of megaspores (dense sharp spines) and microspores (smooth), observed under scanning electronic microscope (following Volkova et al. 2016). This species was previously recorded only for a single local flora (Tumannaya), while we found it in a number of localities across the whole island. The species is known from the most districts of Kamchatka, including K.

Lemnaceae

****Lemna trisulca*** L. Sporadically in central and northern parts of the island in oxbows of rivers with large valleys; also we revealed it in the vicinities of Ossora village. This species was previously known from E, M, T, UB, UK.

****Lemna turionifera*** Landolt. Frequently in the vicinities of abandoned Yagodnoe village. It was reported for all the districts besides K.

Lentibulariaceae

Utricularia intermedia Hayne. Sporadically in the northern part of the island. This species was previously known only for one local flora (Markelovskaya) and is widespread throughout Kamchatka (all districts).

Utricularia macrorhiza Leconte. Sporadically in the central part of the island; in the oxbows of rivers with large valleys. This species was previously known from several districts, including K (E, M, UB, UK). Only morphologically close *U. vulgaris* was reported for the island basing on collection of K.G. Mertens, made in 1878 from the unknown locality (Voroshilov et al. 1971). As our genus revision in non-tropical Eurasia demonstrated that *U. vulgaris* does not go eastwards further West Siberia (Bobrov et al. 2022b), it should be excluded from the island flora.

****Utricularia minor*** L. Rare, in the southern and northern parts of the island. This species was previously known from B, E, S, UK.

****Utricularia* × *ochroleuca*** R.W. Hartm. (*U. intermedia* × *U. minor*). Sporadically in the northern part of the island. This hybrid was previously known only from E, differing from its parental species by flower shape and by presence of setulae, arising from teeth on margin of ultimate leaf segments (Bobrov et al. 2022b).

Nymphaeaceae

Nymphaea tetragona Georgi. Rare, only in few oxbows in the central part of the island (in the valley of Mamikinvayam River near its estuary). The species is included in the Red Book of Kamchatka Territory (Chernyagina 2018) as rare, being known from almost all districts (E, K, O, P, S, T, UB, UK).

Plantaginaceae

****Callitriche anceps*** Fernald. This species was previously known from the Russian Far East as *C. subanceps* Petrov (Bobrov et al. 2014), but we found that the latter is not differentiated both morphologically and genetically from North American *C. anceps* and should be synonymized with it, but not with *C. palustris* (Ivanova et al. 2022). Apart from the island *C. anceps* was reported from A (Volkova et al. 2016, 2018) and UK; also we revealed it in the vicinities of Ossora village.

****Callitriche hermaphroditica*** L. Frequently in different types of fresh waterbodies. This species was previously known from a number of districts (A, B, E, O, UB, UK, M); also we revealed it in the vicinities of Ossora village.

Callitriche palustris L. Frequently in different types of waterbodies including brackish and temporary waters. This species was previously recorded only for one local flora (Tumannaya), while we found it in a number of localities through the whole island. Apart from the island this species is widespread through Kamchatka (all districts).

Hippuris vulgaris L. Frequently in different types of waterbodies including brackish and temporary waters. This species was previously recorded for all local floras on the island and is widespread through Kamchatka (all districts). Besides typical *H. vulgaris*, on Karaginskii Island we found plants that corresponded to *H. tetraphylla* (also reported from the island) by ecology (brackish waters) and morphology (4–5 wide leaves in each node: Kharkevich 1996). However, the morphotypes, referred to as *H. vulgaris* and *H. tetraphylla*, are not genetically differentiated (Yu et al. 2022) and were merged into one species (*H. vulgaris*). Thus, we excluded *H. tetraphylla* from the list of the island flora.

Potamogetonaceae

Potamogeton alpinus Balb. (*P. tenuifolius* Rafin.). Frequently through the island, mostly in oxbows. This species was previously recorded only for one local flora (Markelovskaya). Apart from K this species is known from A, B, E, T, UB.

****Potamogeton berchtoldii*** Fieb. Frequently in different types of fresh waterbodies; one of the most common aquatic plant species; also we revealed it in the vicinities of Ossora village. This species was previously known from B, E, M, UB, UK.

****Potamogeton fryeri*** A. Benn. Frequently in the northern part of the island and in its central part near abandoned Yagodnoe village. This species was previously known from B, E, T, UB. Morphologically similar *P. natans* was reported for one local flora (Markelovskaya). However, the respective specimen (VLA 291779: basin of "Markelovka" River, 31.07.1976, S. Kharkevich, T. Buch) rather corresponds morphologically to *P. fryeri*. Thus, we excluded *P. natans* from the island flora list.

Potamogeton perfoliatus L. Frequently in the northern and southern parts of the island. This species was previously known from a number of districts, including K.

****Potamogeton sibiricus*** A. Benn. Sporadically in the northern half of the island; also we revealed it in the vicinities of Ossora village. This species was reported only for A and P (Volkova et al. 2016), so our findings in K are the southernmost on the Kamchatka Peninsula.

Stuckenia filiformis (Pers.) Börner. Sporadically through the island in waterbodies with brackish and mineralized water. This species was previously known from several districts, including K (E, O, T, UB, UK).

Stuckenia pectinata (L.) Börner. Frequently in the southern part of the island, one locality in the central part of the island. This species was previously recorded only for one local flora (Markelovskaya). Apart from K this species is known from A, E, M, UB.

Ranunculaceae

Ranunculus trichophyllus Chaix. (*Batrachium trichophyllum* (Chaix) Bosch). Sporadically through the island. It was also reported for local flora Markelovskaya as *B. eradicatum* (Laest.) Fries. (our revision of *Ranunculus* (sect. *Batrachium*) in VLA demonstrated that respective specimens correspond to *R. trichophyllus*). This species was previously known from several districts, including K (A, E, O).

Ruppiaceae

Ruppia megacarpa R. Mason (*R. occidentalis* auct., non S. Wats.). Two lakes with brackish water (in the southern part of the island and on the bar Semyonova). This species was previously known from several districts, including K (A, E, UB, UK). *Ruppia megacarpa* is the correct name for Pacific *Ruppia* plants with retuse or truncate leaves apex (Ito et al. 2014).

Scrophulariaceae

Limosella aquatica L. Frequently through the island. This species was previously recorded only on the sea shore near

Semyonova bar (Voroshilov et al. 1971). Apart from the island this species is widespread through Kamchatka (all districts).

Typhaceae

Sparganium angustifolium Michx. Frequently through the island, mostly in lakes. This species was previously known from most districts, including K (A, E, M, T, UB, UK).

****Sparganium glomeratum*** (Laest.) Neuman. Single locality in the central part of the island (lower part of Markelovskaya River valley); also we revealed it in the vicinities of Ossora village. It was previously known from several districts (E, M, UB, UK). Plants both from the island and the mainland were represented by robust morphotype of *S. glomeratum* with remote female heads that was earlier described as *S. glehnii* Meinsh.

Sparganium hyperboreum Laest. Frequently through the island in lakelets and hollows. It was previously known from most of local floras and is widespread in Kamchatka (all districts). *Sparganium hyperboreum* both on the island and on the mainland was represented by two morphotypes, also differing genetically (Bobrov et al. 2023b): a typical one more abundant that is widely spread in temperate Eurasia and the Asian one, more resembling *S. natans* (the latter morphotype was erroneously taken for the hybrid between *S. hyperboreum* and *S. natans* or described as *S. williamsii* Rydb.).

****Sparganium angustifolium* × *S. gramineum*** (*S.* × *speirocephalum* Neuman). Sporadically in the northern half of the island in different types of fresh waterbodies. The specimen (MHA 0283244: Karaginski Island, in lakelet, 08.08.1969, V. Voroshilov et al.), basing on which *S. gramineum* was listed in the island flora, includes very young individuals with unfolded male heads only and corresponds morphologically rather to this hybrid (or *S. angustifolium*). Thus, *S. gramineum* should be excluded from the island flora, unless some unequivocal specimen is found. This hybrid is usual in North Europe and was reliably reported in the Far East only from single localities in southern Kamchatka and the southern Kurils (Volkova et al. 2022, Bobrov et al. 2023b).

****Sparganium angustifolium* × *S. hyperboreum*** (*S.* × *sachalinense* A.A. Bobrov, Volkova, Mochalova et Chemeris). Single locality in the northern part of the island. This rare hybrid is reliably known from several localities, scattered across North Eurasia (Murmansk Region, lower Kolyma River, Sakhalin and the southern Kuril islands: Bobrov et al. 2023b).

Zosteraceae

Zostera marina L. Frequently on the sea coast. It was reported from the island, basing on data of K. Mertens (Voroshilov et al. 1971), but was excluded from the list of island flora, as the herbarium specimen was not available (Barkalov et al. 1986). *Zostera marina* was previously known from E and K.

Terrestrial and bog species, firstly reported for Karaginskii Island

****Achillea millefolium*** L. – meadow with willows near the estuary of Mamikinvayam River, 58.99999°N 163.94276°E, 19.07.2022. This species was reported as alien from A, T, UK, M, and E districts.

****Astragalus sealei*** Lepage – 2 km W of Mt. Peresheek, meadow near ruins, 58.58237°N 163.57886°E, 14.07.2022. This species was included in the Red Book of Kamchatka Territory (Chernyagina 2018) as rare, being known from E, UK, O, and T.

****Betula ermanii*** Cham. × ***B. middendorffii*** Trautv. et C.A. Mey. – vicinity of abandoned Yagodnoe village, 58.88527°N 163.76469°E, 12.08.2022. Likely it is widespread through the island; both parent species grow on it. This hybrid was previously known only for O (Yakubov 2013). It has intermediate size of trunks, leaves and goslings, comparing with parental species. The hybrid differs from *B. ermanii* by ascending trunks with often shiny reddish-brown bark and from *B. middendorffii* by acutate leaf apex.

****Botrychium robustum*** (Rupr.) Underw. – 1.5 km S of abandoned Yagodnoe village, valley of Gnunvayam River, dry meadow, 58.87433°N 163.78345°E, 06.08.2022. This species was reported from A, UB, S, T, E, M, and UK.

Carex aquatilis Wahlenb. – 3 km E of abandoned Yagodnoe village, lake on the pass between Gnunvayam River and Tusatuvayam River, 58.88427°N 163.81009°E, 12.08.2022, IBIW 67559. This species was reported from all Kamchatka districts.

****Carex diandra*** Schrank – 3 km SES of the mouth of Gnunvayam River, valley of inflow of the river, sedge floating bog, 58.87577°N 163.82054°E, 06.08.2022, IBIW 67560. This species was reported from E, M, and UB.

****Carex kellogii*** Boott – 2 km ENE of abandoned Yagodnoe village, lake shore, 58.89164°N 163.79532°E, 11.08.2022. This species was reported in Russia from Kamchatka, Koryakia and Kuril Islands (Kharkevich 1985), but its exact distribution in Kamchatka Territory remains unknown, because *C. kellogii* is mixed with *C. hindsii* C.B. Clarke (reported from A, E, and UB) by most botanists.

****Carex macloviana*** d'Urv – 5.5 km SSE of mouth of Ploksan River, right inflow of Utuvayam River, banks of stream with spring feed, 58.99611°N 164.08464°E, 26.07.2022. This species was reported from E, UK, and northern Koryakiya.

Carex middendorffii Fr. Schmidt – 3 km S of the mouth of Vakplaksovayam River, peat bog, 59.07236°N 164.25409°E, 22.07.2022. This species was reported from all Kamchatka districts.

Carex saxatilis L. – NE shore of lagoon Elnavan, 58.55138°N 163.47574°E, 16.07.2022. This species was reported from all Kamchatka districts.

Cryptogramma acrostichoides R. Br. – 1.5 km SW of Mt. Tumannaya, bank of the upstreams of Mamikinvayam River, among stones, 58.82400°N 164.0971°E, 09.08.2022. This species was reported for UB, T, E, M, B, UK, and K.

****Dryas integrifolia*** Vahl. subsp. ***crenulata*** (Juz.) Ju. Kozhevn. – 2 km of the summit of Mt. Yuzhnaya, southern foot of the mountain, rubbly slope, 58.46819°N 163.47826°E, 15.07.2022. This species was reported only from O by Neshataeva et al. (2020). This Asian-American species occurs from Baikal to Alaska and is confined to limestones and ultrabasic rocks.

Elymus probatovae Tzvel. – 1 km NE of Mt. Eltklen, roadside of unpaved road in tundra, 58.52199°N 163.52536°E, 15.07.2022. This species (as *E. hyperarcticus* (Polun.) Tzvel.) was previously known from E, K, T, UK.

****Eriophorum gracile*** W.D.J. Koch – 2 km SE of Mt. Yuzhnaya, meadow near stream mouth, 58.46969°N 163.49832°E, 15.07.2022, IBIW 74573. This species was previously known from B, E, M, S, and UB.

Gastrolychnis apetala (L.) Tolm. et Kozhanczikov – Mt. Vysokaya, 2 km NW of its summit, 58.98029°N 164.27119°E, 24.07.2022. This species was reported from all Kamchatka districts.

****Hammarbya paludosa*** (L.) O. Kuntze – NE shore of lagoon Elnavan, 58.55138°N 163.47574°E, 16.07.2022. This species was included in the Red Book of Kamchatka Territory (Chernyagina 2018) as rare, being known from E and UB.

****Hordeum brachyantherum*** Nevski – 2.5 km WSW of Mt. Peresheek, seaside meadow, near ruins, 58.58263°N 163.57855°E, 17.07.2022. That species was reported as alien from A, E, and UB.

Lathyrus pilosus Cham. – (1) vicinity of the estuary of Akanovayam (northern) River, seaside meadow, 59.18809°N 164.59366°E, 29.07.2022; (2) 3 km E of abandoned Yagodnoe village, lake on the pass between Gnunvayam River and Tusatuvayam River, 58.88427°N 163.81009° E, 12.08.2022. In general, the species is common in river valleys on the island. It was reported from all Kamchatka districts.

Leontodon autumnalis L. – (1) 2 km W of Mt. Peresheek, meadow near ruins, 58.58237°N 163.57886°E, 14.07.2022; (2) 1 km NE of Mt. Eltklen, roadside of unpaved road in tundra, 58.52199°N 163.52536°E, 15.07.2022. This species was reported as alien from A, UB, E, M, B, and K.

Leymus villosissimus (Scribn.) Tzvel. – vicinity of abandoned Yagodnoe village, 58.88527°N 163.76469°E, 12.08.2022. This species was previously known from E, M, UK, T, and K.

Naumburgia thyrsiflora (L.) Reichenb. – (1) 5 km WNW of Mt. Troika, shore of creek, flowing from large lake to Utuvayam River, 59.00735°N 164.14238°E, 25.07.2022, IBIW 75622; (2) 2 km SE of estuary of Mamikinvayam River, pebble bank of the creek, 59.01957°N 163.98349°E, 04.08.2022, IBIW 75623; (3) 3 km E of abandoned Yagodnoe village, lake on the pass between Gnunvayam River and Tusatuvayam River, 58.88902°N 163.82323° E, 12.08.2022, IBIW 75625. In general it is common in river valleys on the island. This species was reported from all Kamchatka districts.

****Plantago asiatica*** L. – (1) 2 km W of Mt. Peresheek, meadow near ruins, 58.58237°N 163.57886°E, 14.07.2022; (2) vicinity of abandoned Yagodnoe village, 58.88527°N 163.76469°E, 12.08.2022. This species was previously known from B, E, S, T, UB, and UK.

Plantago major L. – 2 km W of Mt. Peresheek, meadow near ruins, 58.58237°N 163.57886°E, 14.07.2022. This species was reported from all Kamchatka districts as alien.

Platanthera oligantha Turcz. (*Lysiella oligantha* (Turcz.) Nevski) – 1.5 km SE of Mt. Yuzhnaya, tundra near mouth of unnamed stream, 58.47577°N 163.49763°E, 15.07.2022. This species was included in the Red Book of Kamchatka Territory (Chernyagina 2018) as rare, being known from A, O, K, and UK.

****Rhinanthus vernalis*** (N. Zing.) Schischk. et Serg. – 2 km W of Mt. Peresheek, meadow near ruins, 58.58237°N 163.57886°E, 14.07.2022. That species was previously known from UB and E as alien.

Rumex longifolius DC. – 1 km W of cape Tynnik, near buildings, 58.54636°N 163.55629°E, 16.07.2022. This species was reported from all Kamchatka districts as alien.

****Trifolium repens*** L. – 2 km W of Mt. Peresheek, meadow near ruins, 58.58237°N 163.57886°E, 14.07.2022. This species was reported as alien from A, B, E, M, S, T, UB, and UK.

DISCUSSION

The large number of aquatic taxa added to the flora of Karaginskii Island during our focused study is quite expected, given the combination of high habitat diversity and favorable microclimate. All the nine aquatic species that have been reported for the island flora from single localities (Barkalov et al. 1986), not counting the four species we excluded from the island flora, are in fact widespread. Other aquatic taxa are also common on the island, and several species with solitary occurrences are exceptions confined to specific habitats: brackish waters (*Ruppia megacarpa*) or sheltered valleys of large rivers (*Lemna trisulca*, *Nymphaea tetragona*, *Sparganium glomeratum*, *Utricularia macrorhiza*) and a sheltered lake on an ancient marine terrace in a lagoon system (*Myriophyllum sibiricum*).

Almost all the aquatic taxa that we added to the flora of the island (except for those little known to botanists, e.g., *Utricularia* × *ochroleuca*) have already been noted from various areas of the Kamchatka Peninsula, including the Karaginskii District (although many taxa were found there only by us). This rather indicates insufficient study of the aquatic flora of Karaginskii Island and the district as a whole, rather than its floristic uniqueness.

In addition to the relatively high aquatic species richness of Karaginskii Island and the adjacent mainland, we revealed high genetic diversity within taxa using *Sparganium* as a model group (Bobrov et al. 2023b). Thus, hybridization between *S. angustifolium* and *S. rothertii* on the mainland occurred at least twice, as the latter parental species was represented by two haplotypes of the phyC nuclear gene. Interestingly, hybrids with different genotypes were spatially separated: all three specimens collected in the bog along Rybnaya Creek were genetically identical and different from the specimen collected in the vicinity of Karaga village (Fig. 1). A similar pattern was observed for the hybrid between *S. angustifolium* and *S. gramineum* on the island. Thus, *S. angustifolium* served as the pollen donor for two nearby southern locations, while all other samples scattered further north across the island had opposite parental combinations (Fig. 1). Interestingly, all mainland *S. angustifolium* hybrids were represented by a nuclear haplotype detected in pure species only in North America. In contrast, all insular *S. angustifolium* (both as pure species and in hybrids with it) were represented by a unique haplotype originating from common in the Far East. Insular *S. glomeratum* was also genetically distinct from the plants collected on the neighboring mainland. The observed mixture of evolutionary lineages is consistent with the complex history and consequent high intrataxonomic genetic diversity recorded for terrestrial high latitude flora (Brochmann & Brysting 2008).

Our additions to the terrestrial and bog flora of the island are mostly represented by common species widely distributed in Kamchatka. The fact that half of them were listed for the first time for the Karaginskii District also testifies to the poorly studied flora of the island and the district as a whole. Almost all of our terrestrial and bog findings were concentrated on the southern end of the island and in the vicinity of the abandoned Yagodnoe village, the two areas where we had temporary base camps and where we were able to collect all available terrestrial and bog species. A similar result was achieved on Urup Island (southern Kurils: Volkova et al. 2022). In particular, we significantly added alien flora, although previous floristic studies (identifying 13 species: Barkalov et al. 1986) were conducted in the early and mid-twentieth century, when the island was inhabited and actively used by humans. Almost all the 7 alien species we added (with the exception of *Achillea millefolium*) were found on the southwestern peninsula, the only part of the island permanently inhabited to date and still unvisited by botanists (Fig. 2). We categorize the remaining novelties of the terrestrial and bog flora into the following groups: (1) common species accidentally missed in previous surveys (*Dryas integrifolia*, *Lathyrus pilosus*, *Naumburgia thyrsiflora*); (2) rare species confined to specific habitats, possibly not included in earlier floristic routes (e.g. *Astragallus sealei*, *Botrychium robustum*, *Cryptogramma acrostichoides*, *Hammarbia paludosa*, *Platanthera oligantha*); (3) representatives of taxonomically complex groups (e.g., some Caryophyllaceae, Cyperaceae, Poaceae, *Betula* hybrid, *Plantago* species, *Rumex longifolius*). We believe that a detailed study of these and other taxonomically complex groups, e.g., Cyperaceae, Juncaceae, Poaceae, on Karaginskii Island will make it possible to add a large number of new species to its

flora. Studies of the unexplored eastern mountainous part of Karaginskii Island should also bring new floristic data.

The documented scarcity of data on the flora of northern Kamchatka (Koryakia) hinders the justified protection of endangered species under conditions of increasing anthropogenic pressure on the region, especially mining (Yakubov 2022). According to the recent data, 15 vascular plant species native to Karaginskii Island (including the five added in this study) are listed in the Red Data Book of Kamchatka Territory (Chernyagina 2018) mostly as rare (only *Rhodiola rosea* L. is listed as declining in abundance). Therefore, the conservation status of the island should be upgraded from a faunistic area to a universal nature reserve, as proposed by Barkalov et al. (1986). Insufficient floristic knowledge also prevents a sound biogeographic zoning of Kamchatka. In particular, the floristic affiliation of Karaginskii Island (i.e. whether it is closer to the east coast of main Kamchatka or to the isthmus of the peninsula (Kharkevich 1996, Yakubov & Chernyagina 2004)) remains unclear. Therefore, the study of the Koryak flora should be continued.

ACKNOWLEDGEMENTS

We thank OOO "Asuas" (head E.P. Koval) for generous logistic help during the whole expedition and the head of Karaginskii District V.N. Gavrilov for overall support. The authors are grateful to P. Jimenez-Mejias for determination of *Carex* specimens and to O.A. Chernyagina (Kamchatka Branch of the Pacific Geographical Institute FEB RAS) for information on Kamchatka flora. We also thank the personnel of the electron microscopy department of IBIW RAS for help with obtaining images of *Isoëtes* spores. The work was supported by the Russian Science Foundation (project 23-14-00115) and was held within the state assignments of IBIW RAS (theme 121051100099-5) and MSU (theme 121032500084-6).

LITERATURE CITED

Barkalov, V.Yu., A.E. Kozhevnikov, S.S. Kharkevich 1986. Vascular plants of isl. Verkhoturova and Karaginskii (Bering Sea) and protection of their genefund. *V.L. Komarov Memorial Lectures* 33:110–168 (in Russian). [Баркалов В.Ю., Кожевников А.Е., Харкевич С.С. 1986. Сосудистые растения островов Верхотурова и Карагинский (Берингово море) и охрана их генофонда // Комаровские чтения. Вып. 33. С. 110–168].

Bobrov, A.A., O.A. Mochalova & E.V. Chemeris 2014. Notes on aquatic and semiaquatic vascular plants of Kamchatka. *Botanicheskii Zhurnal* 99(9):1025–1043 (in Russian with English abstract). [Бобров А.А., Мочалова О.А., Чемерис Е.В. 2014. Заметки о водных и прибрежно-водных сосудистых растениях Камчатки // Ботанический журнал. Т. 99, № 9. С. 1025–1043].

Bobrov, A.A., E.V. Chemeris, V.A. Filippova & S.Yu. Maltseva 2018. European pondweed in East Siberia: evidence of *Potamogeton rutilus* (Potamogetonaceae) in Yakutia (Asian Russia) with evaluation of current distribution and conservation status. *Phytotaxa* 333(1):58–72.

Bobrov, A.A., O.A. Mochalova & E.V. Chemeris 2021. Aquatic vascular plants of the national park "Beringia" (East Chukotka). *Botanicheskii Zhurnal* 106(1):81–99 (in Russian with English summary). [Бобров А.А., Мочалова О.А., Чемерис Е.В. 2021. Водные сосудистые растения национального парка «Берингия» (восточная Чукотка) // Ботанический журнал. Т. 106, № 1. С. 81–99].

Bobrov, A.A., J. Butkuvienė, E.V. Chemeris, J. Patamsytė, C. Lambertini, A. Aučina, Z. Sinkevičienė & D. Naugžemys 2022a. Extensive hybridization in *Ranunculus* section *Batrachium* (Ranunculaceae) in rivers of two postglacial landscapes of East Europe. *Scientific Reports* 12:12088.

Bobrov, A.A., P.A. Volkova, Yu.O. Kopylov-Guskov, O.A. Mochalova, A.E. Kravchuk & D.M. Nekrasova 2022b. Unknown sides of *Utricularia* (Lentibulariaceae) diversity in East Europe and North Asia or how hybridization explained old taxonomical puzzles. *Perspectives in Plant Ecology, Evolution and Systematics* 54:125649.

Bobrov, A.A., O.A. Mochalova & E.V. Chemeris 2023a. The Kava River basin (northern Okhotsk area) as a hotspot of aquatic macrophyte diversity in northern Pacific. *Biology Bulletin* 50(2):145–156.

Bobrov, A.A., P.A. Volkova, O.A. Mochalova & E.V. Chemeris 2023b. High diversity of aquatic *Sparganium* (*Xanthosparganium*, Typhaceae) in North Eurasia is mostly explained by recurrent hybridization. *Perspectives in Plant Ecology, Evolution and Systematics* 60:125746.

Braglia, L, D. Brevario, S. Gianì, F. Gavazzi, J. De Gregori & L. Morello 2021. New insights into interspecific hybridization in *Lemna* L. sect. *Lemna* (Lemnaceae Martinov). *Plants* 10:2767.

Brochmann, C. & A.K. Brysting 2008. The Arctic – an evolutionary freezer? *Plant Ecology & Diversity* 1(2):181–195.

Chernyagina, O.A. (ed.) 2018. *Red data book of Kamchatka Territory. Vol. 2. Plants*. Kamchatpress, Petropavlovsk-Kamchatskii, 388 pp. (in Russian). [Красная книга Камчатского края / под ред. О.А. Чернягиной. Петропавловск-Камчатский: Камчатпресс. 2018. 388 с.].

Chernyagina, O.A. & E.A. Devyatova 2018. Allien plants of the Kamchatka Territory: distribution and diversity. In: *Conservation of the Biodiversity of Kamchatka and Adjacent Waters. Materials of 17–18th International scientific conference*, pp. 92–101, Kamchatpress, Petropavlovsk-Kamchatskii (in Russian). [Чернягина О.А., Девятова Е.А. 2018. Адвентивные растения Камчатского края: распространение и разнообразие // Сохранение биоразнообразия Камчатки и прилегающих морей: Доклады 17–18 Междунар. науч. конф. Петропавловск-Камчатский: Камчатпресс. С. 92–101].

Fehrer, J., M. Nagy Nejedlá, C.B. Hellquist, A.A. Bobrov & Z. Kaplan 2022. Evolutionary history and patterns of geographical variation, fertility, and hybridization in *Stuckenia* (Potamogetonaceae). *Frontiers in Plant Science* 13:1042517.

Ito, Y., T. Ohi-Toma, A.V. Skriptsova, M. Sasagawa, N. Tanaka & J. Murata 2014. *Ruppia megacarpa* (Ruppiaceae): a new species to the floras of Japan, Korea, and Russia. *Botanica Pacifica* 3(1):49–52.

Ivanova, M.O., P.A. Volkova, I.A. Schanzer, N.G. Arutyunyan & A.A. Bobrov 2022. Genetic legacy of ancient lands: *Callitriche* (Plantaginaceae) indicates Beringia and Paratethys Sea as diversification hotspots for aquatic vascular plants in Eurasia. *Aquatic Botany* 181:103543.

Kharkevich, D.S. 1941. Geological and petrographic sketch of the Karaginskii island. In: *Proceedings of the Kamchatka Complex Expedition 1936–1937*, pp. 3–32, Izdatelstvo AN SSSR, Moscow, Leningrad (in Russian). [Харкевич Д.С. 1941. Геолого-петрографический очерк острова Карагинского // Труды Камчатской комплексной экспедиции 1936–1937 гг. М.; Л.: Изд-во АН СССР. Вып. 3. С. 3–32].

Kharkevich, S.S. 1985–1996. *Vascular plants of the Soviet Far East, vols 1–8*. Nauka, Leningrad – Saint-Petersburg (in Russian).

[Харкевич С.С. 1985–1996. Сосудистые растеня Советского Дальнего Востока. Ленинград – Санкт-Петербург: Наука. Т. 1–8].

Mochalova, O.A. & V.V. Yakubov 2004. *Flora of Commander Islands*. BPI DVO RAN, Vladivostok, 120 pp. (in Russian). [Мочалова О.А., Якубов В.В. 2004. Флора Командорских островов. Владивосток: БПИ ДВО РАН. 120 с.].

Moody, M.L. & D.H. Les 2007. Geographic distribution and genotypic composition of invasive hybrid watermilfoil (*Myriophyllum spicatum* × *M. sibiricum*) populations in North America. *Biological Invasions* 9:559–570.

Neshataeva, V.Yu., V.V. Yakubov, E.Yu. Kuzmina & V.E. Kirichenko 2020. Vegetation cover of the Vetveysky Ridge in the upper reaches of the Vetvey River (Olyutorsky District, Kamchatsky Krai). In: *Conservation of the Biodiversity of Kamchatka and Adjacent Waters. Materials of 21st International scientific conference*, pp. 102–105, Kamchatpress, Petropavlovsk-Kamchatskii (in Russian). [Нешатаева В.Ю., Якубов В.В., Кузьмина Е.Ю., Кириченко В.Е. 2020. Растительный покров Ветвейского хребта в верхнем течении р. Ветвей (Олюторский район, Камчатский край) // Сохранение биоразнообразия Камчатки и прилегающих морей: материалы 21 Международной научной конференции. Петропавловск-Камчатский: Камчатпресс. С. 102–105].

Seregin, A.P. 2023. *Moscow University Herbarium (MW), Version 1.226*, Moscow State Univ. Available from: https://doi.org/10.15468/cpnhcc. Last accessed 14.04.2023.

Volkova, P.A., A.A. Bobrov, Yu.O. Kopylov-Guskov, N.P. Tikhomirov & O.A. Mochalova 2016. Notes on the flora of Commander Islands. *Botanicheskii Zhurnal* 44:829–842 (in Russian with English summary). [Волкова П.А., Бобров А.А., Копылов-Гуськов Ю.О., Тихомиров Н.П, Мочалова О.А. 2016. Заметки по флоре Командорских островов // Ботанический журнал. Т. 44. С. 829–842].

Volkova, P.A., M.O. Ivanova, M.Yu. Grigoryan, Yu.O. Kopylov-Guskov & A.A. Bobrov 2022. Floristic findings and revision of aquatic flora of the Kuril Archipelago reveal no clear differences between biogeographical regions. *Inland Water Biology* 15(6):794–804.

Volkova, P.A., Yu.O. Kopylov-Guskov, N.P. Tikhomirov, M.O. Ivanova & A.A. Bobrov 2018. Notes on the flora of Mednyi Island. *Botanicheskii Zhurnal* 103:528–540 (in Russian with English summary). [Волкова П.А., Копылов-Гуськов Ю.О., Тихомиров Н.П., Иванова М.О., Бобров А.А. 2018. Заметки по флоре острова Медный // Ботанический журнал. Т. 103. С. 528–540].

Voroshilov, V.N., N.N. Gurzenkov & P.G. Gorovoi 1971. To the flora of Karaginskii isand (Kamchatka Territory). In: *Biological resources of terrestrial area of Northern Far East, vol. 1*, pp. 141–152, DVNTs RAN, Vladivostok (in Russian). [Ворошилов В.Н., Гурзенков Н.Н., Горовой П.Г. 1971. К флоре острова Карагинский (Камчатская область) // Биологические ресурсы суши Севера Дальнего Востока. Владивосток: ДВНЦ АН СССР. Т. 1. С. 141–152].

Yakubov, V.V. 2013. Materials for the flora of Kamchatka and Northern Koryakiya. *Conservation of the Biodiversity of Kamchatka and Adjacent Waters. Materials of 14th International scientific conference*, pp. 127–130, Kamchatpress, Petropavlovsk-Kamchatskii (in Russian). [Якубов В.В. 2013. Материалы к флоре Камчатки и Северной Корякии // Сохранение биоразнообразия Камчатки и прилегающих морей: тезисы докладов 14 Международной научной конференции. Петропавловск-Камчатский: Камчатпресс. С. 127–130].

Yakubov, V.V. 2022. Flora of the Mount Seinav surroundings (Vetveisky Range, Koryak Highlands, Kamchatka Krai, Russia). *Biota i sreda prirodnykh territorii* 10(1):5–25 (in Russian with English abstract). [Якубов В.В. 2022. Флора окрестностей горы Сейнав на Ветвейском хребте Корякского нагорья (Камчатский край, Россия) // Биота и среда природных территорий. Т. 10, № 1. С. 5–25].

Yakubov, V.V. & O.A. Chernyagina 2004. *Catalog of the flora of Kamchatka (vascular plants)*. Kamchatpress, Petropavlovsk-Kamchatskii, 165 pp. (in Russian). [Якубов В.В., Чернягина О.А. 2004. Каталог флоры Камчатки (сосудистые растения). Петропавловск-Камчатский: Камчатпресс. 165 с.].

Yu, Y., Q. Lu, A.G. Lapirov, J. Freeland & X. Xu 2022. Clear phylogeographical structures shed light on the origin and dispersal of the aquatic boreal plant *Hippuris vulgaris*. *Frontiers in Plant Science* 13:1046600.