



Exploring species diversity and host plant associations of leaf-mining micromoths (Lepidoptera: Gracillariidae) in the Russian Far East using DNA barcoding

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Abstract

The Russian Far East (RFE) is an important hotspot of biodiversity whose insect fauna remains understudied, particularly its Microlepidoptera. Here we explore the diversity of leaf-mining micromoths of the family Gracillariidae, their distribution and host plant associations in RFE using a combination of field observations and sampling, DNA barcoding, morphological analysis and literature review.

We collected 91 gracillariid specimens (45 larvae, 9 pupae and 37 adults) in 12 localities across RFE and identified 34 species using a combination of DNA barcoding and morphology. We provide a genetic library of 57 DNA barcodes belonging to 37 Barcode Index Numbers (BINs), including four BINs that could potentially represent species new to science. Leaf mines and leaf shelters are described and illustrated for 32 studied species, male or female genitalia as well as forewing patterns of adults are shown, especially for those species identified based on morphology.

Three species, *Micrurapteryx caraganella* (Hering), *Callisto insperatella* (Nickerl), and *Phyllonorycter junoniella* (Zeller) are newly recorded from RFE. Five species previously known from some regions of RFE, were found for the first time in Amurskaya Oblast: *Phyllonorycter populifoliella* (Treitschke), Primorskii Krai: *Ph. sorbicola* Kumata and Sahkalin Island: *Caloptilia heringi* Kumata, *Ph. ermani* (Kumata) and *Ph. ulmifoliella* (Hübner). Eight gracillariid–plant associations are novel to science: *Caloptilia gloriosa* Kumata on *Acer pseudosieboldianum*, *Cameraria nipponica* Kumata on *A. caudatum* subsp. *ukurundense*, *Parornix ermolaevi* Kuznetsov on *Corylus sieboldiana*, *Phyllonorycter ermani* (Kumata) on *Betula platyphylla*, *Ph. nipponicella* (Issiki) on *Quercus mongolica*, *Ph. orientalis* (Kumata) and *Ph. pseudojezoniella* Noreika on *Acer saccharum*, *Ph. sorbicola* on *Prunus maakii*. For the first time we documented the “green island” phenotype on *Phyllonorycter cavella* (Zeller) mines on *Betula platyphylla*.

Two pestiferous species have been recorded during our surveys: *Micrurapteryx caraganella* on ornamental *Caragana arborescens* in urban plantations in Amurskaya Oblast, and the lime leafminer *Phyllonorycter issikii* (Kumata), a species known to be native to RFE and invasive elsewhere in Russia and in European countries.

A revised checklist of RFE gracillariids has been compiled. It accounts for 135 species among which 17 species (13%) are only known to occur in RFE. The gracillariid fauna of RFE is more similar to the Japanese fauna (49%), than to the fauna of the rest of Russia (i.e. European part and Siberia) (32%).

Key words: Asian part of Russia, COI, faunal checklist, biogeography, insect–plant interactions, invasive species, pests, putative new species

Introduction

Situated between Eastern Siberia and the Pacific Ocean, the Russian Far East (RFE) is known as a hotspot of biodiversity (Urusov 1993; Krestov 2003). The variability of climatic conditions from continental to maritime and the presence of several mountain ranges both inland and on the islands make this region highly diverse for both flora and fauna (Krestov 2003; Kuzmin 2008; Beljaev 2016). The RFE, particularly its southern territory has a unique biota formed by species from the Siberian boreal forest and Manchurian subtropical forest occupying an area which was not covered by an ice sheet during the last glacial maximum (Dominick 2011). Historically the Japan sea region including southern part of RFE, Sakhalin, southeast China, Korea, and Japan was assumed to be the center of origin of a multitude of species that evolved under large paleogeographic transformations during the late Pleistocene to the beginning of Holocene (Beljaev 1996; Grichuk & Borisova 2009; Novenko 2009).

The insect fauna of RFE still remains understudied with many new species and host plant interactions to be discovered (Ponomarenko & Zinchenko 2013; Chernikova & Ponomarenko 2016; Fedotova 2018; Mutin & Barkalov 2018; Rybalkin *et al.* 2018). One particularly neglected group of insects is the micromoths, a polyphyletic group of small-sized Lepidoptera excluding Macroheterocera and butterflies. Here we focus on the micromoth family Gracillariidae, whose larvae are mainly leaf miners, i.e. feed and live the whole or part of their life inside leaf tissues of their host plants.

With over 2000 species, gracillariids represent one of the most species-rich families of Lepidoptera and have diversified on woody plants in the Palearctic (Lopez-Vaamonde *et al.* 2003, 2006). A total of 132 species of gracillariids feeding on plants from 31 families are known to occur in RFE (Caradja 1920; Kuznetsov 1960, 1979a, 1979b, 1981, 1999; Kuznetsov & Baryshnikova 1998; Ermolaev 1977, 1979, 1981a, 1981b, 1986a, 1986b, 1987; Noreika 1994; Baryshnikova & Dubatolov 2007, 2016; Baryshnikova 2008, 2016). These lepidopterists described a total of 33 new species to science from the region (i.e. 25% of all gracillariids in RFE) and recorded dozens of gracillariid species earlier described by T. Kumata from Japan (Kumata 1963, 1967; see Table S1). Furthermore, 8 species described from RFE were later recorded from Japan, Korea and / or China (Kumata 1982; Kuznetsov & Baryshnikova 1998; Kawahara *et al.* 2010; Hu *et al.* 2011; Kobayashi. & Hirowatari 2011; Baryshnikova 2016; Kirichenko *et al.* 2018a).

DNA barcoding has been extensively used to explore the diversity of gracillariid communities and their interactions with host plants (Lees *et al.* 2013). Since 2009, we have been running a DNA barcoding campaign of leaf-mining insects in Asian Russia, mainly in Siberia. We have used DNA barcodes to discover and describe new-to-science gracillariid species from Siberia (Kirichenko *et al.* 2016, 2018a), to characterize leaf-mining insect communities feeding on species of *Betula*, *Salix* and *Populus* commonly distributed in Asian Russia (Kirichenko *et al.* 2017a, 2018b), to revise the distribution of gracillariids in Siberia, and define their trophic interactions (Kirichenko *et al.* 2017b, 2017c, 2017d; Akulov *et al.* 2018; Knyazev *et al.* 2018). So far, we have generated ca. 700 DNA barcodes for 95 gracillariid species from Asian Russia.

One of the many advantages of using DNA barcodes is to be able to identify leaf-mining insect species based on their immature stages, which often have fewer or no diagnostic characters and are in many cases still unknown to science. DNA barcodes can be even obtained from remains of larvae found inside leaf mines (Lees *et al.* 2013; Mlynareka *et al.* 2016). In addition, the use of Barcode Index Numbers (BINs), as species proxies (Ratnasingham & Hebert 2013) allows the characterization and comparison of taxonomically poorly known Lepidoptera communities across regions and habitats (Delabye *et al.* 2019; Lopez-Vaamonde *et al.* 2019).

The main aims of this study are: 1) to assess the gracillariid species diversity of RFE using DNA barcoding and morphology; 2) to document host plant associations of gracillariids in RFE and to illustrate leaf mines and leaf shelters, adults and their genitalia; 3) to compile a revised checklist of RFE Gracillariidae and compare its taxonomic composition with other regions and countries (Siberia, European part of Russia and Japan); 4) to discover new species.

Material and methods

Field Sampling. Sampling of gracillariid mines was done in twelve localities in four administrative regions of RFE: Amurskaya Oblast (Blagoveshchensk, Skovorodino) (AO), Khabarovskii Krai (Komsomolsk-na-Amure) (KK), Primorskii Krai (Vladivostok, Gornotaezhnoe—two localities, Glukhovka, Rakovka, Chuguevka) (PK), and

Sakhalinskaya Oblast (Sakhalin Island: Yuzhno-Sakhalinsk—three localities) (SO) in 2010–2017 (Fig. 1). Insects were sampled in various ecosystems: in the botanical gardens (Komarov Mountain-Taiga Station FEB RAS, Gornotaezhnoe; Botanical Garden-Institute FEB RAS, Sakhalin Branch, Yuzhno-Sakhalinsk), city parks (Friendship park, Blagoveshchensk; Gagarin park, Yuzhno-Sakhalinsk) and other city tree plantations (Skovorodino, Komsomolsk-na-Amure, Vladivostok), forests (Gornotaezhnoe, Glukhovka and Rakovka villages), and mountainous areas—Sikhote-Alin Mountains (Primorskii Krai) and Susunay mountain range (Sakhalin Island) (Fig. 2).

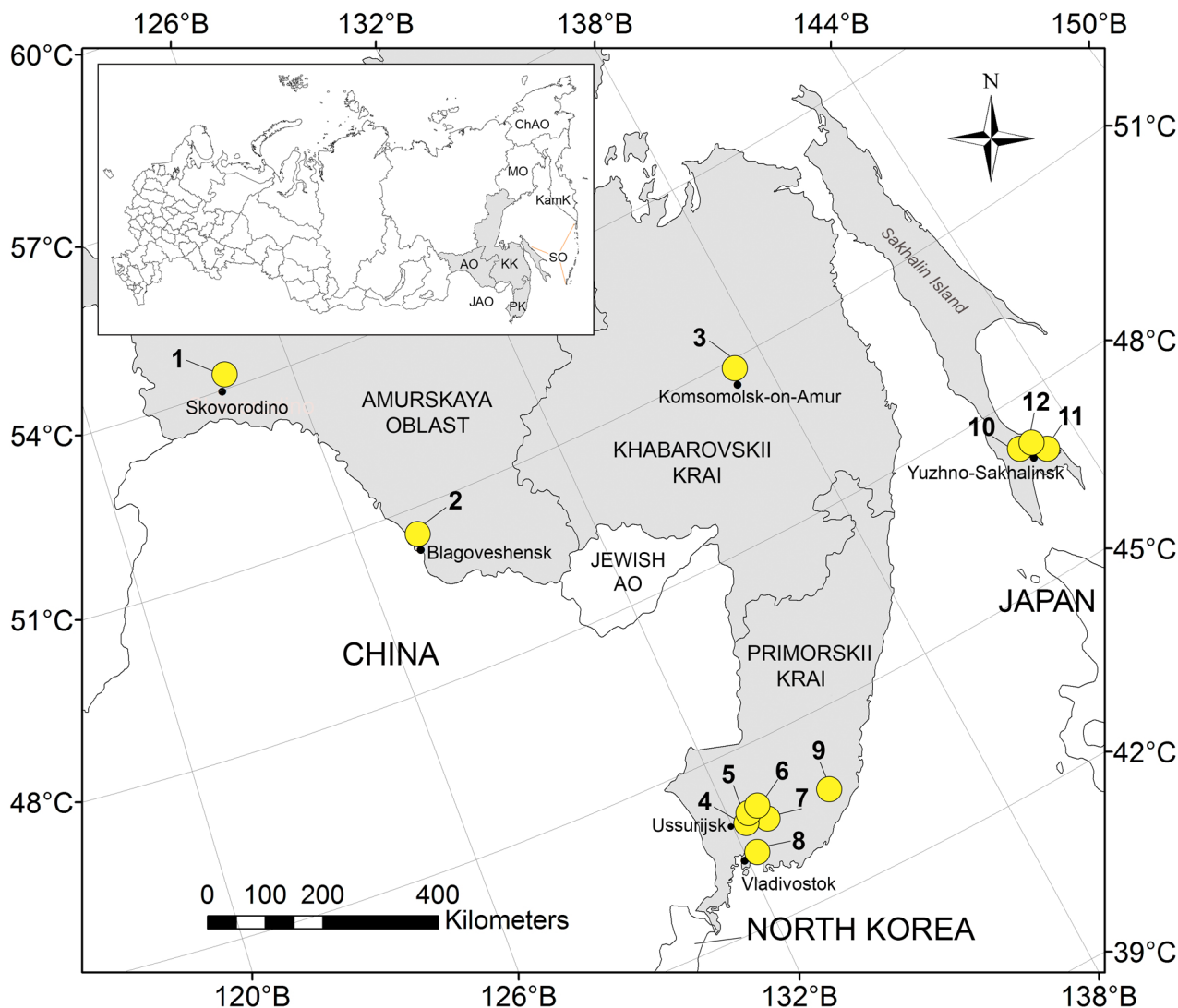


FIGURE 1. The area of study in the Russian Far East, June–July 2010–2017. Black circles indicate cities, yellow circles with the numbers 1–12 are the sampling locations: (1) AO, Skovorodino, tree plantation nearby train station; (2) AO, Blagoveshchensk, Friendship park; (3) KK, Komsomolsk-na-Amure, tree lines along the road; (4) PK, Gornotaezhnoe, MTS; (5) ibidem, forest; (6) PK, Glukhovka, forest; (7) PK, Rakovka, forest; (8) PK, Vladivostok, suburb, tree plantation; (9) PK, Sikhote-Alin Mountains, national park “Zov tigra”; (10) SO, Sakhalin Isl., Yuzhno-Sakhalinsk, Botanical garden FEB RAS Sakhalin Branch; (11) ibidem, Gagarin park; (12) SO, Sakhalin Isl., Susunay mountain range, pass “Verblyud”. In the left corner, on the map of Russia the sampled area is shaded in gray. Regions: (ChAO) Chukotsky Autonomous Okrug, (KamK) Kamchatskii Krai, (MA) Magadanskaya Oblast, (AO) Amurskaya Oblast, (KK) Khabarovskii Krai, (JAO) Jewish Autonomous Oblast, (AO) Amurskaya Oblast, (PK) Primorskii Krai, (SO) Sakhalinskaya Oblast (includes Sakhalin Island and Kuril Islands).

Leaf mines were collected from woody plants of the families Betulaceae, Caprifoliaceae, Ericaceae, Fabaceae, Fagaceae, Juglandaceae, Malvaceae, Oleaceae, Rosaceae, Salicaceae, Sapindaceae, and Ulmaceae. Additionally, leaf mines of one gracillariid species were sampled from herbaceous Fabaceae species.

Overall, 91 gracillariid specimens were collected in RFE: 45 larvae, 9 pupae, 37 adults. They were all obtained from leaf mines collected on various host plants, except 5 adult moths (4 *Phyllonorycter junoniella* (Zeller) and 1

Ph. ulmifoliella (Hübner)) that were collected by sweep netting in the field. Immature stages (larvae and/ or pupae) were excised from their leaf mines and placed singly in 1.5 ml tubes with 96% ethanol. Mined leaves (often with larvae inside leaf mines) were dried and placed in the annotated herbarium collection as traces of feeding activity of gracillariids.

Leaves with feeding larvae in mines found in significant numbers (> 5 mines per a host plant) were kept indoors in plastic boxes at constant conditions (22 °C, 55% RH, L:D 18:6) following rearing protocols described in Hering (1951) and Ohshima (2005) in order to rear adults. Additionally, four adults of *Phyllonorycter pterocaryae* (Kumata) were obtained from leaf mines on *Juglans mandshurica* in Japan in 2018 (Honshu, Okayama, Niimi, 34.98N, 133.42E, 184 m alt., 1 ♂, *J. mandshurica*, 20.VIII.2018 em.; Miyagi, Sendai, Mt. Aoba, 38.26N, 140.82E, 693 m alt., 3 ♀, *J. mandshurica*, 06.IX.2018 em., I. Ohshima leg.) for comparing with RFE's *Juglans*-feeding *Phyllonorycter*.

DNA barcoding. DNA was extracted from 57 gracillariid individuals sampled in RFE, i.e. 45 larvae, 5 pupae and 7 adults (Table 1), and additionally from 4 adults of *Phyllonorycter pterocaryae* (Kumata) from Japan using the NucleoSpin® tissue XS kit, Macherey-Nagel, Germany, following the manufacturer's protocol. Whole bodies of larvae, most commonly represented by tiny individuals (sampled in early larval instars) and whole pupae were used for DNA extraction. In adults, DNA was extracted from the abdomen saving genitalia for morphological identification. The COI barcode fragment (658 bp) was amplified via PCR at the standard conditions for the reaction using the primers LCO (5' GGT CAA CAA ATC ATA AAG ATA TTG G 3') and HCO (5' TAA ACT TCA GGG TGA CCA AAA AAT CA 3') for the COI gene (Folmer *et al.* 1994). Purification of PCR products was done using the NucleoSpin® Gel and PCR Clean-up kit Macherey-Nagel, Germany. For sequencing the Sanger method with Abi Prism® Big Dye® Terminator 3.1 cycle sequencing kit was applied (25 cycles of 10s at 96°C, 5s at 50°C, 4 min at 60°C) and the sequence products were processed using a 3500 ABI genetic analyzer. All reactions were performed at INRA (Orléans, France), except for the specimens of *Phyllonorycter pterocaryae* which were processed in Kyoto Prefectural University (Kyoto, Japan). Sequences were aligned using CodonCode Aligner 3.7.1. (CodonCode Corporation). DNA sequences, along with the voucher data, images, and trace files, are stored in the Barcode of Life Data Systems (BOLD) (Ratnasingham & Hebert 2007; www.barcodinglife.org) and the sequences were also deposited in GenBank. All barcode records are publicly available in the BOLD data set "DS-GRARFE", accessed at: dx.doi.org/10.5883/DS-GRARFE. The specimens, BOLD and GenBank accession numbers, collection region, and BIN are listed in Table 1.

BOLD was used to identify species and assign BINs (Ratnasingham & Hebert 2013). Intra- and interspecific genetic distances were estimated using the Kimura 2-parameter. A neighbor-joining tree was rooted using *Tischeria* sp. (Tischeriidae) collected at larval stage in RFE. To assess confidence limits in clades, a multiparametric bootstrap test was performed with 2000 iterations. All computations were done in MEGA 7.0.

Morphological identification. Identification of 37 adults (32 were reared from mines and five captured in the field) was done on the basis of their forewing patterns and male (rarely female) genitalia (Kumata, 1963; Kuznetsov, 1981; Kuroko, 1982; Noreika, 1997; Kumata *et al.* 2013). A total of 31 genitalia dissections and slide mounts were prepared (Robinson, 1976) (Table 1). Genitalia slides were photographed with an Olympus CX411 microscope and an incorporated digital camera. Photographs of leaf mines and leaf shelters were taken using a digital camera Sony Nex 3. Images were revised in Adobe Photoshop®CS2 (v.9).

Distribution and host plant records. We searched the literature for records of Gracillariidae–host plant associations (Kumata 1963; Noreika 1997; Kuznetsov & Baryshnikova 1998; Baryshnikova 2016; Kim & Byun 2017; De Prins & De Prins 2018; Ellis 2018). Gracillariid species that developed exclusively on plants of one genus were considered as monophagous; and species feeding on several plant genera of one family as oligophagous (Hering 1951).

The 12 localities where we documented Gracillariidae species in RFE were compared with earlier published records (Noreika 1997; Baryshnikova & Dubatolov 2007, 2016; Baryshnikova 2008, 2016; De Prins & De Prins 2018) to confirm the novelty of findings for the regions.

Comparing gracillariid faunas. The taxonomic diversity of Gracillariidae in RFE was compared with that of Japan, the neighboring country, which has one of the best known Gracillariidae faunas in the world, and with the rest of Russia. Both Siberia and European part of Russia were pooled together as they have rather similar gracillariid faunas (Kirichenko *et al.* 2017a, 2018b).

TABLE 1. Specimen data of gracillariid species included in the study. Sample IDs are specimen identifiers; Process IDs are sequence identifiers in BOLD; BINs are Barcode Identification numbers (proxy of species) in BOLD. Specimens without Process ID and BIN were examined morphologically but not barcoded.

No	Species	Host plant	Country & region	Life stage, sex	Sample ID / genit. slide no. []	Process ID	GenBank accession no.	BIN ²
ORNIXOLINAE Kuznetsov et Baryshnikova								
1	<i>Micrurapteryx caraganella</i> †	<i>Caragana arborescens</i>	RU: AO	P	P1	–	–	–
2	<i>M. caraganella</i>	<i>C. arborescens</i>	RU: AO	P	P2	–	–	–
3	<i>M. caraganella</i>	<i>C. arborescens</i>	RU: AO	P	P3	–	–	–
4	<i>M. caraganella</i>	<i>C. arborescens</i>	RU: AO	P	P3	–	–	–
5	<i>M. caraganella</i>	<i>C. arborescens</i>	RU: AO	A, male	[38-male]	–	–	–
6	<i>M. caraganella</i>	<i>C. arborescens</i>	RU: AO	A, female	[39-female]	–	–	–
7	<i>Micrurapteryx gradatella</i>	<i>Vicia</i> sp.	RU: AO	L	NK589	SIBLE078-17	MK403682	BOLD:AAG3706
GRACILLARIINAE Stainton								
8	<i>Caloptilia acericola</i>	<i>Acer pseudosieboldiana-num</i>	RU: PK	L	NK539	SIBLE028-17	MK403697	BOLD:ACL5904
9	<i>C. alni</i>	<i>Alnus hirsuta</i>	RU: SO	L	NK619	SIBLE108-18	MK403684	BOLD:ADJ8665
10	<i>C. betulicola</i>	<i>Betula platyphylla</i>	RU: SO	L	NK622	SIBLE111-18	MK403700	BOLD:AAE3420
11	<i>C. gloriosa</i>	<i>Acer pseudosieboldiana-num</i>	RU: PK	A, male	NK532	SIBLE021-17	MK403705	BOLD:ADF4675
12	<i>C. gloriosa</i>	<i>A. pseudosieboldianum</i>	RU: PK	A, male	[13-male]	–	–	–
13	<i>C. heringi</i> ††	<i>Acer pictum</i>	RU: SO	L	NK624	SIBLE113-18	MK403704	BOLD:ADK1669
14	<i>C. stigmatella</i>	<i>Salix</i> sp.	RU: AO	L	NK565	SIBLE054-17	MK403711	BOLD:AAA9984
15	<i>C. stigmatella</i>	<i>Salix</i> sp.	RU: SO	L	NK620	SIBLE109-18	MK403678	BOLD:ACR7387
16	<i>Gracillaria</i> sp.	<i>Syringa amurensis</i>	RU: PK	L	NK549	SIBLE038-17	MK403699	BOLD:ADF4930
17	<i>Gracillaria</i> sp.	<i>Fraxinus mandshurica</i>	RU: PK	L	NK547	SIBLE036-17	MK403728	BOLD:ADF4930
18	<i>Callisto insperatella</i> †	<i>Prunus padus</i>	RU: PK	L	NK590	SIBLE079-17	MK403725	BOLD:AAK2078
19	<i>C. insperatella</i>	<i>P. padus</i>	RU: SO	L	NK625	SIBLE114-18	MK403693	BOLD:AAK2078
20	<i>Callisto</i> sp.	<i>Malus</i> sp.	RU: PK	L	NK548	SIBLE037-17	MK403677	{BOLD:ADF4428}
21	<i>Parornix ermolaevi</i>	<i>Corylus sieboldiana</i>	RU: PK	L	NK546	SIBLE035-17	MK403727	BOLD:ACU5509
22	<i>P. ermolaevi</i>	<i>C. sieboldiana</i> †	RU: PK	L	NK544	SIBLE033-17	MK403689	BOLD:ACU5509
LITHOCOLLETINAE Stainton								

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TABLE 1. (Continued)

No	Species	Host plant	Country & region	Life stage, sex	Sample ID / genit. slide no. []	Process ID	GenBank accession no.	BIN ²
23	<i>Phyllonorycter caraganella</i>	<i>Caragana fruticosa</i>	RU: PK	L	NK525	SIBLE014-17	MK403690	{BOLD:ADF2805}
24	<i>Ph. caraganella</i>	<i>C. fruticosa</i>	RU: PK	L	NK522	SIBLE011-17	MK403694	{BOLD:ADF2805}
25	<i>Ph. caraganella</i>	<i>C. fruticosa</i>	RU: PK	A, male	NK-184-16-9A / [2Pc-2016-male]	-	-	-
26	<i>Ph. caraganella</i>	<i>C. fruticosa</i>	RU: PK	A, male	NK-184-16-12A / [3Pc-2016-male]	-	-	-
27	<i>Ph. caraganella</i>	<i>C. fruticosa</i>	RU: PK	A, male	NK-184-16-13A / [4Pc-2016-male]	-	-	-
28	<i>Ph. cavella</i>	<i>Betula platyphylla</i>	RU: PK	L	NK541	SIBLE030-17	MK403713	BOLD:ADC1842
29	<i>Ph. cavella</i>	<i>B. platyphylla</i>	RU: PK	A, male	111.1 / [11-2016-male]	-	-	-
30	<i>Ph. cretata</i>	<i>Quercus mongolica</i>	RU: SO	L	NK629	SIBLE118-18	MK403709	BOLD:AAD4754
31	<i>Ph. cretata</i>	<i>Q. mongolica</i>	RU: SO	A, male	NK-85-17-4 / [16-male]	-	-	-
32	<i>Ph. ermani</i> ††	<i>Betula platyphylla</i> ‡	RU: SO	L	NK623	SIBLE112-18	MK403679	BOLD:ACU5862
33	<i>Ph. issikii</i>	<i>Tilia mandshurica</i>	RU: PK	A, male	NK596 [NK596-male]	SIBLE085-17	MK403708	BOLD:AAAC9940
34	<i>Ph. issikii</i>	<i>Tilia taquetii</i>	RU: PK	L	NK310	ISSIK269-14	KX818601	BOLD:AAAC9940
35	<i>Ph. issikii</i>	<i>Tilia amurensis</i>	RU: PK	A, male	NK141	ISSIK186-14	KX818667	BOLD:AAAC9940
36	<i>Ph. japonica</i>	<i>Corylus mandshurica</i>	RU: PK	L	NK545	SIBLE034-17	MK403698	BOLD:ACU6993
37	<i>Ph. japonica</i>	<i>C. mandshurica</i>	RU: PK	A, male	36.2 / [4-2016-male]	-	-	-
38	<i>Ph. japonica</i>	<i>C. mandshurica</i>	RU: PK	A, male	NK-142-16-1A / [4.1-2016-male]	-	-	-
39	<i>Ph. jozanae</i>	<i>Crataegus</i> sp.	RU: PK	P	NK543	SIBLE032-17	MK403717	BOLD:AAH8488
40	<i>Ph. jozanae</i>	<i>Crataegus</i> sp.	RU: PK	A, male	41.1 / [14P]-2016-male]	-	-	-
41	<i>Ph. jozanae</i>	<i>Crataegus chlorosarca</i>	RU: SO	L	NK627	SIBLE116-18	MK403683	BOLD:AAH8488
42	<i>Ph. jozanae</i>	<i>C. chlorosarca</i>	RU: SO	A, male	NK-98-17-1 / [14-male]	-	-	-
43	<i>Ph. jozanae</i>	<i>C. chlorosarca</i>	RU: SO	A, male	NK-98-17-1 / [23-male]	-	-	-
44	<i>Ph. junoniella</i> †	<i>Vaccinium vitis-idaea</i>	RU: SO	A	NK628	SIBLE117-18	MK403691	BOLD:ACU6968
45	<i>Ph. junoniella</i>	<i>V. vitis-idaea</i>	RU: SO	A, male	Sakh-Sw-2 / [18-male]	-	-	-
46	<i>Ph. junoniella</i>	<i>V. vitis-idaea</i>	RU: SO	A, male	Sakh-Sw-3 / [20-male]	-	-	-
47	<i>Ph. junoniella</i>	<i>V. vitis-idaea</i>	RU: SO	A, male	Sakh-Sw-4 / [21-male]	-	-	-

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TABLE 1. (Continued)

No	Species	Host plant	Country & region	Life stage, sex	Sample ID / genit. slide no. []	Process ID	GenBank accession no.	BIN ²
48	<i>Ph. junoniella</i>	<i>V. vitis-idaea</i>	RU: SO	A, female	Sakh-Sw-5 / [22-female]	–	–	–
49	<i>Ph. kisoensis</i>	<i>Alnus hirsuta</i>	RU: PT	A, male	45.1 / [5Pk-2016-male]	–	–	–
50	<i>Ph. nigristella</i>	<i>Quercus dentata</i>	RU: PK	A, male	NK528	SIBLE017-17	MK403687	BOLD:ACU6311
51	<i>Ph. nipponicella</i>	<i>Q. mongolica</i> †	RU: PK	A, female	58.1 / 8-2016-female	–	–	–
52	<i>Ph. orientalis</i>	<i>Acer pictum</i>	RU: PK	A, male	NK536	SIBLE025-17	MK403726	BOLD:AAC1748
53	<i>Ph. orientalis</i>	<i>A. pictum</i>	RU: PK	L	NK535	SIBLE024-17	MK403729	BOLD:AAC1748
54	<i>Ph. orientalis</i>	<i>A. saccharum</i> †	RU: PK	L	NK538	SIBLE027-17	MK403707	BOLD:AAC1748
55	<i>Ph. pastorella</i>	<i>Salix</i> sp.	RU: PK	L	NK594	SIBLE083-17	MK403714	BOLD:AAD9785
56	<i>Ph. pastorella</i>	<i>Salix</i> sp.	RU: PK	A, male	49.1 / [12Pp-2016-male]	–	–	–
57	<i>Ph. pastorella</i>	<i>Populus balsamifera</i>	RU: AO	L	NK563	SIBLE052-17	MK403688	BOLD:AAD9785
58	<i>Ph. pastorella</i>	<i>P. balsamifera</i>	RU: AO	L	NK562	SIBLE051-17	MK403681	BOLD:AAD9785
59	<i>Ph. populifoliella</i>	<i>Populus</i> sp.	RU: KK	P	NK88	GRPAL1132-13	MK403730	BOLD:AAD8619
60	<i>Ph. populifoliella</i> ††	<i>P. balsamifera</i>	RU: AO	P	NK561	SIBLE050-17	MK403712	BOLD:AAD8619
61	<i>Ph. populifoliella</i>	<i>P. balsamifera</i>	RU: AO	A, male	NK561-1, [NK561-1-male]	–	–	–
62	<i>Ph. pseudojezoniella</i>	<i>Acer saccharum</i>	RU: PK	A, male	NK-182-16-1A / [20Pps-2016-male]	–	–	–
63	<i>Ph. reduncata</i>	<i>Lonicera maackii</i>	RU: PK	A, male	55.3 / [23Pr-2016-male]	–	–	–
64	<i>Ph. ringoniella</i>	<i>Malus mandshurica</i>	RU: PK	A, male	NK-179-16-1A / [10Prin-2016-male]	–	–	–
65	<i>Ph. ringoniella</i>	<i>Malus</i> sp.	RU: PK	A, female	70.1 / [3Prin-2016-female]	–	–	–
66	<i>Ph. salictella</i>	<i>Salix rorida</i>	RU: SO	L	NK630	SIBLE119-18	MK403703	BOLD:ADM1578
67	<i>Ph. similis</i>	<i>Quercus dentata</i>	RU: PK	L	NK593	SIBLE082-17	MK403702	BOLD:AAL5146
68	<i>Ph. similis</i>	<i>Q. dentata</i>	RU: PK	A, male	42.1 / [8Psim-62016-male]	–	–	–
69	<i>Ph. similis</i>	<i>Q. mongolica</i>	RU: PK	L	NK592	SIBLE081-17	MK403692	BOLD:AAL5146
70	<i>Ph. sorbicola</i> ††	<i>Prunus maackii</i> †	RU: PK	L	NK591	SIBLE080-17	MK403721	BOLD:ACU5756
71	<i>Ph. strigulatella</i>	<i>Alnus hirsuta</i>	RU: SO	A, male	NK-75-17-2 / [19-male]	–	–	–
72	<i>Ph. ulmifoliella</i>	–	RU: PK	A, male	37.1 / [15Pu-2016-male]	–	–	–
73	<i>Ph. ulmifoliella</i> ††	<i>Betula platyphylla</i>	RU: PK	A, female	NK-66-17-1 / [17-female]	–	–	–
74	<i>Phyllonorycter</i> sp. 1	<i>Tilia</i> sp.	RU: PK	L	NK31	ISSIK031-12	[KX818885]	{BOLD:ACC3074}

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TABLE 1. (Continued)

No	Species	Host plant	Country & region	Life stage, sex	Sample ID / genit. slide no. []	Process ID	GenBank accession no.	BIN ²
75	<i>Phyllonorycter</i> sp. 1	<i>T. mandshurica</i>	RU: PK	P	NK205	ISSIK069-14	[KX818718]	{BOLD:ACC3074}
76	<i>Phyllonorycter</i> sp. 1	<i>T. taquetii</i>	RU: PK	L	NK236	ISSIK100-14	[KX818723]	{BOLD:ACC3074}
77	<i>Phyllonorycter</i> sp. 1	<i>T. mandshurica</i>	RU: PK	L	NK208	ISSIK072-14	[KX818721]	{BOLD:ACC3074}
78	<i>Phyllonorycter</i> sp. 1	<i>T. amurensis</i>	RU: PK	A	NK601	SIBLE090-17	MK403722	{BOLD:ACC3074}
79	<i>Phyllonorycter</i> sp. 2	<i>Malus mandshurica</i>	RU: PK	L	NK534	SIBLE023-17	MK403676	{BOLD:ADF3338}
80	<i>Phyllonorycter</i> sp. 3	<i>Prunus padus</i>	RU: AO	L	NK566	SIBLE055-17	MK403696	{BOLD:ACY3732}
81	<i>Phyllonorycter</i> sp. 4	<i>Alnus hirsuta</i>	RU: SO	L	NK618	SIBLE107-18	MK403695	{BOLD:DMI1303}
82	<i>Phyllonorycter</i> sp. 5	<i>Betula platyphylla</i>	RU: SO	L	NK621	SIBLE110-18	MK403716	{BOLD:DM2521}
83	<i>Phyllonorycter</i> sp. 6	<i>Acer pseudosieboldia-num</i>	RU: PK	L	NK540	SIBLE029-17	MK403701	{BOLD:ADF4563}
84	<i>Phyllonorycter</i> sp. 7	<i>Ulmus glabra</i>	RU: PK	P	NK550	SIBLE039-17	MK403718	{BOLD:ACN4282}
85	<i>Phyllonorycter</i> sp. 7	<i>U. davidiana</i> var. <i>ja-ponica</i>	RU: SO	L	NK626	SIBLE115-18	MK403715	{BOLD:ACN4282}
86	<i>Phyllonorycter</i> sp. 8	<i>Juglans mandshurica</i>	RU: PK	L	NK533	SIBLE022-17	MK403680	{BOLD:ADF3451}
87	<i>Chrysaster hagicola</i>	<i>Lespedeza bicolor</i>	RU: PK	L	NK551	SIBLE040-17	MK403724	BOLD:ADF3949
88	<i>Cameraria niponica</i>	<i>Acer caudatum</i> †	RU: PK	L	NK537	SIBLE026-17	MK403685	BOLD:AAI3878
89	<i>C. niponica</i>	<i>A. pseudosieboldianum</i>	RU: PK	L	NK529	SIBLE018-17	MK403719	BOLD:AAI3878
90	<i>C. niponica</i>	<i>A. pseudosieboldianum</i>	RU: PK	A, male	109.3 / [1Cn-2016-male]	–	–	–
PHYLLOCNISTINAE Herrich-Schäffer								
91	<i>Phyllocnistis</i> sp. 1	<i>Salix</i> sp.	RU: PK	L	NK595	SIBLE084-17	[MG191427]	BOLD:ADF2906
Further material examined								
1	<i>Phyllonorycter pterocarya</i>	<i>Juglans mandshurica</i>	JP: MP	A	MM-071	SIBLE144-18	MK403720	{BOLD:ADQ9355}
2	<i>Ph. pterocarya</i>	<i>J. mandshurica</i>	JP: MP	A	MM-072	SIBLE145-18	MK403723	{BOLD:ADQ9355}
3	<i>Ph. pterocarya</i>	<i>J. mandshurica</i>	JP: MP	A	MM-073	SIBLE146-18	MK403706	{BOLD:ADQ9355}
4	<i>Ph. pterocarya</i>	<i>J. mandshurica</i>	JP: OP	A	MM-074	SIBLE147-18	MK403686	{BOLD:ADQ9355}
5	<i>Tischeria</i> sp., outgroup	<i>Tilia taquetii</i>	RU: PK	L	NK238	ISSIK102-14	ISSIK102-14	BOLD:ACM8285

Indication: † new record for RFE, †† new record for the particular region in RFE, ‡ new host plant; RU—Russia, AO—Amurskaya Oblast, KK—Khabarovskii Krai, PK—Primorskii Krai, SO—Sakhalinskaya Oblast (for the exact sampling locations and coordinates, see the faunistic list); JP—Japan, MP—Miyagi Prefecture, OP—Okayama Prefecture; L—larva, P—pupa, A—adult. Cells with dash mean no data available. ¹GenBank accession numbers given in [] were borrowed from our recent papers: Kirichenko *et al.* (2017c, 2018a). ² BINs given in {} are novel to BOLD.



FIGURE 2. Sampling localities in the Russian Far East. (A–C) PK, Gornotaezhnoe, MTS: (A) European woody plant species zone, (B) *Juglans mandshurica* plantation, (C) East Asian woody plant species zone; (D) PK, 20 km west of MTS, artificial lake on the way to Glukhovka and Rakovka; (E–H) SO, Sakhalin Isl., Susunay mountain range: (E–G) pass “Verblud”, sampling and camping area, (H) foothills of the Susunay mountain range, the Erman’s birch grove. Personalities: (C) S. Gorokhova, (F) V. Sheiko, (H) N. Kirichenko (the photographs are published with the permission of SG, VS and NK). (PK) Primorskii Krai, (SO) Sakhalinskaya Oblast (includes Sakhalin Island and Kuril Islands).

Gracillariid species diversity was assessed based on literature records for RFE (Noreika 1997; Kuznetsov & Baryshnikova 1998; Baryshnikova & Dubatolov 2007, 2016; Baryshnikova 2016; Kirichenko *et al.* 2017b), European part of Russia and Siberia (Baryshnikova 2016; Anikin *et al.* 2016; Kirichenko *et al.* 2016, 2017a, 2017b, 2017c, 2017d, 2018a, 2018b; Kozlov *et al.* 2017; Akulov *et al.* 2018; Knyazev 2018) and Japan (Kumata 1963; Baryshnikova 2016; De Prins & De Prins 2018; Liu *et al.* 2018; Kirichenko *et al.* 2018a). Gracillariid faunas were compared using the Sørensen–Dice coefficient (or Dice similarity coefficient, DSC): $DSC = 2 \times C / (A + B)$, where A and B are the numbers of species in each location, C is the number of species common for two compared locations (Magurran 2004).

Pests and invasive species. We checked the literature for any evidence of invasiveness and or ecological and economic damage among the gracillariids identified in our study (Kuznetsov 1960, 1979a, 1979b, 1981, 1999; Ermolaev 1977, 1979, 1981a, 1981b, 1981c, 1986a, 1986b, 1987, 1988; Noreika 1994, 1997).

Revised check list. Kawahara *et al.* (2017) reconstructed a molecular phylogeny and provided a revised subfamily classification of Gracillariidae based on morphological and molecular data and analyses, recognising eight subfamilies. In their recent checklist of Neotropical Gracillariidae, de Prins *et al.* (2019) treated Parornichinae as a tribe (Parornichini) within Gracillariinae. This debatable change in the higher classification of Gracillariidae has been followed by some authors (Liao *et al.* 2019) but not others who argue that this change in rank is unjustified (Hoare *et al.* 2019). We prefer to keep the subfamily Parornichinae, because whilst there is solid morphological (forewing and hindwing venation, larval chaetotaxy), biological (host plant associations) and phylogenetic evidence to keep Parornichinae as a unique subfamily, there is no such unequivocal evidence that they should form a monophylum with Gracillariinae.

Gracillariid species sampled in our study are given in the text. Each species is provided with sampling data: location, GPS coordinates (in decimal degrees), host plant, date of sampling, insect stage, sample ID, GenBank accession number (starts with two letters—KX or MK), genitalia slide number (in square brackets), and specimen depository (in parentheses). The collector of RFE gracillariids is N. Kirichenko, except for two specimens (*Phyllonorycter issikii* and *Phyllonorycter* sp. 1) sampled by M. Ponomarenko (indicated in the text). In the species section, the Material examined is followed by leaf mine description and host plant notes. Uncertain taxonomic cases and putative new species to science are discussed in Remarks. Revised check list is provided in the Table S1.

Specimen depositories

SIF: Sukachev Institute of Forest, Siberian Branch of Russian Academy of Sciences, Krasnoyarsk, Russia (pinned moths, genitalia slides, typical leaf mines in the annotated herbarium collection).

MSNV: Museo Civico di Storia Naturale, Verona, Italy (pinned moths, genitalia slides).

INRA: Institut National de Recherche Agronomique, Unité de Recherche Zoologie Forestière, Orléans, France (vouchers of the sequenced specimens and extracted DNA).

Abbreviations. Regions: ChAO (Chukotsky Autonomous Okrug), KamK (Kamchatskii Krai), MA (Magganskaya Oblast), KK (Khabarovskii Krai), JAO (Jewish Autonomous Oblast), AO (Amurskaya Oblast), PK (Primorskii Krai), SO (Sakhalinskaya Oblast that includes Sakhalin Island and Kuril Islands). Botanical gardens: MTS (Komarov Mountain-Taiga Station FEB RAS), BGIS (Botanical Garden-Institute FEB RAS, Sakhalin Branch).

Results

DNA barcoding. A total of 56 full-length (658 bp) barcodes were obtained from 45 larvae, 5 pupae and 7 adults belonging to 26 BINs and 26 taxonomic species respectively (Table 1, Fig. 3). Additionally, we discovered 11 BINs of species not present in genetic data bases and belonging to the genera *Caloptilia* (1), *Gracillaria* (1), *Phyllocnistis* (1), and *Phyllonorycter* (8) (Fig. 3, Table 1, 2). Seven of these BINs: *Phyllonorycter* sp. 2, ex. *Malus mandshurica* (Maxim.) Kom. ex Juz.; *Phyllonorycter* sp. 3, ex. *Prunus padus* L.; *Phyllonorycter* sp. 4, ex. *Alnus hirsuta* (Spach) Rupr.; *Phyllonorycter* sp. 5, ex. *Betula platyphylla* Sukaczew; *Phyllonorycter* sp. 7, ex. *Ulmus glabra* Huds. and *U. davidiana* var. *japonica* (Rehder) Nakai, and *Phyllonorycter* sp. 8, ex. *Juglans mandshurica* Maxim. likely represent already described species which are known to develop on the above-mentioned woody plants, but for which

no DNA barcodes are available in BOLD yet (Table 2). The remaining four BINs, i.e. *Callisto* sp. (from *Malus* sp.), *Phyllocnistis* sp. 1 (*Salix* sp.), *Phyllonorycter* sp. 1 (*Tilia* spp.) and *Phyllonorycter* sp. 6 (*Acer pseudosieboldianum* (Pax) Kom.) did not match any previously sequenced gracillariid species. These unknown gracillariids were collected feeding on host plants for which no other gracillariids have been recorded so far (Table 2). Bearing in mind the generally high host specificity of gracillariids and marked genetic distances to the nearest neighbors we consider those four cases as potential new species to science.

Morphological identification. Representatives of twenty-two species were identified based on adult morphology (forewing pattern and male and/ or female genitalia) (Table 1; Figs 4–8). Fourteen species out of these 22 species, i.e. *Caloptilia gloriosa* Kumata, *Cameraria nipponica* Kumata, *Phyllonorycter caraganella* (Ermolaev), *Ph. cavella* (Zeller), *Ph. cretata* (Kumata), *Ph. issikii* (Kumata), *Ph. japonica* (Kumata), *Ph. jozanae* (Kumata), *Ph. junoniella* (Zeller), *Ph. nigristella* (Kumata), *Ph. orientalis* (Kumata), *Ph. pastorella* (Zeller), *Ph. populifoliella* (Treitschke), and *Ph. similis* Kumata were also DNA barcoded (Table 1; Fig. 3). Other eight species—*Micrurapteryx caraganella* (Hering), *Phyllonorycter kisoensis* Kumata et Park, *Ph. nipponicella* (Issiki), *Ph. pseudojezoniella* Noreika, *Ph. reduncata* (Ermolaev), *Ph. ringoniella* (Matsumura), *Ph. strigulatella* (Zeller), and *Ph. ulmifoliella* were determined based exclusively on adult morphology (Table 1; Figs 4, 5, 7, 8).

In total we identified 34 gracillariid species sampled from the continental and insular regions of RFE using a combination of DNA barcoding and morphology (Table 1).

New host plant records. In RFE, gracillariid leaf mines were found on 45 plant species from 19 genera, 12 families and 8 orders (Fig. 9). Nearly half of all gracillariids recorded in this study were found on plants from the order Fagales (4 families—Betulaceae, Fabaceae, Fagaceae and Juglandaceae), followed by Sapindales (8 gracillariid BINs), Rosales (6), and Malpighiales (5). All gracillariids were found feeding on woody plant species, except *Micrurapteryx gradatella* that was collected on herbaceous legumes, *Vicia* sp. Leaf mines and leaf shelters of the sampled gracillariids are described below (see the taxonomic list) and illustrated for the majority of species (Figs 10–14).

Eight gracillariid-host plant associations in RFE are new to science. We recorded for the first time *Caloptilia gloriosa* Kumata feeding on *Acer pseudosieboldianum*, *Cameraria nipponica* Kumata on *A. caudatum* subsp. *ukurundense*, *Parornix ermolaevi* Kuznetsov on *Corylus sieboldiana*, *Phyllonorycter ermani* (Kumata) on *Betula platyphylla*, *Ph. nipponicella* (Issiki) on *Quercus mongolica*, *Ph. sorbicola* (Kumata) on *Prunus maackii*, *Ph. orientalis* (Kumata) and *Ph. pseudojezoniella* Noreika on *Acer saccharum*. In the first six associations, host plants are native to East Asia, whereas in the last two associations the host is North American species (*Acer saccharum*) introduced in the collection of the botanical garden of the Komarov Mountain-Taiga Station in Primorskii Krai.

Overall, 72% of gracillariids sampled in this study are monophagous and 28% are oligophagous. No polyphagous species attacking a wide range of plant species from unrelated families and orders was documented.

For the first time, “green islands” were recorded on mines of *Phyllonorycter cavella* (Zeller), on abscised leaves of *Betula platyphylla* in RFE.

Distribution ranges and fauna similarity. Eight species in our study represented new regional records. Among them, three species have been documented for RFE for the first time: *Micrurapteryx caraganella* (Hering) from AO, *Callisto insperatella* (Nickerl) from PK and SO (Sakhalin Island), *Phyllonorycter junoniella* (Zeller) from SO (Sakhalin Island). Other five species, previously known from some regions of RFE, have been found for the first time in AO (*Ph. populifoliella* Treitschke), PK (*Ph. sorbicola* (Kumata)) and SO (*Caloptilia heringi* Kumata, *Phyllonorycter ermani* (Kumata) and *Ph. ulmifoliella* (Hübner)).

A compiled checklist of RFE Gracillariidae comprises 135 species including three species new to the region (Table S1). The number of gracillariid species known in RFE is about two times less than in Japan (235 species) and similar to the number of species known from the European part of Russia and Siberia altogether (140 species) (Fig. 15). RFE shares 91 gracillariid species with Japan so that the similarity of Gracillariidae faunas of these two areas assessed by Sørensen–Dice coefficient reaches 49%. Overall 45 gracillariid species are common for RFE, European Russia and Siberia (Sørensen–Dice coefficient = 32%) (Fig. 15). The European part of Russia and Siberia altogether share only 23 gracillariid species with Japan, showing only 12% of similarity of their Gracillariidae faunas (Fig. 15).

Pest and invasive species. Among identified gracillariids, four species are known to be able to significantly increase their population densities to outbreak levels on woody plants in Russia according to literature (see Material and methods). Among them *Micrurapteryx caraganella* (Hering) on *Caragana arborescens* (Fabaceae),

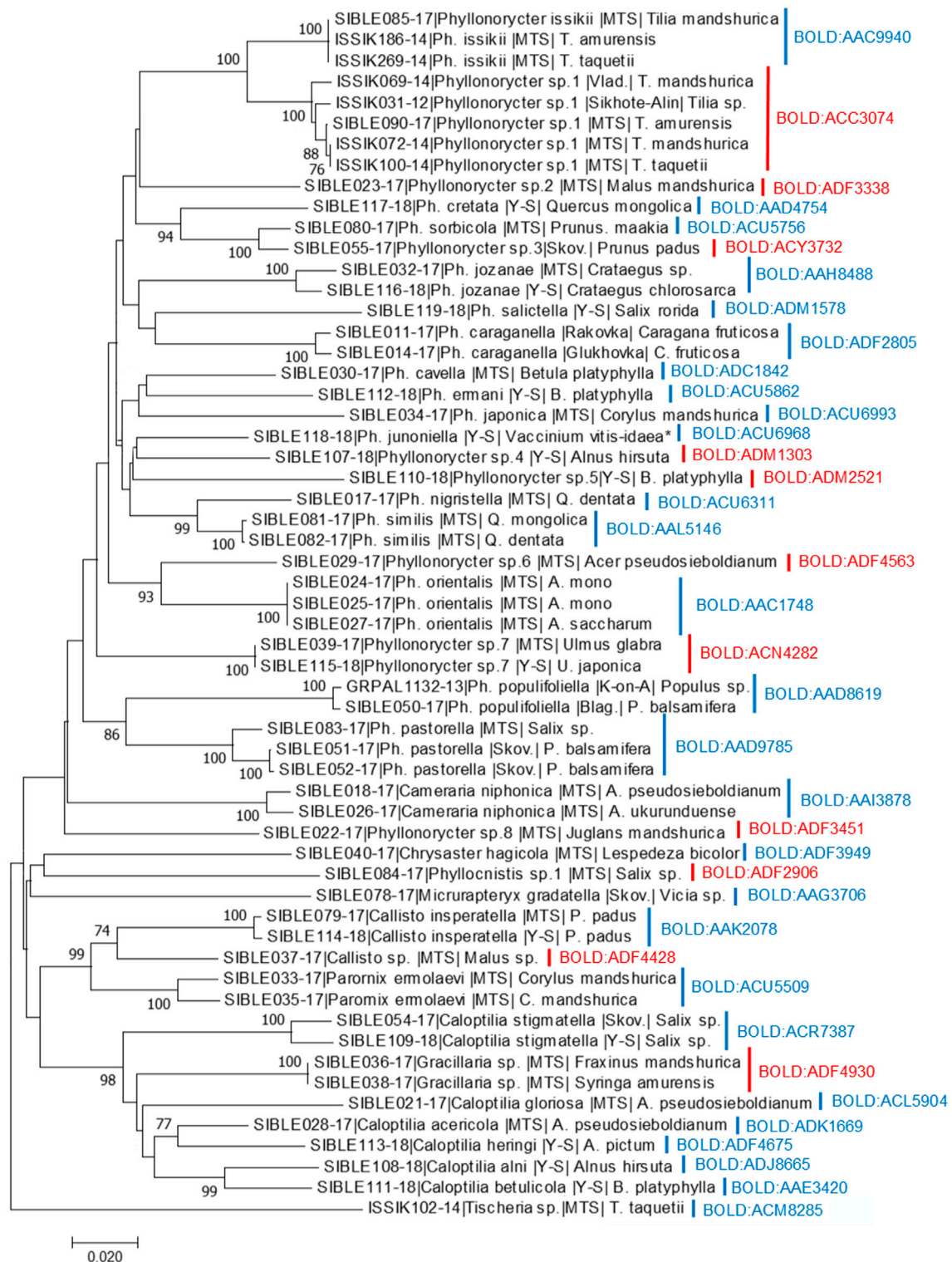


FIGURE 3. COI Neighbor-Joining tree of Gracillariidae species sampled in the Russian Far East. Each specimen is accompanied by its sequence number (BOLD “process ID”), species name, sampling location and host plant. Sampling locations are given between two vertical lines, i.e. [Skov.] Skovorodino; [Blag.] Blagoveshchensk; [MTS] Komarov Mountain-Taiga Station FEB RAS and the forest around; [Rakovka], [Glukhovka] forest around the villages Rakovka and Glukhovka respectively; [Vlad.] Vladivostok; [Sikhote-Alin] Sikhote-Alin Mountains, national park “Zov tigr”, [Y-S] Yuzhno-Sakhalinsk and the area around including Susunay mountain range (see Fig. 1 for details). Host plants: *A. pseudosieb.—Acer pseudosieboldianum*; * sampling done by sweep netting from the bush, whereas all other gracillariids were collected/ reared directly from their mines. Each leafminer species is supplied with its BIN number retrieved from BOLD; blue BINs correspond to known species, red—new BINs.

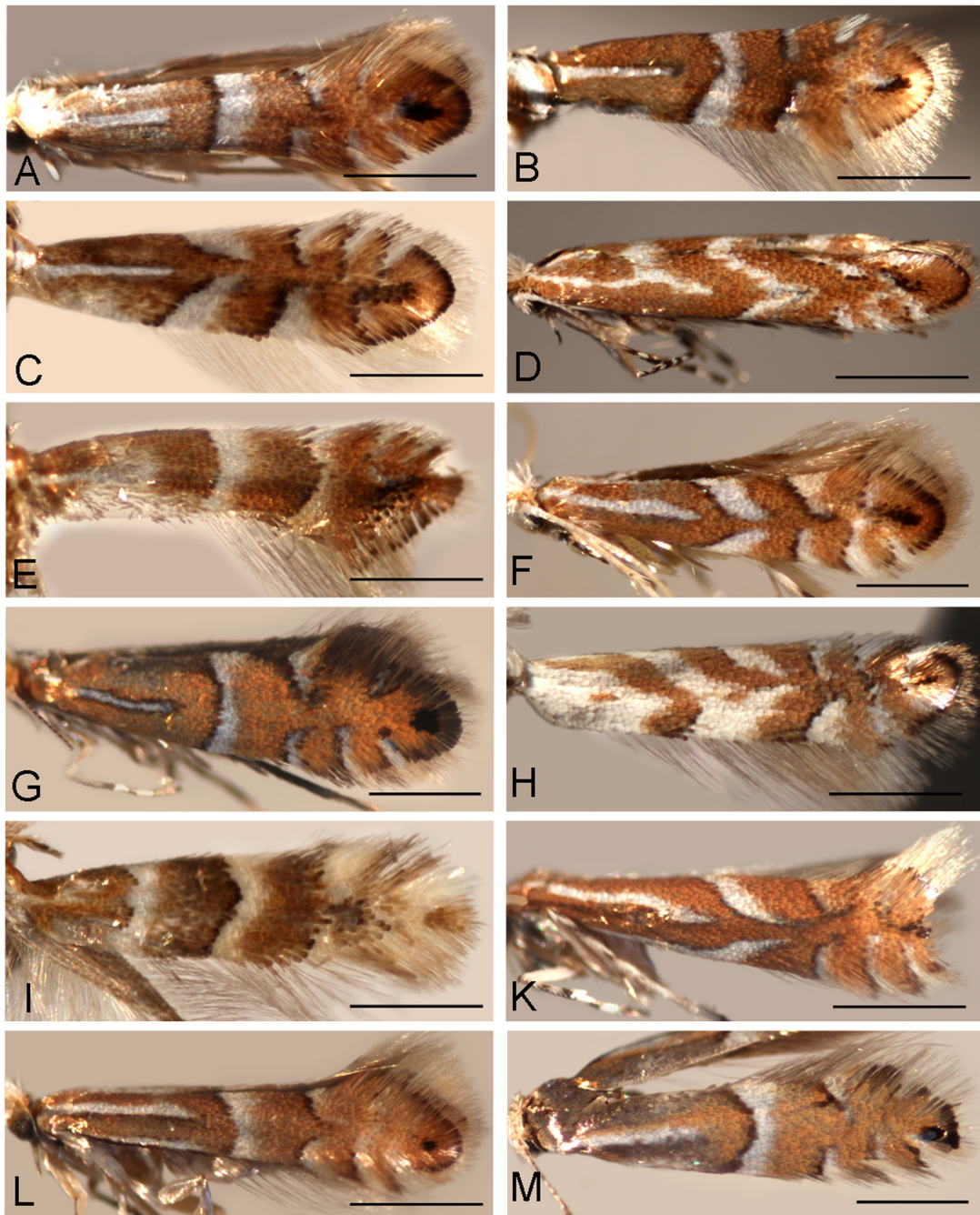


FIGURE 4. Forewing pattern of *Phyllonorycter* spp. from the Russian Far East. (A) *Ph. caraganella*, host plant *Caragana fruticosa*, NK-184-16-9A; (B) *Ph. cavella*, *Betula dahurica*, 111.1; (C) *Ph. cretata*, *Quercus mongolica*, NK-85-17-4; (D) *Ph. issikii*, *T. mandshurica*, NK596; (E) *Ph. japonica*, *Corylus mandshurica*, 36.2; (F) *Ph. jozanae*, *Crataegus* sp., 44.1; (G) *Ph. kisoensis*, *Alnus hirsuta*, 45.1; (H) *Ph. pastorella*, *Salix* sp., 49.1; (I) *Ph. reduncata*, *Lonicera maackii*, 55.3; (K) *Ph. ringoniella*, *Malus mandshurica*, NK-179-16-1A; (L) *Ph. similis*, *Quercus dentata*, 42.1; (M) *Ph. ulmifoliella*, 37.1. Sampling locations: (A) PK, Rakovka, 27.VII.2016; (B, D–M) ibidem, Gornotaezhnoe, 16.VII.2013 (D), 22-25.VII.2016 (B, E–M); (C) SO, Sakhalin Isl., Yuzhno-Sakhalinsk, 12.VII.2017. Scale bars 1 mm.

Phyllonorycter issikii (Kumata) on *Tilia* spp. (Malvaceae), *Caloptilia betulicola* (Hering) on *Betula* spp. (Betulaceae), and *Ph. populifoliella* (Treitschke) on *Populus* spp. (Salicaceae). Outbreaks of these species were occasionally recorded in the European part of Russia or Siberia. We found no data in literature regarding outbreaks of these species in RFE. During our surveys, only *Micrurapteryx caraganella* has been found in mass on bushes of the Siberian peashrub in the urban plantations of Skovorodino, AO (Kirichenko *et al.* 2017b).

The lime leafminer *Phyllonorycter issikii*, known to be native to RFE, is an invasive species that nowadays is found in Siberia, European part of Russia and in many European countries (Kirichenko *et al.* 2017c).

Taxonomic list of Gracillariidae species discovered in RFE in 2010–2017

Subfamily ORNIXOLINAE Kuznetsov et Baryshnikova, 2001

Micrurapteryx caraganella (Hering, 1957)

(Figs 5A, 10A–B)

Material examined. Russia: AO, Skovorodino, 53.98N, 123.93E, 431 m alt., *Caragana arborescens*, 26.VI.2016, 4 pupae, 2 adults (reared from leaf mines), 1 male / genitalia slide [38-male], 1 female / [39-female] (Fig. 5A), deposited in SIF.

Leaf mine. Flat whitish green blotch, slightly branched, on the upper side of the leaflet above the midrib, often occupies entire leaflet (Fig. 10A); starts as a relatively long narrow epidermal tunnel on the lower surface of the leaflet (Fig. 10B). Hardly any frass is accumulated in the blotch part of the mine as the larva regularly ejects frass pellets from the mine protruding rear part of the body through a small slit on the underside of leaflet. When most of parenchyma is eaten out, the larva vacates the mine and creates a new one on the same or a neighboring leaf. Vacated mine soon turns brownish, the epidermis covering mine cracks and gets loose. Pupation on the lower surface of a leaflet (occasionally on the upper side), in a transparent glossy cocoon (Fig. 10B).

Trophic specialization. Oligophagous on Fabaceae: *Caragana arborescens*, *C. frutex*, *C. boisii*, *Medicago sativa* (Kirichenko *et al.* 2016).

Distribution. Russia: RFE—AO (Kirichenko *et al.* 2017b), southern Siberia (Kirichenko *et al.* 2016); European part (Kozlov *et al.* 2017).

Remarks: In early literature, the species was confused with *M. gradatella* (Herrich-Schäffer), which feeds on other Fabaceae: *Lathyrus* and *Vicia* and has distinctive characters in male genitalia (see literature revision and the species diagnosis in Kirichenko *et al.* (2016)). In 2016, numerous mines of *M. caraganella* were documented on *C. arborescens* in Scovorodino, AO (Kirichenko *et al.* 2017b).

Micrurapteryx gradatella (Herrich-Schäffer, 1855)

(Fig. 10C)

Material examined. Russia: AO, Skovorodino, nearby the train station, 53.98N, 123.93E, 431 m alt., *Vicia* sp., 26.VI.2016, 1 larva, NK589, MK403682, deposited in INRA.

Leaf mine. Mine is similar to *M. caraganella*, but often is smaller as host plant leaves are generally small (Fig. 10C). The preceding tunnel on the lower side of the leaflet (Fig. 10C) can be much longer than that of *M. caraganella*. Pupation is on the leaf surface, in a cocoon similar to *M. caraganella*.

Trophic specialization. Oligophagous on Fabaceae: *Lathyrus* spp., *Vicia amoena*, *V. sepium* (Kirichenko *et al.* 2016; De Prins & De Prins 2018).

Distribution. Russia: RFE—AO (Baryshnikova 2016); Europe (De Prins & De Prins 2018).

Remarks: Earlier records in literature mentioning *Micrurapteryx gradatella* on *Caragana arborescens* (Dovnar-Zapol'skiy 1969; Dovnar-Zapol'skiy & Tomilova 1978; Kuznetsov & Baryshnikova 1998; Kuznetsov 1981; Noreika 1997; Baryshnikova 2016) to be attributed to *M. caraganella* (Kirichenko *et al.* 2016).

Subfamily GRACILLARIINAE Stainton, 1854

Caloptilia acericola Kumata, 1966

(Fig. 10D)

Material examined. Russia: PK, Gornotaezhnoe, forest around MTS, 43.70N, 132.15E, 264 m alt., *Acer pseudosieboldianum*, 22.VII.2016, 1 larva, NK539, MK403697, deposited in INRA.

Leaf mine. The mine is a small, slightly contorted brownish blotch along main vein or between secondary veins (Fig. 10D), usually on the lower side of the leaf, with or without short epidermal tunnel. Black grains of frass are accumulated in the blotch mine along its margin. After vacating the mine, the larva creates up to three shelters (usually on the same leaf): at the beginning, it feeds in the folded downwards leaf margin, then moves to another margin and rolls it downwards starting from leaf tip, soon after it rolls downwards a bigger part of the leaf and feeds in this construction (Fig. 10D). Pupation in a whitish shining cocoon attached to the leaf margin.

Trophic specialization. Monophagous on *Acer*: *A. japonicum*, *A. palmatum*, *A. pictum*, *A. pseudosieboldianum* (Sapindaceae) (Baryshnikova 2016; De Prins & De Prins 2018).

Distribution. Russia: RFE—PK (Ermolaev 1988; Baryshnikova 2008), Japan (Kumata 1966).

***Caloptilia alni* Kumata, 1966**

(Fig. 10E)

Material examined. Russia: SO, Sakhalin Island, Yuzhno-Sakhalinsk, Gagarin Park, 46.96 N, 142.75E, 69 m alt., *Alnus hirsuta*, 11.VII.2017, 1 larva, NK619, MK403684, deposited in INRA.

Leaf mine. The mine is a small, slightly contorted brown blotch between secondary veins near leaf margin (Fig. 10E), with scattered dark grains of frass. The larva soon leaves the mine and continues feeding in the two successive shelters: first in the downwards folded (or slightly rolled) leaf margin, usually on the same leaf, then in a neighboring leaf rolled downwards (commonly rolled starting from the tip; often a half or more leaf is rolled) (Fig. 10E). Pupation site is unknown.

Trophic specialization. Monophagous on *Alnus*: *A. hirsuta*, *A. japonica* (Betulaceae) (De Prins & De Prins 2018).

Distribution. Russia: RFE—AO, KK, JAO, PK, SO (Baryshnikova 2008; Baryshnikova & Dubatolov 2016); Japan (Kumata 1966), Korea, China (Baryshnikova 2016).

***Caloptilia betulicola* (Hering, 1928)**

(Fig. 10F)

Material examined. Russia: SO, Sakhalin Island, Yuzhno-Sakhalinsk, Gagarin Park, 46.96N, 142.75E, 69 m alt., *Betula platyphylla*, 11.VII.2017, 1 larva, NK622, MK403700, deposited in INRA.

Leaf mine. The mine is a small, slightly contorted brown blotch with an inconspicuous epidermal corridor on the lower side of the leaf (rarely on the upper surface), along the main vein or near leaf margin. Black grains of frass are scattered inside mine along its margin. After vacating the mine, the larva feeds under a folded (or slightly rolled) leaf margin, usually on the same leaf, afterward moves to a neighbor leaf rolling a significant part of it downwards, starting either from the leaf tip, as observed in Europe (Ellis 2018), or from the leaf margin as we noted in RFE (Fig. 10F). Pupation in a white shining cocoon attached to the leaf surface near leaf margin.

Trophic specialization. Monophagous on Betulaceae: *Betula pendula*, *B. platyphylla*, *B. pubescens* (De Prins & De Prins 2018; Ellis 2018).

Distribution. Russia: RFE—AO, KK, SO (Sakhalin Islands), PK (Ermolaev 1977; Baryshnikova & Dubatolov 2007; Baryshnikova 2008); Japan (Kumata 1982), China (Baryshnikova 2016), Europe, Caucasus (De Prins & De Prins 2018).



FIGURE 5. Female genitalia of gracillariids sampled in the Russian Far East. (A) *Micrurapteryx caraganella*, host plant *Caragana arborescens*, Skovorodino, Amurskaya Oblast, 26.VI.2016; genitalia slide [39-female]; (B) *Phyllonorycter nipponicella*, *Quercus mongolica*, PK, Gornotaezhnoe, 23.VII.2016, [8-2016-female]. Scale bars: (A) 550, (B) 100 μ m.

***Caloptilia gloriosa* Kumata, 1966**

(Fig. 6A)

Material examined. Russia: PK, Gornotaezhnoe, forest around MTS, 43.68N, 132.15E, 224 m alt., *Acer pseudosieboldianum*, 25.VII.2016, 1 male (reared from leaf mine), same location, host and date, NK532; 1 male (reared from leaf mine), 109.1, adult male and genitalia slide deposited in SIF, DNA in INRA.

Leaf mine. The mine and the leaf rolls are indistinguishable from those of *C. acericola*.

Trophic specialization. Monophagous on *Acer*: *A. japonicum*, *A. palmatum*, *A. pictum*, *A. sieboldianum* (Sapindaceae) (De Prins & De Prins 2018), *A. pseudosieboldianum* (**new record**).

Distribution. Russia: RFE—KK (Baryshnikova & Dubatolov 2016), PK, SO (Kuril Islands) (Ermolaev 1977; Baryshnikova 2008); Japan (Kumata 1966).

***Caloptilia heringi* Kumata, 1966**

(Fig. 10G)

Material examined. Russia: SO, Sakhalin Island, Yuzhno-Sakhalinsk, Gagarin Park, 46.96N, 142.75E, 69 m alt., *Acer pictum*, 11.VII.2017, 1 larva, NK624, MK403704, deposited in INRA.

Leaf mine. The mine and the leaf rolls are similar to those of *C. acericola* and *C. gloriosa*, however the mine of *C. heringi* is smaller and the folded leaf margin stage is often missing (instead larvae make a cone from the leaf tip right after vacating mine) (Fig. 10G).

Trophic specialization. Monophagous on *Acer pictum* (Sapindaceae) (Kumata 1966).

Distribution. Russia: RFE—KK, PK (Ermolaev 1977; Baryshnikova & Dubatolov, 2007; Baryshnikova 2008, 2016), SO (Sakhalin Island) (**new record**); Japan (Kumata 1966).

***Caloptilia stigmatella* (Fabricius, 1781)**

(Fig. 10H)

Material examined. Russia: AO, Skovorodino, nearby the train station, 53.98N, 123.93E, 431 m alt., *Salix* sp., 26.VI.2016, 1 larva, NK565, MK403711; SO, Sakhalin Island, Yuzhno-Sakhalinsk, Gagarin Park, 46.97N, 142.75E, 69 m alt., *Salix* sp., 11.VII.2017, 1 larva, NK620, MK403678, deposited in INRA.

Leaf mine. The blotch mine is usually bigger than in other *Caloptilia* spp. listed above, more strongly contorted (that reminds *Phyllonorycter* mines), situated along the leaf margin, and is preceded by a relatively long, easily distinguishable epidermal tunnel which starts near the main or a secondary vein (Fig. 10H). After vacating the mine, the larva moves to the leaf tip (often on the neighbor leaf), bends it downwards creating a triangular cone in which it continues feeding (Fig. 10H). Pupation is external, in a cocoon on the low side of the leaf.

Trophic specialization. Mainly oligophagous on Salicaceae: *Salix*, *Populus*, *Chosenia*, rarely found on Betulaceae (*Betula*), Myricaceae (*Myrica gale*), Fabaceae (*Robinia pseudoacacia*) (Baryshnikova 2016; De Prins & De Prins 2018; Ellis 2018).

Distribution. Russia: RFE—AO, KK, PK, SO, KamK; Siberia, European part (Baryshnikova 2008, 2016); Japan, China, Korea, Mongolia, India, North Africa, Central Asia, Asia Minor, Caucasus, Europe, Canada (De Prins & De Prins 2018).

***Gracillaria* sp.**

(Fig. 11A)

Material examined. Russia: PK, Gornotaezhnoe, MTS, 43.69N, 132.15E, 152 m alt., *Syringa amurensis*, 22.VII.2016, 1 larva, NK549, MK403699, (INRA); same location, *Fraxinus mandshurica*, 25.VII.2016, 1 larva, NK547, MK403728, deposited in INRA.

Leaf mine. The mine is a big silvery blotch, slightly branched, on the upper side of the leaf often at some distance from the leaf margin (Fig. 11A). It begins as a short distinctive epidermal tunnel which soon widens into a blotch. In the tunnel, frass forms an orange-brown central line; in the blotch part, the frass line is darker and more pronounced, covering the mine epidermis from beneath. Later, silk is deposited within the blotch mine which contracts slightly (Fig. 11A). The mine somewhat reminds of the one of *Callisto*. Pupation site unknown.

Trophic specialization. Oligophagous on Oleaceae: *Fraxinus mandshurica*, *Syringa reticulata* subsp. *amurensis*.

Distribution. Russia: RFE—PK.

Remarks. BIN of unknown species—BOLD: ADF4930. The two larvae of *Gracillaria* sp. showed no divergence in COI barcoding fragment and were assigned to one BIN in BOLD (Table 1). Overall, in the Palearctic, seven *Gracillaria* species are known to develop on Oleaceae (De Prins & De Prins 2018). Among them four species have distribution in East Asia: *Gracillaria albicapitata* Issiki (hosts: *Fraxinus*, *Syringa*), *G. arsenievi* (Ermolaev) (*Fraxinus*, *Syringa*), *G. japonica* Kumata (*Ligustrum*) and *G. ussuriella* (Ermolaev) (*Fraxinus*). Others are known from Europe: *G. loriolella* Frey (*Fraxinus*), *G. syringella* (Fabricius) (*Fraxinus*, *Syringa*) and one from North Africa *G. toubkalella* De Prins (*Fraxinus*). The minimum genetic divergence of *Gracillaria* sp. from other *Gracillaria* species known to feed on Oleaceae varied from 6.5 to 9.8%. Among them, the closest neighbor to *Gracillaria* sp. is *G. loriolella* (6.5%), followed by *G. cf. japonica* (6.8%), *G. syringella* (8.0%) and *G. ussuriella* (9.8%) (Table 2). A DNA barcode of *G. albicapitata* is present in BOLD but not accessible; nevertheless, this species does not appear in the list of top matches with our specimens. BIN BOLD:ADP4930 to which both *Gracillaria* sp. from RFE and *Gracillaria* sp. RN-2016 from Japan (deposited in BOLD) may belong to *G. arsenievi* (Ermolaev) whose larvae develop on *Fraxinus* and *Syringa*. However, *G. arsenievi* barcodes are unavailable in genetic databases and we could not examine any adult moth of *Gracillaria* sp. in the present study.

Subfamily PARORNICHINAE Kawahara et Ohshima, 2016

(Ref.: Kawahara *et al.* 2017)

Callisto insperatella (Nickerl, 1864)

Material examined. Russia: PK, Gornotaezhnoe, forest around MTS, 43.68N, 132.17E, 224 m alt., *Prunus padus*, 23.VII.2016, 1 larva, NK590, MK403725, SO, Yuzhno-Sakhalinsk, BGIS, 47.05N, 142.74E, 57 m alt., *P. padus*, 12.VII.2017, 1 larva, NK625, MK403693, deposited in INRA.

Leaf mine. Similar to *Callisto* sp. but generally with no pronounced folds on the epidermis covering the mine (Ellis 2018).

Trophic specialization. Oligophagous on Rosaceae: *Cerasus*, *Prunus* (De Prins & De Prins 2018; Ellis 2018).

Distribution. Russia: RFE—PK, SO (Sakhalin Island) (**new record**), European part of Russia (Baryshnikova 2008, 2016); Europe (De Prins & De Prins 2018).

Callisto sp.

(Figs 11B–C)

Material examined. Russia: PK, Gornotaezhnoe, MTS, 43.69N, 132.15E, 152 m alt., *Malus* sp., 24.VII.2016, 1 larva, NK548, MK403677, deposited in INRA.

Leaf mine. Blotch mine between two secondary veins in parenchyma, with a preceding short (not always visible) epidermal tunnel, with a central frass line, on the lower or upper side of the leaf (Fig. 11B). The blotch is flat but soon gets tentiform-like (similar to *Phyllonorycter*) due to silk deposited by the larva in the mine that dries and shrinks the mine causing 1–2 wrinkles on the epidermis covering mine. The larva vacates the mine through the hole in the lower epidermis, in the corner of the mine (Fig. 11B), and continues living in a shelter, under the leaf margin folded downwards, on the same or neighboring leaf (Fig. 11C). When about one third of a half parenchyma layer is eaten out in the shelter, the larva creates a new shelter (Fig. 11C).

Trophic specialization. Monophagous on *Malus* sp. (Rosaceae).

Distribution. Russia: RFE—PK.

Remarks. BIN of unknown species—BOLD: ADF4428. *Callisto* sp. does not match any known *Callisto* species in BOLD or NCBI. Overall, in the Palearctic, three *Callisto* species are known on Rosaceae: *C. albicinctella* Kuznetsov (RFE; host: *Prunus*), *C. denticulella* (Thunberg) (Europe; Rosaceae, including *Malus*), and *C. insperatella* (Nickerl) (Europe, RFE; host: Rosaceae, including *Prunus*) (De Prins & De Prins 2018). *C. denticulella* (DNA barcodes from Canada and France) is the closest relative to our *Callisto* sp., with minimum interspecific divergence 2.2% (Table 2). The distance from *C. insperatella* sampled for the first time in RFE reaches 3.7% and from *C. insperatella* collected in Poland—4.3% (Table 2). There are no DNA barcode sequences of *C. albicinctella* in the

genetic databases. *C. albicinctella* is known to develop on *Prunus* (Kuznetsov 1979b); no record of this species from *Malus* is known. If the latter species remains trophically linked only to *Prunus*, our *Callisto* sp. may represent a new species.

***Parornix ermolaevi* Kuznetsov, 1979**

(Fig. 11D)

Material examined. Russia: PK, Gornotaezhnoe, forest around MTS, 43.68N, 132.15E, 224 m alt., *Corylus sieboldiana*, 22.VII.2016, 1 larva, NK546, MK403727; same location, *C. sieboldiana*, 22.VII.2016, 1 larva, NK544, MK403689, deposited in INRA.

Leaf mine. The mine is a small blotch, first flat and later slightly contracted (*Phyllonorycter*-like mine shape), with a short preceding epidermal tunnel, on the lower surface of the leaf between secondary veins close to leaf margin or deeper in the leaf lamina (Fig. 11D). The vacated mine soon gets brown (Fig. 11D). Frass in loose grains. Soon the larva leaves the mine and continues feeding under a downfolded leaf margin that is fixed by some spinning. Usually two such shelters are created on the mined leaf (Fig. 11D), less frequently on a neighboring leaf. Pupation is on the leaf surface.

Trophic specialization. Monophagous on *Corylus*: *C. heterophylla* (Betulaceae) (Baryshnikova 2016); *C. sieboldiana* (new record).

Distribution. Russia: RFE—AO, KK, PK (Kuznetsov 1979a; Baryshnikova 2016).

Subfamily LITHOCOLLETINAE Stainton, 1854

***Phyllonorycter caraganella* (Ermolaev, 1986)**

(Figs 4A, 11E–F)

Material examined. Russia: PK, Glukhovka, 43.74N, 132.13E, 68 m alt., *Caragana fruticosa*, 27.VII.2016, 1 larva, NK525; Rakovka, forest, along the road, 43.80N, 132.19E, 140 m alt., *C. fruticosa*, 27.VII.2016, 1 larva, NK522, MK403694, deposited in INRA; same location, host and date, 3 males (reared from leaf mine), NK-184-16-9A / [2Pc-2016-male] (Fig. 4A), deposited in MSNV, K-184-16-12A / [3Pc-2016-male], NK-184-16-13A / [4Pc-2016-male], deposited in SIF.

Leaf mine. The mine is an elongated blotch with a relatively long epidermal tunnel (Fig. 11E) that may not be visible when mine is spread on the surface; on the lower side of the leaflet at any location. In the late stage, the mine may cover the whole leaflet, gets significantly contracted, with 4–5 folds on the epidermis covering the mine (Fig. 11F). From the upper side, the damaged leaf has mottled appearance due to partially eaten out parenchyma layers; later becomes brownish. Frass in scattered grains, some are accumulated in the middle part of the mine. Pupation in the mine.

Trophic specialization. Monophagous on *Caragana fruticosa* (Fabaceae) (Ermolaev 1986b).

Distribution. Russia: RFE—PK (Baryshnikova 2008, 2016).

***Phyllonorycter cavella* (Zeller, 1846)**

(Figs 4B, 6B, 11G–H)

Material examined. Russia: PK, Gornotaezhnoe, forest around MTS, 43.68N, 132.15E, 224 m alt., *Betula platyphylla*, 23.VII.2016, 1 larva, NK541, MK403713, deposited in INRA; same location, *B. dahurica*, 25.VII.2016, 1 male (reared from leaf mine), 111.1 / [11-2016-male] (Fig. 4B, 6B), deposited in SIF.

Leaf mine. The mine is initially a flat elongated blotch between the two secondary veins or along the main vein on the lower side of the leaf; later gets significantly contracted, with 5–7 pronounced folds (Fig. 11G). From the upper side the leaf is significantly bent. At the late stage, the larva consumes deeper layers of parenchyma so that from the upper side of the leaf, the mine gets white (eaten area), with still some green dots (uneaten tissue) (Fig. 11H). Frass in loose grains, accumulated in the middle part of the mine. Pupation is in the mine.

Trophic specialization. Commonly monophagous on *Betula* spp. (Betulaceae) (Ellis 2018). Records of *Alnus* (Betulaceae), *Cerasus* (Rosaceae), *Salix* (Salicaceae) and *Ulmus* (Ulmaceae) (Kuznetsov & Baryshnikova 1998) need confirmation. European subspecies *Ph. cavella milleri* (Povolný et Gregor) feeds on *Prunus padus* (Povolný & Gregor 1950).

Distribution. Russia: RFE—AO, KK, PK, SO (Sakhalin Island) (Baryshnikova & Dubatolov 2007; Baryshnikova 2008, 2016), Siberia (Kuznetsov & Baryshnikova 1998), including new record for Omsk Oblast (Knyazev *et al.* 2018), European part; Japan, Central Asia, Europe (De Prins & De Prins 2018).

Remarks. For the first time in RFE, we recorded the “green island” phenotype in *Ph. cavella* mining leaves of *Betula platyphylla* (Fig. 11H).

***Phyllonorycter cretata* (Kumata, 1957)**

(Figs 4C, 12A)

Material examined. Russia: SO, Sakhalin Island, Yuzhno-Sakhalinsk, BGIS, 47.05N, 142.74E, 57 m alt., *Quercus mongolica*, 12.VII.2017, 1 larva, NK629, MK403709, deposited in INRA; same location, host and collection date, 1 male (reared from leaf mine), NK-85-17-4 / [16-male] (Fig. 4C), deposited in SIF.

Leaf mine. The mine is contracted white elongated blotch, with one pronounced fold on the epidermis; situated between the two secondary veins on the lower side of the leaf (Fig. 12A). Occasionally up to seven mines per a leaf were recorded in RFE. Pupation in the mine.

Trophic specialization. Monophagous on *Quercus*: *Q. mongolica* subsp. *crispula*, *Q. mongolica*, *Q. serrata* (Fagaceae) (De Prins & De Prins 2018).

Distribution. Russia: RFE—AO, KK, PK, SO (Baryshnikova 2008, 2016); Japan (Kumata 1957), South Korea (Kim & Byun 2017).

***Phyllonorycter ermani* (Kumata, 1963)**

(Fig. 12B)

Material examined. Russia: SO, Sakhalin Island, Yuzhno-Sakhalinsk, Gagarin Park, 46.96N, 142.75E, 69 m alt., *Betula platyphylla*, 11.VII.2017, 1 larva, NK623, MK403679, deposited in INRA.

Leaf mine. The mine is similar to *Ph. cavella* but with hardly any folds visible. Up to three mines per leaf were recorded in RFE. At later stages, the leaf is significantly deformed (Fig. 12B). Pupation in the mine.

Trophic specialization. Oligophagous on Betulaceae: *Alnus maximowiczii*, *Betula ermanii* (Kumata 1963; Ermolaev 1987), *Betula platyphylla* (**new record**).

Distribution. Russia: RFE—SO (Kuril Islands) (Baryshnikova 2016), Sakhalin Island (**new record**); Japan (Kumata 1963).

***Phyllonorycter issikii* (Kumata, 1963)**

(Figs 4D, 6E, 12C)

Material examined. Russia: PK, Gornotaezhnoe, MTS, arboretum, 43.69N, 132.16E, 160 m alt., *Tilia taquetii*, 8.VII.2011, 1 larva, NK310, KX818601; same location, *T. amurensis*, 16.VII.2013, 1 male (reared from leaf mine), NK141, KX818667, deposited in INRA; same location, *T. mandshurica*, 21.VIII.2015, 1 male (reared from leaf mine), M. Ponomarenko leg., NK596, NK596 / [NK596-male], MK403708 (Figs 4D, 6E), all deposited in INRA.

Leaf mine. The mine is a flat roundish white blotch with a short preceding epidermal tunnel (which however, may be indistinct), most commonly on the lower side of the leaf (Fig. 12C). At the later stage the mine is contracted, with few weak folds on the epidermis covering the mine. Frass in loose grains accumulated in the middle part of the mine. Pupation in the mine, in a light cocoon.

Trophic specialization. Monophagous on *Tilia* (Malvaceae): in East Asia—*T. maximowicziana*, *T. japonica*, *T. kiusiana*, *T. taquetii*, *T. japonica* (Kumata 1963; Ermolaev 1977; Kumata *et al.* 1983), in Europe, Western Russia and Siberia (in nature and / or in botanical gardens)—*T. cordata*, *T. platyphyllos*, *T. tomentosa*, *T. × euchlora*, *T. × europaea*, *T. sibirica*, *Tilia americana* (Kirichenko *et al.* 2017c).

Distribution. Native in Russia: RFE—KK, PK (Ermolaev 1977; Baryshnikova & Dubatolov 2007); Japan (Kumata 1963), Korea (Kumata *et al.* 1983), China (Kirichenko *et al.* 2017c). Invasive in Russia: Siberia (Kirichenko 2014; Kirichenko *et al.* 2017c), European part; Europe (Šefrová 2002; Ermolaev 2014).

***Phyllonorycter japonica* (Kumata, 1963)**

(Fig. 4E, 6C, 12D)

Material examined. Russia: PK, Gornotaezhnoe, MTS, 43.69N, 132.15E, 152 m alt., *Corylus mandshurica*, 24.VII.2016, 1 larva, NK545, MK403698, deposited in INRA; same location and host, 22.VII.2016, 2 males (reared from leaf mine), 36.2 / [4-2016-male] (Figs 4E, 6C), NK-142-16-1A / [4.1-2016-male], deposited in SIF.

Leaf mine. The mine is an elongated whitish blotch above the main vein on the upper side of the leaf (Fig. 12D). The mine is initially flat but later gets contracted, with no visible folds on the epidermis. Pupation in the mine.

Trophic specialization. Oligophagous on Betulaceae: *Carpinus laxiflora*, *C. tschonoskii*, *Corylus heterophylla*, *C. mandshurica*, *Ostrya japonica* (De Prins & De Prins 2018).

Distribution. Russia: RFE—AO, KK, PK (Baryshnikova 2008, 2016); Japan (Kumata 1963), Korea (Kim & Byun 2017).

***Phyllonorycter jozanae* (Kumata, 1967)**

(Figs 4F, 6D)

Material examined. Russia: PK, Gornotaezhnoe, forest around MTS, 43.68N, 132.15E, 224 m alt., *Crataegus* sp., 20.VII.2016, 1 pupa, NK543, MK403717, deposited in INRA; same location, host and date, 1 male (reared from leaf mine), 41.1 / [14Pj-2016-male] (Figs 4F, 6D), deposited in SIF; SO, Sakhalin Island, Yuzhno-Sakhalinsk, BGIS, 47.05N, 142.74E, 57 m alt., *C. chlorosarca*, 12.VII.2017, 1 larva, NK627, MK403683, deposited in INRA; same location, host and date, 2 males (reared from leaf mine), NK-98-17-1 / [14-male], deposited in MSNV, NK-98-17-1 / [23-male], deposited in SIF.

Leaf mine. The mine is a whitish slightly contracted blotch between the secondary veins on the lower side of the leaf. We recorded up to three mines per a leaf in RFE. Pupation in the mine.

Trophic specialization. Monophagous on *Crataegus*: *C. chlorosarca*, *C. jozana*, *C. maximowiczii*, *C. pinnatifida* (Rosaceae) (De Prins & De Prins 2018).

Distribution. Russia: RFE—KK, PK, SO (Sakhalin Island) (Baryshnikova & Dubatolov 2008; Baryshnikova 2008, 2016); Japan (Kumata 1967), Korea (Kim & Byun 2017).

***Phyllonorycter junoniella* (Zeller, 1846)**

(Figs 7A, 12E)

Material examined. Russia: SO, Sakhalin Island, Yuzhno-Sakhalinsk, Susunaiskiy mountain range, pass Verblud, 47.00N, 142.83E, 983 m alt., 14.VII.2017, 1 male (sampled by sweep netting from *Vaccinium vitis-idaea*, Fig. 12E), NK628, MK403691, deposited in INRA; same location, date and sampling method, 3 males, 1 female, Sakh-Sw-2 / [18-male], Sakh-Sw-3 / [20-male], Sakh-Sw-4 / [21-male], Sakh-Sw-5 / [22-female] (Fig. 7A), deposited in SIF.

Leaf mine. No mines were sampled in RFE. According to Ellis (2018), in Europe this species makes a blotch mine on the lower side of the leaf, occupying almost the entire leaf. At the later stage, the mine is significantly contracted so that the leaf margins are strongly pulled together. From the upper side, the leaf surface has a mottled pattern due to partially eaten parenchyma layers; later becomes brown. Pupation in the mine.

Trophic specialization. Monophagous on *Vaccinium vitis-idaea* (Ericaceae) (Ellis 2018).

Distribution. Russia: RFE—SO (Sakhalin Island) (**new record**), Siberia (Dovnar-Zapol'skiy & Tomilova 1978; Baryshnikova 2008), European part (Kuznetsov & Baryshnikova 1998); Europe (De Prins & De Prins 2018); Japan (Kumata & Nakatani 1995).

***Phyllonorycter kisoensis* Kumata et Park, 1978**

(Fig. 4G, 7E)

Material examined. Russia: PK, Gornotaezhnoe, MTS, 43.69N, 132.15E, 152 m alt., *Alnus hirsuta*, 22.VII.2016, 1 male (reared from leaf mine), 45.1 / [5Pk-2016-male] (Fig. 4G, 7E), deposited in SIF.

Leaf mine. The mine is indistinguishable from *Phyllonorycter strigulatella*.

Trophic specialization. Monophagous on *Alnus hirsuta* (Betulaceae) (Kumata & Park 1978).

Distribution. Russia: RFE—KK, PK, SO (Sakhalin Island) (Baryshnikova 2016); Japan (Kumata & Park 1978).

***Phyllonorycter nigristella* (Kumata, 1957)**

(Fig. 12F)

Material examined. Russia: PK, Gornotaezhnoe, MTS, 43.69N, 132.15E, 152 m alt., *Quercus dentata*, 22.VII.2016, 1 male (reared from leaf mine), NK528, MK403687, deposited in INRA.

Leaf mine. The mine is whitish blotch between secondary veins on the lower side of the leaf (Fig. 12F). No preceding epidermal tunnel. In the later stage, the mine is significantly contracted (Fig. 12F). Pupation in the mine.

Trophic specialization. Monophagous on *Quercus*: *Q. dentata*, *Q. mongolica*, *Q. serrata* (Fagaceae) (De Prins & De Prins 2018).

Distribution. Russia: RFE—KK, PK (Ermolaev 1981b; Baryshnikova 2008, 2016); Japan (Kumata 1957).

***Phyllonorycter nipponicella* (Issiki, 1930)**

(Fig. 5B)

Material examined. Russia: PK, Gornotaezhnoe, MTS, 43.69N, 132.15E, 152 m alt., *Quercus mongolica*, 23.VII.2016, 1 female (reared from leaf mine), 58.1 / [8-2016-female] (Fig. 5B), deposited in SIF.

Leaf mine. The mine is similar to *Ph. nigristella*.

Trophic specialization. Monophagous on *Quercus*: *Q. acutissima*, *Q. variabilis* (Fagaceae) (Kumata 1963; Kumata *et al.* 1983; Fujihara *et al.* 2000); *Q. mongolica* (**new record**).

Distribution. Russia: RFE—KK, PK, SO (Kuril Islands) (Baryshnikova 2016); Japan (Kumata 1963), Korea (Kumata *et al.* 1983).

***Phyllonorycter orientalis* (Kumata, 1963)**

(Fig. 12G)

Material examined. Russia: PK, Gornotaezhnoe, forest around MTS, 43.68N, 132.15E, 224 m alt., *Acer pictum*, 22.VII.2016, 1 male (reared from leaf mine), NK536, MK403726; same location, *A. pictum*, 23.VII.2016, 1 larva, NK535, MK403729; same location, *A. saccharum*, 26.VII.2016, 1 larva, NK538, MK403707, all deposited in INRA.

Leaf mine. The mine is an elongated contracted whitish blotch, without preceding epidermal tunnel, with one pronounced fold on the epidermis; situated on the lower side of the leaf nearby the leaf margin (Fig. 12G). Loose grains of frass are accumulated in the central part of the mine. From the upper side, the mine is white (Fig. 12G). Pupation in the mine.

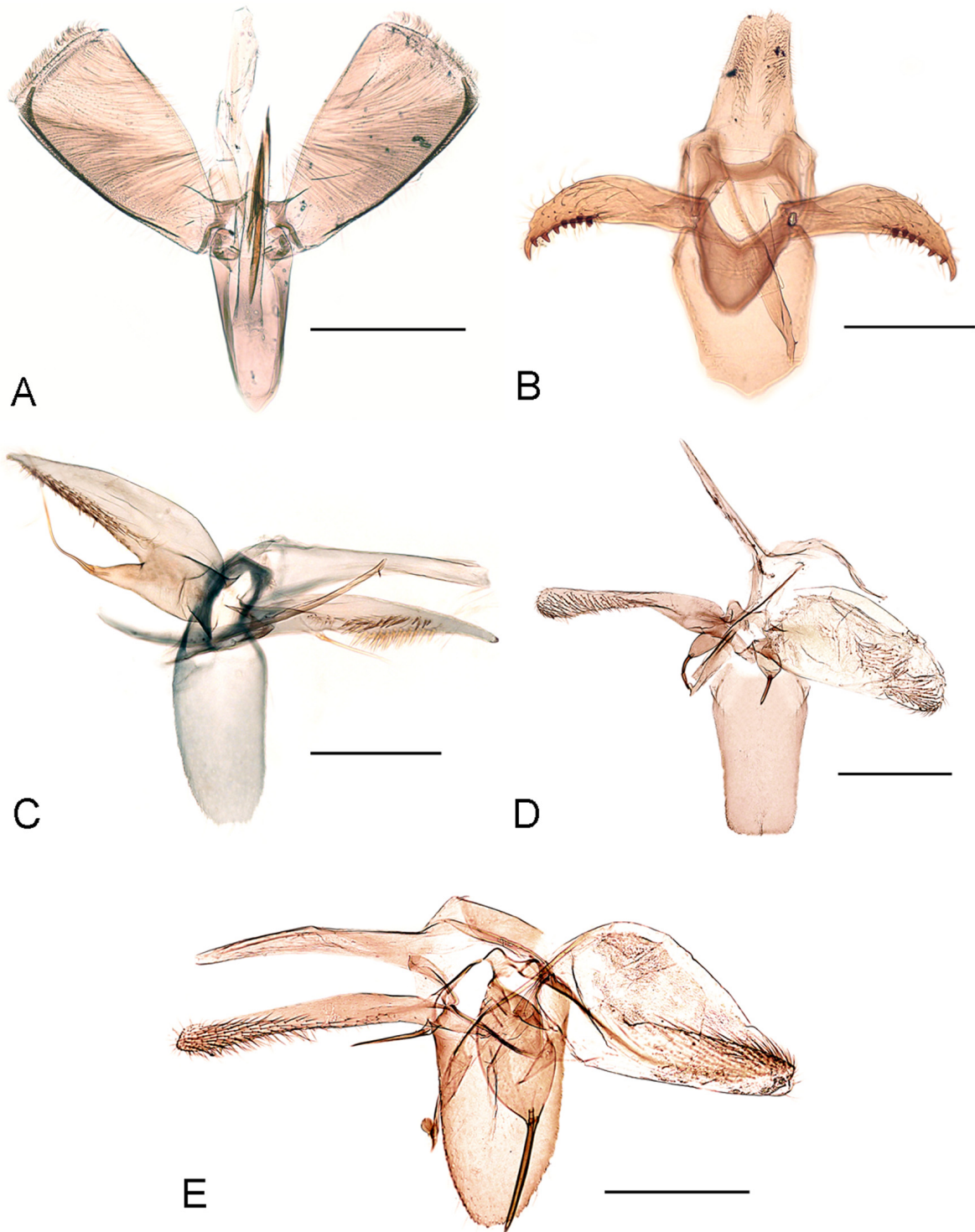


FIGURE 6. Male genitalia of *Caloptilia* and *Phyllonorycter* spp. from the Russian Far East. (A) *Caloptilia gloriosa*, host plant *Acer pseudosieboldianum*, genitalia slide [13-male]; (B) *Phyllonorycter cavella*, *Betula dahurica*, [11-2016-male]; (C) *Ph. japonica*, *Corylus mandshurica*, [4-2016-male]; (D) *Ph. jozanae*, *Crataegus* sp. [14Pj-2016-male]; (E) *Ph. issikii*, *T. mandshurica*, [NK596-male]. Sampling locations: PK, Gornotaezhnoe, (A–D) 22–25.VII.2016, (E) 21.VIII.2015. Scale bars: (A) 350, (B–E) 200 μ m.

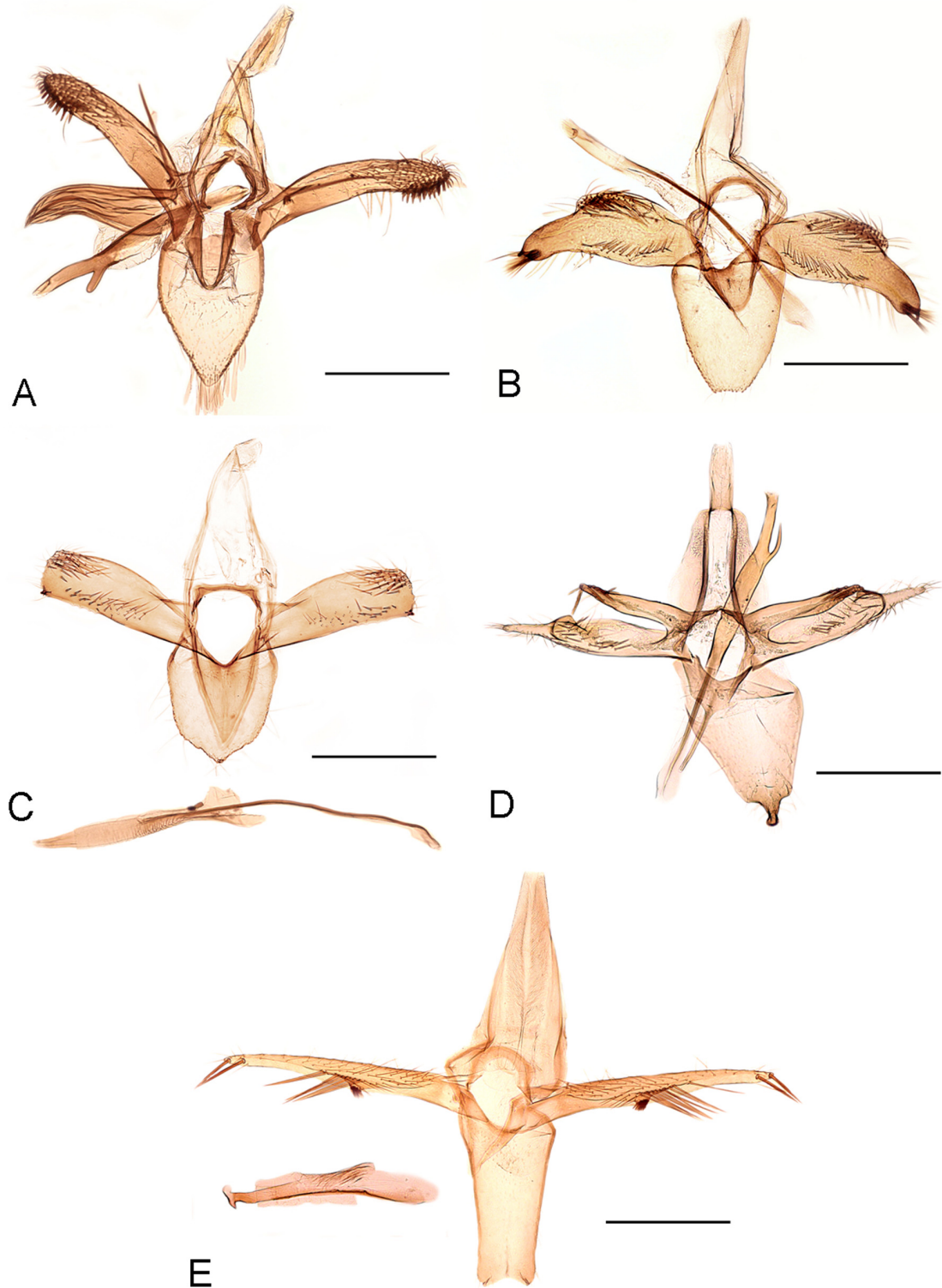


FIGURE 7. Male genitalia of *Phyllonorycter* spp. from the Russian Far East. (A) *Phyllonorycter junoniella*, genitalia slide [21-male]; (B) *Ph. pastorella*, host plant *Salix* sp., [12Pp-2016-male]; (C) *Ph. populifoliella*, *Populus balsamifera*, [NK-561-1-male]; (D) *Ph. pseudojezoniella*, *Acer saccharum*, [20Pps-2016-male]; (E) *Ph. kisoensis*, *Alnus hirsuta*, [5Pk-2016-male]. Sampling location: (A) SO, Sakhalin Isl., 14.VII.2017; (B, D) PK, Gornotaezhnoe, MTS, 22–26.VII.2016; (C) AO, Blagoveshchensk, 27.VI.2016. Scale bars 200 μ m.

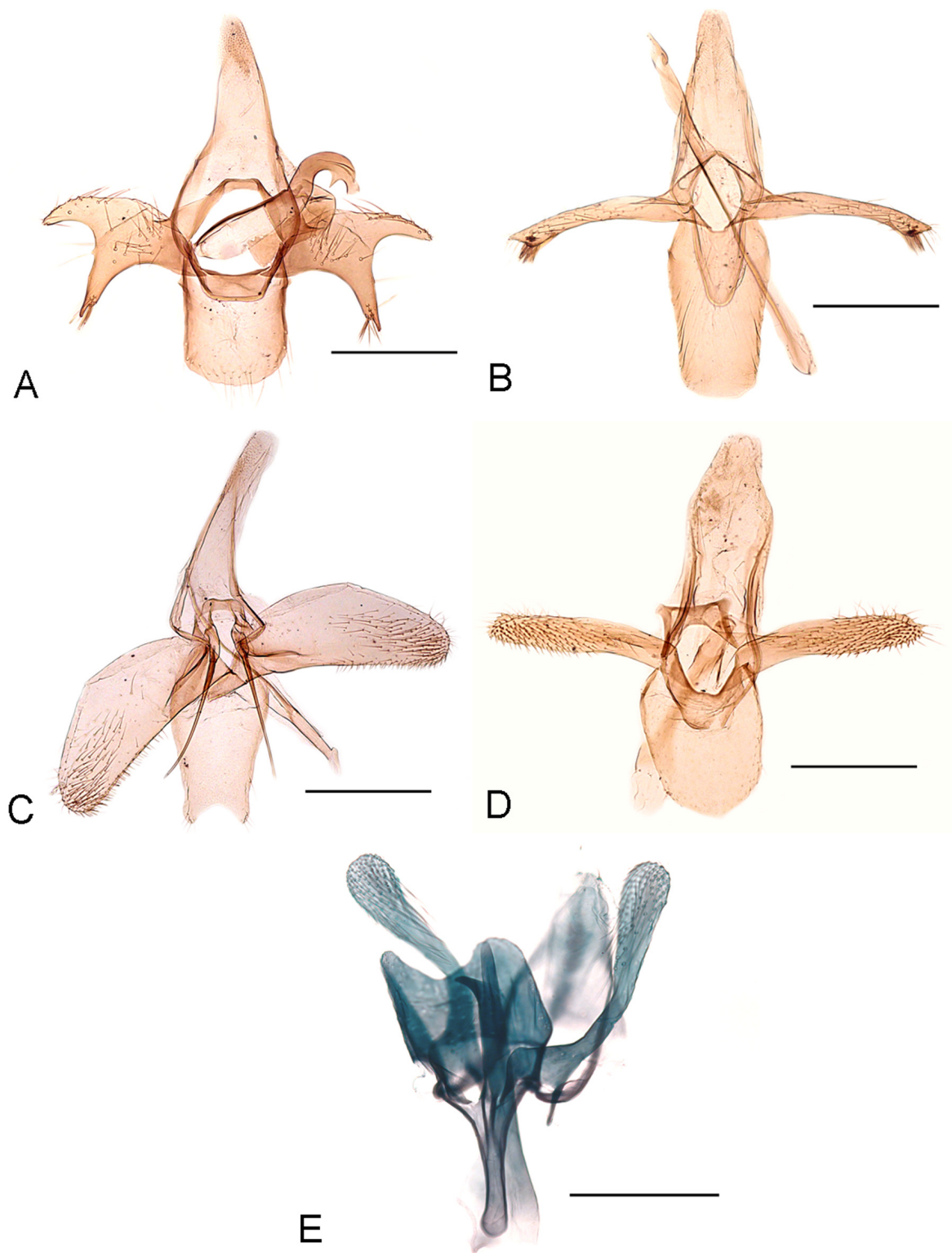


FIGURE 8. Male genitalia of *Phyllonorycter* and *Cameraria* spp. from the Russian Far East. (A) *Ph. reduncata*, host plant *Lonicera maackii*, [23Pr-2016-male]; (B) *Ph. ringoniella*, *Malus mandshurica*, [10Prin-2016-male]; (C) *Ph. similis*, *Quercus dentata*, [8Psim-2016-male]; (D) *Ph. ulmifoliella* [15Pu-2016-male]; (E) *Cameraria nipponica*, *Acer pseudosieboldianum*, [1Cn-2016-male]. Sampling location: Gornotaezhnoe, Primorskii Krai, 22–26.VII.2016. Scale bars: (A–D) 200, (E) 250 μm .

Trophic specialization. Monophagous on *Acer*: *A. carpinifolium*, *A. palmatum*, *A. pictum*, *A. pseudosieboldianum* (Sapindaceae) (De Prins & De Prins 2018), *A. saccharum* (**new record**).

Distribution. Russia: RFE—PK, SO (Kuril Islands) (Ermolaev 1977; Baryshnikova 2016), European part (Baryshnikova 2008); Japan, Taiwan (Kumata 1963), Korea (Park & Han 1986).

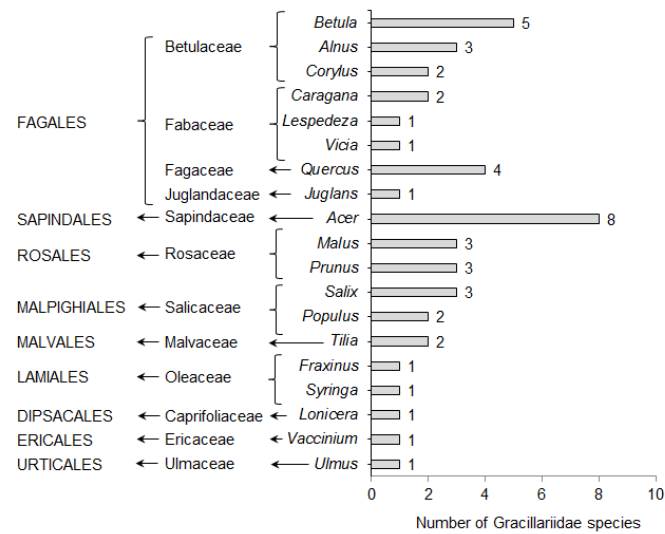


FIGURE 9. Number of gracillariid species found on various plant plants in the Russian Far East in 2010–2017. In some cases, the same gracillariid species were found on more than one plant genus (for example, *Gracillaria* sp. on *Syringa* and *Fraxinus*, *Phyllonorycter pastorella* on *Salix* and *Populus* etc.), therefore the sum of all bars is more than the total number of species identified in the study.

Phyllonorycter pastorella (Zeller, 1846)

(Figs 4H, 7B, 12H)

Material examined. Russia: PK, Gornotaezhnoe, forest around MTS, 43.68N, 132.17E, 224 m alt., *Salix* sp., 23.VII.2016, 1 larva, NK594, MK403714, deposited in INRA; same location, host and date, 1 male (reared from leaf mine), 49.1 / [12Pp-2016-male] (Figs 4H, 7B), deposited in SIF; AO, Skovorodino, near the train station, tree line along the road, 53.98N, 123.93E, 431 m alt., *Populus balsamifera*, 26.VI.2016, 1 larva, NK563, MK403688, same location and date, 1 larva, NK562, MK403681, deposited in INRA.

Leaf mine. The mine is an oval white blotch with 1–2 light folds on the epidermis covering the mine, with distinct epidermal tunnel; situated on the lower side of the leaf along, on narrow leaves of *Salix* along the main vein (Fig. 12H). Loose grains of frass are accumulated in the corner of the mine (Fig. 12H). Pupation in the mine, in the central part (Fig. 12H).

Trophic specialization. Oligophagous on Salicaceae: *Populus*, *Salix*, *Chosenia* (De Prins & De Prins 2018).

Distribution. Russia: RFE—AO, KK, PK, SO (Sakhalin Island) (Baryshnikova & Dubatolov 2007; Baryshnikova 2016), Siberia (Baryshnikova 2008), European part (Baryshnikova 2008); Japan (Kumata 1963), Korea (Park 1983), Central Asia (Noreika 1991), Europe (De Prins & De Prins 2018).

Phyllonorycter populifoliella (Treitschke, 1833)

(Fig. 7C)

Material examined. Russia: KK, Komsomolsk-na-Amure, city plantation, 50.58N, 137.04E, 32 m alt., *Populus* sp., 13.VII.2010, 1 pupa, NK88, MK403730; AO, Blagoveshchensk, Friendship park, 50.29N, 127.53E, 137 m alt., *P. balsamifera*, 27.VI.2016, 1 pupa, NK561, MK403712, 1 male (reared from mine), NK561-1 / [NK561-1-male] (Fig. 7C), deposited in INRA.

Leaf mine. The mine is a blotch similar to that of *Ph. pastorella*, but with a shorter preceding epidermal tunnel that can be seen in the later stage when the blotch part of the mine spreads on the surface. The mine is usually on the lower side of the leaf between secondary veins or nearby leaf margin. Often several mines per leaf. In dense populations, upper side mines can be found. Pupation in the mine.

Trophic specialization. Monophagous on *Populus*: *P. nigra*, *P. suaveolens*, *P. laurifolia*, *P. balsamifera*, *P. deltoids*, *P. simonii*, and the hybrids—*Populus x canadensis*, *Populus x canescens* (Salicaceae) (Ellis 2018; De Prins & De Prins 2018). Records of *P. alba* and *P. tremula* may need confirmation as *Ph. populifoliella* mines can be mixed up with those of several other *Phyllonorycter* species developing on these plants: *Ph. apparella*, *Ph. comparella*, *Ph. connexella*, *Ph. pastorella* (Ellis 2018).

Distribution. Russia: RFE—KK (Baryshnikova 2016), AO (**new record**), Siberia, European part (Baryshnikova 2008); Central Asia, Europe (De Prins & De Prins 2018).

***Phyllonorycter pseudojezoniella* Noreika, 1994**

(Fig. 7D)

Material examined. Russia: PK, Gornotaezhnoe, forest around MTS, 43.68N, 132.15E, 224 m alt., *Acer saccharum*, 26.VII.2016, 1 male (reared from leaf mine), 26.VIII.2016 em., NK-182-16-1A / [20Pps-2016-male] (Fig. 7D), deposited in SIF.

Leaf mine. Blotch mine on the lower side of the leaf, between two secondary veins, at the later stage gets contracted. Pupation in the mine.

Trophic specialization. Host plant was not known (Noreika 1994). We found mines solely on the plant species originating from North America, *Acer saccharum* (Sapindaceae) (**new record**).

Distribution. Russia: RFE—PK (Noreika 1994).

***Phyllonorycter reduncata* (Ermolaev, 1986)**

(Figs 4I, 8A)

Material examined. Russia: PK, Gornotaezhnoe, MTS, 43.69N, 132.15E, 152 m alt., *Lonicera maackii*, 23.VII.2016, 1 male (reared from leaf mine), 55.3 / [23Pr-2016-male] (Fig. 4I, 8A), deposited in SIF.

Leaf mine. The mine is similar to the European species *Phyllonorycter emberizaepenella* (Ellis 2018). Strongly contracted blotch on the lower side of the leaf, often covers a significant part of the leaf. Pupation in the mine.

Trophic specialization. Monophagous on *Lonicera*: *L. edulis* Turcz. ex Freyn, *L. maackii* (Rupr.) Maxim., *L. praeiflorens* Batalin (Caprifoliaceae) (Ermolaev 1986a, 1987).

Distribution. Russia: RFE—PK, SO (Kuril Islands) (Baryshnikova 2016).

***Phyllonorycter ringoniella* (Matsumura, 1931)**

(Figs 4K, 8B, 13A–B)

Material examined. Russia: PK, Gornotaezhnoe, forest around MTS, 43.68N, 132.15E, 224 m alt., *Malus mandshurica*, 25.VII.2016, 1 male (reared from leaf mine), NK-179-16-1A / [10Prin-2016-male] (Figs 4K, 8B); same location, *Malus* sp. 24.VII.2016, 1 female (reared from leaf mine), 70.1 / [3Prin-2016-female], deposited in SIF.

Leaf mine. The mine is a white elongated contracted blotch with very short or without preceding epidermal tunnel, along the leaf margin or between the secondary veins (Figs 13A–B). Epidermis covering mine soon becomes brownish (Fig. 13B). From the upper side of the leaf, the mine has a marbled appearance (Fig. 13B). Pupation in the mine.

Trophic specialization. Oligophagous on Rosaceae: *Malus baccata*, *M. domestica*, *M. mandshurica*, *M. pumila*, *M. sieboldii*, *M. totingo*, *Prunus padus*, *P. salicina*, *Pyrus* sp. (De Prins & De Prins 2018).

Distribution. Russia: RFE—AO, PK, SO (Sakhalin Island) (Baryshnikova 2008, 2016), Siberia (Kirichenko *et al.* 2017b); Japan (Kumata 1959), Korea (Nakayama & Okamoto 1940), China (Kumata *et al.* 1983).

***Phyllonorycter salictella* (Zeller, 1846)**

Material examined. Russia: SO, Sakhalin Island, Yuzhno-Sakhalinsk, BGIS, 47.05N, 142.74E, 57 m alt., *Salix rorida*, 17.VII.2017, 1 larva, NK630, MK403703, deposited in INRA.

Leaf mine. The mine is similar to other *Phyllonorycter* species, on the lower side of the leaf. Pupation in the mine.

Trophic specialization. Monophagous on *Salix* (Salicaceae) (De Prins & De Prins 2018).

Distribution. Russia: RFE—AO, KK, PK, SO (Sakhalin Island) (Baryshnikova 2016), European part (Baryshnikova 2008); Japan (Kumata 1963), Europe (De Prins & De Prins 2018).

***Phyllonorycter similis* Kumata, 1982**

(Figs 4L, 8C)

Material examined. Russia: PK, Gornotaezhnoe, forest around MTS, 43.68N, 132.17E, 224 m alt., *Quercus dentata*, 22.VII.2016, 1 larva, NK593, MK403702, deposited in INRA; same location, host and date, 1 male (reared from leaf mine), 42.1 / [8Psim-2016-male] (Fig. 4L, 8C), deposited in SIF; same location, *Q. mongolica*, 23.VII.2016, 1 larva, NK592, MK403692, deposited in INRA.

Leaf mine. The mine is similar to other *Phyllonorycter* species, on the lower side of the leaf. Pupation in the mine.

Trophic specialization. Monophagous on *Quercus*: *Q. acutissima*, *Q. cerris*, *Q. crispula*, *Q. dentate*, *Q. mongolica*, *Q. serrata* (Fagaceae) (Kumata 1982; De Prins & De Prins 2018).

Distribution. Russia: RFE—AO, KK, PK (Baryshnikova & Dubatolov 2007; Baryshnikova 2016); Japan, Korea (Kumata 1982).

***Phyllonorycter sorbicola* (Kumata, 1963)**

(Figs 13C–D)

Material examined. Russia: PK, Gornotaezhnoe, forest around MTS, 43.68N, 132.17E, 224 m alt., *Prunus maackii*, 23.VII.2016, 1 larva, NK591, MK403721, deposited in INRA.

Leaf mine. The mine is a white elongated, contracted blotch with indistinguishable folds on the epidermis covering the mine, with a relatively short preceding epidermal tunnel, between secondary veins on the lower side of the leaf (Figs 13C–D). Pupation in the mine.

Trophic specialization. Oligophagous on Rosaceae: *Malus asiatica*, *M. pumila*, *Prunus padus*, *Sorbus alnifolia*, *S. commixta*, *S. matsumurana* (Kumata 1982; De Prins & De Prins 2018), *Prunus maackii* (**new record**).

Distribution. Russia: RFE—SO (Baryshnikova 2016), PK (**new record**); Japan (Kumata 1963).

***Phyllonorycter strigulatella* (Zeller, 1846)**

(Fig. 13E)

Material examined. Russia: SO, Sakhalin Island, Yuzhno-Sakhalinsk, Gagarin Park, 46.96N, 142.75E, 69 m alt., *Alnus hirsuta*, 11.VII.2017, 1 male (reared from leaf mine), NK-75-17-2 / [19-male], deposited in SIF.

Leaf mine. The mine is a white oval blotch, with 2–3 folds on the epidermis surface, between the main vein and secondary veins, and may have a short preceding epidermal tunnel, on the lower side of the leaf (Fig. 13E). Pupation in the mine.

Trophic specialization. Monophagous on *Alnus*: *A. alnobetula*, *A. hirsuta*, *A. incana*, *A. minor*, *A. rugosa* (Betulaceae) (De Prins & De Prins 2018). Records on *A. glutinosa* need confirmation.

Distribution. Russia: RFE—KK, PK, SO (Ermolaev 1977; Noreika 1997; Baryshnikova 2016), Siberia, European part (Baryshnikova 2008); Europe (De Prins & De Prins 2018), Japan (Kumata 1963).

***Phyllonorycter ulmifoliella* (Hübner, [1817])**

(Figs 4M, 8D)

Material examined. Russia: PK, Gornotaezhnoe, MTS, 43.69N, 132.15E, 152 m alt., 22.VII.2016, 1 male (collected by sweep netting from *Aesculus hippocastanum*), 37.1 / [15Pu-2016-male] (Figs 4M, 8D); SO, Sakhalin Island, Yuzhno-Sakhalinsk, Gagarin Park, 46.96N, 142.75E, 69 m alt., *Betula platyphylla*, 11.VII.2017, 1 female (reared from leaf mine), NK-66-17-1 / [17-female], deposited in SIF.

Leaf mine. The mine is indistinguishable from the one of *Ph. ermani* on *Betula platyphylla* (Fig. 12B). Pupation in the mine.

Trophic specialization. Monophagous on *Betula*: *B. nigra*, *B. papyrifera*, *B. pendula*, *B. platyphylla*, *B. pubescens* (Betulaceae) (De Prins & De Prins 2018).

Distribution. Russia: RFE—AO, KK, PK, SO (Kuril Islands) (Baryshnikova & Dubatolov, 2007; Baryshnikova 2016), SO (Sakhalin Island) (**new record**), Siberia, European part (Baryshnikova 2008; Kirichenko *et al.* 2017a); Japan (Kumata 1963), Kazakhstan (Kuznetsov & Baryshnikova 1998), Europe (De Prins & De Prins 2018).

***Phyllonorycter* sp. 1**

(Fig. 13F)

Material examined. Russia: PK, Sikhote-Alin Mts, National park “Zov tигра”, 43.60N, 134.30E, 690 m alt., *Tilia* sp., 10.VII.2010, 1 larva, NK31, KX818885, (INRA); Vladivostok, Akademgorodok, city plantation, 43.19N, 131.92E, 82 m alt., *T. mandshurica*, 15.VII.2013, 1 pupa, NK205, KX818718; Gornotaezhnoe, MTS, arboretum, 43.69N, 132.16E, 160 m alt., *T. taquetii*, 25.VIII.2011, 1 larva, NK236, KX818723; same location, *T. mandshurica*, 16.VII.2013, 1 larva, NK208, KX818721; same location, *T. amurensis*, 10.VII.2015, 1 male (reared from leaf mine), M. Ponomarenko leg., NK601, MK403722, all deposited in INRA.

Leaf mine. The mine (Fig. 13F) is not distinguishable from that of *Ph. issikii* (Fig. 12C).

Trophic specialization. Monophagous on *Tilia* (Malvaceae). *T. amurensis*, *T. mandshurica*, *T. taquetii*, *Tilia* sp.

Distribution. Russia: RFE—AO, KK, PK (Baryshnikova 2006); Japan (Kumata 1963), Korea (Kumata *et al.* 1983), China (Kirichenko *et al.* 2017c). *Phyllonorycter* sp. 1 and *Ph. issikii* occur in sympatry (Kirichenko *et al.* 2017c).

Remarks. BIN of unknown species—BOLD:ACC3074. The maximum intraspecific divergence in the cluster represented by five unidentified specimens (Fig. 3) is 1.2%. In East Asia, only one *Tilia*-feeding *Phyllonorycter* species is known—*Ph. issikii* (Kumata 1963). The minimum interspecific genetic distance between our unidentified species and *Ph. issikii* is 5.4% (Table 2), suggesting that *Phyllonorycter* sp. 1 may be an undescribed species. This putative new cryptic species was already mentioned in our previous study (Kirichenko *et al.* 2017c). To confirm its novelty, a representative series of adults is needed for morphological analysis.

***Phyllonorycter* sp. 2 (cf. *malicola* Kuznetsov)**

Material examined. Russia: PK, Gornotaezhnoe, forest around MTS, 43.68N, 132.15E, 224 m alt., *Malus mandshurica*, 25.VII.2016, 1 larva, NK534, MK403676, deposited in INRA.

Leaf mine. Mine similar to *Ph. ringoniella*. Pupation in the mine.

Trophic specialization. Monophagous on *Malus mandshurica* (Rosaceae).

Distribution. Russia: RFE—PK.

Remarks. BIN of unknown species—BOLD: ADF3338. In East Asia, three *Malus*-feeding *Phyllonorycter* are

known: *Ph. malicola* Kuznetsov, *Ph. ringoniella* (Matsumura) and *Ph. sorbicola* (Kumata) (De Prins & De Prins 2018). No DNA barcodes exist in BOLD for *Ph. malicola* Kuznetsov. DNA barcode of *Phyllonorycter* sp. 2 does not match the other two species. The nearest neighbor to *Phyllonorycter* sp. 2 is *Ph. ringoniella*, with minimum genetic distance 3.3% (Table 2). The divergence with the *Ph. sorbicola* reaches 9.4% (Table 2). Our specimen may possibly represent *Ph. malicola* that is known to develop in RFE on *M. mandshurica* (Kuznetsov 1979b).

***Phyllonorycter* sp. 3 (cf. *sorbicola* Kumata)**

Material examined. Russia: AO, Skovorodino, nearby the train station, 53.98N, 123.93E, 431 m alt., *Prunus padus*, 26.VI.2016, 1 larva, NK566, MK403696, deposited in INRA.

Leaf mine. The mine is a white elongated contracted blotch, with up to five folds on epidermis-covering mine, along the main vein. Pupation in the mine.

Trophic specialization. Monophagous on *Prunus padus* (Rosaceae).

Distribution. Russia: RFE—AO.

Remarks. BIN of unknown species—BOLD: ACY3732. In East Asia, only three *Phyllonorycter* species are known to develop on *Prunus*: *Ph. cerasicolella* (Herrich-Schäffer), *Ph. ringoniella* (Matsumura) and *Ph. sorbicola* (Kumata) (De Prins & De Prins 2018). Additionally, *Phyllonorycter laurocerasi* Kuznetsov also develops on *Prunus*, but is known only from Georgia (Kuznetsov 1979b) and from the West Caucasian region of Russia (Baryshnikova 2008). Our DNA barcoded specimen of *Phyllonorycter* does not match any of these three species in BOLD. No DNA barcode of *Ph. laurocerasi* exists in BOLD. The nearest neighbor is *Ph. sorbicola*, with minimal genetic distance of 2% but with different BIN (Table 2). The other two species are distant from *Ph. ringoniella* (7.9%) and *Ph. cerasicolella* (10.2%) (Table 2). *Phyllonorycter* sp. 3 represents a novel BIN in BOLD closely related to *Ph. sorbicola*.

***Phyllonorycter* sp. 4**

Material examined. Russia: SO, Sakhalin Island, Yuzhno-Sakhalinsk, Gagarin Park, 46.96N, 142.75E, 69 m alt., *Alnus hirsuta*, 11.VII.2017, 1 larva, NK618, MK403695, deposited in INRA.

Leaf mine. The mine is similar to *Ph. strigulatella* and was found on the same trees. Pupation in the mine.

Trophic specialization. Monophagous on *Alnus hirsuta* (Betulaceae).

Distribution. Russia: RFE—PK.

Remarks. BIN of unknown species—BOLD: ADM1303. In East Asia, eight *Phyllonorycter* species develop on *Alnus*, among which five species, besides other hosts, feed on *Alnus hirsuta*: *Ph. hancola* (Kumata), *Ph. kisoensis* Kumata et Park, *Ph. longispinata* (Kumata), *Ph. maculata* (Kumata), *Ph. strigulatella* (Zeller) (De Prins & De Prins 2018). The three other species develop on other alder in East Asia: *Ph. ermani* (Kumata) (host plant: *Alnus maximowiczii*, however the main host is *Betula*), *Ph. fruticosella* (Kuznetsov) (*A. viridis*), *Ph. takagii* (Kumata) (*A. japonica*). From this list of *Alnus*-feeding species, only *Ph. strigulatella* has been barcoded and it shows 3.9% genetic distance from *Phyllonorycter* sp. 4 (Table 2). Our specimen could be one of these four species—*Ph. hancola*, *Ph. kisoensis*, *Ph. longispinata*, or *Ph. maculata*.

***Phyllonorycter* sp. 5 (cf. *dakekanbae* Kumata)**

Material examined. Russia: SO, Sakhalin Island, Yuzhno-Sakhalinsk, Gagarin Park, 46.96N, 142.75E, 69 m alt., *Betula platyphylla*, 11.VII.2017, 1 larva, NK621, MK403716, deposited in INRA.

Leaf mine. The mine is similar to one of *Ph. ulmifoliella* on *Betula platyphylla* (Fig. 12B). Pupation in the mine.

Trophic specialization. Monophagous on *Betula platyphylla* (Betulaceae).

Distribution. Russia: RFE—SO.

Remarks. BIN of unknown species—BOLD: ADM2521. In East Asia, four species of *Phyllonorycter* develop

on *Betula*: *Ph. cavella* (Zeller), *Ph. dakekanbae* (Kumata), *Ph. ulmifoliella* (Hübner), and *Ph. ermani* (Kumata) (De Prins & De Prins 2018). The first three species are known to colonize *Betula platyphylla*, the latter species develops only on *B. ermanii*. The nearest neighbor to *Phyllonorycter* sp. 5 is *Ph. ulmifoliella* with a genetic distance 3.0% (Table 2). The other two *Betula*-feeding species, *Ph. cavella* and *Ph. ermani*, are genetically more divergent (>11%) comparing to *Phyllonorycter* sp. 5 (Table 2). No DNA barcode sequences of *Ph. dakekanbae* exist in genetic databases. Keeping in mind that it feeds on the same host plant as *Phyllonorycter* sp. 5, the latter could be *Ph. dakekanbae*.

***Phyllonorycter* sp. 6**

(Figs 13G–H)

Material examined. Russia: PK, Gornotaezhnoe, forest around MTS, 43.68N, 132.15E, 224 m alt., *Acer pseudosieboldianum*, 25.VII.2016, 1 larva, NK540, MK403701, deposited in INRA.

Leaf mine. The mine is a white elongated contracted blotch with three to four folds on the epidermis covering mine, between secondary veins or along leaf margin on the lower side of the leaf (Fig. 13G–H). Pupation in the mine.

Trophic specialization. Monophagous on *Acer pseudosieboldianum* (Sapindaceae).

Distribution. Russia: RFE—PK.

Remarks. BIN of unknown species—BOLD: ADF4563. DNA barcode of *Phyllonorycter* sp. 6 does not match any *Acer*-feeding *Phyllonorycter* species in BOLD. In East Asia, only *Ph. orientalis* (Kumata) is known to develop on *A. pseudosieboldianum* (De Prins & De Prins 2018). *Phyllonorycter* sp. 6 is significantly divergent from *Ph. orientalis* (7.4% genetic distance) (Table 2). *Phyllonorycter* sp. 6 may potentially be a new species.

***Phyllonorycter* sp. 7**

(Fig. 14A)

Material examined. Russia: PK, Gornotaezhnoe, forest around MTS, 43.68N, 132.17E, 224 m alt., *Ulmus glabra*, 23.VII.2016, 1 pupa, NK550, MK403718; SO, Sakhalin Island, Yuzhno-Sakhalinsk, BGIS, 47.05N, 142.74E, 57 m alt., *U. davidiana* var. *japonica*, 12.VII.2017, 1 larva, NK626, MK403715, deposited in INRA.

Leaf mine. The mine is an elongated, significantly contracted blotch, strictly between the secondary veins on the lower side of the leaf (Fig. 14A). Later, the epidermis-covering mine becomes brown as usually happens to vacated mines, but in this case the larva is still present in the mine (Fig. 14A). Pupation in the mine.

Trophic specialization. Monophagous on *Ulmus*: *U. glabra*, *U. davidiana* var. *japonica* (Ulmaceae).

Distribution. Russia: RFE—PK, SO (Sakhalin Island).

Remarks. BIN of unknown species—BOLD: ACN4282. No genetic divergence detected between the two DNA barcoded specimens of *Phyllonorycter* sp. 7 from *Ulmus glabra* and *U. davidiana* var. *japonica*. In BOLD, the closest neighbor to *Phyllonorycter* sp. 7 is an unidentified *Phyllonorycter* sampled from *Ulmus* in Taiwan, with minimal interspecific distance 4.9%, followed by the European species, *Ph. tristrigella*, 5.5%. In East Asia, five *Ulmus*-feeding species occur: *Ph. bicinctella* (Matsumura) (hosts: *Ulmus davidiana* var. *japonica*, *U. pumila*), *Ph. laciniatae* (Kumata) (*U. davidiana* var. *japonica*, *U. laciniata*, *U. pumila*), *Ph. pumilae* (Ermolaev) (*U. pumila*), *Ph. ulmi* (Kumata) (*U. davidiana*, *U. davidiana* var. *japonica*, *U. laciniata*, *Zelkova serrata*, and *Ph. valentina* (Ermolaev) (*U. davidiana* var. *japonica*, *U. macrocarpa*) (De Prins & De Prins 2018). Among these species, the sequences of two species, *Ph. pumilae* and *P. ulmi*, are only available in genetic databases. The minimum interspecific divergence between *Phyllonorycter* sp. 7 and the two species *Ph. ulmi* and *Ph. pumila* reaches 7.5% and 12.2%, respectively (Table 2). *Phyllonorycter* sp. 7 may potentially be *Ph. laciniatae* that develops on *U. davidiana* var. *japonica* in East Asia, but less likely *Ph. bicinctella* or *Ph. valentina* that feed on other *Ulmus* species.

***Phyllonorycter* sp. 8 (cf. *pterocaryae* Kumata)**

(Figs 14B–C)

Material examined. Russia: PK, Gornotaezhnoe, forest around MTS, 43.68N, 132.15E, 224 m alt., *Juglans mandshurica*, 23.VII.2016, 1 larva, NK533, MK403680, deposited in INRA.

Leaf mine. The mine is a small oval silvery white blotch, slightly contracted in the late stage, usually without preceding epidermal tunnel; situated at the leaf margin on the upper side of the leaf (Fig. 14B). Pupation in the mine, at the corner of the mine, in a slight depression similar to that observed in *Phyllocnistis* (Fig. 14C).

Trophic specialization. Monophagous on *Juglans mandshurica* (Juglandaceae).

Distribution. Russia: RFE—PK.

Remarks. BIN of unknown species—BOLD: ADF4351. DNA barcode of *Phyllonorycter* sp. 8 is 3.1% divergent from the DNA barcodes of four *Ph. pterocaryae* (Kumata) specimens collected in Japan on *J. mandshurica*, whose identity was confirmed by adult morphology (Ohshima: personal observation). The fact that *Phyllonorycter* sp. 8 larvae feed on the same host as *Ph. pterocaryae* and make similar mines suggests that our finding may correspond to *Ph. pterocaryae*, which might have high intraspecific genetic variability. According to early records, *Ph. pterocaryae* is known in the southern part of Primorskiy Krai (Baryshnikova 2008, 2016). In BOLD, there are three other BINs corresponding to *Phyllonorycter* feeding on Juglandaceae: the two unidentified species on *Platycarya* (Taiwan), *Pterocarya* (Vietnam), and one *Phyllonorycter juglandis* (Japan). *Phyllonorycter* sp. 8 matches none of these species, showing the divergence from them: 4.4, 7.5 and 11.8%, respectively (Table 2).

***Chrysaster hagicola* Kumata, 1961**

(Figs 14D–E)

Material examined. Russia: PK, Gornotaezhnoe, forest around MTS, 43.68N, 132.17E, 224 m alt., *Lespedeza bicolor*, 3.VII.2016, 1 larva, NK551, MK403724, deposited in INRA.

Leaf mine. The mine is a whitish flat blotch, with a short preceding tunnel that starts nearby the main vein on the upper side of the leaf (Fig. 14D). The frass is attached to the epidermis and the bottom of the mine, making the central part of the mine darker. The larva uses this area as a shelter hiding itself especially when disturbed (Fig. 14E). It vacates the mine through a semicircular slip in the upper epidermis and pupates in an oval cocoon at the leaf margin.

Trophic specialization. Oligophagous on Fabaceae: *Lespedeza bicolor*, *L. cyrtobotrya*, *Robinia pseudoacacia* (De Prins & De Prins 2018).

Distribution. Russia: RFE—PK (Kumata 1963; Baryshnikova 2008); Japan (Kumata 1961), Korea (Kumata *et al.* 1983), China (Liu *et al.* 2015).

***Cameraria nipponica* Kumata, 1963**

(Figs 8E, 14F–G)

Material examined. Russia: PK, Gornotaezhnoe, forest around MTS, 43.68N, 132.15E, 224 m alt., *A. caudatum* subsp. *ukurundense*, 22.VII.2016, 1 larva, NK537, MK403685; same location, *A. pseudosieboldianum*, 25.VII.2016, 1 larva, NK529, MK403719, deposited in INRA; same location, host and date, 1 male (reared from leaf mine), 109.3 / [1Cn-2016-male] (Fig. 8E), deposited in SIF.

Leaf mine. The mine is a relatively large elongated flat blotch, with a very short preceding epidermal tunnel that usually starts nearby secondary vein on the upper side of the leaf (Fig. 14F). The mine is white (Fig. 14F); an exceptionally dark mine was found on *A. caudatum* subsp. *ukurundense* (Fig. 14G). The frass is not granular, like in *Phyllonorycter* species, but has a tar-like aspect and covers the bottom of the mine. Pupation in mine.

Trophic specialization. Monophagous on *Acer*: *A. barbinerve*, *A. japonicum*, *A. palmatum*, *A. pseudosieboldianum* (Sapindaceae) (De Prins & De Prins 2018), *A. caudatum* subsp. *ukurundense* (**new record**).

Distribution. Russia: RFE—PK (Baryshnikova 2008); Japan (Kumata 1963).

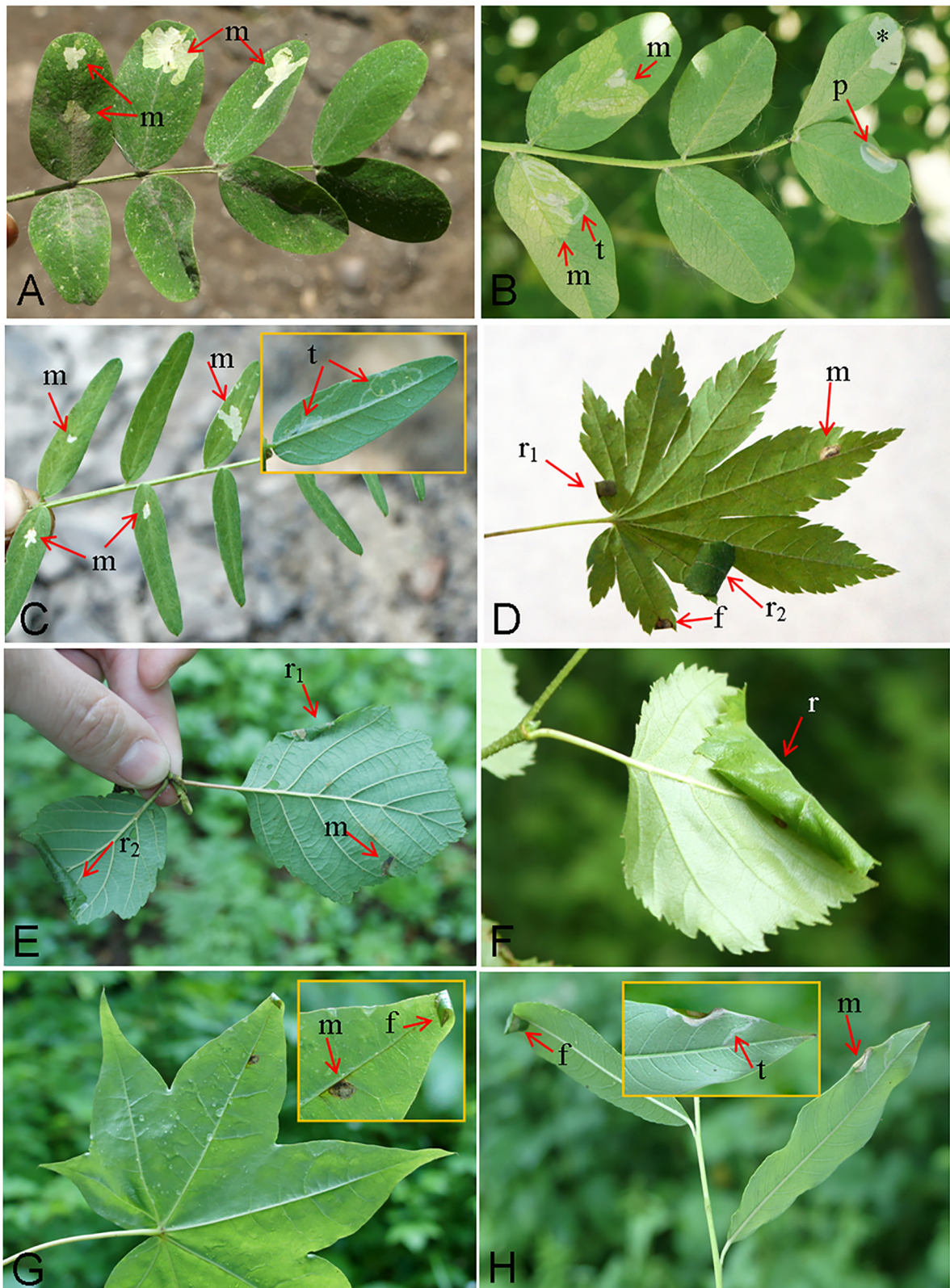


FIGURE 10. Mines, leaf shelters and pupation sites of *Micrurapteryx* and *Caloptilia* spp. from the Russian Far East. (A–B) *Micrurapteryx caraganella*, host plant *Caragana arborescens*; (C) *M. gradatella*, *Vicia* sp.; (D) *Caloptilia acericola*, *Acer pseudosieboldianum*; (E) *C. alni*, *Alnus hirsuta*; (F) *C. betulicola*, *Betula platyphylla*; (G) *C. heringi*, *A. pictum*; (H) *C. stigmatella*, *Salix* sp. Indications: (m) mine; (t) epidermal tunnel; (p) pupation site; (f) folded leaf margin or leaf tip; (r₁–r₂) rolled leaf margin or leaf tip (the indexes ₁ and ₂ indicate the order of construction appearance); *mine of Diptera. Close up: (C, G, H) mine. Sampling locations: (A–C) AO, Skovorodino, 26.VI.2016; (D) PK, Gornotaezhnoe, MTS and forest, 22–27.VII.2016; (E–H) SO, Sakhalin Isl., Yuzhno-Sakhalinsk, 11–20.VII.2017.

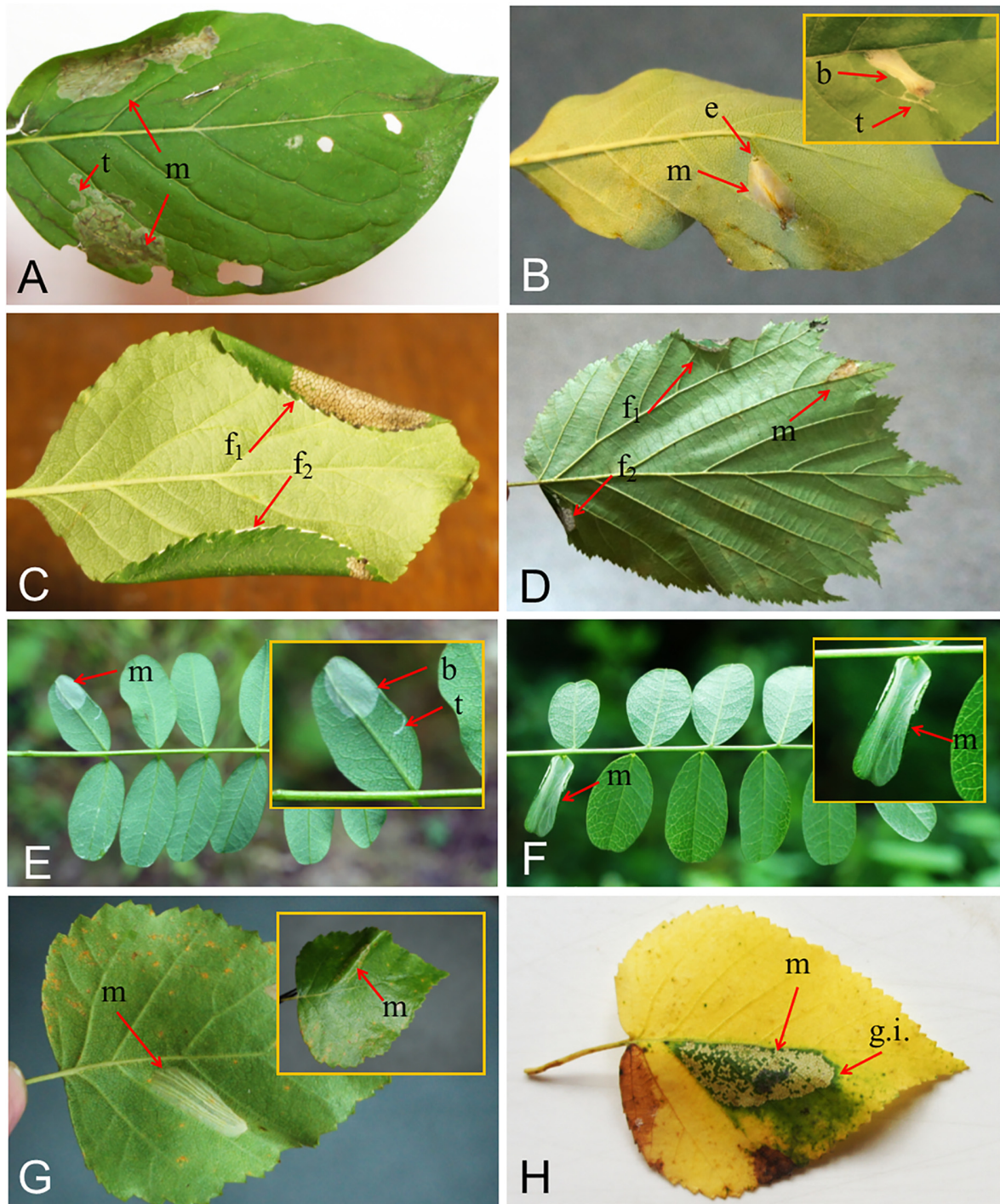


FIGURE 11. Mines and leaf shelters of *Gracillaria*, *Callisto*, *Parornix* and *Phyllonorycter* spp. from the Russian Far East. (A) *Gracillaria* sp., host plant *Syringa amurensis*; (B–C) *Callisto* sp. on *Malus* sp.; (D) *Parornix ermolaevi*, *Corylus sieboldiana*; (E–F) *Ph. caraganella*, *Caragana fruticosa*; (G–H) *Ph. cavella*, *Betula platyphylla*, (H) “green island” and the mine. Indications: (m) mine; (b) blotch part of the mine; (t) epidermal tunnel; (e) exit hole; (f–f₂) folded leaf margin or leaf tip (the indexes ₁ and ₂ indicate the order of construction appearance); (g.i.) green island region. Close up: (B, E–G) mine. Sampling locations: (A–D, G–H) PK, Gornotaezhnoe, MTS and forest, 22–27.VII.2016; (E–F) ibidem, Glukhovka, forest, 27.VII.2016.

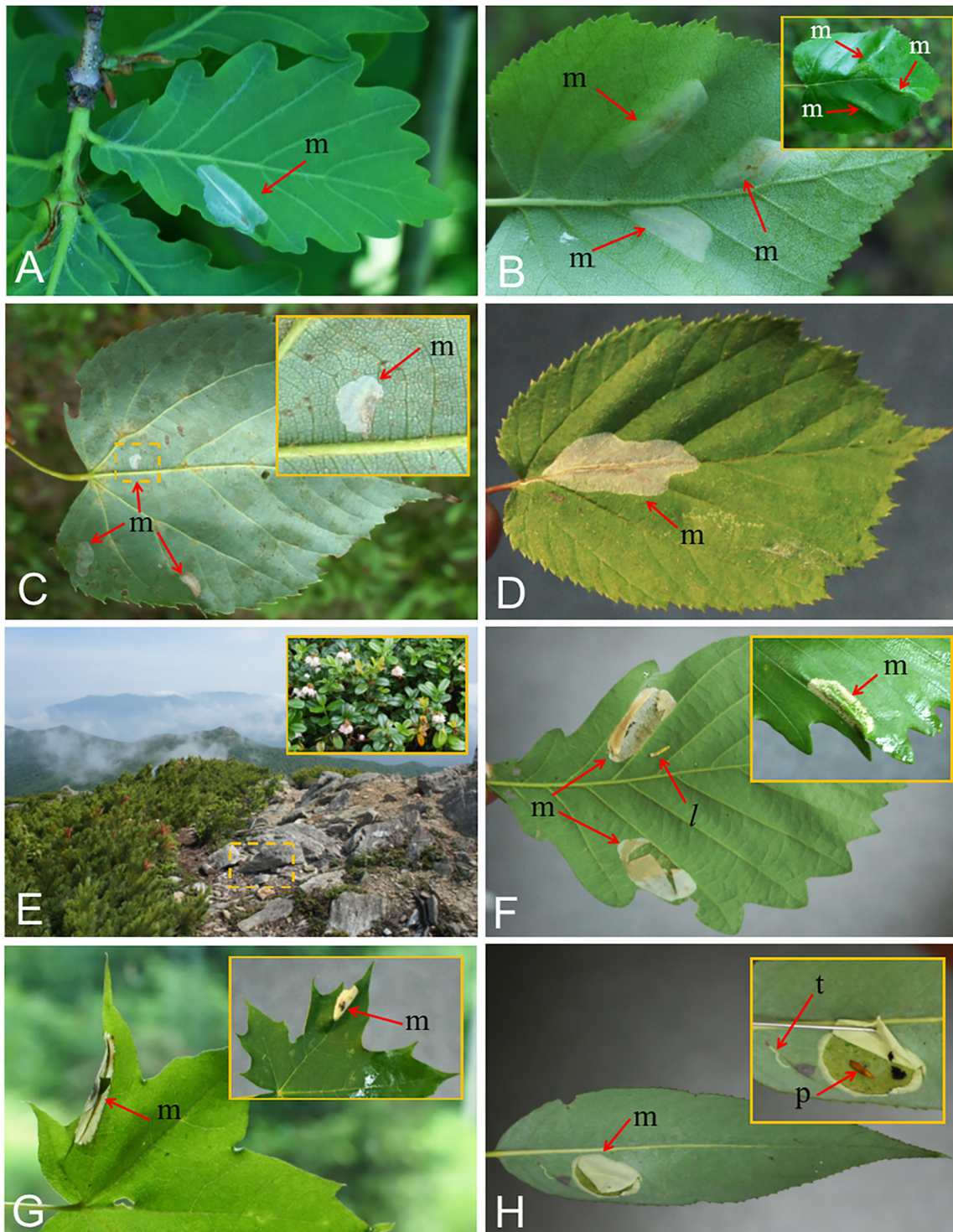


FIGURE 12. Mines of *Phyllonorycter* spp. from the Russian Far East. (A) *Ph. cretata*, host plant *Quercus mongolica*; (B) *Ph. ermani*, *B. platyphylla*; (C) *Ph. issikii*, *Tilia mandshurica*; (D) *Ph. japonica*, *Corylus mandshurica*; (E) sampling location of *Ph. junoniella*; (F) *Ph. nigristella*, *Quercus dentata*; (G) *Ph. orientalis*, *Acer pictum*; (H) *Ph. pastorella*, *Salix* sp. Indications: (m) mine; (t) epidermal tunnel; (l) larva; (p) pupa. Close up: (B) deformation of the leaf due to mines (the view from the upper side); (C, F–H) mine, (E) the bush from that the specimens were collected. Sampling locations: (A–B, F) SO, Sakhalin Isl., Yuzhno-Sakhalinsk, Gagarin’s Park, 11–20.VII.2017; (E) SO, Sakhalin Isl., Susunay mountain range, 14.VII.2017; (C–D, G–H) PK, Gornotaezhnoe, MTS and forest, 22–26.VII.2016.

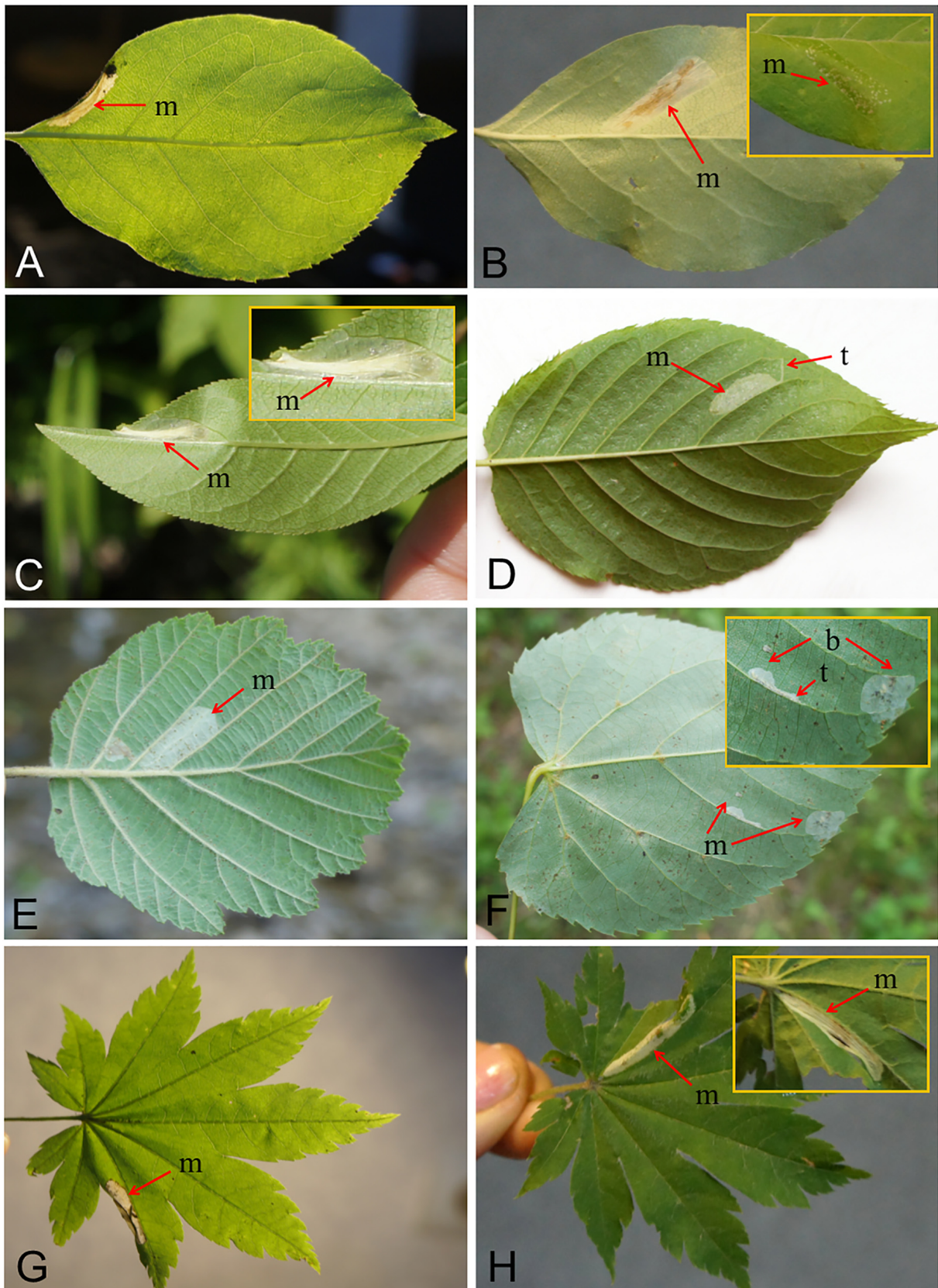


FIGURE 13. Mines of *Phyllonorycter* spp. from the Russian Far East. (A–B) *Ph. ringoniella*, host plant *Malus mandshurica*; (C–D) *Ph. sorbicola*, *Prunus padus* and *Prunus maackii* respectively; (E) *Ph. strigulatella*, *Alnus hirsuta*; (F) *Phyllonorycter* sp. 1, *Tilia mandshurica*; (G–H) *Phyllonorycter* sp. 6, *Acer pseudosieboldianum*. Indications: (m) mine; (t) epidermal tunnel; (b) blotch. Close up: (B–C, F, H) mine. Sampling locations: (A–D, F–H) PK, Gornotaezhnoe, MTS and forest, 22–26.VII.2016; (E) SO, Sakhalin Isl., Yuzhno-Sakhalinsk, 11–20.VII.2017.

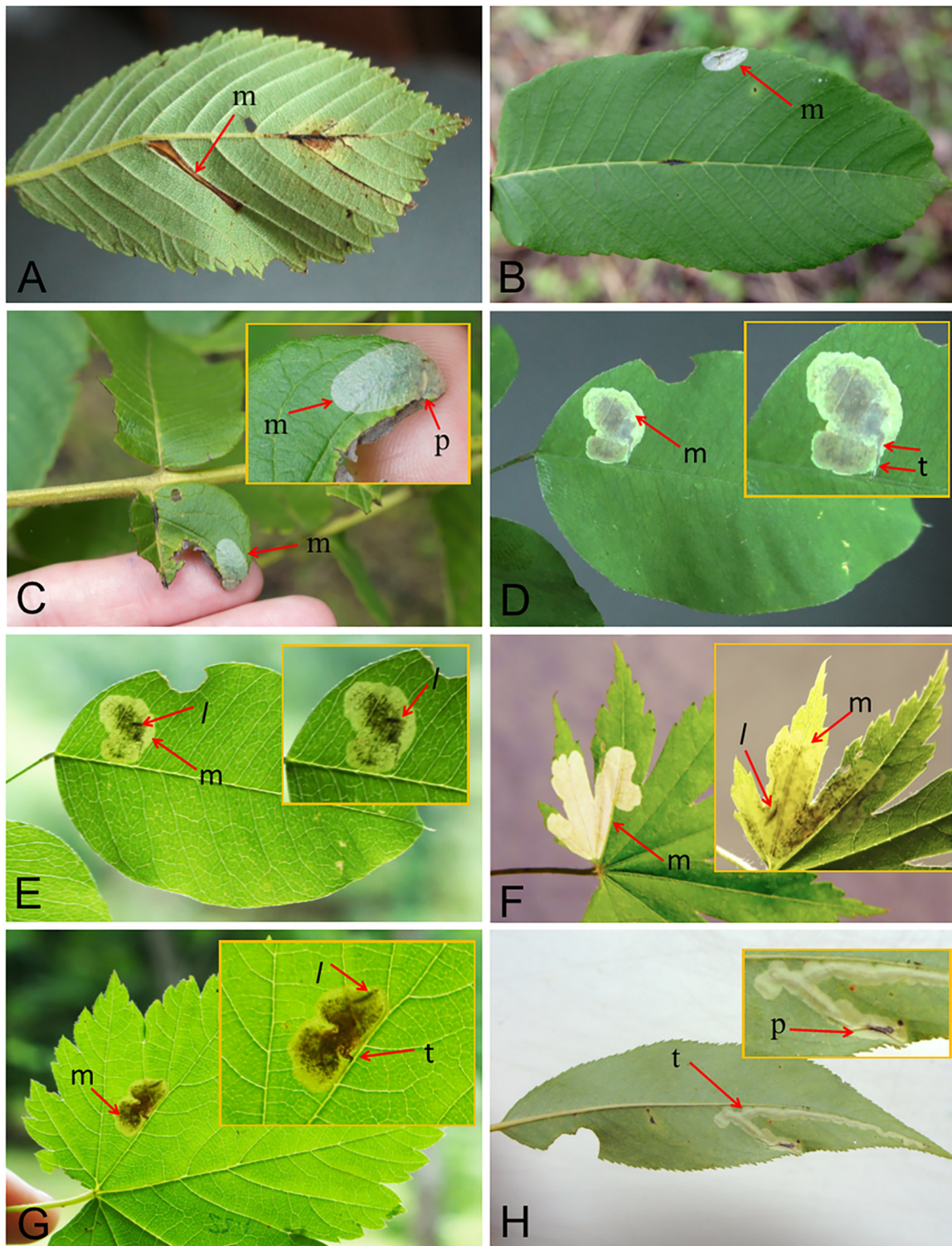


FIGURE 14. Mines, leaf shelters and pupation sites of *Phyllonorycter*, *Chrysaster* and *Cameraria* spp. from the Russian Far East. (A) *Phyllonorycter* sp. 7, host plant *Ulmus glabra*; (B–C) *Phyllonorycter* sp. 8, *Juglans mandshurica*; (D–E) *Chrysaster hagicola*, *Lespedeza bicolor*; (F–G) *Cameraria nipponica*, *Acer pseudosieboldianum* and *A. caudatum* subsp. *ukurundense*, respectively; (H) *Phyllocnistis* sp. 1, *Salix* sp. Indications: (m) mine; (b) blotch part of the mine; (t) epidermal tunnel; (l) larva; (p) pupation site. Close up: (C–G) mine; (H) pupation site. Sampling locations: (A) SO, Sakhalin Isl., Yuzhno-Sakhalinsk, 11–20.VII.2017; (B–H) PK, Gornotaezhnoe, MTS and forest, 22–26.VII.2016.

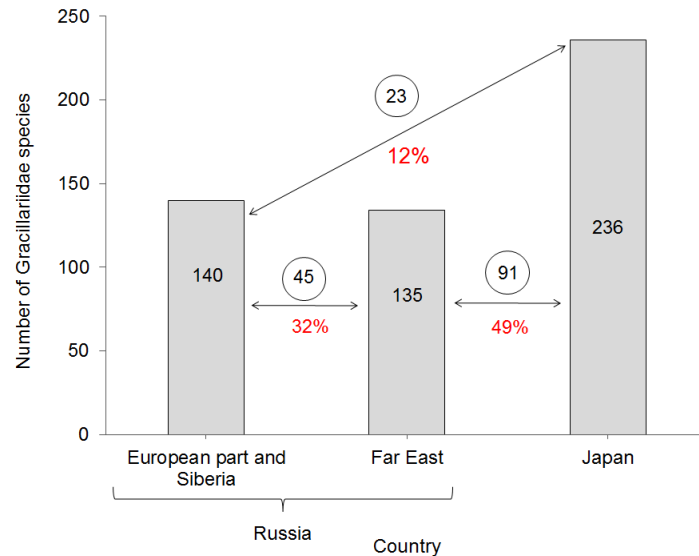


FIGURE 15. Similarity of gracillariid faunas of the Russian regions and Japan. Gracillariid species number is given in the corresponding bar, number of shared species is in the circles. The similarity Sørensen–Dice coefficient is given in red.

Subfamily PHYLLOCNISTINAE Herrich-Schäffer, 1857

Phyllocnistis sp. 1

(Fig. 14H)

Material examined. Russia: PK, Gornotaezhnoe, forest around MTS, 43.68N, 132.17E, 224 m alt., *Salix* sp., 23.VII.2016, 1 larva, NK595, MG191427, deposited in INRA.

Leaf mine. The mine is a long relatively slender whitish epidermal tunnel, slightly wavy, usually starting at the leaf tip and proceeding along the main vein, on the lower side of the leaf (Fig. 14H). The growing mine increases in width insignificantly. Pupation in the mine, in the cocoon, near the leaf margin on the lower side (Fig. 14H).

Trophic specialization. Monophagous on *Salix* sp. (Salicaceae).

Distribution. Russia: RFE—PK.

Remarks. BIN of unknown species—BOLD: ADF2906. Overall, only two *Salix*-feeding *Phyllocnistis* are known in East Asia: *Ph. gracilistylella* Kobayashi, Jinbo et Hirowatari and *Ph. saligna* (Zeller) (De Prins & De Prins 2018). Other three species that develop on *Salix*, occurs in the western part of the Palearctic: *Ph. canariensis* Hering, *Ph. ramulicola* Langmaid et Corley and *Ph. valentinensis* Hering (De Prins & De Prins 2018). The DNA barcode sequence of *Phyllocnistis* sp. 1 does not match any of these species. The closest neighbor, with 4.9% divergence, is *Ph. valentinensis* from Austria, followed by *Ph. gracilistylella* from Japan, 6.4% (Table 2). Other three species are significantly genetically distant from *Phyllocnistis* sp. 1, i.e. > 12.9 % (Table 2). *Phyllocnistis* sp. 1 is a putative new species to science. It was mentioned in our recent study (Kirichenko *et al.* 2018a).

Discussion

Based largely on DNA barcoding, our study provides an updated view of the diversity of the gracillariid fauna in RFE. Combining DNA barcoding with a morphological analysis, we identified 34 gracillariid species and discovered eight species that represent new distribution records in RFE, namely *Callisto insperatella* (Nickerl), *Caloptilia heringi* Kumata, *Phyllonorycter ermani* (Kumata), *Ph. junoniella* (Zeller), *Ph. populifoliella* (Treitschke), *Ph. sorbicola* Kumata, and *Ph. ulmifoliella* (Hübner), and *Micrurapteryx caraganella* (Hering). They may have been previously overlooked probably due to their rare occurrence or fragmented distribution in RFE.

TABLE 2. Unidentified gracillariids from the Russian Far East (RFE) and minimal genetic distances to the nearest neighbor and related species³ known to feed on the same plants in East Asia or other parts of the Palearctic.

No	Unidentified gracillariids from RFE, host plant, BIN ¹	Nearest species in BOLD and related species feeding on the same host	Country (region) ²	Collector ³	Process ID	GenBank accession No.	BIN	Min interspecific distance ⁴ , %
1	<i>Gracillaria</i> sp., host: <i>Syringa amurensis</i> , BOLD:ADF4930	<i>Gracillaria</i> sp. RN-2016 <i>G. lortiolella</i> <i>G. cf. japonica</i> <i>G. syringella</i> <i>G. ussuriella</i>	Japan Austria Japan Germany Japan	– PH – AH –	GBMIN81243-17 LASTS612-14 GBMIN81242-17 FBLMS076-09 GBMIN81245-17	LC127822 – LC127810 GU706354 LC127798	BOLD:ADF4930 BOLD:AAI6855 BOLD:ADK0759 BOLD:AAC0054 BOLD:ADJ9144	0.2 6.5 6.8 8.0 9.8
2	<i>Callisto</i> sp., host: <i>Malus</i> sp., {BOLD:ADF4428}	<i>Callisto denticulella</i> <i>C. denticulella</i> <i>C. insperatella</i> <i>C. insperatella</i>	Canada France (RFE) Poland	– AC NK JB	RRSSC1570-15 GRPAL449-11 SIBLE114-18 GRPAL094-10	MG364846 KX045846 MK403693 HM902895	BOLD:AAK2080 BOLD:AAK2080 BOLD:AAK2078 BOLD:AAK2078	2.2 2.2 3.7 4.3
3	<i>Phyllonorycter</i> sp. 1, host: <i>Tilia mandshurica</i> , {BOLD:ACC3074}	<i>Phyllonorycter issikii</i>	Japan	KT	ISSIK310-14	KX818734	BOLD:AAC9940	5.4
4	<i>Phyllonorycter</i> sp. 2, host: <i>Malus mandshurica</i> , {BOLD:ADF3338}	<i>Phyllonorycter ringoniella</i> <i>Ph. sorbicola</i>	Japan Japan	S CD, CvdB	GRACI113-07 WOGRA371-15	– –	BOLD:AAJ1250 BOLD:ACU5756	3.3 9.4
5	<i>Phyllonorycter</i> sp. 3, host: <i>Prunus padus</i> , {BOLD:ACY3732}	<i>Phyllonorycter sorbicola</i> <i>Ph. sorbicola</i> <i>Ph. ringoniella</i> <i>Ph. cerasicolella</i>	Japan (RFE)* China Czech Rep.	CD, CvdB NK EJVN AL	WOGRA371-15 SIBLE080-17 WOGRA379-15 GRACI187-08	– MK403721 – KX071356	BOLD:ACU5756 BOLD:ACU5756 BOLD:ACU6879 BOLD:AAE6560	2.0 2.0 7.9 10.2
6	<i>Phyllonorycter</i> sp. 4, host: <i>Alnus hirsuta</i> , {BOLD:ADM1303}	<i>Phyllonorycter strigulatella</i> <i>Ph. ermani</i>	Czech Republic (RFE)*	A.L NK	GRACI501-09 SIBLE112-18	HM902813 MK403679	BOLD:AAD5287 BOLD:ACU5862	3.9 10.7
7	<i>Phyllonorycter</i> sp. 5, host: <i>Betula platyphylla</i> , {BOLD:ADM2521}	<i>Phyllonorycter ulmifoliella</i> <i>Ph. cavella</i> <i>Ph. cavella</i> <i>Ph. ermani</i>	France Japan (RFE)* (RFE)*	AC CD, CvdB NK NK	GRPAL194-11 WOGRA194-15 SIBLE030-17 SIBLE112-18	JN280204 – MK403713 MK403679	BOLD:ABY9921 BOLD:ADC1842 BOLD:ADC1842 BOLD:ACU5862	3.0 11.4 11.4 11.9
8	<i>Phyllonorycter</i> sp. 6, host: <i>Acer pseudosieboldianum</i> , {BOLD:ADF4563}	<i>Phyllonorycter orientalis</i> <i>Ph. orientalis</i>	Japan (RFE)*	CD, CvdB NK	WOGRA253-15 SIBLE025-17	– MK403726	BOLD:ACU5862 BOLD:AAC1748	7.4 7.4

.....continued on the next page

TABLE 2. (Continued)

No	Unidentified gracillariids from RFE, host plant, BIN ¹	Nearest species in BOLD and related species feeding on the same host	Country (region) ²	Collector ³	Process ID	GenBank accession No.	BIN	Min interspecific distance ⁴ , %
9	<i>Phyllonorycter</i> sp. 7, host: <i>Ulmus glabra</i> , <i>U. davidiana</i> var. <i>japonica</i> , {BOLD: ACN4282}	<i>Phyllonorycter Ulmus Taiwan</i> <i>Ph. tristrigella</i> <i>Ph. ulmi</i>	Taiwan Belgium Japan	C.D, EvN J&WDP S	WOGRA359-15 GRPAL069-10 GRACI115-07	— HM392569 —	BOLD:AAE4625 BOLD:AAAY1137	4.9 5.5 7.5
10	<i>Phyllonorycter</i> sp. 8, host: <i>Juglans mandshurica</i> , {BOLD:ADF4351}	<i>Ph. pumila</i> <i>Ph. pterocarya</i>	Spain Japan	AL IO	GRACI263-08 SIBLE144-18 SIBLE145-18	KC567647 MK403720 MK403723	BOLD:AAH8430 BOLD:ADQ9355	12.2 3.1
		<i>Phyllonorycter Platycarya</i>	Taiwan	CD, EvN	WOGRA236-15	—	BOLD:ACU5572	4.4
		<i>Phyllonorycter Pterocarya</i>	Vietnam	EvN, CD	WOGRA038-13	—	BOLD:ACD4375	7.5
		<i>Ph. juglandis</i>	Japan	CD, EvN	WOGRA263-15	—	BOLD:ACU6420	11.8
11	<i>Phyllocnistis</i> sp. 1, host: <i>Saxifraga</i> sp., {BOLD:ADF2906}	<i>Phyllocnistis valentinensis</i> <i>Ph. gracilistylella</i> <i>Ph. saligna</i> <i>Ph. ramulicola</i> <i>Ph. canariensis</i>	Austria Japan Japan France Spain	— SK SK JN EvN	GRPAL515-11 GBGL7455-11 GBGL7449-11 PHLAD379-11 WOGRA059-13	KX046218 AB614506 AB614512 KX042734 MG935413	BOLD:AAZ7894 BOLD:AAZ7400 BOLD:AAL5481 BOLD:ACG6599	4.9 6.4 12.9 13.1 13.5

¹BINs given in {} are novel to BOLD; ²Region, RFE—Russian Far East; ³Collectors: AC—A. Cama, AH—A. Haslberger, AL—A. Lastvka, CD—C. Doorenweerd, CvdB—C. van den Berg, EvN—E. van Niekerken, J&WDP—J. & W. De Prins, JB—J. Buszko, JN—J. Nel, IO—I. Ohshima, KT—K. Tokashi, NK—N. Kirichenko, PH—P. Huemer, S—Sugisima, SK—S. Kobayashi. ⁴Minimum genetic distance between unidentified specimens from RFE (first column) and the members of the same genus that are known to feed on same plants in the Palearctic. Cells with dash mean no data available.

Barcoding immature stages of gracillariids collected from their leaf mines is a very efficient method to unveil insect–plant interactions, especially when field conditions make it difficult to rear the adults. By DNA barcoding immature stages, we discovered four potentially new species as inferred from the facts that no other gracillariid species are known to feed on their host plants and that gracillariids are usually highly host specific. In addition, DNA barcodes of larvae revealed eight gracillariid–host plant associations novel to science. The presence of alien plants in the environment, especially those having taxonomic proximity to common host plants of leafminers can lead to host plant shifts (Auerbach & Simberloff 1988; Péré *et al.* 2010; Kirichenko *et al.* 2013; Kirichenko & Kenis 2016). For instance, *Phyllonorycter orientalis* (Kumata), known to develop exclusively on East Asian maple species (De Prins & De Prins 2018), and *Ph. pseudojezoniella* Noreika, for which the host plant was not known previously (Noreika 1994) were found for the first time on North American sugar maple, *Acer saccharum* cultivated in a botanical garden in RFE. These and other findings show the usefulness of botanical gardens and arboreta, growing together native and alien plants from various floristic regions, for studying trophic interactions and host shifts in folivorous insects (Kirichenko & Kenis 2016). The occurrence of both *Ph. pseudojezoniella* and *Ph. orientalis* on *Acer saccharum* also raises the possibility that these species might be conspecific with a *Phyllonorycter* from eastern North America. Indeed, a recent barcoding study showed that 30 species of Microlepidoptera previously known from either the Palearctic or the Nearctic had an overlooked Holarctic distribution (Landry *et al.* 2013). Two *Phyllonorycter* species are known to attack *Acer saccharum* in North America: *Phyllonorycter clemensella* and *Phyllonorycter lucidicostella*. *Ph. orientalis* shows a 12.6% and 13.6% divergence with *Phyllonorycter clemensella* and *Phyllonorycter lucidicostella*, respectively. *Ph. pseudojezoniella* has not been barcoded yet. More sampling and a deeper study would be needed to check conspecificity of these *Acer*-feeding *Phyllonorycter* species.

We recorded for the first time the “green island” phenotype in *Phyllonorycter cavella* leaf mines on *Betula platyphylla* in Primorskii Krai. Leaf miners can induce green islands, which are characterized by photosynthetically active green patches in otherwise senescing leaves (Giron *et al.* 2007). Green islands have been reported for several gracillariids (Gutzwiller *et al.* 2015), and other micromoths and Hymenoptera species in Europe (Hering 1951; Giron *et al.* 2007). They have recently been discovered in Brazil in leaf-gallers (Santos *et al.* 2017). It has been shown that *Wolbachia* endosymbionts could play an important role in green island induction (Kaiser *et al.* 2010; Gutzwiller *et al.* 2015). It would be necessary to screen the sample of *Ph. cavella* from RFE for *Wolbachia* to test that hypothesis.

We have not documented significant damage caused by leaf mining gracillariids on woody plants in RFE, with one exception. *Micrurapteryx caraganella* was recorded in large numbers in the city plantations severely damaging bushes of Siberia peashrub, *Caragana arborescens* in Skovorodino in Amurskaya Oblast in 2016 (Kirichenko *et al.* 2017b). This species has been erroneously identified in past studies as *M. gradatella* (Dovnar-Zapol'skiy & Tomilova 1978; Kuznetsov 1981). Here we showed that these *Micrurapteryx* species occur in sympatry in Amurskaya Oblast but develop on different legume hosts: *M. caraganella* on *Caragana arborescens* and *M. gradatella* on *Vicia* sp. The other pest known from AO, *Acrocercops amurensis* Lam. Kuznetsov, which was recorded in high densities on Mongolian oak, *Quercus mongolica* in the middle of the 20th century (Kuznetsov 1960), was not found in our surveys. The lime leafminer, *Phyllonorycter issikii* (Kumata), native to East Asia (including RFE) but invasive and a pest elsewhere in Russia and in Europe, was never recorded in outbreak density in RFE in 2010–2017.

As expected, the gracillariid fauna of RFE is more similar to that of Japan, than to the rest of Russia, i.e. the European part of Russia and Siberia. This can be explained by the geographic proximity and common paleogeographic history of RFE and Japan (Otofujii *et al.* 1985), which is reflected in some similarity of their climatic conditions and floral composition (Krestov 2003; Grichuk & Borisova 2009; Novenko 2009). Therefore, some species known only from RFE might also occur in neighboring East Asian countries, such as Japan, Northeast China and North Korea (Beljaev 1996). As an example, our recent study showed that *Phyllocnistis cornella* Ermolaev, formerly known only for RFE (particularly, Kunashir Island), is present also in Japan on Hokkaido Island (Kirichenko *et al.* 2018a).

The DNA barcoding campaign that we have initiated in the Easternmost Russia is an on-going project that will allow a deeper exploration of gracillariid diversity, the interaction with their host plants and endosymbionts in the remote corners of RFE, as well as to detect emerging pests and invaders and discover species new to science. Our ultimate goal is to compile a reliable DNA barcode reference library covering all gracillariids of RFE, with their verified distribution and trophic interactions. At present, out of the 135 gracillariidae species known to occur in the Far East of Russia, only 12 species (i.e. 7%) do not have full DNA barcodes available in BOLD: *Aristaea bathracma* (Meyrick), *Caloptilia issikii* Kumata, *C. pulverea* Kumata, *C. pyrrhaspis* (Meyrick), *C. schisandrae* Kumata, *C.*

ulmi Kumata, *Parornix alni* Kumata, *P. extrema* Kuznetsov et Baryshnikova, *Phyllonorycter bicinctella* (Matsumura), *Ph. jezoniella* (Matsumura), *Ph. hancola* (Kumata), *Spulerina astaurota* (Meyrick). It will be our priority to obtain full DNA barcodes of these 12 species.

We hope that our campaign will promote similar studies in other understudied microlepidopteran groups in this unique region of Russia.

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TABLE S1. Revised checklist of Gracillariidae species of the Russian Far East (RFE), their host plants and distribution*. This revised checklist places all RFE Gracillariidae in the subfamilies defined by Kawahara *et al.* (2017).

№	Species	Host plant	Distribution	
			RFE ¹	elsewhere
ORNIXOLINAE Kuznetsov et Baryshnikova, 2001				
1	<i>Epicephala relictella</i> Kuznetsov, 1979	<i>Flueggea suffruticosa</i> (Euphorbiaceae)	PK	Korea, China
2	<i>Liocrobyla desmodiella</i> Kuroko, 1982	<i>Desmodium oldhamii</i> , <i>Hylodesmum podocarpum</i> , <i>Lespedeza cyrtobotrya</i> , <i>Ohwia caudata</i> (Fabaceae)	KK, JAO, PK	Japan
3	<i>L. kumatai</i> Kuroko, 1982	<i>Desmodium</i> , <i>Lespedeza bicolor</i> (Fabaceae)	PK	Japan
4	<i>Micrurapteryx caraganella</i> (Hering, 1957) †	<i>Caragana arborescens</i> (Fabaceae)	AO	Russia (European part—introduced; Siberia)
5	<i>M. gerasimovi</i> Ermolaev, 1989	<i>Melilotus suaveolens</i> , <i>Vicia cracca</i> (Fabaceae)	AO, KK, PK	Russia (Siberia—Transbaikal region)
6	<i>M. gradatella</i> (Herrich-Schäffer, 1855) †	<i>Lathyrus linifolius</i> , <i>L. montanus</i> , <i>Vicia amoena</i> , <i>V. septium</i> (Fabaceae). Findings on <i>Caragana</i> spp. to be referred to <i>M. caraganella</i>	AO	Russia (European part and Siberia), China, Mongolia, Central Asia, Europe
7	<i>Ornixola caudatella</i> (Zeller, 1839)	<i>Salix acutifolia</i> , <i>Salix</i> sp. (Salicaceae)	KK, JAO, PK	Russia (European part and Siberia), Europe
GRACILLARIINAE Stainton, 1854				
8	<i>Aristaea bathracma</i> (Meyrick, 1912)	<i>Aster ageratoides</i> Turcz. var. <i>ovatus</i> (Asteraceae)	PK	Japan, Korea, Thailand, South Africa
9	<i>A. pavoniella</i> (Zeller, 1847)	<i>Aster</i> (Asteraceae)	AO, KK, PK	Japan, China, Asia Minor, Europe
10	<i>Caloptilia acericola</i> Kumata, 1966	<i>Acer japonicum</i> , <i>A. pictum</i> , <i>A. palmatum</i> , <i>A. pseudosieboldianum</i> (Sapindaceae)	PK	Japan
11	<i>C. aceris</i> Kumata, 1966	<i>A. miyabei</i> , <i>A. palmatum</i> , <i>A. pictum</i> , <i>A. saccharum</i> (Sapindaceae)	AO, KK, PK	Japan, Korea, China
12	<i>C. alchimiella</i> (Scopoli, 1763)	<i>Fagus sylvatica</i> , <i>Quercus</i> (Fagaceae)	KK	Kazakhstan, Caucasus, Asia Minor, Europe
13	<i>C. alni</i> Kumata, 1966	<i>Alnus hirsuta</i> , <i>A. japonica</i> (Betulaceae)	AO, KK, JAO, PK, SO	Japan, Korea, China
14	<i>C. almivorella</i> (Chambers, 1875)	<i>Alnus</i> (main host), <i>Betula papyrifera</i> (Betulaceae), <i>Quercus garryana</i> (Fagaceae), <i>Acer negundo</i> (Sapindaceae)	PK	Russia (Siberia—Buryatia Rep.), North America
15	<i>C. betulicola</i> (Hering, 1928)	<i>Betula</i> (Betulaceae)	AO, KK, PK, SO (Sakhalin Isl)	Russia (European part, Siberia), Japan, China, Caucasus, Europe
16	<i>C. cuculipennella</i> (Hubner, 1796)	<i>Fraxinus</i> , <i>Jasminum</i> , <i>Ligustrum</i> , <i>Syringa</i> (Oleaceae)	KamK, AO, PK	Russia (European part), Japan, China, Turkmenistan, Caucasus, Asia Minor, Europe, North America
17	<i>C. chrysolampra</i> (Meyrick, 1936)	<i>Populus</i> , <i>Salix</i> (Salicaceae)	KK	Japan, Korea, China, Taiwan

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TABLE S1. (Continued)

№	Species	Host plant	Distribution	
			RFE ¹	elsewhere
18	<i>C. dubatolovi</i> Baryshnikova, 2007	unknown	KK	–
19	<i>C. elongella</i> (Linnaeus, 1761)	<i>Alnus</i> (Betulaceae)	KK	Russia (Siberia), Kazakhstan, Caucasus, Turkey, Europe, North America
20	<i>C. gloriosa</i> Kumata, 1966	<i>Acer japonicum</i> , <i>A. palmatum</i> , <i>A. pictum</i> , <i>A. sieboldianum</i> , <i>A. pseudosieboldianum</i> (Sapindaceae)	KK, PK, SO (Kunashir Isl)	Japan
21	<i>C. heringi</i> Kumata, 1966	<i>Acer pictum</i> (syn. <i>A. mono</i>) (Sapindaceae)	KK, PK, SO (Sakhalin Isl)	Japan
22	<i>C. hidakensis</i> Kumata, 1966	<i>Acer pictum</i> (Sapindaceae)	PK, SO (Kuril Isl)	Japan
23	<i>C. issikii</i> Kumata, 1982	<i>Acer japonicum</i> , <i>Acer</i> spp. (Sapindaceae)	KK, PK	Japan, China
24	<i>C. kisoensis</i> Kumata, 1982	<i>Acer ginnala</i> , <i>A. pictum</i> (Sapindaceae)	PK, SO (Kuril Isl)	Japan, Korea
25	<i>C. korbiella</i> (Caradja, 1920)	unknown	KK	–
26	<i>C. leucothoes</i> Kumata, 1982	<i>Menziesia pentandra</i> , <i>Leucothoe grayana</i> , <i>Rhododendron</i> (Ericaceae)	KK, JAO, PK, SO (Kuril Isl)	Russia (Siberia), Japan, Korea, China
27	<i>C. mandshurica</i> (Christoph, 1882)	<i>Quercus</i> , <i>Castanea crenata</i> (Fagaceae)	AO, KK, PK	Japan, China
28	<i>C. monticola</i> Kumata, 1966	<i>Acer</i> (Sapindaceae)	KK, PK, SO	Japan, China
29	<i>C. orientalis</i> Ermolaev, 1979	<i>Lonicera maackii</i> (Caprifoliaceae)	PK	–
30	<i>C. populetorum</i> (Zeller, 1839)	<i>Alnus</i> , <i>Betula</i> (Betulaceae)	KK, PK	Russia (European part and Siberia), Kazakhstan, Caucasus, Europe
31	<i>C. puberea</i> Kumata, 1966	<i>Alnus</i> (Betulaceae)	MO, AO, KK, PK, SO	Russia (Siberia), Japan, China
32	<i>C. pyrrhaspis</i> (Meyriek, 1931)	<i>Betula</i> (Betulaceae)	AO, KK, JAO, PK, SO (Kuril Isl)	Japan, China
33	<i>C. sachalinella</i> Ermolaev, 1984	<i>Alnus hirsuta</i> (Betulaceae)	AO, KK, SO (Sakhalin Isl)	Russia (Siberia), Japan, Korea, China
34	<i>C. sapporella</i> (Matsumura, 1931)	<i>Quercus</i> , <i>Castanea crenata</i> (Fagaceae)	AO, KK, PK, SO	Japan, Korea, China
35	<i>C. schisandrae</i> Kumata, 1966	<i>Schisandra chinensis</i> (Magnoliaceae)	KK, PK	Japan, Korea, China
36	<i>C. stigmatella</i> (Fabricius, 1781) †	<i>Salix</i> , <i>Populus</i> , <i>Chosenia</i> (Salicaceae)	KamK, AO, KK, PK, SO	Russia (European part and Siberia), Japan, Korea, China, Mongolia, Kazakhstan, Central Asia, Caucasus, Asia Minor, Europe, North Africa, North America, India

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TABLE S1. (Continued)

№	Species	Host plant	Distribution	
			RFE ¹	elsewhere
37	<i>C. suberinella</i> (Tengström, 1848)	<i>Betula platyphylla</i> (Betulaceae)	KamK, AO, KK, SO (Sakhalin Isl), KK, PK, SO	Russia (European part and Siberia), North Caucasus, China, Europe, North America Japan, China
38	<i>C. ulmi</i> Kumata, 1982	<i>Ulmus laciniata</i> , <i>U. davidiana</i> var. <i>japonica</i> , <i>U. davidiana</i> , <i>Zelkova serrata</i> (Ulmaceae)	KK, PK	China
39	<i>C. variegata</i> Kuznetsov et Baryshnikova, 2001	unknown		
40	<i>Calybites phasianipenella</i> (Hübner, [1813])	Amaranthaceae, Boraginaceae, Chenopodiaceae, Clusiaceae, Lythraceae, Poaceae, Polygonaceae, Primulaceae	AO, KK, PK, SO (Kunashir Isl)	Russia (European part and Siberia), Japan, Korea, China, Kazakhstan, Central Asia, Caucasus, Asia Minor, Middle East, Europe, Southeast Asia, India, Indonesia
41	<i>C. securinella</i> (Ermolaev, 1986)	<i>Flueggea suffruticosa</i> (Euphorbiaceae)	PK	Korea
42	<i>Euspilapteryx aureola</i> (Kumata, 1982)	<i>Hypericum erectum</i> (Hypericaceae)	SO (Kuril Isl)	Japan
43	<i>Gracillaria albicapitata</i> Issiki, 1930	<i>Fraxinus</i> , <i>Syringa</i> (Oleaceae)	KK, JAO, PK, SO	Japan
44	<i>G. arsenievi</i> (Ermolaev, 1977)	<i>Fraxinus</i> , <i>Syringa</i> (Oleaceae)	KK, PK, SO (Sakhalin Isl)	Japan
45	<i>G. ussuriella</i> (Ermolaev, 1977)	<i>Fraxinus mandshurica</i> (Oleaceae)	AO, KK, PK, SO	Japan
PARORNICHINAE Kawahara et Ohshima, 2016				
46	<i>Callisto albicinctella</i> Kuznetsov, 1979	<i>Prunus cerasifera</i> (Rosaceae)	PK, SO (Sakhalin Isl)	–
47	<i>C. elegantella</i> Kuznetsov, 1979	unknown	PK	–
48	<i>C. insperatella</i> (Nickerl, 1864) †	<i>Cerasus</i> , <i>Prunus</i> (Rosaceae)	PK	Russia (European part), Europe
49	<i>Parornix alni</i> Kumata, 1965	<i>Alnus hirsuta</i> (Betulaceae)	PK, SO (Sakhalin Isl), Kuril Isl)	Japan, Korea
50	<i>P. betulae</i> (Stainton, 1854)	<i>Betula</i> (Betulaceae)	AO, KK, PK, SO (Kuril Isl)	Russia (European part and Siberia), Japan, Korea, North America (Canada)
51	<i>P. ermolaevi</i> Kuznetsov, 1979 †	<i>Corylus heterophylla</i> , <i>C. sieboldiana</i> (Betulaceae)	AO, KK, PK	–
52	<i>P. extrema</i> Kuznetsov et Baryshnikova, 2003	unknown	KK, PK	–
53	<i>P. fumidella</i> Kuznetsov, 1979	<i>Malus mandshurica</i> (Rosaceae)	KK, PK	Russia (Siberia—Transbaikal region)
54	<i>P. kumatai</i> Ermolaev, 1993	<i>Crataegus maximowiczii</i> (Rosaceae)	KK, PK	Russia (Siberia), Caucasus
55	<i>P. loganella</i> (Stainton, 1848)	<i>Betula</i> (Betulaceae)	AO, KK, PK	Russia (European part and Siberia), Kazakhstan, Europe

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TABLE S1. (Continued)

№	Species	Host plant	Distribution	
			RFE ¹	elsewhere
56	<i>P. maliphaga</i> Kuznetsov, 1979	<i>Malus</i> (Rosaceae)	PK	Russia (Siberia)
57	<i>P. multimaculata</i> (Matsumura, 1931)	<i>Prunus</i> (Rosaceae)	PK, SO (Kurul Isl)	Japan, Korea
58	<i>P. retrusella</i> Kuznetsov, 1979	<i>Crataegus pinnatifida</i> (Rosaceae)	KK, PK	–
59	<i>P. scoticella</i> (Stainton, 1850)	<i>Cotoneaster</i> , <i>Cydonia</i> , <i>Dryas octopetala</i> , <i>Malus</i> , <i>Prunus</i> , <i>Sorbus</i> (Rosaceae), <i>Viburnum lantana</i> (Caprifoliaceae)	PK, SO (Sakhalin Isl)	Russia (European part and Siberia), Kazakhstan, Europe
60	<i>P. traugotti</i> Svensson, 1976	<i>Betula</i> (Betulaceae)	KK	Russia (Siberia—Transbaikal region), Europe
LITHOCOLLETINAE Stainton, 1854				
61	<i>Cameraria acericola</i> Kumata, 1963	<i>Acer pictum</i> , <i>A. pseudosieboldianum</i> (Sapindaceae)	PK	Japan
62	<i>C. nipponica</i> Kumata, 1963 †	<i>Acer barbinerve</i> , <i>pseudosieboldianum</i> , <i>A. caudatum</i> subsp. <i>ukurunduense</i> (Sapindaceae)	PK	Japan
63	<i>Chrysaster hagicola</i> (Kumata, 1961) †	<i>Lespedeza bicolor</i> , <i>L. cyrobotrya</i> (Fabaceae)	PK	Japan, Korea
64	<i>Hylcoconis improvisella</i> (Ermolaev, 1986)	<i>Lespedeza bicolor</i> (Fabaceae)	PK	–
65	<i>H. lespedezae</i> Kumata, 1963	<i>Lespedeza bicolor</i> (Fabaceae)	PK	Japan, Korea
66	<i>H. puerariae</i> Kumata, 1963	<i>Amphicarpaea bracteata</i> , <i>A. edgeworthia</i> var. <i>japonica</i> , <i>Pueraria lobata</i> , <i>Falcata japonica</i> , <i>Lespedeza bicolor</i> (Fabaceae)	PK	Japan
67	<i>Phyllonorycter acutissimae</i> (Kumata, 1963)	<i>Quercus</i> , <i>Castanea crenata</i> (Fagaceae)	PK	Japan, Korea
68	<i>Ph. apparella</i> (Herrich-Schäffer, 1855)	<i>Populus</i> , <i>Salix</i> (Salicaceae)	AO, KK	Russia (European part and Siberia), Kazakhstan, Caucasus, Asia Minor, Europe, North America
69	<i>Ph. bicinctella</i> (Matsumura, 1931)	<i>Ulmus</i> (Ulmaceae), <i>Quercus crispula</i> (Fagaceae)	PK	Japan
70	<i>Ph. caraganella</i> (Ermolaev, 1986) †	<i>Caragana fruticosa</i> (Fabaceae)	PK	–
71	<i>Ph. carpini</i> (Kumata, 1963)	<i>Carpinus cordata</i> , <i>C. laxiflora</i> , <i>C. tschonoskii</i> (Betulaceae)	PK	Japan
72	<i>Ph. cavella</i> (Zeller, 1846) †	<i>Betula</i> (Betulaceae), <i>Cerasus</i> , <i>Prunus</i> (Rosaceae), <i>Salix</i> (Salicaceae), <i>Ulmus</i> (Ulmaceae)	AO, KK, PK, SO (Sakhalin Isl)	Russia (European part and Siberia), Japan, Europe
73	<i>Ph. celtidis</i> (Kumata, 1963)	<i>Celtis</i> (Cannabaceae)	SO (Kurul Isl?)	Japan
74	<i>Ph. cretata</i> (Kumata, 1957) †	<i>Quercus mongolica</i> , <i>Q. serrata</i> (Fagaceae)	AO, KK, PK, SO	Japan
75	<i>Ph. dakekanbae</i> (Kumata, 1963)	<i>Betula ermani</i> , <i>B. platyphylla</i> (Betulaceae)	PK, SO (Sakhalin Isl)	Japan

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TABLE S1. (Continued)

№	Species	Host plant	Distribution	
			RFE ¹	elsewhere
76	<i>Ph. ermani</i> (Kumata, 1963) †	<i>Alnus maximowiczii</i> , <i>Betula ermanii</i> , <i>B. platyphylla</i> (Betulaceae)	SO (Sakhalin Isl)	Russia (Siberia), Japan
77	<i>Ph. fruticosella</i> (Kuznetsov, 1979)	<i>Alnus viridis</i> subsp. <i>fruticosa</i> (Betulaceae)	Kuril Isl	Russia (Siberia)
78	<i>Ph. ginnalae</i> (Ermolaev, 1981)	<i>Acer ginnala</i> (Sapindaceae)	PK	Japan
79	<i>Ph. gracilis</i> Noreika, 1994	unknown	KK, PK	–
80	<i>Ph. hancola</i> (Kumata, 1958)	<i>Alnus hirsuta</i> , <i>A. japonica</i> (Betulaceae)	PK	Japan
81	<i>Ph. issikii</i> (Kumata, 1963) †	<i>Tilia</i> (Malvaceae)	KK, PK	Russia (European part and Siberia), Japan, Korea, Europe
82	<i>Ph. japonica</i> (Kumata, 1963) †	<i>Carpinus</i> , <i>Corylus</i> , <i>Ostrya japonica</i> (Betulaceae)	AO, KK, PK	Japan
83	<i>Ph. jezoniella</i> (Matsumura, 1931)	<i>Acer</i> (Sapindaceae)	PK, SO (Kuril Isl)	Japan
84	<i>Ph. jozanae</i> (Kumata, 1957) †	<i>Crataegus</i> (Rosaceae)	KK, PK, SO (Sakhalin Isl)	Japan
85	<i>Ph. junoniella</i> (Zeller, 1846) †	<i>Vaccinium vitis-idaea</i> (Ericaceae)	SO (Sakhalin Isl)	Russia (European part, Siberia), Japan, Europe, North America (Greenland)
86	<i>Ph. kisoensis</i> Kumata et Park, 1978 †	<i>Alnus hirsuta</i> (Betulaceae)	KK, PK, SO (Sakhalin Isl)	Japan
87	<i>Ph. kuznetzovi</i> (Ermolaev, 1982)	<i>Lespedeza bicolor</i> (Fabaceae)	PK	–
88	<i>Ph. laciniatae</i> (Kumata, 1967)	<i>Ulmus</i> (Ulmaceae)	KK, PK, SO	Japan
89	<i>Ph. malicola</i> (Kuznetsov, 1979)	<i>Malus mandshurica</i> (Rosaceae)	PK	–
90	<i>Ph. matsudai</i> (Kumata, 1986)	<i>Quercus mongolica</i> , <i>Q. crispula</i> (Fagaceae)	PK	Japan
91	<i>Ph. melacoronis</i> (Kumata, 1963)	<i>Rhododendron mucronulatum</i> (Ericaceae)	PK	Japan, Korea
92	<i>Ph. mongolicae</i> (Kumata, 1963)	<i>Quercus</i> (Fagaceae)	SO (Kuril Isl)	Japan
93	<i>Ph. nigristella</i> (Kumata, 1957) †	<i>Quercus</i> (Fagaceae)	KK, PK	Japan
94	<i>Ph. nipponicella</i> (Issiki, 1930) †	<i>Quercus acutissima</i> , <i>Q. variabilis</i> , <i>Q. mongolica</i> (Fagaceae)	KK, PK, SO (Kuril Isl)	Japan, Korea
95	<i>Ph. orientalis</i> (Kumata, 1963) †	<i>Acer saccharum</i> (Sapindaceae)	PK, SO (Kuril Isl)	Japan, China
96	<i>Ph. pastorella</i> (Zeller, 1846) †	<i>Salix</i> , <i>Populus</i> (Salicaceae)	AO, KK, PK, SO (Sakhalin Isl)	Russia (European part and Siberia), Japan, Korea, Kazakhstan, Central Asia, Europe
97	<i>Ph. populifoliella</i> (Treitschke, 1833) †	<i>Populus</i> (Salicaceae)	AO, KK	Russia (European part and Siberia), Japan, Korea, Kazakhstan, Central Asia, Caucasus, Europe

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TABLE S1. (Continued)

№	Species	Host plant	Distribution	
			RFE ¹	elsewhere
98	<i>Ph. pseudojezoniella</i> Noreika, 1994 †	<i>Acer saccharum</i> (Sapindaceae)	PK	–
99	<i>Ph. pseudolautella</i> (Kumata, 1963)	<i>Quercus</i> (Fagaceae)	PK, SO (Kuril Isl)	Japan
100	<i>Ph. pterocaryae</i> (Kumata, 1963)	<i>Pterocarya rhoifolia</i> (Juglandaceae)	PK	Japan
101	<i>Ph. pumilae</i> (Ermolaev, 1981)	<i>Ulmus pumila</i> (Ulmaceae)	PK	Russia (Siberia), Japan, China
102	<i>Ph. quinqueguttella</i> (Stainton, 1951)	<i>Salix</i> (Salicaceae)	KK	Russia (European part), Europe
103	<i>Ph. reduncata</i> (Ermolaev, 1986) †	<i>Lonicera edulis</i> , <i>L. maackii</i> , <i>L. praeflorens</i> (Caprifoliaceae)	PK, SO (Kuril Isl)	–
104	<i>Ph. ringoniella</i> (Matsumura 1931) †	<i>Malus</i> , <i>Prunus</i> (Rosaceae)	AO, PK, SO (Sakhalin Isl)	Russia (Siberia), Japan, Korea, China
105	<i>Ph. salicicolella</i> (Sircom, 1848)	<i>Salix</i> (Salicaceae)	AO, KK?, PK, SO	Russia (European part, Siberia), Japan, Europe
106	<i>Ph. salictella</i> (Zeller, 1846) †	<i>Salix</i> (Salicaceae)	AO, KK, PK, SO (Sakhalin Isl?)	Russia (European part, Siberia), Japan, Europe
107	<i>Ph. similis</i> Kumata, 1982 †	<i>Quercus</i> (Fagaceae)	AO, KK, PK	Japan
108	<i>Ph. sorbicola</i> (Kumata, 1963) †	<i>Sorbus</i> , <i>Malus</i> , <i>Prunus</i> , <i>Prunus maackii</i> (Rosaceae)	AO, PK, SO	Russia (Siberia), Japan
109	<i>Ph. strigulatella</i> (Zeller, 1846) †	<i>Alnus</i> (Betulaceae)	KK, PK, SO (Sakhalin Isl)	Russia (European part and Siberia), Japan, Europe
110	<i>Ph. takagii</i> (Kumata, 1963)	<i>Alnus japonica</i> (Betulaceae)	lin Isl)	Europe
111	<i>Ph. uchidai</i> (Kumata, 1963)	<i>Sorbus alnifolia</i> (Rosaceae)	KK, PK	Japan
112	<i>Ph. ulmi</i> (Kumata, 1963)	<i>Ulmus davidiana</i> var. <i>japonica</i> , <i>U. laciniata</i> , <i>Zelkova serrata</i> (Ulmaceae)	PK	Japan
113	<i>Ph. ulmifoliella</i> (Hübner, [1817]) †	<i>Betula</i> (Betulaceae)	PK, SO (Kuril Isl)	Japan, Korea
114	<i>Ph. valentina</i> (Ermolaev, 1981)	<i>Ulmus davidiana</i> var. <i>japonica</i> , <i>U. macrocarpa</i> (Ulmaceae)	AO, KK, PK, SO (Sakhalin Isl, Kuril Isl)	Russia (European part and Siberia), Japan, Kazakhstan, Europe
115	<i>Ph. viciae</i> (Kumata, 1963)	<i>Lathyrus</i> , <i>Vicia</i> (Fabaceae)	PK	–
116	<i>Ph. watanabei</i> (Kumata, 1963)	<i>Pourthiaea villosa</i> (Rosaceae)	KK, PK	Russia (Siberia), Japan
117	<i>Acrocercopinae</i> Kawahara et Ohshima, 2016		KK, PK	Japan
117	<i>Acrocercops amurensis</i> Kuznetzov, 1960	<i>Quercus mongolica</i> (Fagaceae)	AO, KK, PK	Russia (Siberia—Transbaikal region), China
118	<i>A. brongiardiella</i> (Fabricius, 1798)	<i>Quercus</i> , <i>Castanea sativa</i> (Fagaceae)	KK	Russia (Siberia, European part), Caucasus, Kazakhstan, Turkey, Europe

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TABLE S1. (Continued)

№	Species	Host plant	Distribution	
			RFE ¹	elsewhere
119	<i>A. transecta</i> Meyrick, 1931	<i>Carya, Juglans, Pterocarya</i> (Juglandaceae), <i>Lyonia ovalifolia</i> (Ericaceae)	PK	Japan, Korea, China
120	<i>Cryptolectica chrysalis</i> Kumata et Ermolaev, 1988	<i>Quercus mongolica, Q. serrata</i> (Fagaceae)	PK	Japan
121	<i>Eteoryctis deversa</i> (Meyrick, 1922)	<i>Mangifera indica, Rhus, Toxicodendron</i> (Anacardiaceae)	SO (Kuril Isl)	Japan, China, India
122	<i>Leucospilapteryx anaphalidis</i> Kumata, 1965	<i>Anaphalis margaritacea</i> (Asteraceae)	KK, PK, SO (Kuril Isl)	Japan
123	<i>L. omisella</i> (Stainton, 1848)	<i>Artemisia, Dendranthema ornatum</i> (Asteraceae)	KK, PK, SO	Japan, Central Asia, Caucasus, Europe
124	<i>Psydrocercops wisteriae</i> (Kuroko, 1982)	<i>Wisteria floribunda</i> (Fabaceae)	PK	Japan, China
125	<i>Spulerina astaurota</i> (Meyrick, 1922)	<i>Chaenomeles, Malus, Prunus, Pyrus</i> (Rosaceae)	KK, PK	Japan, Korea, China, India
126	<i>S. castaneae</i> Kumata et Kuroko, 1988	<i>Castanea crenata, Quercus</i> (Fagaceae)	PK	Japan, Korea, China,
127	<i>S. corticola</i> Kumata, 1964	<i>Abies sachalinensis, Larix kaempferi, Pinus parviflora</i> var. <i>pentaphylla, Pinus pentaphylla, P. strobus</i> (Pinaceae)	KK, PK	Japan, China
128	<i>S. dissotoma</i> (Meyrick, 1931)	<i>Flemingia lineata, Lespedeza bicolor; L. cyrtobotrya, Pueraria montana, Pueraria montana</i> var. <i>lobata</i> (Fabaceae)	PK	Japan, Korea, China, India
129	<i>Telamoptilia tiliae</i> Kumata et Ermolaev, 1988	<i>Tilia maximowicziana</i> (Malvaceae)	PK	Japan
PHYLLOCNISTINAE Herrich-Schäffer, 1857				
130	<i>Phyllocnistis chloranica</i> Seksjaeva, 1992	<i>Chloranthus japonicus</i> (Chloranthaceae)	PK	Japan, China
131	<i>Ph. cornella</i> Ermolaev, 1987	<i>Cornus controversa</i> (Cornaceae)	SO (Kuril Isl)	Japan
132	<i>Ph. tahyinthella</i> (Bjerkander, 1790)	<i>Populus</i> (Salicaceae)	AO, KK, PK, SO (Sakhalin Isl)	Russia (European part and Siberia), Kazakhstan, Central Asia, Europe
133	<i>Ph. saligna</i> (Zeller, 1839)	<i>Salix</i> (Salicaceae)	KK, PK	Russia (European part and Siberia), Japan, China, Kazakhstan, Central Asia, Caucasus, Israel, Europe, India, Madagascar
134	<i>Ph. unipunctella</i> (Stephens, 1834)	<i>Populus</i> (Salicaceae)	KK, PK	Russia (European part and Siberia), Japan, Kazakhstan, Central Asia, Caucasus, Asia Minor, Europe, Japan
135	<i>Ph. vitella</i> Ermolaev, 1987	<i>Vitis amurensis</i> (Vitaceae)	PK	–