An annotated checklist of gall-forming poplar aphids (Sternorrhyncha: Aphididae, Pemphigini) of the Asian part of Russia

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Here we overviewed the taxonomic diversity and compiled the checklist of gall-forming poplar aphids (Sternorrhyncha: Aphididae, Pemphigini) in the Asian part of Russia. Overall, 20 species, i.e. 18 Pemphigus and two Thecabius spp. were proven to have distribution in this macroregion. Based on our field study, following seven species represented novel geographical records. Among them, Pem. iskanderkuli Narzikulov is new for Asian Russia as per the record in Tuva Republic, and six species, Pem. matsumurai Monzen, Pem. microsetosus Aoki, Pem. plicatus Dolgova, Pem. populi Courchet. protospirae Lichtenstein, Th. latisensorius Hori, are new for some administrative regions of Siberia and/or the Russian Far East. Pemphigus passeki Börner, Pem. spyrothecae Passerini are alien species for the Asian part of Russia. Eight species, Pem. borealis Tullgren, Pem. bursarius (Linnaues), Pem. matsumurai Monzen, Pem. populi Courchet, Pem. passeki Börner, Pem. protospirae Lichtenstein, Pem. spyrothecae Passerini, Th. affinis (Kaltenbach), were documented in the Asian part of Russia as pests of poplars.

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Keywords

Pemphigus, Thecabius, poplars, species diversity, alien species, Siberia, Russian Far East

Introduction

Gall-forming poplar aphids from the genera *Pemphigus* and *Thecabius* (Sternorrhyncha: Aphididae, Pemphigini) are known by their social and complex life style (Stern, Foster 1996; Wool 2005). Some of them have a specialized caste called "soldiers", which protect the colony and clean the galls. The majority of species make galls or pseudogalls on leaves or shoots of trees, where summer generations develop, whereas autumn generations develop on herbaceous plants becoming important agricultural pests in some cases (Dolgova 1969; Zerova et al. 1991; Wool 2005; Holman 2009; Hałaj, Osiadacz 2013).

In the Holarctic, overall 70 species of *Pemphigus* and about 12 species of *Thecabius* are known to feed on *Populus* and herbaceous plants (Blackman, Eastop 2022; Favret 2022). Of them, 27 species have been mentioned for Asian Russia (i.e. Siberia and the Russian Far East) (Mordvilko 1929, 1932; Shaposhnikov 1955; Lyubarskiy 1956; Ivanovskaya 1977; Tomilova 1963, 1977; Pashchenko 1985, 1988; Tokmakov 1987; Yanovskiy 2002, 2003; Florov 2009; Holman 2009; Stekolshchikov, Novgorodova 2015; Blackman, Eastop 2022; Babichev, Kirichenko 2020).

The gall-forming poplar aphids remain poorly studied in the Asian part of Russia. In Siberia, their richness is explored mostly on the south (Kolomiets 1955; Zolotarenko 1959; Tibatina 1963; Tomilova 1963, 1977; Dolgova 1969; Yanovskiy 1996, 2002; Ivanovskaya 1977; Ostanin 1980; Barannik 1981; Tarasova et al. 2004; Stekolshchikov, Novgorodova 2015; Babichev, Kirichenko 2020). Also in the Russian Far East, southern regions are mainly studied (Mordvilko 1929; Kurentsov 1953, 1956; Lyubarskiy 1956; Pashchenko 1985, 1988; Pashchenko, Lobkova 1990). Furthermore, misidentifications, descriptions of the same species by different authors under different names, multiplied errors on local faunas and species distribution in the articles of followers complicate understanding the composition of gall-forming poplar aphids in Asian Russia. Careful overview of existing knowledge and local fauna inventories are important for clarifying the species composition in this part of Asia.

This article revises data on species diversity of *Pemphigus* and *Thecabius* in Asian Russia and provides the checklist of gall-forming poplar aphis for this macroregion.

Materials and methods

The study has been largely based on original field collections of galls and galling aphids done in Siberia in 10 administrative regions: Tyumen Region (in particularly Khanty-Mansi Autonomous Okrug), Omsk Region, Altai Territory, Altai Republic,

Tomsk Region, Kemerovo Region, Khakassia Republic, Krasnovarsk Territory, Tuva Republic,

Irkutsk Region, and in the Russian Far East in two regions: Khabarovsk Territory, Amur Region, in 2005–2022 (Fig. 1). Overall, 54 localities in these regions were visited in Asian Russia (Fig. 1; see Suppl. material 1). To clarify the distribution of *Pem. spyrothecae* on the border of Europe and Asia, the aphids were also collected in Bashkortostan Republic (west of the Urals) (Fig. 1; see Suppl. material 1). Additionally, published records of species in Asian Russia and neighboring regions were summarized (Kurentsov 1953, 1956; Kolomiets 1955; Lyubarskiy 1956; Zolotarenko 1959; Narzikulov 1962; Ivanovskaya-Shubina 1963; Tibatina 1963; Tomilova 1963, 1977; Dolgova 1969; Holman, Szelegiewiez 1972, 1974; Aoki 1975; Ivanovskaya 1977; Ostanin 1980; Barannik 1981; Pashchenko 1985, 1988; Pashchenko, Lobkova1990; Yanovskiy 1996, 2002; Zhang et al. 1999; Gabrid 2005; Barjadze 2010; Ryabinin 2014; Stekolshchikov, Novgorodova 2015; Kadyrbekov 2017; Khusanov et al. 2018; Najmi et al. 2019; Babichev, Kirichenko 2020).

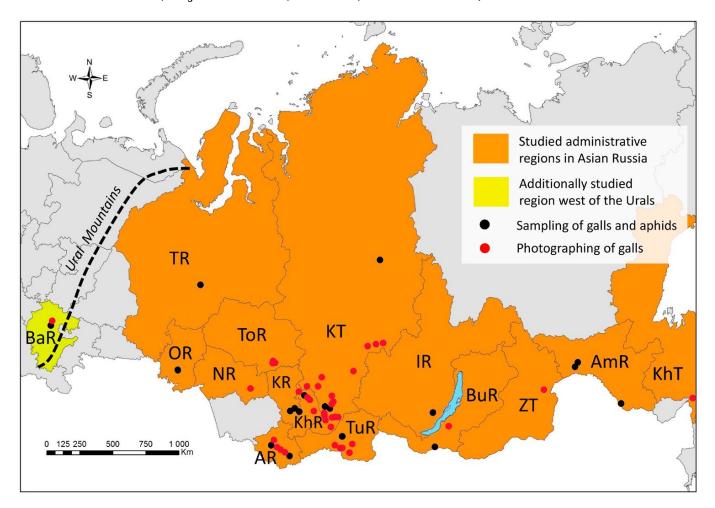


Figure 1. Studied administrative regions in the Asian part of Russia: TR – Tyumen Region, OR – Omsk Region, AR – Altai Republic, TOR – Tomsk Region, NR – Novosibirsk Region, KR – Kemerovo Region, KR – Khakassia Republic, KT – Krasnoyarsk Territory, TUR – TUVA Republic, TVA – Irkutsk Region, TVA – Buryatia Republic, TVA – Zabaikalskiy Territory, TVA – Amur Region, TVA – Khabarovsk Territory. Additionally studied region west of the Urals: TVA – Bashkortostan Republic. Sampled localities are indicated by black and red circles on the map and listed in Suppl. material 1.

The galls and the aphids were sampled in natural stands of poplars (floodplain forests, groves) (Fig. 2) and artificial plantings (forest belts, parks). The galls were placed in plastic zip bags and transported to the laboratory of Forest Zoology SIF SB RAS (Krasnoyarsk). The aphids dissected from the galls were preserved in 70% ethanol solution following Shaposhnikov (1952). The microscopic slides of aphid were prepared using Berlese fluid (Blackman, Eastop 2022). In addition, we studied ethanol-preserved collections, the slides and the photographs of galls from various regions of Asian Russia. Overall, 32 slides (70 specimens of adult winged emigrants, fundatrix and nymphs), 105 original photographs of galls from 54 geographic localities were examined (see Suppl. material 1). All slides and ethanol-preserved specimens are stored in the collection of the

Museum of Forest Ecosystems of the V.N. Sukachev Institute of Forest SB RAS, Krasnoyarsk, Russia (SIF).

The species of aphids were identified by N.S. Babichev and M.K. Dementeva using the key in Blackman, Eastop (2022). Poplars, *Populus nigra* L., *Pop. laurifolia* Ledeb., *Pop.* × *sibirica* Kryl. & Grig. ex Skvort., *Pop. suaveolens* Fisch., were determined using the keys (Lomonosova et al. 1992; Koropachinskiy, Vstovskya 2012). Other poplars, *Pop.alba*L., *Pop.balsamifera* L., *Pop.ciliata* Wall. ex Royle, *Pop. euphratica* Olivier., *Pop. macrocarpa* (Schrenk) N. Pavl. et Lipsch., *Pop. simonii* Carriere., *Pop.tristis* Fisch., *Pop. usbekistanica* Kom., *Pop. yunnanensis* Dode, are listed in our paper as they were mentioned in literature sources (Mordvilko 1929; Kurentsov 1953, 1956; Lyubarskiy 1956; Shaposhnikov 1955; Narzikulov 1962; Aoki 1975; Dolgova 1969; Ivanovskaya 1977; Pashchenko 1988; Buga et al. 2016; Gabrid 2005; Holman 2009; Hałaj, Osiadacz 2013; Baranchikov, Babichev 2015; Kadyrbekov 2017; Babichev, Kirichenko 2020). The taxonomy of *Populus* of gall-forming aphids follows Skvortsov (2010, 2011). Secondary host plants (mostly herbaceous) were not considered in our study, except for *Pem. fuscicornis*, for which primary host is not known.

The checklist of gall-forming poplar aphids of the Asian part of Russia was compiled based on national and international publications, which came out in 1929–2022, and updated with the novel field records collected by our team. The taxonomy of aphids in the checklist follows Favret (2022). In the checklist, the distribution of species in the world is given by macroregions without detalization; for the Asian part of Russia, the distribution is provided by administrative region, following our novel records and published data (Mordvilko 1929; Kurentsov 1953, 1956; Shaposhnikov 1955; Lyubarskiy 1956; Tomilova 1959, 1962, 1963; Holman, Szelegiewiez 1972, 1974; Aoki 1975; Ivanovskaya-Shubina 1963; Ivanovskaya 1977; Ostanin 1980; Barannik 1981; Pashchenko 1988; Pashchenko, Lobkova 1990; Zerova et al. 1991; Zhang et al. 1999; Gabrid 2005; Barjadze 2010; Hałaj, Osiadacz 2013; Ryabinin 2014; Kadyrbekov 2017; Khusanov et al. 2018; Najmi et al. 2019; Babichev, Kirichenko 2020; Blackman, Eastop 2022). According to the same sources and our observations, the aphid species importance (i.e. whether or not some of them are known as pests) is mentioned.

4 / 27

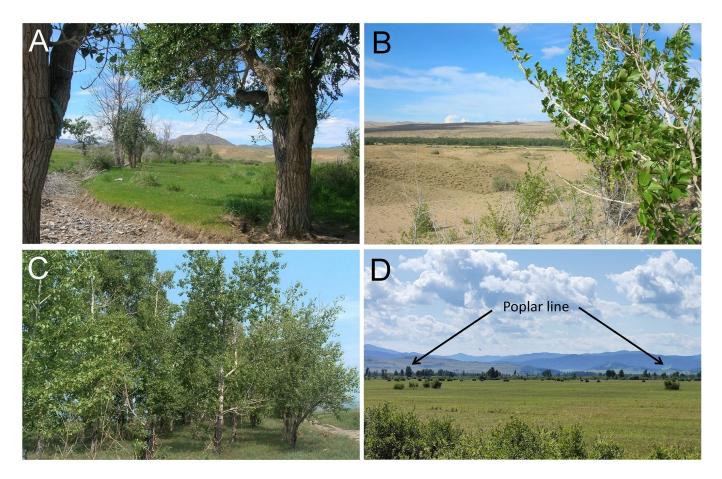


Figure 2. Some studied localities in Siberia. **A** – Tuva Republic, Tandinskiy kozhuun, around village of Kyzyl-Aryg; **B** – ibidem, Erzin kozhuun, Tsugeer-Els; C, D – Khakassia Republic, the surrounding of Beliy Ius River. In all localities, Populus laurifolia was examined. Photos by N.S. Babichev, N.I. Kirichenko.

The following terms and abbreviations were used for development stages and aphid morphs: fundatrix (F) – wingless parthenogenetic female, the founder of the colony; (N) – larva of 4th instar of summer generation; winged migrant (WM) – winged parthenogenetic adult female of summer generation; alatae sexuparae (AS) – winged parthenogenetic adult female of autumnal generation that reproduces sexuales. The gall shape and gall position are indicated as follow: PGWL – pseudogall from a whole leaf; RGLB – rounded galls on the leaf base; RGLS – rolled elongated gall along midrib on lower side of the leaf; RGUS – rolled elongated gall along midrib on upper side of the leaf; SGB – shapeless gall on the leaf base; SGWL – shapeless gall from a whole leaf; SpG – spiral gall on the leaf petiole.

Novel geographical records are indicated by an asterisk: * new for the Asian part of Russia, ** new for administrative region in Siberia or the Russian Far East.

Result

Overall, 20 species, i.e. 18 *Pemphigus* (two species of the subgenus *Pemphiginus* and 16 of the subgenus *Pemphigus*) and two *Thecabius* spp. (by one species of the subgenus *Parathecabius* and *Thecabius*) were proven to have the distribution in the Asian part of Russia. Among them, seven species represented novel geographical records according to our field data collected 2005–2022. *Pemphigus iskanderkuli* is novel for the Asian part of Russia based on the first finding in Tuva Republic in 2016. Six species are new for some administrative regions in Siberia and/or the Russian Far East: *Pemphigus microsetosus* new for Kemerovo Region, *Pem. plicatus* for Altai Republic, *Pem. populi* for Omsk Region, *Pem. protospirae* for Irkutsk Region, *Th. latisensorius* for Khakassia and Tuva Republics, *Pemphigus matsumurai* is new for two administrative regions of Siberia

(Buryatia and Altai Republic) and for Amur Region in the Russian Far East. Two species, *Pemphigus passeki*, *Pem. spyrothecae*, are alien for the Asian part of Russia. According to our observations and early data from literature, eight species can be considered as pests in some parts of the studied macroregion: *Pem. boreali*, *Pem. bursarius*, *Pem. populi*, *Pem. passeki*, *Pem. protospirae*, *Pem. spyrothecae*, *Pem. matsumurai*, and *Th. affinis*.

The checklist of gall-forming poplar aphids of the Asian part of Russia

Aphididae Latreille, 1802

Eriosomatinae Kirkaldy, 1905 (1843)

Pemphigini Herrich-Schaeffer, 1854

Genus Pemphigus Hartig, 1839

Subgenus Pemphiginus Börner, 1930

Pemphigus populi Courchet, 1881

Specimen examined. Omsk Region: 1 WM, Omsk, 03.VII.2020, *Populus* sp., RGLB, slide No. 135 (SIF), S.Yu. Kniazev leg.

Distribution. World: Europe (Hałaj, Osiadacz 2013), Caucasus (Alieva 1980; Barjadze 2010), Asia (Görür et al. 2012; Kadyrbekov 2017; Narzikulov 1962; Zhang et al. 1999). Asian part of Russia: Western Siberia – Omsk Region**, Novosibirsk Region (Ostanin, 1980), Altai Territory (Dolgova 1969), Kemerovo Region (Barannik 1981); Eastern Siberia – Khakassia Republic (Baranchikov, Babichev 2015), Krasnoyarsk Territory (Baranchikov, Babichev 2015), Irkutsk Region (Tomilova 1959).

Primary host plants. Palearctic: *Aigeiros – Pop. nigra* (Dzhibladze 1968; Zerova et al. 1991), *Pop. usbekistanica* (Narzikulov 1962); *Tacamahaca – Pop. laurifolia* (Ivanovskaya 1977), *Pop. macrocarpa* (Yukhnevich 1974). Asian part of Russia: mostly on *Pop. nigra* (Zerova et al. 1991; Babichev, Kirichenko 2020).

Gall. Smooth, light green, rounded (10 mm in diameter) gall on the upper side of the leaf at the base of midrib or in the middle of the leaf (Fig. 3A); the mature gall cracks in several places.

Importance. The species was mentioned as a pest in the Caucasus (Vezirov 1973) and Central Asia (Khusanov et al. 2018). In 2008, it caused premature leaf fall in Krasnoyarsk city, Krasnoyarsk Territory (Babichev, Kirichenko 2020).

Remarks. *Pem. populi* is widely distributed together with *Pop. nigra* (sometimes it switches to other poplars) across the plant range. In Western Siberia, it is widespread and found in floodplain groves of *Pop. nigra* and forest belts up to the River Yenisei. Further east, it is found mainly in cities where it was introduced with plants. It could be found in many localities across Northern and Central Asia.

Pemphigus vesicarius Passerini, 1861

Distribution. World: Europe (Hałaj, Osiadacz 2013), Caucasus (Vezirov 1973; Barjadze 2010), Asia (Narzikulov 1962; Görür et al. 2012; Kadyrbekov 2017; Najmi et al. 2018). Asian part of Russia: Altai Republic (Yukhnevich 1968; Kadyrbekov 2017). Yanovskiy suggested that the species is distributed in Southern Siberia (2003).

6 / 27

Primary host plants. Palearctic: *Aigeiros – Pop. nigra* (Dzhibladze 1968; Zerova et al. 1991; Holman 2009), *Pop. usbekistanica* (Narzikulov 1962); *Tacamahaca–Pop. laurifolia* (Yukhnevich 1974).

Gall. Bumpy, green with a reddish tinge, spherical or shapeless (20–30 mm in diameter) gall on the shoot; the gall base merges with the shoot. The mature gall opens with several holes; the gall lignifies together with the shoot therefore it stays on the shoot the year around (Narzikulov 1962).

Importance. In some years of 2008–2018 in southwest of Central Asia, *Pem. vesicarius* was regularly documented on poplars *Aigeiros* (2–3 galls per a branch on trees) causing deformation of shoots (Khusanov et al. 2018). No data are known from the Asian part of Russia.

Remarks. The species range occupies Western and Central Palearctic. In Central Asia, it is found on floodplain vegetation in plains and mountain-floodplain forests (Yukhnevich 1968; Kadyrbekov 2017). In the Asian part of Russia, it was once mentioned for Southern Siberia (Yanovskiy 2003), but not confirmed by field sampling, and for the regions of Russia bordering with Kazakhstan (i.e. South-Western Altai) (Yukhnevich 1968; Kadyrbekov 2017). Presumably, it can penetrate deep into the steppe zone of Kurgan, Omsk and Novosibirsk Regions, Altai Territory and Altai Republic. The occurrence of the species and its potential distribution in Siberia would need further exploration.

Subgenus Pemphigus Hartig, 1839

Pemphigus birimatus Ivanovskaya, 1973

Distribution. World: East and South-East of Kazakhstan (Kadyrbekov 2017). Asian part of Russia: Western Siberia – Omsk Region (Ivanovskaya 1973, 1977), Altai Republic (Ivanovskaya 1973, 1977; Stekolshchikov, Novgorodova 2015); Eastern Siberia – Tuva Republic (Babichev, Kirichenko 2020).

Primary host plants. Palearctic: *Tacamahaca – Pop. laurifolia* (Ivanovskaya 1973, 1977), *Pop. macrocarpa* (Kadyrbekov 2017). Asian part of Russia: *Pop. laurifo-lia* (Ivanovskaya 1973, 1977; Babichev, Kirichenko 2020).

Gall. Rough, greenish gall of a cone shape with a red streaks on the surface; situated on the petiole at the base of the leaf, with two slits on the top (Ivanovskaya 1973, 1977).

Importance. Not studied.

Remarks. It was described from the mountainous steppe regions of Altai Republic and later found in floodplains of the Omsk Region (Ivanovskaya 1973, 1977); later documented on the north of Pavlodar Region (northern Kazakhstan), the southeast of the Almaty Region of Kazakhstan (Kadyrbekov 2017).

The morphology of WM and the structure and color of galls of *Pem. birimatus* are indistinguishable from *Pemphigusis kanderkuli* Narzikulov, 1957. Furthermore, these two species develop on the same hosts, *Pop. laurifolia*. Further study, including the involvement of molecular genetics, would be needed to understand whether or not *Pem. birimatus* could be synonymized with *Pem. iskanderkuli*.

Pemphigus borealis Tullgren, 1909

Fig. 3B

Distribution. World: Europe (Hałaj, Osiadacz 2013), Caucasus (Barjadze 2010), Asia (Аокі 1975; Zhang et al. 1999; Kadyrbekov 2017; Najmi et al. 2018). Asian part of Russia: Western Siberia – Novosibirsk Region (Ivanovskaya 1977; Ostanin 1980), Altai Territory (Ivanovskaya 1977),

Kemerovo Region (Ivanovskaya 1977; Barannik 1981), Tomsk Region (Ivanovskaya-Shubina 1963); Eastern Siberia – Khakassia Republic (Babichev, Kirichenko 2020), Krasnoyarsk Territory (Babichev, Kirichenko 2020), Irkutsk Region (Tomilova 1977), Buryatia Republic (Tomilova 1977); Russian Far East – Kamchatka Territory (Pashchenko 1988), Khabarovsk Territory (Lyubarskiy 1956; Pashchenko 1988), Primorsky Territory (Pashchenko 1988), Sakhalin Region (Pashchenko 1988). Probably, Magadan Region (Collections of ... 2022).

Primary host plants. Palearctic: Aigeiros – Pop. nigra (Kadyrbekov 2017); Tacamahaca–Pop. laurifolia (Shaposhnikov 1955), Pop. macrocarpa (Kadyrbekov 2017), Pop. simonii (Zhang et al. 1999), Pop. suaveolens (Aoki 1975; Pashchenko 1988), Pop. tristis (Buga et al. 2016), Pop. yunnanensis (Zhang et al. 1999). Asian part of Russia: Pop. laurifolia (Dolgova 1969; Babichev, Kirichenko 2020), Pop. suaveolens (Shaposhnikov 1955; Pashchenko 1988). It also develops on poplar hybrids (Babichev, Kirichenko 2020).

Gall. Smooth, green, often with light or reddish streaks on the surface, spherical (20–25 mm in diameter) or slightly elongated shoot gall with a slit at the top (Fig. 3B). The gall base merges with the shoot without forming a noticeable transition; the gall lignifies together with the shoot therefore it stays on the shoot several years.

Importance. Included in the list of invasive insects of the European part of Russia (Maslyakov, Izhevskiy 2011). It caused noticeable damage to poplars in the Russian Far East on the south of Primorsky Territory in 1950s (Lyubarskiy 1956). According to our observations, in Siberia it can deform shoots of poplars, but it does not cause pronounced damage.

Remarks. One of the most common Palearctic species of *Pemphigus* associated with various poplar species. In north of taiga zone, the species is found in urban areas following the introduction of its hosts.

Pemphigus bursarius (Linnaeus, 1758)

Fig. 3C

Specimen examined. Krasnoyarsk Territory: 2 WM, Evenkijskiy distr., Tura, street planting; 27.VII.2020; *Pop. sibirica*, tubular gall on the petiole, slide No. 139 (SIF), N.S. Babichev leg.

Distribution. World: Northern Africa (Holman, 2009), Europe (Hałaj, Osiadacz 2013), Caucasus (Alieva 1980; Barjadze 2010), Asia (Narzikulov 1962; Holman, Szelegiewicz 1972; Zhang et al. 1999; Görür et al. 2012; Kadyrbekov 2017; Najmi et al. 2018). Native to Eurasia, invasive elsewhere in Canada (Floate 2010) and the Southern Hemisphere (Holman, 2009). Asian part of Russia: Western Siberia

Primary host plants. Palearctic: Aigeiros - Pop. nigra (Dzhibladze 1968; Zerova et al. 1991; Holman 2009), Pop. usbekistanica (Kadyrbekov 2017); Tacamahaca-Pop. balsamifera (Kurentsov 1953), Pop. ciliata (Chakrabarti 2001), Pop. laurifolia (Holman, Szelegiewiez 1972; Yukhnevich 1974; Buga et al. 2016), Pop. macrocarpa (Yukhnevich 1974; Kadyrbekov 2017), Pop. simonii (Zhang et al. 1999), Pop. suaveolens (Tomilova 1959), Pop. tristis (Buga et al. 2016). Asian part of Russia: Pop. balsamifera (Kurentsov 1953), Pop. nigra (Dolgova 1969; Ostanin 1980; Babichev, Kirichenko 2020), Pop. laurifolia (Babichev, Kirichenko 2020). Found on poplar intersectional hybrids (Holman 2009).

Gall. Smooth, from green to red in color, often with light streaks, bulbous or tubular-like (10–20 mm in length) gall with a slit on the top (Fig. 3C). The gall is situated on the petiole of the leaf.

Importance. The pest of poplars and agricultural crops, *Daucus* (Apiaceae), *Cichorium*, *Lactuca* (Asteraceae), in Caucasus (Vezirov 1973) and Central Asia (Khusanov et al. 2018), a vector

of viral diseases of lettuce in Europe (Hałaj, Osiadacz 2013). A pest of black poplar in European part of Russia (Shaposhnikov 1955; Superfamily of true aphids... 1987; Petrov 2019). In Siberia, it was mentioned as pest of poplars in Khakassia Republic in 1950s (Kolomiets 1955) and regularly recorded on poplars in Altai Territory in 1960s (Dolgova 1969). Also indicated as a pest in the Russian Far East in Primorsky Territory in 1950s but without providing exact data (Kurentsov 1953).

Remarks. The aphid is associated with both *Pop. nigra* (considered the main host plant in Europe and Western Siberia) and *Pop. laurifolia* (Eastern Siberia and Mongolia). Geographical populations of the aphid are differentiated based on their trophic relations (Shaposhnikov 1955; Narzikulov 1962; Dolgova 1969; Babichev, Kirichenko 2020).

Pemphigus dorocola Matsumura, 1917

Distribution. World: Asia (Aoki 1975; Zhang et al. 1999; Chakrabarti 1998). Asian part of Russia: Far East - Kamchatka Territory (Pashchenko 1988), Amur Region (Pashchenko 1988), Primorsky Territory (Pashchenko 1988), Sakhalin Region (Pashchenko 1988).

Primary host plants. Palearctic: *Tacamahaca - Pop. ciliata* (Chakrabarti 1998), *Pop. simonii* (Zhang et al. 1999), *Pop. suaveolens* (Aoki 1975; Pashchenko 1988). Asian part of Russia: *Pop. suaveolens* (Pashchenko 1988).

Gall. Green (but later turns red), rounded gall on the shoot, with a slit on the top; lignified together with the shoot (Aoki 1975).

Importance. Not studied.

Remarks. Some researchers consider *Pem. dorocola* to be synonymous with *Pem. borealis* (Aoki 1975; Hałaj, Osiadacz 2013; Blackman, Eastop 2022).

Pemphigus fuscicornis (Koch, 1857)

Distribution. World: Europe (Hałaj, Osiadacz 2013), Caucasus (Barjadze 2010), Central Asia (Kadyrbekov 2017). Asian part of Russia: Western Siberia – Altai Territory (Frolov 2009), Kurgan Region (Ryabinin 2014).

Host plants. As an exceptional species within *Pemphigus*, it develops exclusively on herbaceous plants, mainly on the representatives of Umbelliferae, and others (Amaranthaceae, Chenopodiaceae, Plantaginaceae, Polygonaceae, Solanaceae) (Holman 2009). In the experiments, it did not show the ability to make galls on poplars (Slovokhotova 1977; Berim 2021).

Gall. Does not make galls.

Importance. *Pem. fuscicornis* is a serious pest of root crops (especially harmful to sugar beet) and a vector of viruses causing plant diseases in European countries (Superfamily of true aphids... 1987; Hałaj, Osiadacz 2013). It causes withering of leaves, dying and rotting of root crops resulting in decrease of root crop weight and sugar content, at worse leading to root death; it also affects quality of beet seeds (Golikov 1969; Frolov 2009).

Remarks. *Pem. fuscicornis* develops exclusively on herbaceous plants. The species is distributed in Central Asia mainly in the areas of sugar beet cultivation (Superfamily of true aphids... 1987; Frolov 2009; Berim 2021). The species range, especially in the east, is poorly studied. In Europe, the species seems to expand its range northwards (Berim 2021). The occurrence of *Pem. fuscicornis* in Siberia needs further study as it could be an alien species.

9 / 27

Pemphigus immunis Buckton, 1896

Distribution. World: Africa (Holman, 2009), Europe (Hałaj, Osiadacz 2013), Caucasus (Vezirov 1973; Barjadze 2010), Asia (Narzikulov 1962; Chosh 1984; Zhang et al. 1999; Görür et al. 2012; Kadyrbekov 2017; Najmi et al. 2018). Asian part of Russia: Western Siberia - Kurgan Region (Ryabinin 2014), Kemerovo Region (Ivanovskaya 1977), Altai Territory (Ivanovskaya 1977).

Primary host plants. Palearctic: *Aigeiros - Pop. nigra* (Narzikulov 1962; Zerova et al. 1991; Zhang et al. 1999; Buga et al. 2016); Leuce - *Pop.alba* (Holman 2009); *Tacamahaca-Pop. ciliata* (Chakrabarti 1998), *Pop. laurifolia* (Kadyrbekov 2017), *Pop. macrocarpa* (Zhang et al. 1999), *Pop. simonii* (Zhang et al. 1999); Turanga - *Pop. euphratica* (Zhang et al. 1999). Asian part of Russia: *Pop. nigra* (Ryabinin 2014). The species also develops on poplar hybrids (Narzikulov 1962; Holman 2009).

Gall. Rough, greenish-brown or red, rounded (often arched, 25–40 mm in diameter) gall, with a slit on the top; the gall is situated on the shoot next to the base of the leaf petiole (Narzikuliv 1962; Blackman, Eastop 2022).

Importance. In some years of 2008–2018 in southwest of Central Asia, *Pem. immunis* was documented on poplars *Aigeiros* in a high density (up to 17 galls per a branch on trees) causing deformation of shoots (Khusanov et al. 2018). No data are known from the Asian part of Russia.

Remarks. The aphid inhibits arid areas and mountain-floodplain forests, occasionally penetrates semi-deserts (Narzikulov 1962; Kadyrbekov 2017). The species is rather rare in Western Siberia and it is unclear whether it is native to Siberia. We believe that the northern limit of the species range in Asia runs along the border of southern Siberia with Kazakhstan.

Pemphigus iskanderkuli Narzikulov, 1957

Fig. 3D

Specimen examined. Tuva Republic: 2 WM, Kyzyl, an island on Kaa-Khem River, 12.VII.2016, *Pop. laurifolia*, SGB, slide No. 103 (SIF), N.S. Babichev leg.; ibidem: 1 WM, 1 N, Kyzyl, bank of the Yenisei River, 03.VII.2020, *Pop. laurifolia*, SGB, slide No. 136 (SIF), S.V. Kuzhuget leg.

Distribution. World: Central Asia (Narzikulov 1962; Gabrid 2005). Asian part of Russia* as per the first record in Tuva Republic. The northernmost location is Kyzyl (Tuva Republic).

Primary host plants. Palearctic: *Tacamahaca – Pop. laurifolia* (Gabrid 1989, 2005), *Pop. macrocarpa* (Narzikulov 1957, 1962). Asian part of Russia: *Pop. laurifolia* (present study). In Tuva Republic, the aphid make galls exclusively on young shoots of *Pop. laurifolia* (present study).

Gall. Smooth, green with a reddish shade, shapeless (15-40 mm in diameter) gall on the upper side of the leaf at the base of the mainrib, due to the gall the petiole is shortened (Fig. 3D); mature gall opens with several longitudinal slits; lignified together with the shoot and stays on it the year around.

Importance. Not studied.

Remarks. It is common on the border of floodplain vegetation and arid habitats. *Pem. iskanderkuli* could be a junior synonym of *Pemphigus napaeus* Buckton, 1896 (Gabrid 2005; Blackman, Eastop 2022). Furthermore, we suspect that *Pemphigus birimatus* Ivanovskaja, 1973 described from Western Siberia (Ivanovskaya 1973) could be a junior synonym of *Pemphigus iskanderkuli* Narzikulov, 1957 based on adult morphology and correspondence of morphology of gall specimens collected in Tuva to the describtion in literature (Narzikulov 1957, 1962;

Ivanovskaya 1973; Gabrid 1989, 2005).

Pemphigus laurifoliae Dolgova, 1973

Fig. 4A

Specimen examined. Tuva Republic: 2 WM, Kyzyl distr., along Kaa-Khem River, 20.VI.2020, *Pop. laurifolia*, RGLB, slide No. 134 (SIF), S.V. Kuzhuget leg.

Distribution. World: Asia (Holman, Szelegiewicz 1972; Kadyrbekov 2017). Asian part of Russia: Western Siberia – Novosibirsk Region (Ostanin 1980), Altai Territory (Dolgova 1969), Altai Republic (Dolgova 1969; Stekolshchikov, Novgorodova 2015); Eastern Siberia – Khakassia Republic (Babichev, Kirichenko 2020), Krasnoyarsk Territory (Yanovskiy 1996; Babichev, Kirichenko 2020), Tuva Republic (Babichev, Kirichenko 2020), Buryatia Republic (Babichev, Kirichenko 2020), Yakutia Republic (Novikov 1988; Babichev, Kirichenko 2020).

Primary host plants. Palearctic: *Tacamahaca-Pop. laurifolia* (Holman, Szelegiewiez 1972; Kadyrbekov 2017), *Pop. macrocarpa* (Kadyrbekov 2017). Asian part of Russia: *Pop. laurifolia* (Babichev, Kirichenko 2020). Kadyrbekov (2017) suggest that the species develops exclusively on poplars, which differs from the original species description, where herbaceous plants were listed as secondary hosts (Dolgova 1973).

Gall. Green with a red shade, wrinkled, rounded (10 mm in diameter) gall on the upper side of the leaf at the base of the mainrib; the gall opens with a slit on the lower side of the leaf next to the petiole (Fig. 4A).

Importance. The aphid was never reported as a pest in literature. Neither had we observed it at a high population density in Siberia.

11 / 27

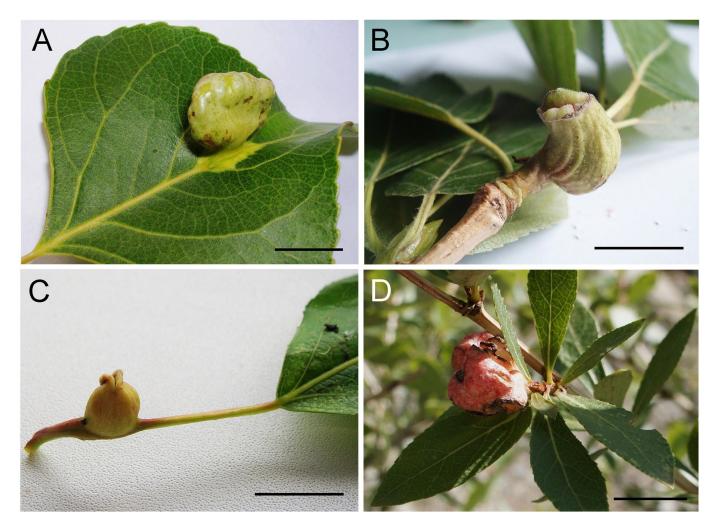


Figure 3. Galls of poplar-feeding aphids in the Asian part of Russia (beginning). $\bf A$ – the gall of Pemphigus populi on the upper side of the leaf of Populus nigra; $\bf B$ – Pem. borealis on the shoot of Pop. laurifolia; $\bf C$ – Pem. bursarius on leaf petiole of Pop. laurifolia; $\bf D$ – Pem. iskanderkuli on the leaf base of Pop. laurifolia; Localies: $\bf A$, $\bf C$ – Khakassia Republic, Shirinskiy district, near Chjernoe Ozero village, poplar line along the road; $\bf B$ – Amur Region, Blagoveshchensk, downtown, street planting; $\bf D$ – Tuva Republic, Erzin kozhuun, river Aryskannyg–Khem. Scale = 20 mm (A–C), 40 mm (D). Photos by N.S. Babichev, N.I. Kirichenko.

Pemphigus matsumurai Monzen, 1927

Fig. 4B-D

Specimen examined. Altai Republic: 4 WM, Ongudai distr., Ongudai village, floodland of Ursul River, 15.VIII.2019, *Pop. laurifolia*, RGLB, slide No. 120 (SIF), N.S. Babichev leg.; Tuva Republic: 4 WM, Kyzyl distr., along Kaa-Khem River; 06.VI.2020, *Pop. laurifolia*, RGLB, slides Nos 141/1-2 (SIF), S.V. Kuzhuget leg.; Buryatia Republic: 8 WM, Dzhidinskiy distr., Borgoiskiy Nature Reserve, Dzhida River, neighborhood of Baian town, 05.VII.2016, *Pop. suavelens*, in gall, slide No. BZ.143 (St. PSU) M.K. Dementeva leg.; Amur Region: 4 WM, Skovorodino distr., Skovorodino, 26.06.2016, *Populus* sp., RGLB, slide No. 114 (SIF), N.I. Kirichenko leg.; ibidem: 2 WM, Blagoveshchensk, street planting, 21.VI.2021, *Populus* sp., RGLB, slide No. 145 (SIF), S. Kniga leg.; ibidem: 2 WM, Tyndinskiy distr., Solovyovsk village, 14-15. VII.2021, *Pop. suaveolens*, RGLB, slide slide No. 150 (SIF), S. Kniga leg.

Distribution. World: Asia (Narzikulov 1962; Holman, Szelegiewiez 1972; Aoki 1975; Chakrabarti 1998; Zhang et al. 1999; Kadyrbekov 2017). Asian part of Russia: Western Siberia – Novosibirsk Region (Ostanin 1980), Altai Territory (Dolgova 1969), Altai Republic**, Kemerovo Region (Barannik 1981); Eastern Siberia – Khakassia Republic (Babichev, Kirichenko 2020), Krasnoyarsk

Territory (Babichev, Kirichenko 2020), Tuva Republic (Babichev, Kirichenko 2020), Irkutsk Region (Tomilova 1977), Buryatia Republic**, Zabaikalskiy Territory (Babichev, Kirichenko 2020); Russian Far East – Amur Region**, Khabarovsk Territory (Pashchenko 1988), Primorskiy Territory (Pashchenko 1988). Based on photos of galls we received, the species may have a distribution in Tomsk Region, which could be a novel record for this region, but further field samplings would be needed to confirm it.

Primary host plants. Palearctic: Aigeiros – Pop. nigra (Zhang et al. 1999), Pop. usbekistanica (Narzikulov 1962); Tacamahaca – Pop. ciliata (Chakrabarti 1998), Pop. laurifolia (Holman, Szelegiewiez 1972; Ivanovskaya 1977), Pop. macrocarpa (Kadyrbekov 2017), Pop. simonii (Zhang et al. 1999), Pop. suaveolens (Aoki 1975; Pashchenko 1988), Pop. yunnanensis (Zhang et al. 1999). Asian part of Russia: Pop. laurifolia (Ivanovskaya 1977; Babichev, Kirichenko 2020), Pop. nigra (Ostanin 1980), Pop. suaveolens (Tomilova 1977; Pashchenko 1988).

Gall. Smooth, light green, rounded (15-25 mm in diameter) gall on the upper side of the leaf at the base of the mainrib (Fig. 4B, C); mature gall cracks with many holes.

Importance. In Khakassia Republic, *Pem. matsumurai* was recorded in mass on *Pop. laurifolia* along Belyi Iyus River in 2011–2016; similarly, high density of galls was noted on the same poplar species in Altai Republic in Ongudai district along Ursul River in 2019 and in Krasnoyarsk Territory in the southern regions in 2016–2022 (Babichev: personal observation).

Remarks. *Pem. matsumurai* inhibits wide range of natural zones: from taiga to semi-deserts but most often it is found in forest-steppe and in intrazonal vegetation (Ivanovskaya 1977; Tomilova 1977; Barannik 1981; Kadyrbekov 2017; Babichev, Kirichenko 2020, present study).

Pemphigus microsetosus Aoki, 1975

Fig. 5A

Specimen examined. Kemerovo Region: 2 WM, Mezhdurechensk distr., Mezhdurechensk and Teba village, street planting, 29-30.07.2013, *Pop. laurifolia*, SGWL, slide No. 125 (SIF), N.S. Babichev leg.; Krasnoyarsk Territory: 2 WM, Kuragino distr., Tuba River, Ust-Shush Village, 08.VII.2021, *Pop. laurifolia*, slide No. 148 (SIF), SGWL, N.S. Babichev leg.

Distribution. World: Eastern Asia (Aoki 1975). Asian part of Russia: Western Siberia – Altai Republic (Stekolshchikov, Novgorodova 2015), Kemerovo Region**; Eastern Siberia – Khakassia Republic (Babichev, Kirichenko 2020), south of Krasnoyarsk Territory (Babichev, Kirichenko 2020); Russian Far East – Primorskiy Territory (Pashchenko 1988).

Primary host plants. In the Asian part of Russia and Japan, it develops exclusively on poplars of the section *Tacamahaca*: *Pop. laurifolia* (Babichev, Kirichenko 2020), *Pop. suaveolens* (Aoki 1975; Pashchenko 1988).

Gall. Smooth, green, bag- or teardrop-shaped (30–50 mm in length) gall, made from the entire leaf, attached to a shortened petiole (Fig. 5A); mature gall cracks with many holes on the surface. The gall lignifies with the shoot and stays on it the year around.

Importance. No data are known.

Remarks. According to our observations in southern Siberia, it avoids arid habitats, often found along the banks of rivers and lakes. We believe that *Pem. microsetosus* is an alien species in Western Siberia (Babichev, Kirichenko 2020).

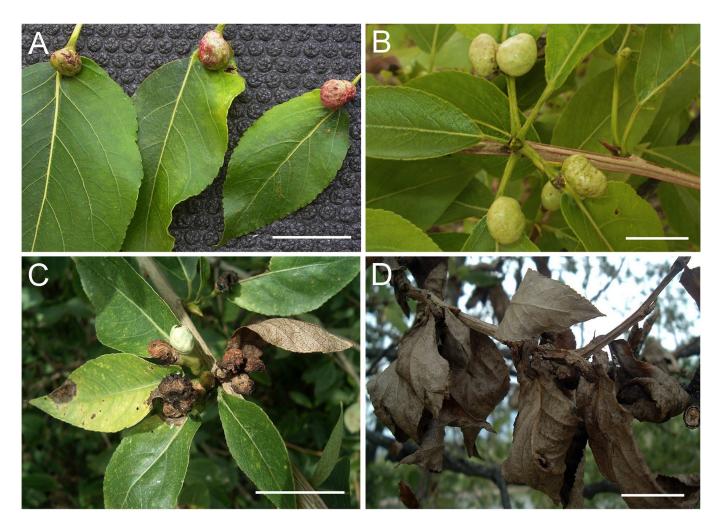


Figure 4. Galls of poplar-feeding aphids in the Asian part of Russia (continuation). $\bf A$ – the gall of Pemphigus laurifoliae on the leaf base of Populus laurifolia; $\bf B-C$ – Pem. matsumurai on the leaf base of Pop. laurifolia resulting in drying shoots and leaves ($\bf D$). Localies: $\bf A$ – Tuva Republic, Erzin kozhuun, sands Zugeer-Els; $\bf B$ – Krasnoyarsk Territory, Ermakovskiy district, near Verkhneusinskoye village; $\bf C$, $\bf D$ – Khakassia Republic, Shirinskiy district, near Chjernoe Ozero village. Scale = 40 mm ($\bf A$, $\bf C$), 20 mm ($\bf B$, $\bf D$). Photos by N.S. Babichev, N.I. Kirichenko.

Pemphigus mongolicus Holman et Szelegiewicz, 1974

Specimen examined. Altai Republic: 3 AS, Kosh-Agach distr., floodplain of Chuya River, Chagan-Uzun village, 17.VII.2012, Pop. laurifolia, SGB, slide No. 140/1 (SIF), N.I. Kirichenko leg.

Distribution. World: Central Asia (Holman, Szelegiewicz 1972). Asian part of Russia: Western Siberia – Altai Republic (Stekolshchikov, Novgorodova 2015); Eastern Siberia – Irkutsk Region (Tomilova 1959, 1962); Russian Far East – Primorskiy Territory (Shaposhnikov 1955).

Primary hostplants. In the Asian part of Russian and Mongolia, it develops on poplars of *Tacamahaca* section: *Pop. laurifolia* (Holman, Szelegiewiez 1974). The aphid develops exclusively on poplars, thus, has no secondary hosts (Holman, Szelegiewiez 1974; Blackman, Eastop 2022).

Gall. Smooth, green shapless (20–30 mm in length) gall which later turns red; situated on the base of the leaf; mature gall cracks with many holes on its surface (Holman, Szelegiewicz 1974).

Importance. No data are known.

Remarks. Blackman & Eastup (2022) suggest that records of *Pemphigus semenovi* Mordvilko ex Shaposhnikov, 1955 on *Pop. suaveolens* in Siberia and the Russian Far East (Shaposhnikov 1955;

Tomilova 1959, 1962) may refer to *Pemphigus mongolicus* Holman et Szelegiewicz, 1974. Due to the limited distribution, low abundance and presence only in certain biomes, the species would need additional study.

Pemphigus passeki Börner, 1952

Fig. 5B

Specimen examined. Krasnoyarsk Territory: 2 WM, Karatuzskiy distr., Amyl River, Kachulka village, 06.VII.2021, *Pop. nigra*, RGUS, slide No. 146 (SIF), N.S. Babichev leg.

Distribution. World: Europe (Hałaj, Osiadacz 2013). Asian part of Russia: Western Siberia – Novosibirsk Region (Ostanin 1980; Babichev, Kirichenko 2020), Kemerovo Region (Barannik 1981; Babichev, Kirichenko 2020), Altai Territory (Dolgova, 1969; Babichev, Kirichenko 2020); Eastern Siberia – Khakassia Republic (Babichev, Kirichenko 2020), south of Krasnoyarsk Territory (Babichev, Kirichenko 2020). The species range expansion to the north of the forest-steppe of Krasnoyarsk Territory was noted (Babichev, Baranchikov 2012).

Primary host plants. Across its present range, the aphid develops exclusively on *Pop. nigra* (*Aigeiros*) (Buga et al. 2016; Najmi et al. 2019; Babichev, Kirichenko 2020; Blackman, Eastop 2022).

Gall. Smooth, most often red, rolled elongated (15–30 mm in length) gall on the upper side of the leaf along the mainrib; on the lower side, it opens with a longitudinal slit (Fig. 5B).

Importance. Ornamental pest of *Pop. nigra* causing early fall of leaves in Khakassia Republic (Babichev, Kirichenko 2020).

Remarks. In the Asian part of Russia, *Pem. passeki* was initially misidentified as *Pemphigus phenax* Börner et Blunck, 1916, which is similar in ecological and morphological features (Dolgova 1969; Ivanovskaja 1977). This mistake was discovered later, when the distribution of *Pem. passeki* in Siberia was revised (Babichev, Baranchikov 2012; Babichev, Kirichenko 2020; Blackman, Eastop 2022). Thus, early records of *Pem. phenax* in Western Siberia, i.e. Kurgan Region (Ryabinin 2014), Novosibirsk Region (Ostanin 1980), Kemerovo Region (Barannik 1981), Altai Territory (Dolgova 1969) corresponded to *Pem. passeki. Pem. phenax* was indicated for Kazakhstan (Smailova 1980), but not confirmed by field samplings (Kadyrbekov 2017). We suggested that *Pem. passeki* was introduced to Siberia with planting material (Babichev, Baranchikov 2012; Babichev, Kirichenko 2020), thus, it and can be considered an alien species in Siberia.

Pemphigus plicatus Dolgova, 1973

Fig. 5C

Specimen examined. Altai Republic: 2 WM, Kosh-Agach distr., bank of Chuya River, Chagan-Uzun village; *Pop. laurifolia*, 17.VII.2012, RGLS, slide No. 64 (SIF), N.I. Kirichenko leg.; ibidem: 4 WM, Ongudai distr., Ongudai village, bank of Ursul River, *Pop. laurifolia*, 15.VIII.2019, RGLS, slide No. 121 (SIF), N.S. Babichev leg.; Khakassia Republic: 2 WM, Askiz distr., Balyksa village, *Pop. laurifolia*, 02.VIII.2013, RGLS, slide No. 127 (SIF), N.S. Babichev leg.

Distribution. World: Central Asia (Kadyrbekov 2017). Asian part of Russia: Western Siberia – Novosibirsk Region (Ostanin 1980), Altai Territory (Dolgova 1969, 1973), Altai Republic**, Kemerovo Region (Barannik 1981); Eastern Siberia – Khakassia Republic (Babichev 2011; Babichev, Kirichenko 2020), south of Krasnoyarsk Territory (Babichev, Kirichenko 2020).

Primary host plants. Palearctic: *Tacamahaca - Pop. laurifolia* (Kadyrbekov 2017). Asian part of Russia: *Pop. laurifolia* (Dolgova 1969, 1973; Babichev, Kirichenko 2020). The ability of the species

to develop on *Pop. nigra* (Dolgova, Ivanovskaya 1973; Kadyrbekov 2017) and *Pop. macrocarpa* (Kadyrbekov 2017) needs confirmation.

Gall. Yellowish, rolled, elongated (10-15 mm in length) smooth gall on the underside of the leaf along the mainrib; on the upper side it opens with a longitudinal slit (Fig. 5C).

Importance. No data are known.

Remarks. In the Asian part of Russia, it is found on poplars growing next to the rivers, in foothills and intermountain basins in forest-steppe, steppe and semi-desert zones. Biology and life cycle have been studied in Altai Territory and Khakassia Republic (Dolgova 1969; Babichev 2011). So far, the species has been rarely documented in Asia (Ivanovskaya 1973; Kadyrbekov 2017); its distribution and abundance would need further study.

Pemphigus populinigrae (Schrank, 1801)

Fig. 5D

Specimen examined. Tyumen Region, Khanty-Mansi Autonomous Okrug: 1 WM, 1 N, Surgut, 30.VI.2017; *Pop. nigra*, slide No. 116 (SIF), N.I. Kirichenko leg.; Omsk Region: 1 F, 1 WM, Omsk, 07.VII.2020, *Pop. nigra*, RGUS, slide No. 138 (SIF), S.Yu. Kniazev leg.; Irkutsk Region: 2 WM; Bayanday distr., near Bayanday village, 27.VII.2021, *Pop. nigra*, RGUS, slide No. 523 (St.PSU), M.K. Dementeva leg.

Distribution. World: Northren Africa (Holman 2009), Europe (Hałaj, Osiadacz 2013), Caucasus (Alieva 1980; Barjadze 2010), Asia (Narzikulov 1962; Zhang et al. 1999; Görür et al. 2012; Kadyrbekov 2017; Najmi et al. 2018). Asian part of Russia: Western Siberia – Kurgan Region (Ryabinin 2014), Tyumen Region (Tibatina 1963), Omsk Region**, Novosibirsk Region (Ostanin 1980), Tomsk Region (Ivanovskaya- Shubina 1963), Altai Territory (Dolgova 1969), Kemerovo Region (Barannik 1981); Eastern Siberia – Khakassia Republic (Babichev, Kirichenko 2020), Krasnoyarsk Territory (Babichev, Kirichenko 2020), Irkutsk Region (Tomilova 1959, 1962), Zabaikalskiy Territory (Tomilova 1963); Russian Far East – Khabarovsk Territory (Pashchenko 1988), Primorsky Territory (Pashchenko 1988).

Primary host plants. Palearctic: Aigeiros - Pop. nigra (Dzhibladze 1968; Zerova et al., 1991; Zhang et al. 1999; Buga et al., 2016), Pop. usbekistanica (Narzikulov 1962); Tacamahaca - Pop. macrocarpa (Zhang et al. 1999; Kadyrbekov 2017), Pop. suaveolens (Tomilova 1959; Narzikulov 1962). Asian part of Russia (Siberia): Pop. nigra (Babichev, Kirichenko 2020), Pop. suaveolens (Tomilova 1959). It also develops on intersection hybrids of poplars (Aigeiros×Tacamahaca). In the Russian Far East, it feeds exclusively on herbaceous plants (Pashchenko 1988).

Gall. Most often red, wrinkled, rolled elongated (15–20 mm in length) gall on the upper side of the leaf along the mainrib; on the lower side it opens with a longi- tudinal slit (Fig. 5D).

Importance. No data are known.

Remarks. It is one of the most common Pempigus species associated with *Pop.nigra* in the Palearctic. In the Asian part of Russia, the species is usually found in southern taiga, forest-steppe and steppe from Urals to Primorsky Territory; in taiga regions, it is found only in urban area (Tomilova 1959, 1962, 1963; Ivanovskaya- Shubina 1963).

Pemphigus protospirae Lichtenstein, 1885

Fig. 6A

Specimen examined. Altai Republic: 2 WM, Ongudai distr., Ongudai village, bank of Ursul River, 15.VIII.2019, *Pop. laurifolia*, SpG, slide No. 122 (SIF), N.S. Babichev leg.; Irkutsk Region: 2 WM; Bayanday distr., near Bayandai village, 27.VII.2021, *Pop.nigra*, SpG, slide No. 522 (St.PSU), M.K. Dementeva leg.

Distribution. World: Europe (Hałaj, Osiadacz 2013), Caucasus (Barjadze 2010), Asia (Narzikulov 1962; Zhang et al. 1999; Görür et al. 2012; Kadyrbekov 2017; Najmi et al. 2018). Asian part of Russia: Western Siberia – Kurgan Region (Ryabinin 2014), Tyumen Region (Tibatina 1963), Novosibirsk Region (Ostanin 1980), Tomsk Region (Ivanovskaya-Shubina 1963), Altai Territory (Dolgova, 1969), Altai Republic (Ivanovskaya 1977; Stekolshchikov, Novgorodova 2015), Kemerovo Region (Barannik, 1981); Eastern Siberia – Khakassia Republic (Babichev, Kirichenko 2020), south of Krasnoyarsk Territory (Babichev, Kirichenko 2020), Irkutsk Region**.

Primary host plants. Palearctic: *Aigeiros - Pop. nigra* (Dzhibladze 1968; Zerova et al. 1991; Zhang et al. 1999; Buga et al. 2016), *Pop. usbekistanica* (Narzikulov 1962; Zerova et al. 1991; Gabrid 2005); *Tacamahaca - Pop. laurifolia* (Kadyrbekov 2017), *Pop. macrocarpa* (Zhang et al. 1999; Kadyrbekov 2017). Asian part of Russia: *Pop. nigra* (Ivanovskaya 1977; Babichev, Kirichenko 2020), *Pop.laurifolia* (Babichev, Kirichenko 2020).

Gall. Green, wrinkled, spiral (15-40 mm in length) gall on the petiole; mature gall opens with slits inbetween spiral coil (Fig. 6A).

Importance. High densities of the species on *Pop. laurifolia* was documented in Khakassia, Tuva and Altai Republics in 2011–2016 and 2022 (Babichev: personal observation).

Remarks. Trophic association of the species with *Pop. nigra* in Europe (Shaposh-nikov 1955; Zerova et al. 1991; Hałaj, Osiadacz 2013) and *Pop. laurifolia* in Eastern Siberia (Babichev, Kirichenko 2020) as well as species distribution in Norther Asia require further study.

Pemphigus spyrothecae Passerini, 1860

Fig. 6B

Specimen examined. Bashkortostan Republic: 4 AS, Ordzhonikidzevskiy distr., Votikeevo village, 28.VI.2019, *Pop. nigra*, SpG, slides Nos 117/1-2 (SIF), Sh. Martazin leg.

Distribution. World: Northren Africa (Holman, 2009), Europe (Hałaj, Osiadacz 2013), Caucasus (Alieva 1980; Barjadze 2010), Bashkortostan Republic (Martazin: personal communication, 2019); Asia (Narzikulov 1962; Ghosh 1984; Zhang et al. 1999; Görür et al. 2012; Kadyrbekov 2017; Najmi et al. 2018); introduced to Nearctic (Canada). Asian part of Russia: Western Siberia – Kurgan Region (Ryabinin 2014), Tyumen Region (Tibatina 1963), Omsk Region (Ivanovskaya 1977); Eastern Siberia

Primary host plants. Palearctic: *Aigeiros - Pop. nigra* (Dzhibladze 1968; Zerova et al. 1991; Buga et al. 2016; Kadyrbekov 2017); *Tacamahaca- Pop. ciliata* (Chakrabarti 1998), *Pop. laurifolia* (Kadyrbekov 2017), *Pop. macrocarpa* (Kadyrbekov 2017). Asian part of Russia: *Pop. nigra* (Ivanovskaya 1977). The species associated only with poplars, not with herbaceous plants (Shaposhnikov 1955; Zerova et al. 1991; Stern, Foster 1996; Wool 2005; Hałaj, Osiadacz 2013; Blackman, Eastop 2022).

Gall. Green (with shades of yellow or red), smooth, spiral (10–20 mm in length) gall on the petiole; mature gall opens with slits in-between spiral coil (Fig. 6B).

Importance. A pest of poplars affecting ornamental plantings and natural tree stands, as well as nurseries, arboreta in Europe (Superfamily of true aphids... 1987; Hałaj, Osiadacz 2013; Petrov

2019) and Siberia (Babichev, Kirichenko 2020). Provides permanent outbreaks in Krasnoyarsk (Krasnoyarsk Territory), deformates leaf petioles and young shoots (Babichev, Kirichenko 2020). It is listed as an alien pest in Belarus (Buga, Zhorov 2016).

Remarks. In Siberia, it is considered an alien species (Babichev, Kirichenko 2020). Only few galls were documented in some regions of Western Siberia: Kurgan Region (Ryabinin 2014), Tyumen Region (Tibatina 1963), Omsk Region (Ivanovskaya 1977), whereas in Krasnoyarsk and its suburb (Krasnoyarsk Territory) the species is numerous (Baranchikov, Babichev 2006; Babichev, Kirichenko 2020).

Genus Thecabius Koch, 1857

Subgenus Parathecabius Börner, 1950

Thecabius latisensorius Hori, 1938

Fig. 6C

Specimen examined. Khakassia Republic: 4 WM, Shira distr., along Belyi Iyus River, 11.VII.2011, *Pop. laurifolia*, PGWL, slides Nos 99/1-3 (SIF), N.S. Babichev leg.; Tuva Republic: 4 WM, Kyzyl, floodplain of Yenisei River, 12.VII.2016, *Pop. laurifolia*, PGWL, slides Nos 107, 109 (SIF), N.S. Babichev leg.

Distribution. World: Central and Eastern Asia (Aoki 1975; Kadyrbekov 2017). Asian part of Russia: Western Siberia – Novosibirsk Region (Ostanin 1980), Altai Territory (Dolgova 1969), Altai Republic (Dolgova 1971; Stekolshchikov, Novgoro- dova 2015); Eastern Siberia – Khakassia Republic**, Krasnoyarsk Territory (Baranchikov, Babichev 2015), Tuva Republic**, Zabaikalskiy Territory (Dolgova 1971); Russian Far East – Primorsky Territory (Pashchenko 1985), Sakhalin Region (Pashchenko 1988).

Primary host plants. Palearctic: *Tacamahaca - Pop. laurifolia* (Dolgova 1971), *Pop. macrocarpa* (Kadyrbekov 2017); *Pop. suaveolens* (Aoki 1975; Pashchenko 1985, 1988). Asian part of Russia: *Pop. laurifolia* (Dolgova 1971; Ostanin 1980; present study), *Pop. suaveolens* (Pashchenko 1985, 1988).

Gall. Fundatrix and its progeny (emigrants) make two different pseudogalls on poplar leaves. The pseudogal of fundatrix is red, volumistic, roller-shaped (10–15 mm in length) on the upper side of the leaf, parallel to the mainrib; on the lower side, the pseudogal opens with a narrow longitudinal slit. The pseudogal of emigrants is often situated on the apical leaves. The gall is bright red to purple in color, roller-shaped or ctenoid (over 30 mm in lenght), on the upper side of the leaf on the sides of the mainrib; on the lower side, it opens with a wide longitudinal slit (Fig. 6C).

Importance. No data are known.

Remarks. It was first described in Japan as *Pemphigus latisensorius* (Hori, 1938) (Aoki 1975), later listed in Altai as *Thecabius altaicus* Dolgova, 1971 (Dolgova 1969, 1971; Ivanovskaya 1977). In the Asian part of Russia, *Th. latisensorius* found almost exclusively in floodplain forests of southern forest, forest-steppe, steppe and semi-desert zones (Dolgova 1969, 1971; Ivanovskaya 1977).

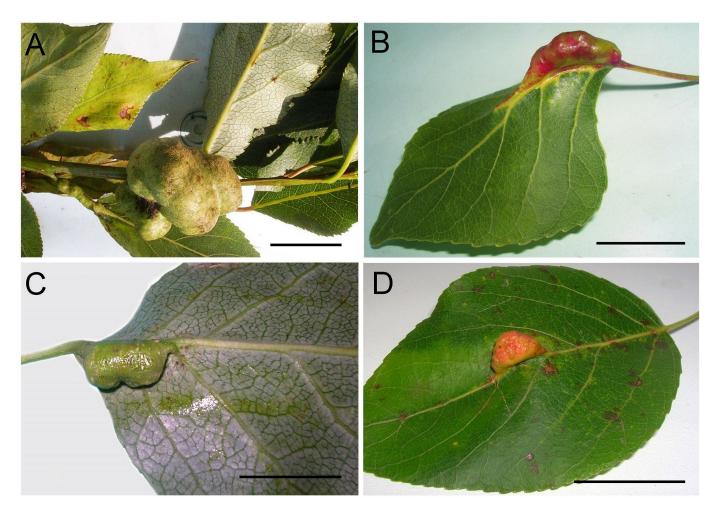


Figure 5. Galls of popular-feeding aphids in the Asian part of Russia (continuation). $\bf A$ – the gall of Pemphigus microsetosus formed from the whole leaf on Populus laurifolia; $\bf B$ – Pem. passeki on the upper side of the leaf of Pop. nigra; $\bf C$ – Pem. plicatus on the lower side of the leaf of Pop. laurifolia; $\bf D$ – Pem. populinigrae on the leaf of Populus sp. Localities: $\bf A$, $\bf B$ – Khakassia Republic, Shirinskiy district, near Chjernoe Ozero village, forest belt; $\bf C$, $\bf D$ – Kemerovo Region, Mezhdurechensk, street planting. Scale = 40 mm ($\bf A$, $\bf C$), 20 mm ($\bf B$, $\bf D$). Photos by N.S. Babichev, N.I. Kirichenko.

Subgenus Thecabius Koch, 1857

Thecabius affinis (Kaltenbach, 1843)

Fig. 6D

Specimenexamined. Krasnoyarsk Territory: 2 WM, Karatuzskiy distr., Amyl River, near Kachulka village, 06.VII.2021, *Pop. nigra*, PGWL, slide No. 142 (SIF), N.S. Babichev leg.

Distribution. World: Europe (Hałaj, Osiadacz 2013), Caucasus (Dzhibladze 1968), Asia (Holman, Szelegiewiez 1972; Aoki 1975; Ghosh 1984; Zhang et al. 1999; Gabrid 2005; Holman 2009; Kadyrbekov 2017); introduced to Nearctic (Canada) (Blackman, Eastop 2022). Asian part of Russia: Western Siberia – widely distributed (Dolgova 1971; Ivanovskaya 1977; Ostanin 1980; Zerova et al. 1991); Eastern Siberia – Khakassia Republic (Baranchikov, Babichev 2015), Krasnoyarsk Territory (Zerova et al. 1991; Baranchikov, Babichev 2015), Irkutsk Region (Tomilova 1977), Yakutiya Republic (Novikov 1988), Zabaikalskiy Territory (Tomilova 1963); Russian Far East – Kamchatka Territory (Pashchenko 1988; Pashchenko, Lobkova 1990), Khabarovsk Territory (Lyubarskiy 1956), Primorsky Territory (Lyubarskiy 1956; Pashchenko 1988; Pashchenko, Lobkova 1990).

Primary host plants. Palearctic: Aigeiros - Pop. nigra (Dzhibladze 1968; Zerova et al., 1991; Buga

et al. 2016; Kadyrbekov 2017); *Tacamahaca – Pop. laurifolia* (Holman, Szelegiewiez 1972; Kadyrbekov 2017), *Pop. macrocarpa* (Kadyrbekov 2017), Pop. simonii (Holman 2009), *Pop. suaveolens* (Aoki 1975; Pashchenko 1988). Asian part of Russia: *Pop. nigra* (Dolgova 1971; Ivanovskaya, 1977), *Pop. suaveolens* (Lyubarskiy 1956; Pashchenko 1988). It also develops on intersection hybrids of pop- lars (*Aigeiros×Tacamahaca*) (Holman 2009).

Gall. Fundatrix and its progeny (emigrants) form two different pseudogalls on poplar leaves. The pseudogal of fundatrix is red, folded, up 5 mm in length, on the edge of the leaf blade underside of the leaf; slightly opened along the entire length with a narrow slit. The pseudogal of emigrants is red, volumistic, up 20-40 mm in length, made from the whole apical leaf; the pseudogal opens from the lower side of the leaf (Fig. 6D).

Importance. In 1950s, the species was documented in mass on *Pop. suaveolens* in Khabarovsk Territory (Lyubarskiy 1956). No much data are known from the Asian part of Russia, except mentioning of the moderate damage caused by the species to *Pop. suaveolens* in Irkutsk Region and Buryatia Republic in 1960s–1970s (Tomilova 1977).

Remarks. In East Asia, it is described as *Thecabius orientalis* Mordvilko, 1935 and *Th. ranunculi* (Shinji, 1922), which are presently considered as synonums of *Th. affinis* (Pashchenko 1988; Blackman, Eastop 2022).

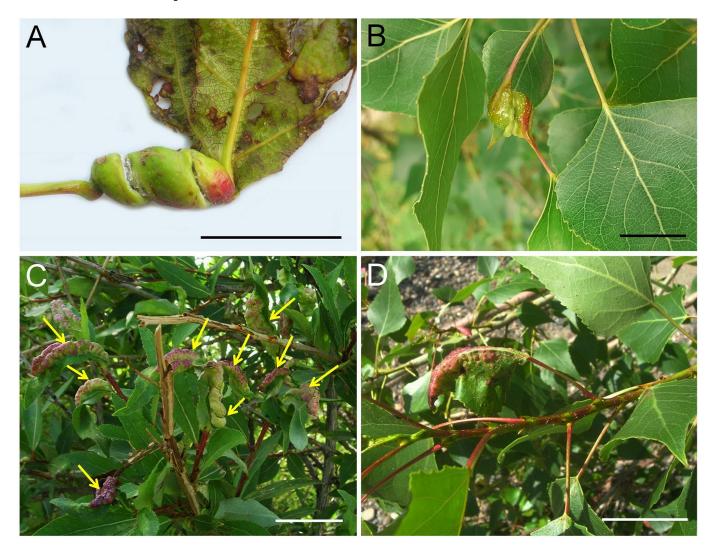


Figure 6. Galls of popular-feeding aphids in the Asian part of Russia (end). $\bf A$ – the gall of Pemphigus protospirae on the leaf petiole of Populus laurifolia; $\bf B$ – Pem. spyrothecae on the leaf petiole of Pop. nigra; $\bf C$ – Thecabius latisensorius on the upper

side of the leaf of Pop. laurifolia; \mathbf{D} – Th. affinis on the upper side of the leaf of Pop. nigra. Localities: \mathbf{A} – Khakassia Republic, Shirinskiy district, near Chjernoe Ozero village, forest belt; \mathbf{B} – Krasnoyarsk Territory, Krasnoyarsk, Akademgorodok, street planting; \mathbf{C} – Tuva Republic, Tes-Khemsky kozhuun; \mathbf{D} – Krasnoyarsk Territory, Karatuzskiy district. Scale = 20 mm (\mathbf{A} , \mathbf{B}), 60 mm (\mathbf{C} , \mathbf{D}). Photos by N.S. Babichev.

Discussion

Careful revision of distributional data on gall-forming poplar aphids from the genera Pemphigus and Thecabius and our field sampling allowed to confirm the pres- ence of 20 species in Northen Asia. Other six species of these two genera mentioned in the literature for this macroregion, namely Pemphiaus baicalensis Cholodkovsky, 1920, Pem, niissimae (Matsumura, 1917), Pem. saccosus Mordvilko ex Shaposhnikov, 1955, Pem. semenovi Mordvilko ex Shaposhnikov, 1955; Thecabius orientalis Mordvilko, 1935, Th. ranunculi (Shinji, 1922) (Shaposhnikov 1955; Lyubarskiy 1956; Ivanovskaya 1977; Pashchenko 1988; Pashchenko, Lobkova 1990; Favret 2022) are either now treated under different species names (or under different genera) or synonymized with those provided in our present study. Among these six species, Pem. baicalensis Cholodkovsky, 1920 and Pem. niissimae (Matsumura, 1917), previously mentioned for the Asian part of Russia (Shaposhnikov 1955; Lyubarskiy 1956; Tokmakov 1987), are treated in modern taxonomic system under other genera. In particular, Pemphigus baicalensis was transferred to the genus Prociphilus (Paraprociphilus) Mordvilko, 1923 (Mordvilko 1935; Ivanovskaya 1977; Favret 2022) and Pem. niissimaeto Epipemphiqus (Matsumura, 1917) (Aoki 1975; Pashchenko 1988; Blackman, Eastop 2022; Favret 2022). Some species have controversial or uncertain taxonomic position, or they have been synonymized. For example, Pem. saccosus Mordvilko ex Shaposhnikov, 1955, singly documented in the Russian Far East, Primorskiy Territory (Shaposhnikov 1955), was not formally described and thus, it was not recorded anywhere else, therefore it does not appear in modern keys and in our checklist. To our mind, the gall of this species may correspond to Pem. borealis or Pem. dorocola. Other species, Pemphigus semenovi Mordvilko ex Shaposhnikov, 1955, found in Baikal region and Primorskiy Territory (Shaposhnikov 1955; Tomilova 1959, 1962), is presently recognized as junior synonym of Pem. mongolicus Holman et Szelegiewicz, 1974 (Blackman, Eastop 2022; Favret 2022). Two species, Thecabius orientalis Mordvilko, 1935 and Th. ranunculi (Shinji, 1922) (Shaposhnikov 1955; Lyubarskiy 1956; Aoki 1975; Pashchenko 1985; Pashchenko, Lobkova 1990) were synonymized with Th. affinis (Kaltenbach, 1843) (Remaudière, Remaudière 1997; Pashchenko 1988; Blackman, Eastop 2022).

Other species included in the checklist would need further study. We suspect that *Pem. birimatus* described from Siberia (Ivanovskaya 1973, 1977) and *Pem. iskanderkuli* described from Central Asia (Narzikulov 1962; Gabrid 1989, 2005) are one species as they are hardly distinguishable morphologically (both galls and aphids) and share the same host (*Populus laurifolia*) (Gabrid 1989, 2005). The systematic position of *Pem. borealis* and *Pem. dorocola*, both described from the Far East (Aoki 1975), would also need clarification, since the latter species may be a variety of the former species (Aoki 1975; Hałaj, Osiadacz 2013; Blackman, Eastop 2022).

Conclusions

An intensive literature survey and our recent field data from Siberia and the Russian Far East allowed to compile the checklist of gall-forming poplar aphids of the Asian part of Russia, which presently comprises 18 species of *Pemphigus* and two species of *Thecabius*. An accurate taxonomic revision and the development of DNA barcoding library would be needed to resolve taxonomic issues of some galling aphids discussed in the paper and to assure accurate taxonomic identification of all species of this group. Further range exploration of galling aphids in the Asian part of Russia, especially along the border with Central Asia from where some species could penetrate into Siberia, would be necessarily. Moreover, a special study of trophic associations with both poplars and herbaceous plants would be essential as it may allow clarifying the pathways of species distribution.

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Supplementary material 1

Table S1. The localities in the Asian part of Russia where gall-forming poplar aphids were sampled by our team in 2005-2022.

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Data type: table

Explanation note: The table contains the names and coordinates of the collection sites of gall-forming poplar aphids in 2005–2022.

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