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BIODIVERSITY STUDIES

Driftwood lichens on the Commander Islands (Russia)

Anna S. Zueva[1]*, Irina S. Stepanchikova[1,2], Dmitry E. Himelbrant[1,2], Ivan V. Frolov[3,4], Galina L. Gusarova[2,5], Anna V. Stepanova[1], Viktoria V. Tabakina[1], Irina A. Galanina[6,7]

Anna S. Zueva [1]*
e-mail: annazueva5@gmail.com

Irina S. Stepanchikova [1,2]
e-mail: stepa_ir@mail.ru

Dmitry E. Himelbrant [1,2]
e-mail: d_brant@mail.ru

Ivan V. Frolov [3,4]
e-mail: ivfrolov@gmail.com

Galina L. Gusarova [2,5]
e-mail: galina.gusarova@ibv.uio.no

Anna V. Stepanova [1]
e-mail: stepanovabot@mail.ru

Viktoria V. Tabakina [1]
e-mail: viktoria.pankova.97@gmail.com

Irina A. Galanina [6,7]
e-mail: gairka@yandex.ru

[1] Komarov Botanical Institute RAS, St. Petersburg, Russia

[2] St. Petersburg State University, St. Petersburg, Russia

[3] Institute Botanic Garden UB RAS, Yekaterinburg, Russia

[4] Botanical Garden-Institute FEB RAS, Vladivostok, Russia

[5] The Arctic University Museum of Norway, UiT – Arctic University of Norway, Tromsø, Norway

[6] Federal Scientific Center of East Asian Terrestrial Biodiversity FEB RAS, Vladivostok, Russia

[7] G.B. Elyakov Pacific Institute of Bioorganic Chemistry FEB RAS, Vladivostok, Russia

* corresponding author

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ABSTRACT

Here we present data on 113 driftwood lichen species and two lichenicolous fungi species from the Commander Islands (Bering and Medny islands). Eighty-seven of these species are reported for the Commander Islands for the first time. In addition, 29 species are new to Kamchatka Territory, 14 of them are new to the Russian Far East, and five of them – *Hafellia fosteri*, *Lecania granulata*, *Lecanora aleutica*, *Lichenodiplis fallaciosa*, and *Puttea caesia* – are new to Russia. For all species, we provide coordinates and descriptions of sample plots, as well as the genus to which the substrate wood belongs. A total of 604 lichen specimens were examined and deposited in the LE and LECB herbaria. For four species (*Bacidina indigens*, *B. mendax*, *Lecanora aleutica*, and *Myriolecis* aff. *flowersiana*), ITS sequences were obtained and uploaded to GenBank. We also analysed the distribution of driftwood lichens in relation to influencing factors (substrate species, ornithogenic influence, distance from the coast, altitude, and location of the sample plot on the western or eastern coast of Bering or Medny islands). According to our data, distance from the coast and altitude slightly influence the distribution of lichen species.

Keywords: biodiversity, lichenicolous fungi, new records, North Pacific, Asia

РЕЗЮМЕ

Зуева А.С., Степанчикова И.С., Гимельбрант Д.Е., Фролов И.В., Гусарова Г.Л., Степанова А.В., Табакина В.В., Галанина И.А. Лишайники древесного плавника на Командорских островах (Россия). Приведены данные о 113 видах лишайников и двух видах лихенофильных грибов Командорских островов (о. Беринга и о. Медный), растущих на бревнах плавника. 87 из этих видов приводятся впервые для Командорских островов. Также 29 видов являются новыми для Камчатского края, 14 – для Дальнего Востока и пять (*Hafellia fosteri*, *Lecania granulata*, *Lecanora aleutica*, *Lichenodiplis fallaciosa* и *Puttea caesia*) – для территории Российской Федерации. Для всех видов приведены координаты и описание пробных площадей, а также родовая принадлежность древесины субстрата. Всего исследовано и вложено в гербарии LE и LECB 604 образца лишайников. Для четырёх видов (*Bacidina indigens*, *B. mendax*, *Lecanora aleutica*, and *Myriolecis* aff. *flowersiana*) были получены и загружены в ГенБанк последовательности ITS. Проведен анализ распространения лишайников в зависимости от влияющих на них факторов (породы дерева, орнитогенного влияния, удалённости от берега, высоты над уровнем моря, расположения пробной площади на восточном или западном берегу острова Медный или Беринга). Согласно нашим данным, расстояние от берега и высота над уровнем моря влияют на распределение видов лишайников.

Ключевые слова: биоразнообразие, лихенофильные грибы, новые находки, Северная часть Тихого океана, Азия

The term driftwood refers to trees, logs, or fragments of wood carried by wind, waves, currents, and ice on or over water (Murphy et al. 2021). Natural sources of driftwood (trees, branches, bark, and root systems) typically pass through the four stages of a "driftwood cycle": treefall, river transport, ocean circulation, and coastal delivery (Alix 2005). This process can take months or years (Häggblom 1982, Alix 2005, Murphy et al. 2021). At the same time, driftwood is exposed to a number of aggressive factors, such as salt water, boring marine invertebrates, mechanical impacts on the shore (i.e. surf, ice floes thrown ashore, sandstorms), rains, droppings of seabirds, and the activity of wood-destroying fungi. As a result, the bark and the surface layer of the wood are destroyed, the wood becomes salinated, and its chemistry is altered. All these factors make driftwood a unique substrate, markedly different from forest wood in its properties and, consequently, in the species composition of the lichens it supports. Owing

to the characteristics of driftwood, lichens from several substrate groups can inhabit it. Firstly, driftwood provides a niche for corticolous and lignicolous lichens in tundras and arctic deserts, where trees and large shrubs are absent. Secondly, owing to the high degree of mineralisation and the long-term exposure of this substrate, driftwood can be inhabited by some saxicolous lichens. Thirdly, logs in late stages of decomposition are accessible to tundra terricolous and muscicolous species. Finally, there are lichens found only on driftwood (Zhurbenko & Vekhov 2001, Himelbrant & Kuznetsova 2002, Skazina & Himelbrant 2008a).

There are very few studies focusing on driftwood lichens. One of the key works in this area is an article on lichens of bare wood on Vaygach Island (Zhurbenko & Vekhov 2001). There are also articles that study in detail the driftwood lichens of the White Sea (Himelbrant & Kuznetsova 2002, Zhdanov & Dudoreva 2003), the Barents Sea (Skazina & Himelbrant 2008a), and the Baltic Sea (Skazina & Himelbrant 2008b). In many floristic studies and guides, driftwood lichens are also mentioned, but their number is usually insignificant (1–25 species) (Brodo et al. 2001, Øvstedal et al. 2009, Zhurbenko & Pino-Bodas 2017, Spribille et al. 2023, Zueva et al. 2025a). Most of the available works on driftwood lichens are devoted to the coasts of the western seas of the Arctic Ocean.

Based on published studies, at least 216 species of lichens and allied fungi have been recorded on driftwood worldwide (e.g. Leuthner 1968, Andreyev 1989, Søchting 1989, Laundon 1992, Kuvaev et al. 1994, Arup 1995, Geiser et al. 1998, Brodo et al. 2001, Zhurbenko & Vekhov 2001, Himelbrant & Kuznetsova 2002, Zhurbenko et al. 2002, Zhdanov & Dudoreva 2003, Nash et al. 2004, Piercey-Normore 2005, Øvstedal & Gremmen 2006, Osyczka & Węgrzyn 2008, Skazina & Himelbrant 2008a, b, Urbanavichus et al. 2009, Øvstedal et al. 2009, Sheard 2010, Blanchon et al. 2013, Spribille et al. 2008, 2010, 2014, 2023, McCune 2017, Zhurbenko & Pino-Bodas 2017, Fryday et al. 2019, Fadeeva & Kravchenko 2021, Ekman 2023, Frolov et al. 2025). In the northern regions, where wood-destroying organisms are less active, driftwood lichens are a significant component (up to 22 %) of the overall lichen diversity (Himelbrant & Kuznetsova 2002). Among them there are representatives of various substrate groups – corticolous and lignicolous (*Cetraria sepincola* (Ehrh.) Ach., *Parmeliopsis ambigua* (Wulfen.) Nyl., *Tuckermannopsis chlorophylla* (Willd.) Hale, species of the genera *Calicium* Pers. and *Evernia* Ach., etc.), saxicolous (*Melanelia hepatizon* (Ach.) A. Thell, *Pseudephebe pubescens* (L.) Choisy, *Rusavskia elegans* (Link) S.Y. Kondr. & Kärnefelt, *Umbilicaria deusta* (L.) Baumg., species of the genus *Rhizocarpon* Ramond ex DC., etc.), terricolous and muscicolous lichens (*Alectoria ochroleuca* (Schrank) A. Massal., *Cetraria islandica* (L.) Ach., *Flavocetraria nivalis* (L.) Kärnefelt & Thell, *Gowardia nigricans* (Ach.) Halonen, Myllys, Velmala & Hyvärinen, etc.), and lichens specific to driftwood (*Lecanora orae-frigidae* R. Sant., *Ramalina subfarinacea* (Nyl. ex Cromb.) Nyl., *Xylographa opegraphella* Nyl.).

Studying lichens on driftwood in the north of European Russia, Skazina & Himelbrant (2008a) concluded that (1) lichen diversity increases in the later stages of log decomposition (mainly due to colonisation by species of *Cladonia* P. Browne) and (2) the further north, the smaller the proportion of corticolous lichens and the greater the proportion of saxicolous and driftwood-specific lichens.

The aim of our research is to study the diversity of driftwood-inhabiting lichens in the Commander Islands, a poorly studied territory rich in driftwood. In this study, we intend to: identify lichen species diversity in the Commander Islands in individual sample plots and as a whole; investigate the relationship between species abundance and various factors (substrate wood species, altitude, distance from the coast, location on one or another coast of Bering Island or Medny Island) and to compare the driftwood lichen biota of the Commander Islands with driftwood lichen biota in other areas.

MATERIAL AND METHODS

Study area

The Commander Islands are located in the northwestern part of the Pacific Ocean, between 55°25' and 54°29'N and 165°04' and 168°10'E, about 190 km from the eastern coast of Kamchatka. From the south they are washed by the Pacific Ocean, and from the north by the Bering Sea. The islands represent the westernmost group of the Aleutian (Commander–Aleutian) Arc, like a bridge connecting Eurasia and North America. The Commander archipelago includes two large islands – Bering (area about 1667 km²) and Medny (186 km²), as well as the small Toporkov (0.4 km²) and Ariy Kamen (0.08 km²) islands. The total area of the archipelago is 1854 km² (Mochalova & Yakubov 2004).

The Commander Islands are oceanic in origin and lie on the seabed. The Aleutian Arc in general, and the Commander Islands in particular, represent the peaks of a single underwater volcanic ridge (Ivaschenko et al. 1984). The modern terrain of the Commander Islands is low- and mid-mountain denudation-tectonic, with a predominance of folded-block and erosion-denudation low mountains (maximum heights up to 750 m a.s.l.). The islands are also characterised by a levelled tiered relief created by a series of sea terraces of different levels (Olyunin 1982).

The climate of the Commander Islands is influenced by air circulation processes developing between areas of low and high pressure (the Aleutian Low and the Honolulu High). In addition to atmospheric circulations, sea currents have a huge influence on the climate of the islands. The Commander Islands are influenced by the warm Alaskan Jet Current and the Western Subarctic Gyre (northern branches of the warm Kuroshio Current) and by the cold East Kamchatka Current (Fig. 1). Under the influence of currents, a temperate oceanic climate is formed, with relatively mild winters and cool summers. The average annual air temperature is +2.1 °C, the annual temperature range is low (about 15°C), and the average annual precipitation is about 500 mm (http://komandorsky.ru/territory.html).

The landscape of the Commander Islands, like that of all the islands of the Aleutian Arc, belongs to the group of meadow-tundra landscapes of island arcs of the northern boreal zone (Mochalova & Yakubov 2004). The soil-forming materials on the Commander Islands are basaltic andesite,

Table 1. List of localities.

Abbreviations: SP – names of sample plots. SPs whose names begin with "B" are located on Bering Island, with "M" – on Medny Island.

SP	Location	Coordinates	Altitude, m a. s. l.	Community	Data	Collector
M-5	Staraya Odinochka Bay, northern shore, mouth of the stream	54°38'34.2"N, 167°53'52.9"E	3	driftwood and fisher's bouis in the creek mouth	04.08.2019	DH, IS
M-9	Nikol'skaya Bay, 50 m to the north of the mouth of a stream	54°39'05.4"N, 167°51'59.1"E	0	supralittoral with driftwood	05.08.2019	DH, IS
M-30	Sen'kina Bay, mouth of the stream	54°42'59.2"N, 167°39'25.2"E	0, 3	driftwood in the stream mouth in the supralittoral	12.08.2019	DH, IS
M-40	Zhirovaya Bay, mouth of the stream	54°45'29.9"N, 167°40'17.4"E	3	heap of driftwood in the stream mouth	19.08.2019	DH, IS
B-7	southern part, Lisinskaya Bay, near the Lisinskaya River mouth	54°49'26.4"N, 166°30'28.2"E	3	supralittoral driftwood surrounded by coastal tall grass	07.25.2020	DH, IS
B-22	Peregryobnaya Bay, central part, mouth of the stream in deep valley	54°50'46.8"N, 166°38'19.8"E	1, 5	rocky bed and sides of the creek valley, driftwood surrounded by seaside tall forbs	30.07.2020	DH, IS
B-25	southern part, Peregryobnaya Bay, Peregryobnaya River valley near the mouth, left bank	54°50'39.1"N, 166°38'06.5"E	11	old wooden hut, outdoor table, benches	30.07.2020	DH, IS
B-28	southern part, Serebryannikova Bay, Serebryannikova River mouth	54°47'26.3"N, 166°29'58.2"E	7	driftwood in the streambed and on the banks	30.07.2020	DH, IS
B-30	southern part, central part of the Golodnaya Bay, coastal rampart	54°49'58.6"N, 166°26'31.0"E	3	scarce drfitwood logs on a coastal ridge (supralittoral) surrounded by *Leymus mollis* and *Calamagrostis* sp. community	05.08.2020	DH, IS
B-38	central part, western coast, to the south of Cape Poludenny, supralittoral	54°58'07.2"N, 166°10'42.9"E	2	driftwood on pebble shore covered with *Leymus mollis* and tall forbs (*Senecio cannabifolius* Less., *Filipendula camtschatica* (Pall.) Maxim., *Artemisia opulenta* Pamp.)	10.08.2020	DH, IS
B-40	central part, western coast, Nepropuskovaya Bay, valley of the Chornaya (Nepropuskovaya) River slightly upper than the river mouth	55°01'06.5"N, 166°09'00.2"E	3	driftwood in the streambed and on the banks of the stream at the bottom of the deeply incised wandering valley surrounded by tall forbs (*Senecio cannabifolius*, *Leymus mollis*, *Heracleum lanatum* Michx) deeply incised winding valley	11.08.2020	DH, IS
B-51	northwestern part, Nikolsky Reid, Nikol'skoe, coastal part	55°11'58.4"N, 165°59'55.7"E	5	anthropogenic communities in an old settlement – silicious stones, concrete, driftwood, very old whale bones	16.08.2020	DH, IS
B-56	northwestern part, plateau 200.6 m («Zabiyaka"), eastern part	55°16'40.8"N, 165°54'34.3"E	150	huge, rather decayed driftwood log and boards	18.08.2020	DH, IS
B-72	southern part, eastern coast, Cape Komandor	54°55'51.4"N, 166°31'17.1"E	4	scarce big pieces of driftwood on the edge of the supralittoral with *Leymus mollis* and *Senecio pseudoarnica*	07.08.2021	DH, IS
B-73	southern part, eastern coast, northern part of Komandor Bay, around the first grave of Bering	54°56'07.8"N, 166°30'16.3"E	12	*Sorbus sambucifolia* (Cham.et Schlecht.) M. Roem. and *Salix* spp. thickets in the supralittoral zone, wooden cross erected in 1991	07.08.2021	DH, IS
B-84	central part, eastern coast, Sudovaya Bay	54°56'38.6"N, 166°29'23.3"E	8	old driftwood protruding from the supralittoral and surrounded by *Leymus mollis*	10.08.2021	DH, IS
B-86	central part, eastern coast, Usovaya Bay	54°59'08.7"N, 166°25'15.1"E	8	old driftwood protruding from the supralittoral and surrounded by *Leymus mollis*; one of the trunks 90 cm in diameter	11.08.2021	DH, IS
B-87	central part, eastern coast, northern end of Usovaya Bay	54°59'41.5"N, 166°24'54.9"E	4	old driftwood protruding from the supralittoral and surrounded by *Leymus mollis*: trunk bases and logs with considerable amount of bird droppings	11.08.2021	DH, IS
B-100	southeastern part, bay ca 1 km to south-southeast of Pasenyuk Cape	55°02'18.2"N, 166°23'26.0"E	3	driftwood in the supralittoral (stumps and logs), surrounded by *Leymus mollis*	11.08.2021	DH, IS
B-111	eastern coast, Sosnovaya Bay, the Myakishevskaya River mouth	55°07'57.8"N, 166°17'02.6"E	2	driftwood in the supralittoral, surrounded by *Leymus mollis*	20.08.2021	DH, IS
B-113	eastern coast, north to the Konets Ukhozha River mouth	55°10'03.3"N, 166°15'38.5"E	2	driftwood in the supralittoral (logs), surrounded by *Leymus mollis*	20.08.2021	DH, IS
B-115	eastern coast, south to Myakishevskaya Bay	55°05'39.7"N, 166°20'17.9"E	3	driftwood at the edge of the supralittoral, surrounded by *Leymus mollis*	21.08.2021	DH, IS
B-116	eastern coast, to the south of the Buyan (Buyanovsky Rif) Cape	55°05'17.0"N, 166°21'03.4"E	4	driftwood at the edge of the supralittoral, surrounded by *Leymus mollis*	21.08.2021	DH, IS
B-119	eastern coast, Staraya Odinochka Bay, river mouth	55°06'45.8"N, 166°17'47.2"E	2	driftwood in the stream mouth (logs and stumps), surrounded by *Leymus mollis* and *Senecio pseudoarnica*	21.08.2021	DH, IS

Table 1. Continued.

SP	Location	Coordinates	Altitude, m a.s.l.	Community	Data	Collector
B-122	northern part, eastern coast, Cape Starogavansky to the south of the Staraya Gavan' Bay	55°13'20.0"N, 166°15'01.3"E	3	old wooden buildings (posts of a fur farm from Soviet times, a wall of an old bathhouse), as well as a large driftwood log in the supralittoral	23.08.2021	DH, IS
B-123	northern part, eastern coast, shore between Staraya Gavan' Bay and Stolbovaya	55°14'00.8"N, 166°15'06.6"E	1	driftwood in the supralittoral, surrounded by *Leymus mollis* and *Senecio pseudoarnica*, ornitocoproph. community	27.07.2022	DH, IS, AZ
B-125	northern part, eastern coast, southern part of Tundrovaya Bay, shoreline	55°15'17.7"N, 166°15'02.6"E	4	driftwood in the supralittoral, surrounded by *Leymus mollis* and *Senecio pseudoarnica*, ornitocoproph. influence	27.07.2022	DH, IS, AZ
B-126	northern part, eastern coast, between Tundrovaya and Drovyanaya Blizhniaya bays, shoreline	55°16'16.0"N, 166°15'34.1"E	4	driftwood in the supralittoral, surrounded by *Leymus mollis* and *Senecio pseudoarnica*, ornitocoproph. influence	27.07.2022	DH, IS, AZ
B-129	northern part, eastern coast, southern part of Pryamaya Bay	55°12'05.5"N, 166°14'26.7"E	3	driftwood in the supralittoral, surrounded by *Leymus mollis* and *Senecio pseudoarnica*, ornitocoproph. influence	27.07.2022	DH, IS, AZ
B-167	northern part of the island, western shore, ca. 400 m south to Kitovaya River mouth	55°07'01.5"N, 166°04'36.6"E	2	driftwood (bases of trunks) on the edge of supralittoral with *Leymus mollis* and *Senecio pseudoarnica*, ornitocoproph. influence	07.08.2022	DH, IS, AZ
B-168	northern part of the island, western shore, ca. 100 m north to Kitovaya River mouth	55°07'21.8"N, 166°05'00.7"E	2	driftwood (bases of trunks) in the supralittoral with *Leymus mollis* and *Senecio pseudoarnica*, ornitocoproph. influence	07.08.2022	DH, IS, AZ
B-172	northern part of the island, western shore, cape 82.2 south of Vkhodnoi Rif Cape and south of Nikolskoe	55°11'12.8"N, 165°59'53.0"E	3	rocks in supralittoral (gneisses), ornitocoproph. influence	09.08.2022	DH, IS, AZ
B-174	northernmost part of the island, former settlement Severnoe	55°21'26.0"N, 165°58'26.0"E	37	woody houses, fens, and posts in settlement	10.08.2022	DH, IS, AZ
B-175	northernmost part of the island, seashore west to mouth Bolshoi Rakushnik River	55°21'23.4"N, 166°00'37.6"E	2	huge rocks up to 6-7 m height (conglomerates) and driftwood in upper littoral and supralittoral, ornitocoproph. influence	11.08.2022	DH, IS, AZ
B-176	northernmost part of the island, seashore between mouths of Bolshoi and Maly Rakushnik rivers	55°21'24.6"N, 165°59'52.8"E	2	driftwood in supralittoral, ornitocoproph. influence	11.08.2022	DH, IS, AZ
B-177	northernmost part of the island, cape between mouths of Moroshnik and Fontanka rivers, seashore	55°20'00.3"N, 165°56'19.9"E	1	large boulders and driftwood in upper littoral and at the edge of supralittoral, ornitocoproph. influence	12.08.2022	DH, IS, AZ
B-178	northernmost part of the island, cape W to Madvezhya Bay, seashore	55°19'20.8"N, 165°54'29.0"E	1	driftwood at the edge of supralittoral, ornitocoproph. influence	12.08.2022	DH, IS, AZ
B-181	northernmost part of the island, northern part of Bolshaya Bay	55°20'19.5"N, 166°04'26.8"E	3	driftwood in supralittoral community with *Leymus mollis* and *Honckenya oblongifolia* Torr. et Gray, ornitocoproph. influence	13.08.2022	DH, IS, AZ
M-a17	southeastern end of the island, near southwestern rookery of *Callorhinus usrinus*	54°30'23.1"N, 168°05'35.9"E		steps of old woody stairs	14.07.2022	Mamaev E. G.
B-186	northern part of the island, seashore between Sarannaya and Bolshaya bays northwest to mouth of Sarannaya River	55°19'34.2"N, 166°06'39.0"E	3	driftwood in supralittoral community with *Leymus mollis*, *Heracleum lanatum* (DC.) Ledeb., *Coelopleurum gmelinii* (DC.) Ledeb., and *Senecio pseudarnica*, ornitocoproph. influence	20.08.2022	DH, IS, AZ
B-191	northern part of the island, Bolshaya Bay SE to Tonky Bay	55°19'10.9"N, 166°16'13.0"E	3	driftwood and old fishing garbage in supralittoral community with *Leymus mollis* and *Senecio pseudarnica*, ornitocoproph. influence	21.08.2022	DH, IS, AZ
B-193	northern part of the island, central part of Zasarannaya Bay	55°19'08.1"N, 166°09'21.0"E	5	driftwood on the edge of supralittoral community with *Leymus mollis*, ornitocoproph. influence	23.08.2022	DH, IS, AZ
B-a32	northern part, eastern coast, central part of Tundrovaya Bay, shoreline	55°15'42.6"N, 166°14'30.6"E	3	driftwood in the supralittoral, surrounded by *Leymus mollis* and *Senecio pseudoarnica*, ornitocoproph. influence	27.07.2022	DH, IS

mudstone, and sea sand. They formed several types of soils. These are mainly tundra podburs, alluvial sod, peat-marsh, and turfy subarctic coastal soils.

On the Medny and Bering Islands there are shrub, coastal meadow, tundra, swamp, tundra-marsh, aquatic, and coastal-aquatic vegetation, open vegetation of seacoasts, vegetation of rocks, rocky slopes, screes, and placers of mountain slopes. For our research, of particular interest are the coastal meadows, where driftwood overgrown with lichens is located. The open vegetation of pebble and

sand-pebble beaches is replaced at the lowest levels of the sea terraces by meadows of *Leymus mollis* (Trin.) Plig. or *L. mollis* and *Senecio pseudoarnica* Less. The overall grass cover in such meadows is quite high (80–100 %).

On the Commander Islands, driftwood covered with lichens is found at the lowest levels of marine terraces in the meadows of *Leymus mollis* and *Senecio pseudoarnica* (Fig. 2). This is because tides, surf, and ice floes are usually unable to push logs further inland, whereas in the littoral zone, driftwood is too mobile and unstable for the growth of lichens. To serve as a substrate for lichens, driftwood should enter the supralittoral and remain there more or less motionless for a long time. The vegetation of coastal meadows anchors driftwood logs and protects their surface from sandstorms, creating more favourable conditions for lichens. At the same time, the tightly packed grass cover overshadows driftwood fragments and, in such areas, the growth of lichens is inhibited or even impossible. As a result, the opportunity for the growth of lichens remains only on logs located on the border with the littoral zone, at the mouths of rivers flowing into the sea, or on logs that protrude significantly above the supralittoral vegetation (i.e., where there is almost no shading). Often such protruding parts of driftwood are used as perches by seabirds, which leads to eutrophication of the substrate with their excrements and creates suitable conditions for the growth of ornithocoprophilic species of the family Teloschistaceae.

On the Commander Islands, most of the driftwood fragments can be found within 0–5 m from the upper boundary of the littoral and supralittoral zones. Some driftwood logs were moved by humans to different distances inland (see Table 1: B:56) and used as building (B:25, 73, 174; M:a17) or decorating (B:51) materials.

History of the study of lichens of the Commander Islands

Prior to our study, only two lichenologists visited the Commander Islands – Ernst Bernhard Almquist in 1879 and Hans-Voldemar Trass in 1960. Based on the processing of the Almquist's collection, 114 lichen species were published (Almquist 1887, Nylander 1888). Also in 1928, on Bering Island lichens were collected by phycologist Evgenia Alekseevna Kardakova. These collections, as well as the collections of Trass, remained unpublished (Trass 1963). Historical specimens collected on the islands are stored in the collections of the Natural History Museum in Stockholm, Sweden (S), in the herbarium of the University of Tartu, Estonia (TU), and in the herbarium of the Komarov Botanical Institute, St. Petersburg, Russia (LE). All of them were critically revised by D.E. Himelbrant and I.S. Stepanchikova.

Some of our data (39 species) obtained during fieldwork in 2019–2022 have been already published (Kuznetsova et al. 2021, Frolov et al. 2021, 2025, Printzen et al. 2023; Stepanchikova et al. 2023).

Field study and identification of species

The field investigations have been conducted on the coast of Medny and Bering Islands (Commander Islands, Aleutsky District of Kamchatka Territory) by Irina Stepanchikova (IS) and Dmitry Himelbrant (DH) in July and August 2019–2021, and in July and August 2022 they were accompanied with Anna Zueva (AZ). Altogether 43 sites with driftwood were studied – 41 standard sample plots (SP, squares 10 × 10 m or 20 × 5 m) and two additional sample plots with varying sizes (Fig. 3). In standard SP, the whole lichen diversity on all available substrates was thoroughly described and in additional SP only the most interesting substrates and species were studied. List of the SPs is given in Table 1. Preparation and analysis of cartographic materials were carried out using the QGIS Desktop 3.24.0 construction system. Geographical coordinates are given in the coordinate system WGS 84.

The laboratory study was carried out following the standard technique (Smith et al. 2009, Stepanchikova & Gagarina 2014) at the Department of Botany, St. Petersburg State University. The specimens were studied using a binocular stereoscopic microscope Leica EZ4, transmitted light microscopes Leitz Laborlux S and Carl Zeiss Axioskop 40, and a standard set of chemical reagents for color spot reactions. IS, DH, and AZ identified most of the specimens, I.V. Frolov (IF) – lichens of the family Teloschistaceae, I.A. Galanina – genus *Rinodina* (Ach.) Gray. Photographs of the specimens were taken with QImaging MicroPublisher 5.0 RTV camera established on transmitted light microscope Carl Zeiss Axioskop 40. Nomenclature of lichens and lichenicolous fungi follows Fryday (2002), Diederich (2003), Deneka (2005), Fryday & Coppins (2012), McCune (2017), Westberg et al. (2021), Spribille et al. (2023) and Frolov et al. (2025). Nomenclature of vascular plants follows the Plants of the World Online database (http://www.plantsoftheworldonline.org). All studied specimens are stored in the herbaria of the Department of Botany, St. Petersburg State University (LECB) and Laboratory of Lichenology and Bryology, Komarov Botanical Institute (LE).

Chemical analysis

Some specimens were studied to confirm species identity using high performance thin-layer chromatography (HPTLC) in solvent systems A, B and C (Orange et al. 2001) by IS and AZ in the laboratory of Lichenology and Bryology of the Komarov Botanical Institute RAS..

Molecular analysis

To identify some species, molecular barcoding was used in addition to morphological and chemical analyses. Specimens of the family Teloschistaceae were studied by IF using methods described in Frolov et al. (2021). Other groups were studied by IS and V. V. Tabakina using primers ITS1F (Gardes & Bruns 1993) and ITS4 (White et al. 1990). The following PCR cycling parameters were applied to amplify nuclear ITS region: 1) 94°C 2 min., 2) 35 cycles: 30 s. at 94°C – 1 min. at 60°C – 1 min. at 72°C; 3) 7 min. at 72°C (Guzow-Krzemińska et al. 2019). Sequence alignment was performed in Unipro UGENE ver. 46.0 and MEGA 11. The obtained sequences were compared with sequences from the GenBank database (http://www.ncbi.nlm.nih.gov/BLAST/) using BLASTn search (Altschul et al. 1990). The research was carried out using the equipment of the resource center of the Science Park of St. Petersburg State University

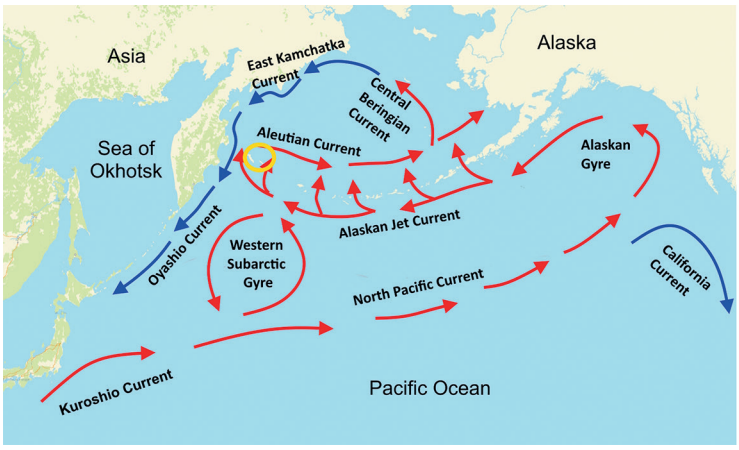

Figure 1 Currents in the North Pacific (based on http://komandorsky.ru/territory.html and Liu et al. 2004). Warm currents are indicated by red and cold currents by blue arrows. Commander Islands are marked with yellow circle)

Figure 2 Driftwood logs on Medny Island. Logs lying in the intertidal zone (white, in the lower half of the photo) are moved by ice and surf and remain uninhabited, whereas logs in the supralittoral zone (darker, in the center of the photo, with one end fixed in the supralittoral and part hanging in the air) are stable and colonized by lichens

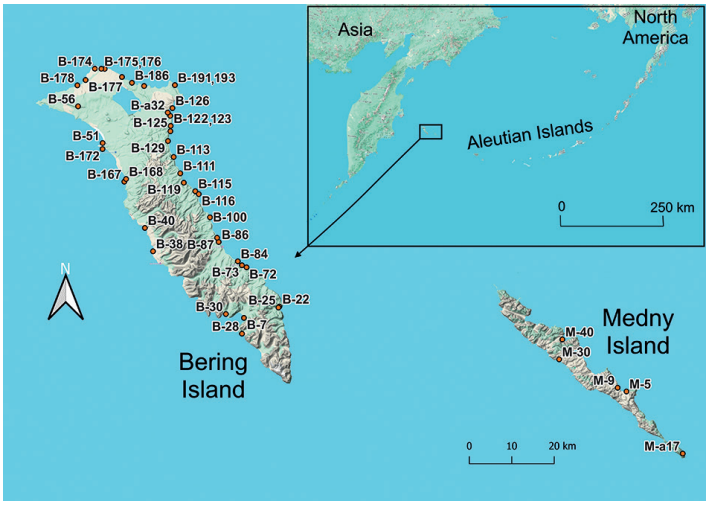

Figure 3 Location of sample plots with driftwood on the Commander Islands

"Development of molecular and cellular technologies" (project 109-28907 "Epixylic lichens of the coasts of the Commander Islands") and in Komarov Botanical Institute RAS. The obtained sequences of *Bacidina indigens*, *B. mendax*, *Lecanora aleutica*, *Myriolecis* aff. *flowersiana* and species of the family Teloschistaceae were loaded into the BLAST (http://www.ncbi.nlm.nih.gov/BLAST/). The GenBank accession numbers are given in the section Results and discussion and in Frolov et al. (2025).

Identification of driftwood tree species

Most substrate wood fragments were identified to genus using anatomical characteristics. The genus identity was determined for all wood fragments on all SPs except substrate at later stages of decomposition, some specimens of fruticose and foliose lichens (genera *Cladonia*, *Peltigera*, *Ramalina*), which were collected without substrate wood, and some species from the genus *Rinodina* and the family Teloschistaceae, submitted to specialists for analysis. For each piece of wood three sections (transverse, radial and tangential) were made with a razor blade. Sections were stained with safranin and methylene blue and discribed using common terminology and rules (Yatsenko-Khmelevsky 1954, Hellman 2013). The taxonomic affiliation of driftwood was identified using the InsideWood electronic database (http://insidewood.lib.ncsu.edu/search) and handbooks Yatsenko-Khmelevsky (1954), Vikhrov (1959), and Budkevich (1961).

Substrate and ecological analyses

Substrate and ecological analyses were carried out using the R/RStudio program. Non-metrical multidimensional scaling (NMDS) was used to analyze sample plots and substrates depending on the similarity of species composition on them. The Jaccard index was used for distance. Using the "*envfit*" function, factors reliably affected on species composition were found ($P<0.05$). The analysis of the SPs considered the influence of factors such as altitude, distance from the coast, the location of the sample plots on western or eastern coast of an island or on Bering or Medny islands. We also assessed how species richness on SPs correlates with ordination. In the analysis of the substrates, the influence of such factors as coniferous or deciduous nature of the substrate and species reachness on substrate was considered. Graphs, showing location of the SPs and substrates in the space of the hypothetical axes NMDS1 and NMDS2, were prepared with package "*ggplot2*". The closer sample plots (or substrate) are located on the graph, the more similar the species composition of lichens on them.

The distribution of species among different woods is shown in the Upset diagram (analogous to the Venn diagram) (Conway et al. 2017).

For occurrence analysis, 6 categories with a step of 20 % (Westhoff & van der Maarel 1973) were established (see Table 2): R1 (rare, singular) – single record – the species was found once, R (rare) – recorded in 2–8 standard sample plots (no more than 20 % of all SP), O (occasional) – 9–16

standard SPs (20–40 % SP), F (frequent) – 17–25 (40–60 % SP), C (common) – 26–33 (60–80 % SP), and VC (very common) – 34–41 (80–100 % SP). Lichens not identified to species level and lichenicolous fungi were not included in the occurrence, substrate and ecological analyses.

The species accumulation curve was made using MS Office Excel.

RESULTS AND DISCUSSION

On driftwood of the Commander Islands, we revealed 126 species of lichens and related groups of fungi. Of those, 113 lichens (including two subspecies of *Cladonia cornuta*) and two species of lichenicolous fungi were identified to species, 10 lichens were identified only to genus level, and one lichen remained unidentified. The total number of species from driftwood of the Commander Islands exceeds the largest number of species reported for this substrate in other areas.

Species diversity on driftwood of the Commander Islands varied from two species to 37 per plot (14.5±1.2 species on average). The species accumulation curve is displayed on Fig. 4. The curve reaches a plateau, indicating a relatively effective detection of lichen diversity.

The list of species is given in Table 2. Eighty-seven species are new to the Commander Islands, 29 – to the Kamchatka Territory, 14 – to the Russian Far East, and five species (*Hafellia fosteri*, *Lecania granulata*, *Lecanora aleutica*, *Lichenodiplis fallaciosa*, *Puttea caesia*) are new to Russia. For *Lecanora aleutica* (PZ197868, PZ197869) and *Bacidina indigens* (PZ197870), we obtained the ITS sequences for the first time. *Bacidina mendax* (PZ197867) was identified using the obtained ITS sequences. The ITS sequence (PZ197866) was also obtained for *Myriolecis* aff. *flowersiana*, a species requiring further identification. All obtained DNA sequences were deposited to GenBank.

Here we provide brief description of species new to Russia.

Hafellia fosteri (Fig. 5A, B) is a species that grows primarily on driftwood, known in western North America from Oregon to British Columbia. Thallus white, light yellow or light grey, apothecia black, up to 2 mm in diameter. Spores 2-septated, 20–30 × 8–11 μm. Hymenium not inspersed with oil drops and become yellow with KOH (McCune 2017). *Hafellia fosteri* may be confused with *Amandinea punctata*, also found on driftwood, but the latter species does not react with K, has an inconspicuous thallus and smaller spores and apothecia. Also, *Buellia disciformis* is a closely related species, but it usually grows inland and has smaller average spore size.

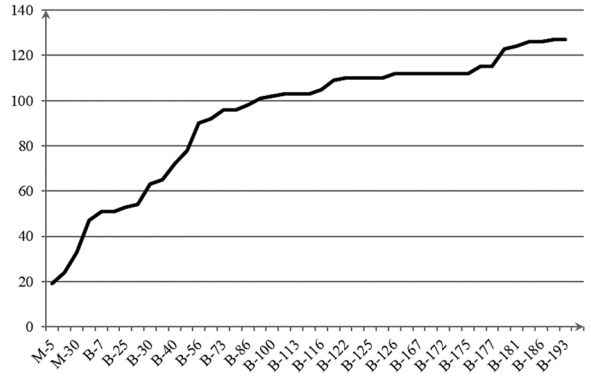

Figure 4 Species accumulation curve. The abscissa axis shows the surveyed sample plots in chronological order, and the ordinate axis shows the total number of species known after surveying a given sample plot

Lecania granulata (Fig. 5D, E) is a species living on nutrient-enriched coastal turf known from Great Britain. Thallus whitish to pale buff, densely granular blastidiate, with no colour spot reactions. Apothecia 2–6 mm diameter, plane or becoming convex. Disc pinkish or light ochre often with patchy brown pigment. The margin of the apothecium is crenulated and bears blastidia. Spores narrowly clavate-fusiform to shortly acicular, 20–25 × 2.5–3.8 μm, 3–5-septate. *Lecania subfuscula* occurs in similar habitats and has similar narrow spores, but a thinner thallus and dark apothecia (dark pink to grey-brown) with a barely visible thalline margin (Fryday & Coppins 2012).

Lecanora aleutica (Fig. 6A, B) occurs in Alaska, the Aleutian Islands, and Asian coast of the Bering Sea, usually growing on rock. Thallus nonlobate, extremely thick, areolate or verrucose, containing zeorin and become yellow with KOH. Apothecia large, 2.5–5 mm diameter, generally scattered. Disk red brown, not pruinose. Epihymenium red brown, olive, or greenish, excipulum usually insperced with POL+ granules. The closely related species *L. xylophila*, also found on driftwood, has much smaller apothecia (0.6–1.8 mm diameter) and contains different terpenoids but not zeorin (McCune 2017).

Lichenodiplis fallaciosa (Fig. 5C) – lichenicolous fungi, that forms pycnidia embedded in the apothecia of species of *Buellia*-species. Has aseptate conidia 6–8 × 3–4 μm. Known from North America (Diederich 2003).

Puttea caesia (Fig. 6C, D) – European and North American lignicolous species. Thallus indistinct; apothecia small, to 0.3 mm diameter, usually pale yellow to tan, sometimes gray brown or orange brown, convex, usually without a differentiated margin. Exciple edge brownish, hyaline within; hypothecium hyaline. Epithecium covered with a narrow gelatinous layer overlain by yellowish POL+ crystals. Excipular hyphae thickened at the tips, often with brown caps forming a dark rim. Paraphyses branched and anastomosing. Spores hyaline, nonseptate, small (3–7 × 1–2.5 μm). Contains no lichen substances. The species can be confused with some wood-dwelling *Lecidia* and *Lecanora* (*Lecanora cadubriae* (A. Massal.) Hedl., *Lecidea albohyalina* (Nyl.) Th. Fr., *L. erythrophaea* Flörke ex Sommerf., *L. rubrocastanea* T. Sprib. & Printzen, *Palicella schizochromatica* (Pérez-Ort. et al.) Rodr.-Flakus & Printzen), but all of them have large spore sizes (>3 μm wide). Also, a similar species is *Catillaria erysiboides*, but it has one-septate spores (McCune 2017).

We also provide a description of *Myriolecis* aff. *flowersiana*, a species presumably new to Russia but requiring further study.

Myriolecis flowersiana (Fig. 5F) known from North America, where it usually grows on calcareous rock, occasionally also on wood (Sliwa 2007). Thallus within the substratum, immersed and not apparent (endolithic or endophloedal). Apothecial margin with deep radial cracks, disk plane to slightly convex, smooth, reddish brown, dark brown to blackish, epruinose, excipular cortex not consistently thinning to the upper edge, strongly POL+ throughout the upper part. *Myriolecis crenulata* and *M. percrenata* also have crenulate apotecia, but the first species has pruina and POL+ granules in epihymenium, while *M. percrenata* has immersed apothecia (Sliwa 2007). The specimen shares 90.93 % percent identity with two sequencies of *Myriolecis* aff. *flowersiana* (MZ922155.1, MZ922153.1) from Munger et al. (2022) and has similar morphological features (Sliwa 2007).

Table 2. Annotated list of species.

Species, new to the Commander Islands, are marked with "*", species, new to Kamchatka Territory – with "**", new to Russian Far East – with "!", new to Russia – with "!!". Lichenicolous fungy are marked with "#". For each species, sample plots, frequency of occurrence (OF), the species to which the substrate wood belongs and typical substrates, where the lichen species usually grows. The nearest locations of lichen species known from the literature are also given.

For occurrence analysis, 6 categories with a step of 20% were identified: R1 (rare, singular) – single record – the species was found once, R (rare) – recorded in 2–7 standard sample plots (no more than 20% of all SP), O (occasional) – 8–15 standard sample plots (20–40% SP), F (frequent) – 16–22 (40–60% SP), C (common) – 23–30 (60–80% SP), and VC (very common) – 31–38 (80–100% SP). Lichens not identified to species level and lichenicolous fungi were not included in the occurrence analysis.

A dash in the "wood" column means that the substrate was not collected in sufficient quantity to determine the species.

Species	Sample plot	OF	Wood	Typical substrates	Known from administrative or geographical unit
Amandinea punctata (Hoffm.) Coppins et Sheid.	**B:** 30, 38, 51, 72, 73, 84, 87, 100, 111, 113, 115, 116, 119, 123, 125, 126, 129, 167, 168, 172, 175-178, 181, 186, 191, 193; **M:** 5, 9, 30, 40	C	*Picea* sp., *Populus* sp.	bark, rocks, less often moss and wood	Bering Island (Nylander 1888)
Athallia subrotundispora Stepanchikova, Himelbrant & I.V. Frolov	**B:** 72	R1	*Picea* sp.	driftwood, stones	Commander Islands (Frolov et al. 2025)
Athallia holocarpa (Hoffm.) Arup et al.	**B:** 51, 87, 174, 176, 191; **M:** 40	R	*Picea* sp.	rocks, less often wood and bark	Commander Islands (Frolov et al. 2025)
***Bacidina chloroticula* (Nyl.) Vězda et Poelt	**M:** 30	R1	*Picea* sp.	wood, stones, rusty metal, less often bark	Sakhalin (Chesnokov & Konoreva 2022, Zueva et al. 2024)
***Bacidina indigens* (Vain.) S. Ekman et J. Gerasimova	**B:** 72	R1	*Picea* sp.	mosses on the rocks	Chukotka (Gerasimova & Ekman 2017)
**Bacidina inundata* (Fr.) Vězda	**B:** 22, 28, 86; **M:** 40	R	*Fraxinus* sp., *Picea* sp.	rocks, less often wood and bark	Kamchatka (Savicz 1925)
!*Bacidina mendax* Czarnota et Guz.-Krzem.	**B:** 7	R1	*Populus* sp.	concrete, dolomite, wood of decidious trees	Tula Region (Muchnik et al. 2022), Krasnodar Territory and Leningrad Region (Urbanavichus et al. 2020)
Biatora sp.	**M:** 30, 40	–	*Picea* sp.	–	–
**Biatora sphaeroidiza* (Vain.) Printzen et Holien	**M:** 30	R1	*Picea* sp.	bark of *Picea*, bark of decidious trees	Kamchatka (Himelbrant et al. 2019)
***Biatora subduplex* (Nyl.) Printzen s. l.	**B:** 7, 86; **M:** 40	R	*Picea* sp.	plant debris, moss, bark and wood of shrubs	Sakhalin (Chesnokov & Konoreva 2022, Zueva et al. 2024)
**Bryoria simplicior* (Vain.) Brodo et D. Hawksw.	**B:** 30, 56, 87	R	*Picea* sp.	twigs of Pinus, *Picea*, *Betula* and wood	Kamchatka (Himelbrant et al. 2019)
***Buellia arborea* Coppins et Tønsberg	**B:** 7	R1	*Picea* sp.	wood, less often bark of *Populus* and coniferous	Altai (Davydov & Printzen 2012)
***Calicium salicinum* Pers.	**B:** 191	R1	*Picea* sp.	old wood, less often bark of *Quercus* and *Betula* species	Sakhalin (Tschabanenko 1999, Chesnokov & Konoreva 2022)
Caloplaca caesiorufella (Nyl.) Zahlbr.	**B:** 7, 28, 30, 38, 51, 72, 84, 86, 87, 100, 111, 113, 115, 116, 123, 125, 126, 129, 168, 172, 174-176, 178, 181, 186, 191, 193, a32; **M:** 5, 30, 40	C	*Alnus* sp., *Picea* sp.	bark and wood	Bering Island (Nylander 1888)
Caloplaca fraudans (Th. Fr.) H. Olivier	**B:** 87, 100	R	*Picea* sp.	rocks, less often wood	Commander Islands (Frolov et al. 2025)
Caloplaca sp.	**B:** 72, 84, 100, 113, 176, 178; **M:** 40	–	*Picea* sp.	–	–
Caloplaca stillicidiorum (Vahl) Lynge	**B:** 25, 86, 119, 174, 191; **M:** 5	R	*Picea* sp.	plant debris, moss	Bering Island (Nylander 1888)
Caloplaca turkuensis (Vain.) Zahlbr.	**B:** 86, 111, 119	R	*Picea* sp.	bark of decidious trees, less often bark of coniferous and wood	Commander Islands (Frolov et al. 2025)
**Candelariella aurella* (Hoffm.) Zahlbr.	**B:** 51; **M:** 40	R	*Picea* sp.	stones, bark, soil	Kamchatka (Himelbrant et al, 2021)
Candelariella vitellina (Hoffm.) Müll. Arg.	**B:** 116, 126, 176	R	*Picea* sp.	rocks, wood and bark, often visited by seabirds	Bering Island (Nylander 1888)
**Catillaria erysiboides* (Nyl.) Th. Fr.	**M:** 30, 40	R	*Populus* sp.	wood	Kamchatka (Himelbrant et al. 2019)

Table 2. Continued.

Species	Sample plot	OF	Wood	Typical substrates	Known from administrative or geographical unit
**Catinaria atropurpurea* (Schaer.) Vězda et Poelt	**B:** 38	R1	*Picea* sp.	bark and wood	Kamchatka (Himelbrant et al. 2019)
**Cetraria sepincola* (Ehrh.) Ach.	**B:** 73, 87, 122, 174	R	*Picea* sp.	twigs of trees and shrubs, wood, less often rocks	Kamchatka (Himelbrant et al. 2021)
**Cladonia arbuscula* (Wallr.) Flot. subsp. *arbuscula*	**B:** 56	R1	–	forest soil, marshes, sand dunes, rocks	Kamchatka (Himelbrant et al. 2019)
**Cladonia bacilliformis* (Nyl.) Glück	**B:** 40, 87, 178	R	*Picea* sp.	wood and bark of coniferous, less often soil	Kamchatka (Himelbrant et al. 2019)
Cladonia bellidiflora (Ach.) Schaer.	**B:** 178	R1	*Picea* sp.	rocks, soil	Bering Island (Nylander 1888)
**Cladonia borealis* S. Stenroos	**B:** 56	R1	–	soil	Kamchatka (Himelbrant et al. 2019)
**Cladonia carneola* (Fr.) Fr.	**B:** 56, 178	R	*Picea* sp.	soil and decaing wood	Kamchatka (Himelbrant et al. 2019)
**Cladonia chlorophaea* (Flörke ex Sommerf.) Spreng. s. str.	**B:** 7, 30, 51, 87, 113, 122, 168, 178, 186; **M:** 30, 40	O	*Picea* sp.	plant debris, soil, wood, trunk bases, mossy rocks	Kamchatka (Himelbrant et al. 2019)
**Cladonia coniocraea* (Flörke) Spreng.	**B:** 30, 178; **M:** 30	R	*Picea* sp.	decaing wood	Kamchatka (Himelbrant et al. 2019)
**Cladonia cornuta* (L.) Hoffm. subsp. *cornuta*	**B:** 7, 38, 40, 56, 87, 113, 122, 178, 186	O	*Picea* sp.	reach soil, wood and trunk bases	Kamchatka (Himelbrant et al. 2019)
**Cladonia cornuta* (L.) Hoffm. subsp. *groenlandica* (E. Dahl) Ahti	**B:** 73	R1	*Picea* sp.	soil, wood	Kamchatka (Himelbrant et al. 2019)
**Cladonia crispata* (Ach.) Flot. var. *crispata*	**B:** 56	R1	–	soil, wood	Kamchatka (Himelbrant et al. 2019)
**Cladonia cyanipes* (Sommerf.) Nyl.	**B:** 56	R1	–	mossy rocks, soil	Kamchatka (Himelbrant et al. 2019)
**Cladonia fimbriata* (L.) Fr.	**B:** 51, 113	R	*Picea* sp.	bark, decaing wood, open soil	Kamchatka (Himelbrant et al. 2019)
**Cladonia maxima* (Asahina) Ahti	**B:** 56	R1	–	soil	Kamchatka (Himelbrant et al. 2019)
**Cladonia pleurota* (Flörke) Schaer.	**B:** 87, 178, 186	R	–	wood, soil, mossy rocks	Kamchatka (Himelbrant et al. 2019)
**Cladonia pyxidata* (L.) Hoffm.	**B:** 40, 86, 168, 178; **M:** 30, 40	R	*Picea* sp.	soil, less often wood	Kamchatka (Himelbrant et al. 2019)
**Cladonia rei* Schaer.	**B:** 56	R1	–	soil	Kamchatka (Himelbrant et al. 2019)
**Cladonia squamosa* Hoffm.	**B:** 56, 178	R	*Picea* sp.	marshes, mossy rocks, soil	Kamchatka (Himelbrant et al. 2019)
**Cladonia stygia* (Fr.) Ruoss	**B:** 56	R1	–	soil	Kamchatka (Himelbrant et al. 2019)
Gowardia arctica Halonen et al.	**B:** 56	R1	–	soil, rocks, less often bark of trees and shrubs	Bering Island (Nylander 1888)
!! *Hafellia fosteri* Imshaug & Sheard	**B:** 86, 87; **M:** 40	R	*Picea* sp.	driftwood	North America (McCune 2017)
**Hypogymnia bitteri* (Lynge) Ahti	**B:** 30	R1	*Picea* sp.	bark, wood, less often rocks	Kamchatka (Himelbrant et al. 2019)
**Hypogymnia physodes* (L.) Nyl.	**B:** 56, 174	R	–	bark, less often rocks and wood	Kamchatka (Himelbrant et al. 2019)
#*Intralichen lichenicola* (M.S. Christ. et D. Hawksw.) D. Hawksw. et M. S. Cole	**B:** 51	–	*Picea* sp.	thalli of various lichen species	Adygeya (Urbanavichus et al. 2014)
Japewia tornoensis (Nyl.) Tønsberg	**B:** 40	R1	*Picea* sp.	bark, wood, moss, plant debris, less often rocks	Bering Island (Nylander 1888)
!!*Lecania granulata* Coppins et Fryday	**B:** 38, 111, 119, 125, 126, 168, 178, 186, 191	O	*Picea* sp.	peat turf and rock ledges on the coast	Europe (Fryday & Coppins 2012)
***Lecania naegelii* (Hepp) Diederich et van den Boom	**B:** 119, 168, 176	R	*Picea* sp.	deciduous tree bark, less commonly coniferous tree bark	Vladimir Region (Muchnik et al. 2019)

Table 2. Continued.

Species	Sample plot	OF	Wood	Typical substrates	Known from administrative or geographical unit
***Lecania subfuscula* (Nyl.) S. Ekman	**B:** 28, 123, 126, 178, 186; **M:** 5	R	*Picea* sp., *Populus* sp.	moss, wood and bark	Sakhalin (Konoreva et al. 2018)
**Lecanora aitema* (Ach.) Hepp	**B:** 30, 38, 40, 56, 73, 84, 87, 111, 113, 116, 123, 125, 126, 129, 174, 176, 178, 186	O	*Picea* sp.	bark (branches of dwarf-shrubs, *Pinus* and *Picea*), wood (often processed)	Kamchatka (Himelbrant et al. 2021)
!!*Lecanora aleutica* H. Magn.	**B:** 86, 119, 176, 178, 191; **M:** 5, 9, a17	R	*Picea* sp.	seaside rocks, whale bones, driftwood	North America (Talbot 1991)
**Lecanora boligera* (Norman ex Th. Fr.) Hedl.	**B:** 73, 87	R	*Picea* sp.	plant debris, wood	Kamchatka (Himelbrant et al. 2019)
**Lecanora circumborealis* Brodo et Vitik.	**B:** 40	R1	*Picea* sp.	bark, wood	Kamchatka (Himelbrant et al. 2019)
**Lecanora orae-frigidae* R. Sant.	**B:** 7, 25, 28, 30, 38, 40, 51, 56, 72, 73, 84, 86, 87, 100, 111, 113, 115, 116, 119, 123, 125, 126, 129, 168, 174, 175, 176, 177, 178, 181, 186, 191, 193; **M:** 5, 9, 30, 40	VC	*Alnus* sp., *Picea* sp., *Populus* sp.	old wood on the sea shores	Kamchatka Territory (Himelbrant et al. 2021)
Lecanora polytropa (Ehrh. ex Hoffm.) Rabenh.	**B:** 51, 56	R	*Picea* sp.	rocks, less often dry wood	Bering Island (Nylander 1888)
Lecanora symmicta (Ach.) Ach.	**B:** 25, 30, 38, 73, 87, 113, 125, 168, 174, 181	O	*Alnus* sp., *Picea* sp.	bark, wood (sometimes processed)	Bering Island (Nylander 1888)
!*Lecanora umbrina* (Ach.) A. Massal.	**B:** 51, 86, 87, 113, 119, 191	R	*Picea* sp., *Populus* sp.	rocks, bark, wood	Sakha (Yakutia) (Evdokimov et al. 2022)
!*Lecanora xylophila* Hue	**B:** 87, 186, 193	R	*Picea* sp.	driftwood, processed wood, seaside rocks	Karelia (Himelbrant & Kuznetzova 2002)
***Lecidella elaeochroma* (Ach.) M. Choisy	**B:** 51, 86, 168; **M:** 5, 40	R	*Picea* sp.	deciduous trees bark	Sakhalin (Ezhkin 2022; Zueva et al. 2024)
**Lecidella euphorea* (Flörke) Hertel	**B:** 73, 100; **M:** 40	R	*Picea* sp.	bark, wood, moss	Kamchatka (Himelbrant et al. 2021)
**Lepra panyrga* (Ach.) Hafellner	**B:** 30, 40, 56	R	*Picea* sp.	plant debris, moss, soil, less often bark	Kamchatka (Himelbrant et al. 2019)
!!#*Lichenodiplis fallaciosa* (Hafellner et Kalb) Diederich	**B:** 87	–	*Picea* sp.	thallus of *Amandinea punctata*	North America (Diederich 2003)
Melanohalea olivacea (L.) O. Blanco et al.	**B:** 30, 56, 73, 86	R	*Picea* sp.	bark of deciduous trees, wood, less often rocks	Bering Island (Nylander 1888)
***Micarea lyssacea* (Th. Fr.) Czarnota	**B:** 178	R1	*Picea* sp.	bark, wood	Magadan Region (Konoreva et al. 2024)
**Micarea denigrata* (Fr.) Hedl.	**B:** 7	R1	–	bark, wood	Kamchatka (Himelbrant et al. 2009)
Micarea sp.	**B:** 7	–	–	–	–
Mycoblastus affinis (Schaer.) T. Schauer	**B:** 40	R1	*Picea* sp.	bark, wood, rocks	Bering Island (Nylander 1888)
!!*Myriolecis* aff. *flowersiana* (H. Magn.) Sliva et al.	**B:** 119	R1	*Picea* sp.	rocks, soil	North America (Deneka 2005)
!*Myriolecis persimilis* (Th. Fr.) Śliwa et al.	**B:** 40, 73	R	*Picea* sp.	bark of decidious trees	Krasnodar Territory (Urbanavichus et al. 2020)
Myriolecis sp.	**B:** 119	–	*Picea* sp.	–	–
**Myriolecis straminea* (Ach.) Śliwa et al.	**B:** 84, 87, 100, 115, 116, 123, 126, 129, 175, 177, 178, 191, 193; **M:** 30	O	*Picea* sp.	rocks on the seashore, often visited by birds	Kamchatka (Himelbrant et al. 2019)
**Myriolecis torrida* (Vain.) Śliwa et al.	**B:** 119	R1	*Picea* sp.	limestone rocks	Kamchatka (Himelbrant et al. 2021)
Myriolecis zosterae (Ach.) Śliwa et al.	**B:** 28, 30, 38, 51, 72, 84, 86, 87, 111, 113, 115, 116, 119, 123, 125, 126, 129, 167, 168, 172, 174, 175, 176, 177, 178, 181, 186, 191, 193; **M:** 5, 30	C	*Picea* sp., *Populus* sp.	*Zostera* sp., plant debris, wood, bark of shrubs	Bering Island (Nylander 1888)

Table 2. Continued.

Species	Sample plot	OF	Wood	Typical substrates	Known from administrative or geographical unit
**Ochrolechia androgyna* (Hoffm.) Arnold s. l.	**B:** 178	R1	*Picea* sp.	bark, rocks, less often moss and wood	Kamchatka (Zhurbenko et al. 2018)
Ochrolechia frigida (Sw.) Lynge	**B:** 30, 40, 56, 86, 178, 187; **M:** 5, 9, 40, a17	R	*Fraxinus* sp., *Picea* sp.	soil, plant debris, moss, less often bark	Bering Island (Nylander 1888)
**Ochrolechia subplicans* (Nyl.) Brodo s. l.	**B:** 86; **M:** 9	R1	*Picea* sp.	rocks	Kamchatka (Himelbrant et al. 2019)
**Parmelia saxatilis* (L.) Ach.	**B:** 174, 178, 181; **M:** 5, 9, a17	R	*Picea* sp.	bark, wood and rocks, sometimes overgrown with moss	Kamchatka (Himelbrant et al. 2019)
**Parmelia sulcata* Taylor	**B:** 25, 30, 38, 40, 51, 56, 73, 86, 87, 113, 116, 119, 126, 178, 186, 191; **M:** 5, 9, 30, 40, a17	F	*Picea* sp.	bark, wood, rocks	Kamchatka (Himelbrant et al. 2019)
**Parmeliopsis ambigua* (Wulfen) Nyl.	**B:** 30, 40, 56, 73, 87, 122, 178	R	*Fraxinus* sp., *Picea* sp.	bark, wood, less often rocks	Kamchatka (Himelbrant et al. 2019)
**Parmeliopsis hyperopta* (Ach.) Arnold	**B:** 30, 40, 56, 73, 84, 87	R	*Picea* sp.	bark, wood, less often rocks	Kamchatka (Himelbrant et al. 2019)
**Peltigera canina* (L.) Willd.	**B:** 30	R1	–	moss on rocks and soil, sometimes soil	Kamchatka (Himelbrant et al. 2019)
!*Peltigera lyngei* Gyeln.	**B:** 187	R1	–	soil	Krasnoyarsk (Kharpukhaeva 2021)
**Peltigera membranacea* (Ach.) Nyl.	**B:** 73	R1	*Picea* sp.	soil	Kamchatka (Himelbrant et al. 2019)
Pertusaria sp.	**B:** 187; **M:** a17	–	*Picea* sp.	–	–
**Physcia caesia* (Hoffm.) Fürnr.	**B:** 25, 113, 115, 119, 125, 126, 172, 174–178, 186, 191; **M:** 30, 40, a17	F	*Picea* sp.	rocks, less often bark and wood	Kamchatka (Himelbrant et al. 2019)
**Physcia dubia* (Hoffm.) Lettau	**B:** 25, 51, 72, 84, 87, 119, 174, 175, 176; **M:** 5, 30, 40	O	*Picea* sp.	rocks, less often bark and wood	Kamchatka (Himelbrant et al. 2019)
**Placynthiella dasaea* (Stirt.) Tonsberg	**B:** 122	R1	–	bark, wood	Kamchatka (Himelbrant et al. 2019)
Polycauliona candelaria (L.) Frödén et al.	**B:** 30, 38, 51, 72, 84, 86, 87, 100, 111, 113, 115, 116, 119, 123, 125, 126, 129, 167, 168, 172, 174–178, 186, 191; **M:** 5, 9, 30, 40	C	*Alnus* sp., *Picea* sp.	bark of deciduous trees, rocks often visited by birds, less often wood	Bering Island (Nylander 1888)
Polycauliona comandorica Himelbrant et al.	**B:** 126	R1	–	rocks	Commander Islands (Frolov et al. 2025)
Polycauliona cf. *flavogranulosa* (Arup) Arup et al.	**B:** 191	R1	–	siliceous outcrops and stones	Commander Islands (Frolov et al. 2025)
Polycauliona phlogina (Ach.) Arup et al.	**B:** 116, 126, 129, 174	R	–	bark of decidious trees, less often wood	Commander Islands (Frolov et al. 2025)
Polycauliona pollinarioides (L. Lindblom et D. M. Wright) Frödén et al.	**B:** 25, 123, 178	R	–	bark, usually bark of *Salix* sp. and *Baccharis* sp.	Commander Islands (Frolov et al. 2025)
Polycauliona verruculifera (Vain.) Arup et al.	**B:** 126, 175–178, 186, 191, 193	O	–	rocks on the seashore, often visited by birds	Commander Islands (Frolov et al. 2025)
Polycauliona sp.	**B:** 125, 181, 191, 193	–	–	–	–
Porpidia crustulata (Ach.) Hertel et Knoph	**M:** 40	R1	*Picea* sp.	stones, pebbles	Bering Island (Nylander 1888)
Protopannaria pezizoides (Weber) P. M. Jorg. et S. Ekman	**B:** 187; **M:** 5	R	–	soil, wood	Bering Island (Nylander 1888)
!!*Puttea caesia* (Fr.) M. Svenss. et T. Sprib.	**B:** 176	R1	*Picea* sp.	wood, less often moss	North America (Dillman et al. 2010)
***Ramalina pollinaria* (Westr.) Ach.	**M:** 40	R1	*Picea* sp.	shadowed rocks, old decidious trees	Sakhalin (Joneson et al. 2004)
**Ramalina roesleri* (Hochst. ex Schaer.) Hue	**M:** 30	R1	–	twigs of *Picea*, *Alnus*, *Sorbus*	Kamchatka (Himelbrant et al. 2019)
**Ramalina scoparia* Vain.	**B:** 51, 87, 178, 191; **M:** 5, 9, 30, a17	O	*Picea* sp.	seaside rocks and boulders, driftwood	Kamchatka (Himelbrant et al. 2021)

Table 2. Continued.

Species	Sample plot	OF	Wood	Typical substrates	Known from administrative or geographical unit
**Ochrolechia androgyna* (Hoffm.) Arnold s. l.	**B:** 178	R1	*Picea* sp.	bark, rocks, less often moss and wood	Kamchatka (Zhurbenko et al. 2018)
Ochrolechia frigida (Sw.) Lynge	**B:** 30, 40, 56, 86, 178, 187; **M:** 5, 9, 40, a17	R	*Fraxinus* sp., *Picea* sp.	soil, plant debris, moss, less often bark	Bering Island (Nylander 1888)
**Ochrolechia subplicans* (Nyl.) Brodo s. l.	**B:** 86; **M:** 9	R1	*Picea* sp.	rocks	Kamchatka (Himelbrant et al. 2019)
**Parmelia saxatilis* (L.) Ach.	**B:** 174, 178, 181; **M:** 5, 9, a17	R	*Picea* sp.	bark, wood and rocks, sometimes overgrown with moss	Kamchatka (Himelbrant et al. 2019)
**Parmelia sulcata* Taylor	**B:** 25, 30, 38, 40, 51, 56, 73, 86, 87, 113, 116, 119, 126, 178, 186, 191; **M:** 5, 9, 30, 40, a17	F	*Picea* sp.	bark, wood, rocks	Kamchatka (Himelbrant et al. 2019)
**Parmeliopsis ambigua* (Wulfen) Nyl.	**B:** 30, 40, 56, 73, 87, 122, 178	R	*Fraxinus* sp., *Picea* sp.	bark, wood, less often rocks	Kamchatka (Himelbrant et al. 2019)
**Parmeliopsis hyperopta* (Ach.) Arnold	**B:** 30, 40, 56, 73, 84, 87	R	*Picea* sp.	bark, wood, less often rocks	Kamchatka (Himelbrant et al. 2019)
**Peltigera canina* (L.) Willd.	**B:** 30	R1	–	moss on rocks and soil, sometimes soil	Kamchatka (Himelbrant et al. 2019)
!*Peltigera lyngei* Gyeln.	**B:** 187	R1	–	soil	Krasnoyarsk (Kharpukhaeva 2021)
**Peltigera membranacea* (Ach.) Nyl.	**B:** 73	R1	*Picea* sp.	soil	Kamchatka (Himelbrant et al. 2019)
Pertusaria sp.	**B:** 187; **M:** a17	–	*Picea* sp.	–	–
**Physcia caesia* (Hoffm.) Fürnr.	**B:** 25, 113, 115, 119, 125, 126, 172, 174–178, 186, 191; **M:** 30, 40, a17	F	*Picea* sp.	rocks, less often bark and wood	Kamchatka (Himelbrant et al. 2019)
**Physcia dubia* (Hoffm.) Lettau	**B:** 25, 51, 72, 84, 87, 119, 174, 175, 176; **M:** 5, 30, 40	O	*Picea* sp.	rocks, less often bark and wood	Kamchatka (Himelbrant et al. 2019)
**Placynthiella dasaea* (Stirt.) Tonsberg	**B:** 122	R1	–	bark, wood	Kamchatka (Himelbrant et al. 2019)
Polycauliona candelaria (L.) Frödén et al.	**B:** 30, 38, 51, 72, 84, 86, 87, 100, 111, 113, 115, 116, 119, 123, 125, 126, 129, 167, 168, 172, 174–178, 186, 191; **M:** 5, 9, 30, 40	C	*Alnus* sp., *Picea* sp.	bark of deciduous trees, rocks often visited by birds, less often wood	Bering Island (Nylander 1888)
Polycauliona comandorica Himelbrant et al.	**B:** 126	R1	–	rocks	Commander Islands (Frolov et al. 2025)
Polycauliona cf. *flavogranulosa* (Arup) Arup et al.	**B:** 191	R1	–	siliceous outcrops and stones	Commander Islands (Frolov et al. 2025)
Polycauliona phlogina (Ach.) Arup et al.	**B:** 116, 126, 129, 174	R	–	bark of decidious trees, less often wood	Commander Islands (Frolov et al. 2025)
Polycauliona pollinarioides (L. Lindblom et D. M. Wright) Frödén et al.	**B:** 25, 123, 178	R	–	bark, usually bark of *Salix* sp. and *Baccharis* sp.	Commander Islands (Frolov et al. 2025)
Polycauliona verruculifera (Vain.) Arup et al.	**B:** 126, 175–178, 186, 191, 193	O	–	rocks on the seashore, often visited by birds	Commander Islands (Frolov et al. 2025)
Polycauliona sp.	**B:** 125, 181, 191, 193	–	–	–	–
Porpidia crustulata (Ach.) Hertel et Knoph	**M:** 40	R1	*Picea* sp.	stones, pebbles	Bering Island (Nylander 1888)
Protopannaria pezizoides (Weber) P. M. Jorg. et S. Ekman	**B:** 187; **M:** 5	R	–	soil, wood	Bering Island (Nylander 1888)
!!*Puttea caesia* (Fr.) M. Svenss. et T. Sprib.	**B:** 176	R1	*Picea* sp.	wood, less often moss	North America (Dillman et al. 2010)
***Ramalina pollinaria* (Westr.) Ach.	**M:** 40	R1	*Picea* sp.	shadowed rocks, old decidious trees	Sakhalin (Joneson et al. 2004)
**Ramalina roesleri* (Hochst. ex Schaer.) Hue	**M:** 30	R1	–	twigs of *Picea*, *Alnus*, *Sorbus*	Kamchatka (Himelbrant et al. 2019)
**Ramalina scoparia* Vain.	**B:** 51, 87, 178, 191; **M:** 5, 9, 30, a17	O	*Picea* sp.	seaside rocks and boulders, driftwood	Kamchatka (Himelbrant et al. 2021)

Table 2. Continued.

Species	Sample plot	OF	Wood	Typical substrates	Known from administrative or geographical unit
*R*hizocarpon infernulum* (Nyl.) Lynge f. *sylvaticum* Fryday	**M:** 40	R1	*Picea* sp.	rocks	Kamchatka as *Lecidea infernula* Nyl. (Nylander 1888)
**Rinodina conradii* Körb.	**M:** 40	R1	–	plant debris, mosses, soil, wood, bones	Kamchatka (Sheard et al. 2017)
***Rinodina freyi* H. Magn.	**B:** 30	R1	–	bark of *Alnus*, *Juniperus*, *Populus*, *Picea*	Kamchatka (Sheard et al. 2017)
**Rinodina gennarii* Bagl.	**B:** 176, 191	R	–	rocks on the seashore, often visited by birds, less often wood	Kamchatka (Himelbrant et al. 2021)
**Rinodina* cf. *sibirica* H. Magn.	**M:** 9	R1	*Picea* sp.	bark and wood	Kamchatka (Sheard et al. 2017)
Rinodina turfacea (Wahlenb.) Körb.	**B:** 36, 86, 87, 116, 181, 186, 187, 191; **M:** 5, 9, 30, 40, a17	O	*Picea* sp.	plant debris and moss	Bering Island (Nylander 1888)
Rinodina sp.	**B:** 176, 181; **M:** a17	–	–	–	–
Rusavskia elegans (Link) S. Y. Kondr. et Kärnefelt	**B:** 87, 126, 129, 168, 174, 176, 187, 191, 193; **M:** 9, 30	O	*Picea* sp.	rocks on the seashore, often visited by birds	Bering Island (Nylander 1888)
**Scoliciosporum umbrinum* (Ach.) Arnold	**B:** 51	R1	*Picea* sp.	rocks, pebbles, wood, bark	Kamchatka (Himelbrant et al. 2019)
**Scutula circumspecta* (Nyl. ex Vain.) Kistenich et al.	**B:** 86	R1	*Populus* sp.	bark of decidious trees, less often bark of *Juniperus* sp.	Kamchatka (Himelbrant et al. 2019)
**Scytinium tenuissimum* (Dicks.) Otálora et al.	**B:** 178	R1	–	clay and calcareous soil	Kamchatka (Himelbrant et al. 2019)
sorediate crust 1	**B:** 28	–	*Picea* sp.	–	–
**Sphaerophorus fragilis* (L.) Pers.	**M:** 40	R1	–	rocks, less often soil	Kamchatka (Himelbrant et al. 2019)
Sphaerophorus globosus (Huds.) Vain.	**B:** 56	R1	–	rocks, bark, less often soil	Bering Island (Nylander 1888)
Tephromela atra (Huds.) Hafellner	**B:** 51	R1	*Picea* sp.	rocks, less often bark of decidious trees	Bering Island (Nylander 1888)
**Tetramelas chloroleucus* (Körb.) A. Nordin	**M:** a17	R1	*Picea* sp.	bark of decidious trees and Juniperus sp.	Kamchatka (Himelbrant et al. 2021)
!*Thelenella muscorum* (Fr.) Vain. var. *octospora* (Nyl.) Coppins et Fryday	**B:** 176	R1	*Picea* sp.	dead mosses, lichens and plant debris	Karachayevo-Circassian Republic (Zhurbenko & Kobzeva 2014)
**Thelocarpon epibolum* Nyl.	**B:** 111	R1	*Picea* sp.	dead lichens, decaying wood, peat	Kamchatka (Timofeeva et al. 2025)
!*Thrombium epigaeum* (Pers.) Wallr.	**B:** 72	R1	*Picea* sp.	clay and sandy soil, less often mosses and plant debris	Leningrad Region (Stepanchikova et al. 2011), Republic of Adygeya (Urbanavichus & Urbanavichene 2014)
**Trapeliopsis flexuosa* (Fr.) Coppins et P. James	**B:** 30	R1	–	wood, less often bark	Kamchatka (Himelbrant et al. 2019)
**Vulpicida pinastri* (Scop.) J.-E. Mattson et M. J. Lai	**B:** 25, 73, 87, 122, 178; **M:** 5	R	*Picea* sp.	bark, wood, less often rocks	Kamchatka (Himelbrant et al. 2019)
***Xylographa trunciseda* (Th. Fr.) Minks ex Redinger.	**B:** 36	R1	*Picea* sp.	driftwood	Sakhalin (Chesnokov & Konoreva 2022)
!*Xylographa difformis* (Vain.) Vain.	**B:** 7, 22, 51, 73, 86, 100, 116, 191; **M:** 30, 40	O	*Picea* sp.	wood	Leningrad Region (Himelbrant et al. 2018)
***Xylographa hians* Tuck.	**B:** 7, 30, 40, 84, 86, 113, 186, 193; **M:** 5, 30, 40	O	*Picea* sp., *Populus* sp.	wood in coastal rain forests	Sakhalin (Chesnokov & Konoreva 2022, Zueva et al. 2024, 2025a)
***Xylographa opegraphella* Nyl. ex Rothr.	**B:** 7, 30, 38, 40, 51, 72, 73, 86, 87, 100, 111, 113, 115, 116, 119, 125, 168, 178, 181, 186, 191, 193; **M:** 9, 30, 40	C	*Picea* sp., *Populus* sp.	old wood on the sea shores	Sakhalin (Ezhkin 2022, Zueva et al. 2025a, b)
***Xylographa vitiligo* (Ach.) J. R. Laundon	**B:** 86; **M:** 5, 30, 40	R	*Picea* sp.	wood of *Picea*, *Pinus*, *Juniperus*, *Quercus*	Sakhalin Region (Zueva et al. 2024)

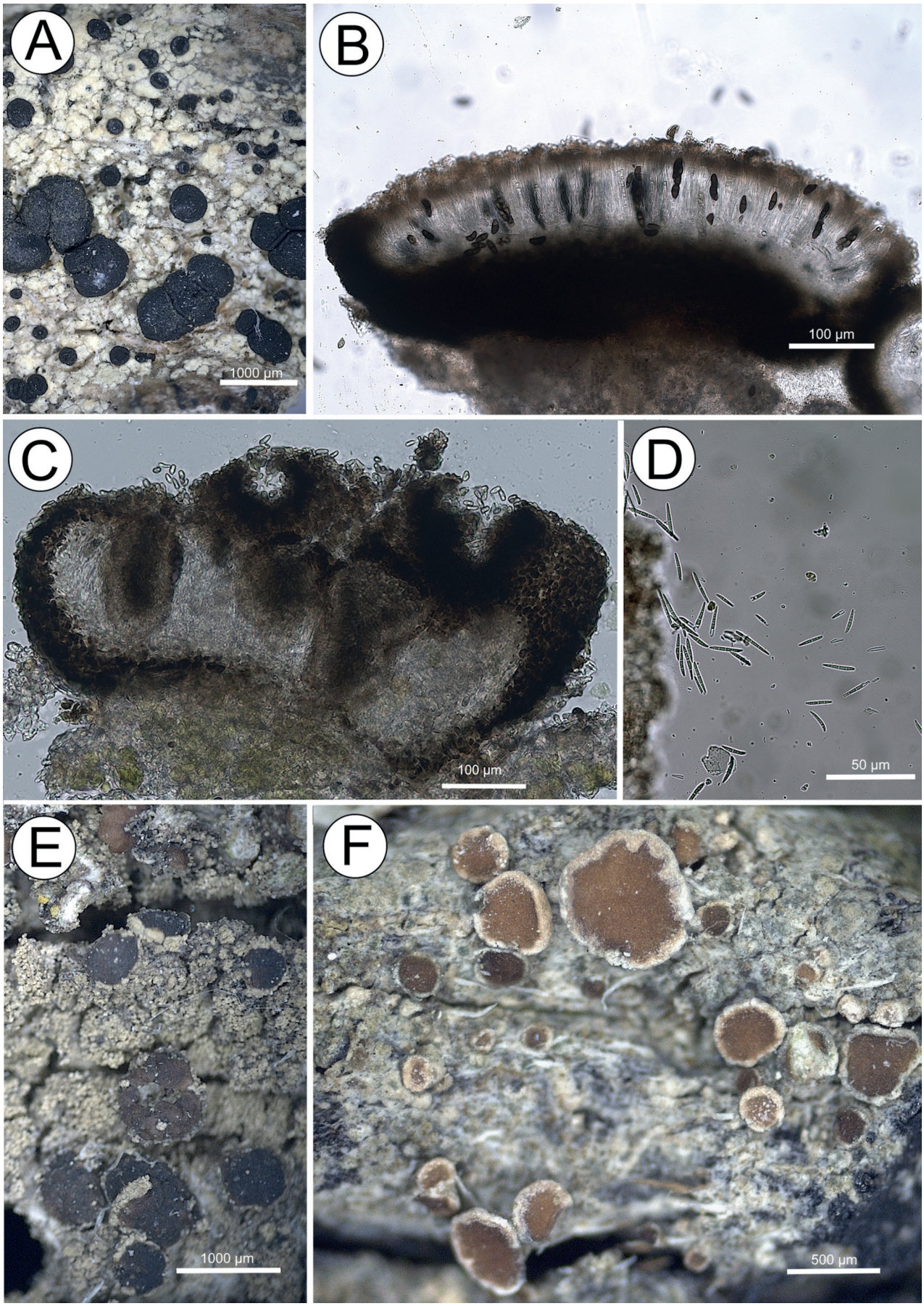

Figure 5 A, B – *Hafellia fosteri* Imshaug & Sheard (general appearance and section of apothecium); C – *Lichenodiplis fallaciosa* (Hafellner et Kalb) Diederich (pycnidia in apothecium of *Amandinea punctata* (Hoffm.) Coppins et Sheid.), D, E – *Lecania granulata* Coppins et Fryday (spores and general appearance); F – *Myriolecis* aff. *flowersiana* (H. Magn.) Sliva et al. (general appearance)

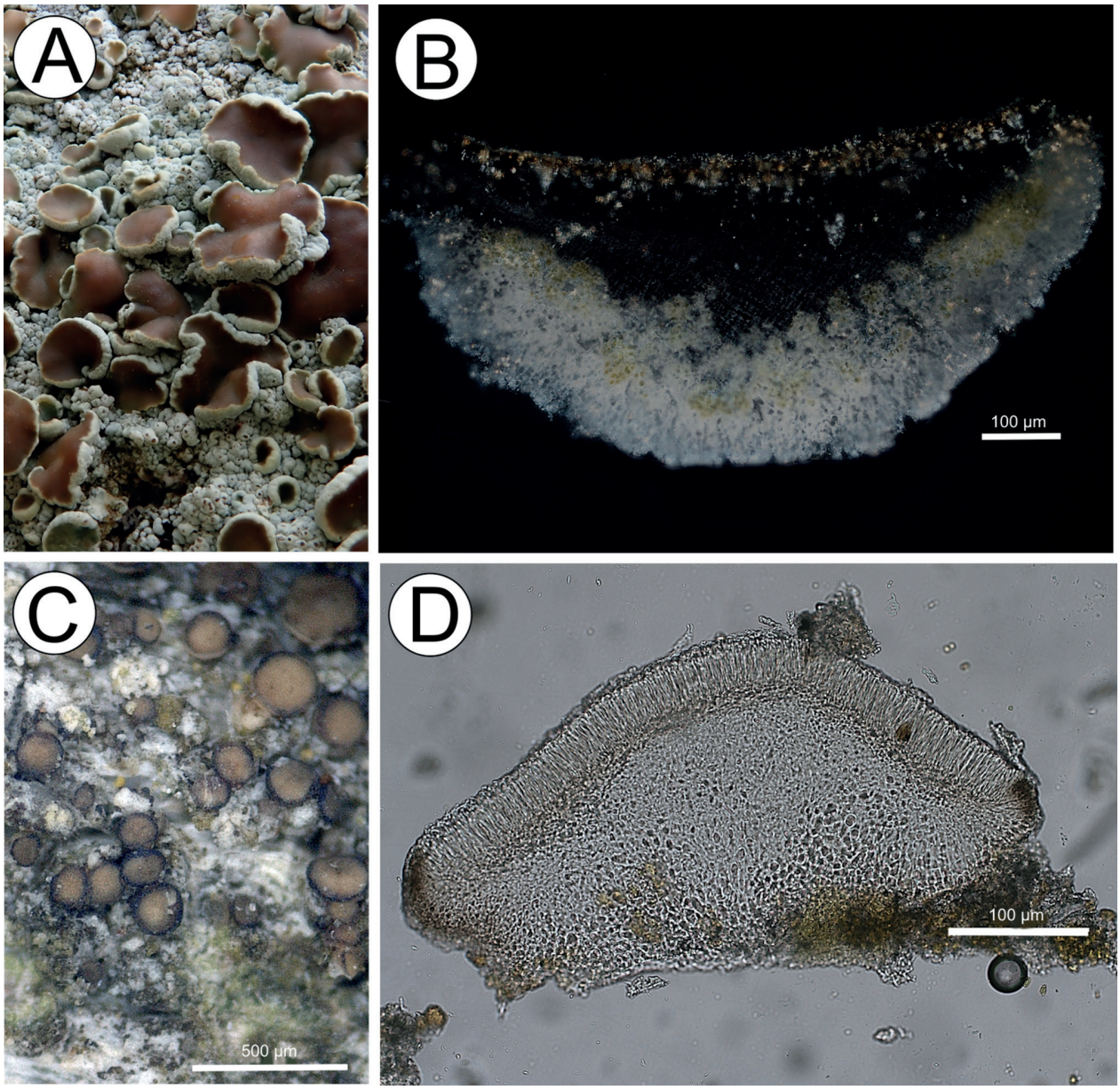

Figure 6 A, B – *Lecanora aleutica* H. Magn. (general appearance and section of apothecium); C, D – *Puttea caesia* (Fr.) M. Svenss. et T. Sprib. (general appearance and section of apothecium)

However, driftwood is not the typical habitat of *Myriolecis flowersiana*, which occurs in desert to montane habitats, mostly at elevations above 1000 m and up to 2870 m (Sliwa 2007).

Species occurrence frequency

Lecanora orae-frigidae is the only species falling into the VC category (found at 35 SP). On most SPs it occupies most of the substrate area and sorediate thalli of this species often makes a light greenish-yellowish aspect of the lichen community on driftwood (Fig. 7). Category C includes 5 species: *Amandinea punctata*, *Caloplaca caesiorufella*, *Myriolecis zosterae*, *Polycauliona candellaria* and *Xylographa opegraphella*. The absolute majority of analyzed species (83.6 %) are found in less than 20 % of SPs and belong to R and R1 groups (47 and 60 species respectively). Such a large number of rare lichens indicates the nonspecificity of most species of driftwood lichen diversity to the substrate they occupy.

Substrate groups

Similar to other studies (Zhurbenko & Vekhov 2001, Himelbrant & Kuznetsova 2002, Zhdanov & Dudoreva 2003), on driftwood we found species with different substrate preferences (see Table 2). Most driftwood lichen species of the Commander Islands are both corticolous and lignicolous (89 species, or 70.1 % of the driftwood lichen diversity). Lichens from saxicolous and terricolous communities also make a significant contribution to the lichen diversity (43 species each, 34.1 %). Terricolous lichens on driftwood include mainly species of the genera *Cladonia*, *Ochrolechia*, and *Peltigera*. Among lichens from saxicolous communities, there are a lot of coastal ornithocoprophilic species. These are mainly lichens of the family Teloschistaceae (*Polycauliona comandorica*, *P. verruculifera*, and *Rusavskia elegans*) as well as species from other groups (*Candelariella vitellina*, *Myriolecis*

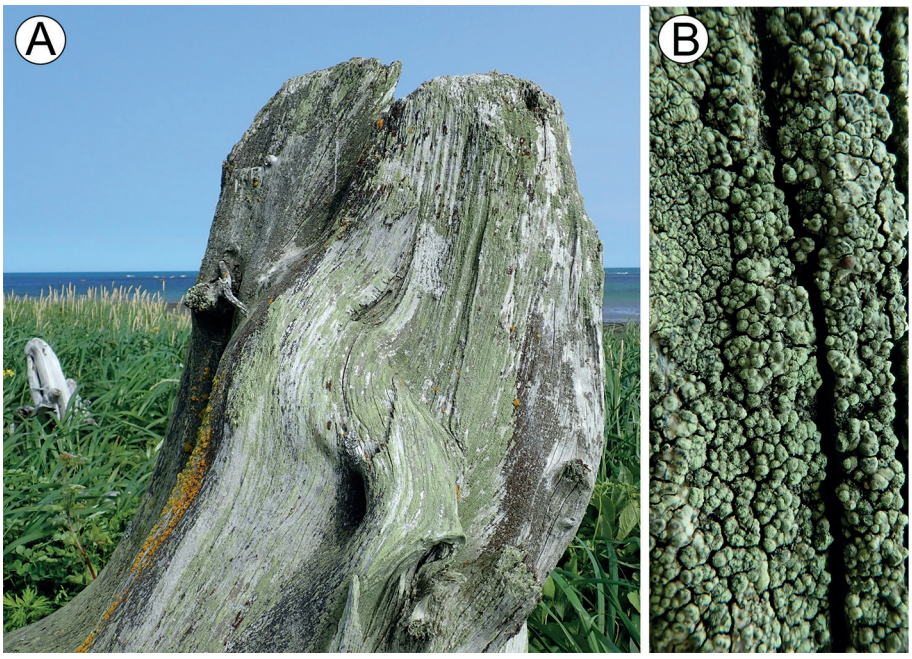

Figure 7 A, B – *Lecanora orae-frigidae* R. Sant. (light greenish-yellowish aspect of the driftwood communities and enlarged view of sorediate thallus)

straminea, and *Rinodina gennarii*). All these substrate groups partially overlap, as some lichens typically grow on several substrates, and the total percentage exceeds 100 %.

Due to the lack of woody vegetation on the Commander Islands, driftwood remains almost the only substrate for many corticolous and lignicolous lichens here. The bark of tundra and floodplain shrubs of the genus *Salix* L. has a very specific and poor corticolous lichen diversity and is not entirely suitable as a substrate for most corticolous lichens from the neighboring continents. That's why most of the boreal corticolous species found on the Commander Islands live on driftwood. They mainly belong to the family Parmeliaceae (*Bryoria simplicior*, *Cetraria sepincola*, *Hypogymnia bitteri*, *H. physodes*, *Melanohalea olivacea*, *Parmelia sulcata*, *Parmeliopsis ambigua*, *P. hyperopta*, *Vulpicida pinastri*).

Few species on the driftwood of the Commander Islands are strictly specialized for this substrate, namely *Hafellia fosteri*, *Lecanora orae-frigidae*, *L. xylophyla*, *Xylographa bjoerkii*, and *X. opegraphella* (5 species, 4 % of total diversity). This number is higher than in other studies (Brodo & Vänskä 1984, Zhurbenko & Vekhov 2001, Skazina & Himelbrant 2008a). However, it is obvious that the vast majority of driftwood lichen species prefer other substrates, and just occasionally occur on driftwood.

The combination of lichens from different substrate groups, their significant contribution to driftwood lichen community and the generally high species diversity on driftwood clearly indicate the unique properties of this substrate and its important role in maintaining the diversity of lichens on the Commander Islands.

Comparison with the driftwood lichen diversity of the Keret Archipelago (White Sea)

The only territory with comparable diversity of lichens on driftwood is the Keret archipelago in the White Sea with 106 lichen species (Himelbrant & Kuznetsova 2002). Despite their remoteness from the Commander Islands, both territories belong to the boreal floristic zone (but much closer to the mainland) and have a comparable driftwood lichen biota. Forty two species (39.6 % for Keret Archipelago and 36.5 %, for Commander Islands) are same, 64 species (60.4 %) are known from the driftwood of the Keret Archipelago only, and 76 species (66.1 %) from the driftwood of the Commander Islands. The Jaccard coefficient between the two lichen communities is 0.43. Typical driftwood lichens (*Lecanora orae-frigidae*, *L. xylophila*, and *Xylographa opegraphella*) and widely distributed corticolous species (*Lecanora symmicta*, *Parmelia sulcata*, *Parmeliopsis ambigua*, *P. hyperopta*) are common on driftwood of both territories. The lichen community of the Keret Archipelago is distinguished by a more significant contribution of the boreal corticolous lichens (*Bryoria fuscescens* (Gyeln.) Brodo & D. Hawksw., *Lecanora cadubriae* (A. Massal.) Hedl., *L. pulicaris* (Pers.) Ach., *Platismatia glauca* (L.) W.L. Culb. & C.F. Culb.). The higher diversity of corticolous and lignicolous species (85 % of driftwood species diversity) is due to the location of the Keret Archipelago close to the mainland and the presence of woody vegetation on it. Among the driftwood lichens of the Commander Islands there is a significant proportion of saxicolous species due to the stronger influence of the ocean. In addition, the lichen community of the driftwood of the Commander Islands contains tundra species (*Cladonia maxima*, *C. cyanipes*, *Gowardia arctica*, *Peltigera lyngei*, *Protopannaria pezizoides*). Thus, it is clear that the composition of the driftwood lichen biota is significantly influenced by the surrounding biotope (boreal forest on the Keret Archipelago and tundra on the Commander Islands). However, there are also circumboreal corticolous and lignicolous lichens, which were found on the Commander Islands' driftwood, but were probably overlooked on the White Sea driftwood (*Biatora sphaeroidiza*, *Catinaria atropurpurea*, *Lecanora boligera*). Also, the driftwood of the Commander Islands is characterized by three species previously known only from North America (*Hafellia fosteri*, *Lecanora aleutica*, *Xylographa bjoerkii*) and two local endemics (*Athallia subrotundispora*, *Polycauliona comandorica*).

Taxonomic affiliation of driftwood and its relationship with lichen diversity

As a result of the analysis of substrate wood sections, 4 genera were identified: *Alnus* Mill., *Fraxinus* L., *Picea* Dietrich, and *Populus* L. The most abundant wood in the collections was *Picea* sp.; it was identified from almost all

sample plots (37 SPs out of 43). Wood from other groups is rare (1–5 SPs).

According to the map of the currents (Fig. 1), most of the driftwood can be delivered to the Commander Islands from the Pacific coast of North America with the Aleutian Jet Current or from Japan through the North Pacific Current (a branch of the Kuroshio Current) and the Western Subarctic Gyre. Transport of driftwood by the Kamchatka Current is less likely, but driftwood from Kamchatka can reach the islands with storms caused by cyclones and with drifting ice floes.

The wood we identified could be equally belong to North American (e.g. *Alnus incana* (L.) Moench., *Fraxinus latifolia* Benth., *Picea engelmanii* Parry ex Engelm., *Populus balsamifera* L., and *P. tremuloides* Michx.) and Asian (e.g. *Alnus hirsuta* (Spach) Rupr., *Fraxinus lanuginosa* Koidz., *F. mandshurica* Rupr., *Picea jezoensis* (Siebold & Zucc.) Carrière and *Populus tremula* L.) tree species (Ohwi 1965, Frenkel & Heinitz 1987, Klinka et al. 1999, http://insidewood.lib.ncsu.edu/search). Therefore, we cannot say with certainty where the driftwood comes from on the Commander Islands.

Ecological-substrate analysis

Substrate analysis was performed for all species for which a substrate was identified. As a result of NMDS (package "*vegan*"), we obtained an ordination diagram of substrate woods (package "*ggplot2*") depending on similarity in the species composition of the lichens living on them (Fig. 8). The distribution across substrate wood species is too uneven, and therefore it is not possible to identify the reliable influence of any factors (woods of coniferous or deciduous trees, lichen species reachness) using the "*envfit*" function (stress nearly zero). We can see that lichens from different substrates do not form clusters. Perhaps further research and more uniform sampling from different types of wood will reveal patterns in the distribution of lichens across substrates that are not visible in our data.

For more detailed characterization and comparison of substrates according to the species composition of lichens, the UpSet diagram (package "*UpsetR*") was calculated (Fig. 9). The largest number of lichen species (83) are found only on *Picea* sp., followed by the species shared by *Picea* sp. and *Populus* sp. (7). On other combinations of substrates, single species of lichens were found.

A multiple regression analysis was also performed to examine the dependence of species richness at the SPs on SP characteristics. Model optimisation yielded a model with a single influencing factor: the location of the SP on either Medny or Bering Island. On average, SPs on Medny Island exhibited higher species richness than those on Bering Island. This may be attributed either to the small sample size of SPs from Medny Island or to the lower anthropogenic impact on the currently uninhabited Medny Island, where driftwood is not burned and therefore accumulates in large amounts. Figure 11 shows the relationship between species richness at the SPs and distance from the coast. A slight increase in species richness was observed with increasing distance from the coast. SP B-56 was excluded from this analysis because its distance from the shore differs significantly from that of the others, thereby obscuring the general pattern.

NMDS of the sample plots depending on the similarity of their species composition of lichens was also carried out (Fig. 10). The influence of such factors as altitude, distance from the water line, significant ornithogenic influence, the location of the SP on western or eastern coast of an island and the location of the SP on Bering or Medny islands was considered. We also assessed how species richness on SP correlates with ordination. Using the "*envfit*" function, we found that the diversity of lichen species on SP is slightly affected by the distance from the sea coast (R^2=0.1808, Pr(>r)=0.048, stress=0.16) and the altitude a.s.l. (R^2=0.1815, Pr(>r)=0.046). This is likely due to the fact that driftwood logs transported more deeply inland are actively colonized by tundra species. Nevertheless, the R^2 value is quite low, and despite statistical significance, the biological impact of these factors is weak. Ornithogenic influence also has a weak effect (R^2 = 0.1159, Pr(>r) = 0.012). Species intolerant of high nitrogen level disappear from SPs subject to strong ornithogenic influence. Conversely, ornithocoprophilous members of the Teloschistaceae family exhibit greater diversity. It should be noted that eutrophication is present to varying degrees at all SPs. Therefore, SPs were categorized into those with strong eutrophication (where the impact of birds is conspicuous) and those with weak eutrophication (where eutrophication was not specifically noted during SP description). Also, the distribution of the species composition of lichens on SP correlates with species rich-

Table 3. R^2 and p-value results for all SP characteristics analyzed by the envfit function.

SP characteristics	R^2	Pr(>r)
Distance from the sea coast	0.1808	0.048
Altitude a.s.l.	0.1815	0.046
Ornithogenic influence	0.1159	0.012
Species richness	0.2127	0.011
Location on west or east coast	0.0011	0.96
Location on Bering or Medny island	0.0124	0.588

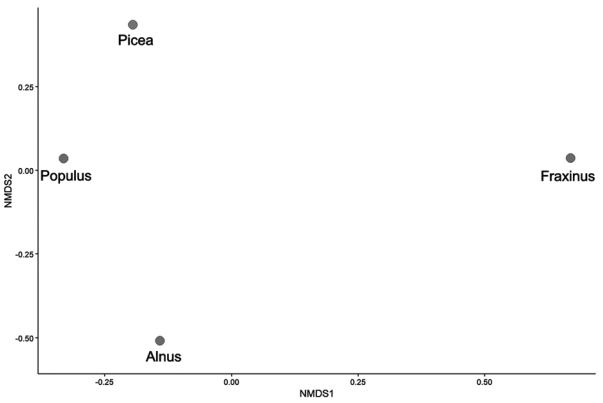

Figure 8 Non-metrical multidimensional scaling of substrate woods. Points corresponding to different types of substrate wood are located in the space of hypothetical axes NMDS1 and NMDS2. The closer the points are located on the graph, the more similar their lichen species composition

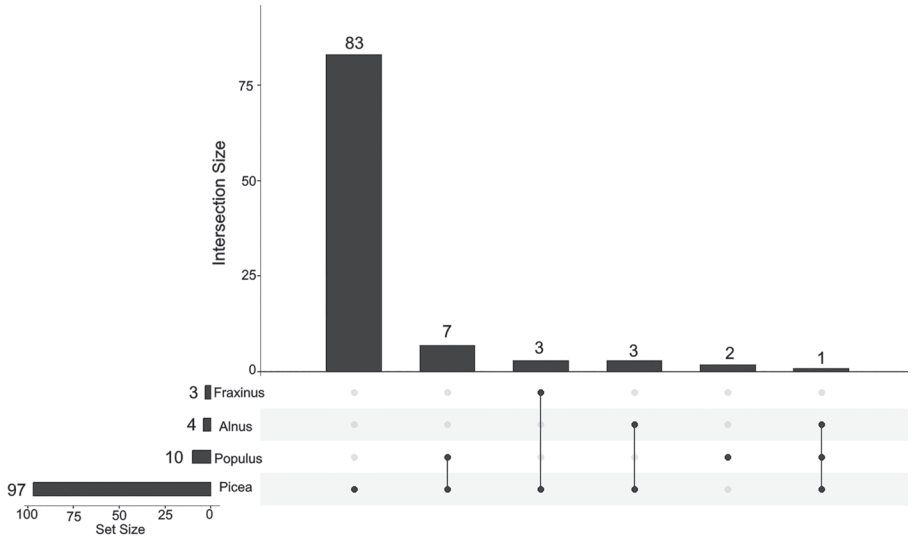

Figure 9 UpSet diagram of common and unique sets of lichen species on different woods. Horizontal bars show the total number of species on each substrate. Vertical bars show the number of the species shared by the substrates, highlighted with black circles

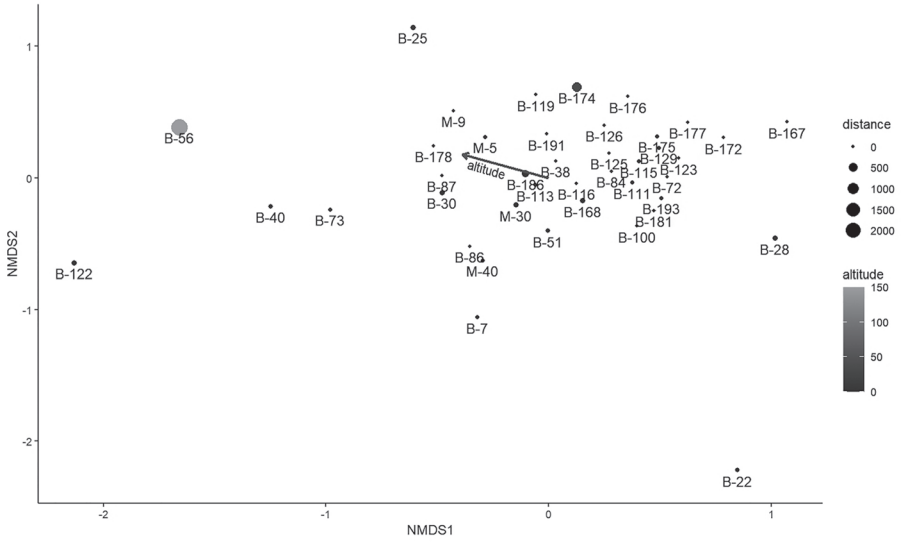

Figure 10 Non-metrical multidimensional scaling of sample plots. The points corresponding to different sample plots are located in the space of the hypothetical axes NMDS1 and NMDS2. The closer the points on the graph are, the more similar their lichen species composition. Color reflects altitude, and size indicates distance from the coast. Altitude is also shown with vector

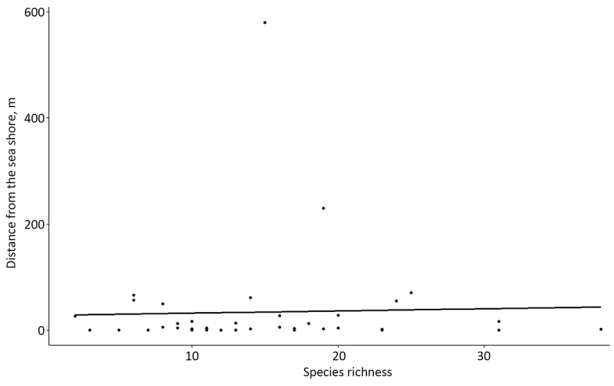

Figure 11 Scatter plot showing the relationship between species richness and distance from the sea

ness (R^2=0.2127, Pr(>r)=0.011). The remaining factors were not significant (the location of the sample plot on west or east coast of island (R^2=0.0011, Pr(>r)=0.96), the location of the sample plot on Bering or Medny islands (R^2=0.0124, Pr(>r)=0.588)) (Table 3).

The SPs on the graph (Fig. 10) form one cluster based on the lichen species composition on them. Only few SPs (B-22, B-56, B-122) fall outside this cluster. The reasons for falling outside the cluster are different: B-22 contains driftwood heavily shaded by vegetation with only two lichen species on it; B-56 has a log moved further inland and is dominated by tundra species; B-122, due to the log's proximity to wooden structures, contains a number of boreal forest species. All other points on the graph are located quite compactly. Therefore, we can conclude that almost all surveyed sample plots represent a single more or less uniform driftwood lichen community on the Commander Islands.

Unfortunately, in our study, we were unable to account for the age and decomposition of the logs, which clearly influence the lichen species composition. Perhaps by considering this and other unaccounted factors, it will be possible to identify patterns in lichen distribution within the driftwood community.

CONCLUSION

Driftwood is a unique substrate, significantly different in its characteristics from inland wood. Consequently, driftwood is colonized by lichens from various substrate groups (70.1 % are corticolous and lignicolous, 34.1 % are saxicolous, 34.1 % are terricolous and 4 % are specialized driftwood species). We identified 115 species of lichens and lichenicolous fungi growing on driftwood. This is the largest known list of driftwood lichen biota. Of these, 87 species are new to the Commander Islands, 28 species are also new to the Kamchatka Territory, 14 are new to the Russian Far East, and five (*Hafellia fosteri*, *Lecania granulata*, *Lecanora aleutica*, *Lichenodiplis fallaciosa*, and *Puttea caesia*) are new to Russia. The most common species are *Lecanora orae-frigidae* (found at 35 SP) and a small number of other

species specialized in colonizing driftwood, wood, and seashore. The majority of the lichen species found on driftwood are not substrate-specific and are encountered rarely or as single occurence. Compared with the lichen biota of the driftwood of the Keret Archipelago of the White Sea, the Jaccard coefficient is 0.43. Typical driftwood lichens and multizonal multiregional corticolous species are common to driftwood of both territories. The driftwood community of the Keret Archipelago is distinguished by a more significant contribution of boreal corticolous lichens, and the driftwood community of the Commander Islands is distinguished by a more significant proportion of saxicolous species. As a result of the analysis of substrate wood sections, 4 genera growing in North America as well as in Asia were identified. The most abundant is *Picea* sp. wood. The ecological-substrate analysis revealed that the diversity of lichen species on SP is slightly affected by the distance from the sea coast, the altitude a.s.l., ornithogenic influence, and it also correlates with species richness on SP. The location of the sample plot on the western or eastern coast of Bering or Medny Island does not have a significant effect. Almost all SPs form one cluster based on the lichen species composition on them. Therefore, we can conclude that all the sample plots we surveyed represent a single driftwood lichen community on the Commander Islands. Further studies of the driftwood lichen biota on the Commander Islands and in other locations, along with the consideration of factors such as the age and stage of log decomposition, may make it possible to identify patterns in lichen distribution within the driftwood community.

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Author contribution

A.S. Zueva – collection of specimens, photography of specimens, identification of lichenicolous fungus and lichens, HPTLC, substrate and ecological analyses, writing original draft and its editing; I.S. Stepanchikova – collection of specimens, photography of specimens, identification of lichenicolous fungus and lichens, HPTLC, molecular analysis, editing draft; D.E. Himelbrant. – collection of specimens, photography of habitats, identification of lichenicolous fungus and lichens, editing draft; I.V. Frolov – identification of lichens, molecular analysis, editing draft; G.L. Gusarova – substrate and ecological analyses, editing draft; A.V. Stepanova – identification of substrate woods; V.V. Tabakina – molecular analysis; I.A. Galanina – identification of lichens. All the authors have read and agreed with the final submitted version the manuscript.

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