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Contribution to the Fauna and Bionomics of Entomophagous Insects Feeding on the Small Spruce Bark Beetle *Ips amitinus* (Eichh.) (Coleoptera, Curculionidae: Scolytinae) in West Siberia

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Abstract—A total of 29 species of entomophagous insects from 15 families of 4 orders were found for the first time in the galleries of the small spruce bark beetle *Ips amitinus* within its invasive range in West Siberia; 26 species were predators of *Ips amitinus*, including 11 species of obligate and 15 species of facultative zoophages. The most abundant obligate predators were *Thanasimus femoralis* (Zett.) (Coleoptera, Cleridae) and *Medetera fasciata* Frey (Diptera, Dolichopodidae); the most abundant facultative predator was *Placusa complanata* Er. (Coleoptera, Staphylinidae). The larval ectoparasitoids *Dinotiscus eupterus* (Walk.) and *Rhopalicus tutela* (Walk.) (Pteromalidae) and the endoparasitoid of adults *Ropalophorus clavicornis* (Wesm.) (Braconidae) develop on *I. amitinus* both in its native range and in the secondary ranges. Widespread representatives of the local fauna that have established new trophic links with *I. amitinus* absolutely predominate among its entomophages in West Siberia. The European species *Phloeonomus sjoebergi* A. Strand (Staphylinidae) and *Epuraea dolosa* Kir. (Nitidulidae) were found for the first time in Siberia. *Ips amitinus* has been included in the prey spectrum of *Medetera penicillata* Neg., which is an obligate predator of *Polygraphus proximus* Blandf., another invasive bark beetle of Far Eastern origin.

Keywords: entomophages, small spruce bark beetle, *Ips amitinus*, invasion, West Siberia, new trophic links

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The small spruce bark beetle *Ips amitinus* (Eichhoff, 1872) is a species of Central European origin that has by now become quite widespread in Europe. This bark beetle was first detected in West Siberia in 2019 (Kerchev et al., 2019). The Siberian invasion of *I. amitinus* probably originated from the northwest of the Russian Federation (Kerchev et al., 2021), where this species appeared as the result of its rapid dispersal across Fennoscandia in the late 20th and early 21st centuries (Økland et al., 2019).

Outbreaks of the alien bark beetle destroy the Siberian pine *Pinus sibirica* Du Tour over vast areas of dark coniferous forests in the south of West Siberia. According to the data of the Tomsk branch of the Russian Center for Forest Protection, the total area of known *I. amitinus* outbreaks by the end of 2021 was 1498 ha in Tomsk Province and 1584 ha in Kemerovo Province.

Invasion of the aggressive alien species is accompanied by establishment of its associations with members

of the local biota, including entomophages. The latter regulate the abundance of this serious dendrophagous pest and may serve as agents of its biological control.

Information on entomophages of *I. amitinus* within its native range was published in a few papers (Nuorteva, 1957; Mills, 1983; Noyes, 2001) and summarized in a review of natural enemies of bark beetles in Europe (Kenis et al., 2004), which listed 11 species of parasitoid wasps (Hymenoptera) associated with *I. amitinus* but included no data on predatory insects feeding on this species. Three previously known species of parasitoids were recorded in the galleries of *I. amitinus* in its largest outbreak focus in Slovenia (Jurc and Bojović, 2006). Only one European study (Händel and Wegensteiner, 2004) mentioned predatory beetles of the families Cleridae, Nitidulidae, and Staphylinidae, as well as members of the orders Homoptera, Hemiptera, and Diptera found in the galleries of *I. amitinus* on heavily infested branches of the Swiss stone pine *Pinus cembra* L. in the Tyrolean Alps, but did not include the exact species' names. The relatively poor knowledge of the European predators of *I. amitinus* probably reflects the low numbers and minor economic importance of this bark beetle within its native range, as compared to its invasive populations (Jurc and Bojović, 2006; Økland et al., 2019).

The only publication on entomophages of *I. amitinus* in Siberia is a brief report by Krivosheina and Kerchev (2020), in which three species of the genus *Medetera* Fisch. (Diptera, Dolichopodidae) were listed for the invasion region: *M. penicillata* Neg., *M. pinicola* Kow., and *M. signaticornis* Loew.

This paper summarizes all the data obtained in 2019–2022 on the species composition and localities of the natural enemies of *I. amitinus* in its invasion regions in West Siberia.

MATERIALS AND METHODS

The material was collected in the habitats of *I. amitinus* in the south of Tomsk Province. In natural dark coniferous forests, entomophages were collected on *Pinus sibirica*, which is the main host plant of this bark beetle in its invasion region. Other plants infested with *I. amitinus*, namely the Siberian spruce *Picea obovata* Ledeb. and the introduced Korean pine *Pinus koraiensis* Sieb. et Zucc. of Far Eastern origin, were studied in the conifer arboretum at the Kedr research base of the Institute of Monitoring of Climatic and Ecological Systems, Siberian Branch of the Russian Academy of Sciences.

We used the generally accepted methods of collecting and rearing entomophages of forest pests (Krivosheina and Mamaev, 1967; Kolomiets and Bogdanova, 1973a; Nikitsky, 1980; Gorokhovnikov and Lebedeva, 1984). Most of the insects were collected (manually or using an aspirator) from *I. amitinus* galleries exposed by removing the bark from wind-broken and deadfall trees and broken branches of Siberian pines. Adults of some species were collected from tree bark and from traps baited with *Ips typographus* (L.) pheromone installed in the tree stands. In the conifer arboretum, entomophages were extracted from under the bark of standing young trees damaged by the small spruce bark beetle. The immature stages of parasitoids found on the larvae and pupae of *I. amitinus* were kept in the laboratory until emergence of the adults. The feeding of some entomophages of *I. amitinus* was observed in Petri dishes and on sandwich plates, the design of which had been earlier described by Kerchev (2014).

A total of 732 insects were collected and identified. The entomophages were identified by the authors: rove beetles, by A.S. Babenko (National Research Tomsk State University), xylophilous dipterans, by M.G. Krivosheina (Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow), Hymenoptera, by E.V. Tselikh (Zoological Institute, Russian Academy of Sciences, St. Petersburg; ZIN), and other species, by S.A. Krivets and I.A. Kerchev (Institute of Monitoring of Climatic and Ecological Systems, Siberian Branch of the Russian Academy of Sciences, Tomsk). We thank A.G. Kirejtshuk (ZIN) for identifying the sap beetle *Epuraea dolosa* Kir.

RESULTS

Altogether, 29 species of entomophages of the small spruce bark beetle were identified in West Siberia; they belong to 15 families of 4 orders of insects.

Order HEMIPTERA

Family ANTHOCORIDAE

Scoloposcelis pulchella (Zetterstedt, 1838)

Material. Russia. *Tomsk Province*: Tomskii District, env. of Ipatovo, Luchanovo-Ipatovskii Siberian pine

forest, 17.VI.2020 (S.A. Krivets); Kurlek, Kedr research base, 6.VII.2020 (S.A. Krivets). In galleries of *I. amitinus* under bark of *Pinus sibirica*, 3 adults.

This species is an obligate predator of xylophagous beetles, mainly those developing on conifers. It is widespread in the forest zone of the Palaearctic. Nymphs and adults feed by sucking eggs, larvae, pupae, and young adult beetles. In Europe, the species actively exterminates bark beetles (Nikitsky, 1980; Dippel et al., 1997; Kenis et al., 2004).

In West Siberia, it was previously found on Siberian spruce *Picea obovata*, Siberian pine *Pinus sibirica*, and Scots pine *Pinus sylvestris* L. in the galleries of the bark beetles *Dendroctonus micans* (Kug.), *Ips sexdentatus* (Boern.), *I. typographus* (L.), *Orthotomicus proximus* (Eichh.), and *Tomicus piniperda* (L.) (Kiseleva, 1946; Krivolutskaya, 1965; Kolomiets and Bogdanova, 1980), and in colonies of the invasive bark beetle *Polygraphus proximus* Blandf. on Siberian fir *Abies sibirica* Ledeb. (Krivets and Kerchev, 2016).

Order COLEOPTERA

Family CARABIDAE

Tachyta nana (Gyllenhal, 1810)

Material. Tomskii District, 18.5 km N of Petropavlovka, mixed dark coniferous forest, under the dead bark of a fallen *Pinus sibirica* tree processed by bark beetles, including *Ips amitinus*, 16.V.2022 (S.A. Krivets), 2 adults.

A Holarctic species. According to some authors, both larvae and adults are obligate predators destroying eggs, larvae, pupae, and new, still incompletely colored adults of bark beetles under the bark of coniferous and deciduous trees (Kolomiets and Bogdanova, 1980). According to other data, the species develops under dead bark of trees inhabited, or more often abandoned, by bark beetles or other xylobionts, and combines predation with mycetophagy (Nikitsky et al., 1996).

In West Siberia, the species was previously found in the galleries of the bark beetles *Ips acuminatus* (Gyll.), *I. sexdentatus*, *I. subelongatus* Motch., *I. typographus*, and *Orthotomicus proximus* (Kolomiets and Bogdanova, 1980).

Family STAPHYLINIDAE

Homalota plana (Gyllenhal, 1810)

Material. Tomskii District, env. of Ipatovo, Luchanovo-Ipatovskii Siberian pine forest, 28.IX.2020; env. of Aksenovo, Aksenovskii Siberian pine forest, 29.IX.2020 (N.A. Smirnov). A total of 11 adults in galleries of *I. amitinus* under bark of *Pinus sibirica*.

The species is distributed in Europe, North Asia, and North America (Löbl and Smetana, 2004) and inhabits bark beetle galleries under the bark of coniferous and deciduous trees (Kirschenblat, 1965; Goreslavets, 2010).

In West Siberia, it was previously recorded on *Pinus sylvestris* in colonies of *Orthotomicus proximus* (Kolomiets and Bogdanova, 1980).

Nudobius lentus (Gravenhorst, 1806)

Material. Pervomaiskii District, env. of Tuendat, Siberian pine forest, 26.VIII.2020 (N.A. Smirnov). Tomskii District, Kurlek, Kedr research base, 7.VI.2020 (S.A. Krivets); env. of Aksenovo, Aksenovskii Siberian pine forest, 29.IX.2020 (N.A. Smirnov); env. of Bogashevo, Bogashevskii Siberian pine forest, 2.X.2020 (S.A. Krivets). A total of 5 adults in galleries of *I. amitinus* under bark of *Pinus sibirica*.

A widespread Palaearctic species; an obligate polyphagous predator of beetles developing under the bark of coniferous and deciduous trees. Its adults and larvae destroy eggs, larvae, and pupae of bark beetles, jewel beetles (Buprestidae), weevils of the genus *Pissodes* (Curculionidae), and longhorn beetles (Cerambycidae) (Nuorteva, 1956; Mamaev et al., 1977; Ounap, 1992; Kenis et al., 2004).

In West Siberia, the species commonly inhabits the tunnels of xylophagous insects on *Abies sibirica*, *Picea obovata*, *Pinus sibirica*, and *P. sylvestris*; recorded in colonies of the bark beetles *Dendroctonus micans*, *Dryocoetes autographus* (Ratz.), *Hylurgops glabratus* (Zett.), *H. palliatus* (Gyll.), *Ips duplicatus* (Sahlb.), *I. typographus*, *Orthotomicus laricis* (F.), *O. proximus*, *O. suturalis* (Gyll.), *Pityogenes chalcographus* (L.), *Polygraphus poligraphus* (L.), *P. subopacus* Thoms., *P. proximus*, *Tomicus minor* (Hart.), and *T. piniperda* (Krivolutskaya, 1965; Kolomiets and Bogdanova, 1980; Babenko, 1991; Krivets and Kerchev, 2016).

Philonthus decorus (Gravenhorst, 1802)

Material. Tomskii District, env. of Ipatovo, Luchanovo-Ipatovskii Siberian pine forest, trap baited with *Ips typographus* pheromone in outbreak focus of *I. amitinus*, 30.IV.2020 (S.A. Krivets), 2 adults.

A Euro-Siberian, predominantly forest species. In the south of West Siberia, it is the most abundant in the litter of small-leaved forests in the first half of summer and mainly feeds on small invertebrates (Babenko, 1989, 2000). According to the data of Krivolutskaya (1965) and Kolomiets and Bogdanova (1980), the species sporadically occurs in the dark coniferous forests of West Siberia and feeds as a predator in the galleries of bark beetles.

Phloeonomus sjoebergi A. Strand, 1937

Material. Tomskii District, env. of Ipatovo, Luchanovo-Ipatovskii Siberian pine forest, 28.IX.2020; env. of Bogashevo, Bogashevskii Siberian pine forest, 1.X.2020, (N.A. Smirnov). A total of 10 adults in galleries of *I. amitinus* under bark of *Pinus sibirica*.

The species is distributed in Europe (Löbl and Smetana, 2004), including European Russia (Kirschenblat, 1965). It is found under the bark of coniferous trees, usually in the galleries of bark beetles (Jonsell and Hansson, 2011). Here, the species is recorded for the first time for Siberia.

Data on the diet of *Phloeonomus* species are contradictory: according to some authors (Mamaev et al., 1977), these beetles are saprophagous; according to others (Nikitsky, 1980), both adults and larvae combine facultative predation with facultative sapro- and mycetophagy.

Placusa complanata Erichson, 1839

Material. Tomskii District, Kurlek, Kedr research base, 1.VI–6.VII.2020 (S.A. Krivets); env. of Aksenovo, Aksenovskii Siberian pine forest, 29.IX.2020 (N.A. Smirnov); same locality, 1.X.2020 (S.A. Krivets); env. of Bogashevo, Bogashevskii Siberian pine forest, 1.X.2020 (N.A. Smirnov); same locality, 2.X.2020 (S.A. Krivets); env. of Ipatovo, Luchanovo-Ipatovskii Siberian pine forest, 11.VI–30.IX.2020 (S.A. Krivets); same locality, 28.IX.2020 (N.A. Smirnov). Kozhevnikovskii District, env. of Bazoi, Bazoiskii Siberian pine forest, 18.VIII.2020 (N.A. Smirnov). A total of 165 adults in galleries of *I. amitinus* under bark of *Pinus sibirica* and *Picea obovata*.

A Holarctic species. Its larvae occur on conifers, feeding on eggs and possibly early instar larvae of bark beetles (Mamaev et al., 1977). According to Nikitsky (1980), it is a facultative predator of bark beetles.

The species is common in West Siberia; it was previously found under the bark of *Pinus sibirica* and *Picea obovata*, where it destroyed eggs and early instar larvae of *Ips acuminatus* (Gyll.), *I. sexdentatus*, *I. typographus*, *Orthotomicus proximus*, and *Polygraphus subopacus* (Krivolutskaya, 1965; Kolomiets and Bogdanova, 1980).

Family HISTERIDAE

Cylister linearis (Erichson, 1834)

Material. Tomskii District, 18.5 km N of Petropavlovka, mixed coniferous forest, 16.V.2022 (S.A. Krivets, N.A. Smirnov); env. of Ipatovo, Luchanovo-Ipatovskii Siberian pine forest, 18.IX.2019 (I.A. Kerchev); Kurlek, Kedr research base, 1.VI–6.VII.2020 (S.A. Krivets). A total of 27 adults in galleries of *I. amitinus* under bark of *Pinus sibirica* and *Picea obovata*.

A forest species, widespread in the Palaearctic and closely associated with conifers. A broadly polyphagous predator feeding under the bark on eggs, larvae, pupae, and young adults of bark beetles with weakly sclerotized integuments, as well as small larvae of other xylophages (Mamaev et al., 1977; Rauhut et al., 1993; Schroeder and Weslien, 1994; Kenis et al., 2004).

In West Siberia, the species was previously found under the bark of *Larix sibirica* Ledeb., *Picea obovata*, *Pinus sibirica*, and *P. sylvestris* in the galleries of the bark beetles *Hylurgops palliatus*, *Ips acuminatus*, *I. sexdentatus*, *I. subelongatus* Motsch., *I. typographus*, *Orthotomicus laricis*, *O. proximus*, *Pityogenes bidentatus* (Hbst.), *Tomicus minor*, *T. piniperda*, and *Trypodendron lineatum* (Oliv.) (Kiseleva, 1946; Krivolutskaya, 1965; Kolomiets and Bogdanova, 1980).

Paromalus parallelepipedus (Herbst, 1792)

Material. Tomskii District, env. of Ipatovo, Luchanovo-Ipatovskii Siberian pine forest, 18.IX.2019

(S.A. Krivets); env. of Petukhovo, Petukhovskii Siberian pine forest, 11.VII.2019 (S.A. Krivets). In galleries of *I. amitinus* under bark of *Pinus sibirica*, 3 adults.

A forest species, widespread in the Palaearctic, develops under the bark of conifers infested or abandoned by bark beetles (Mamaev et al., 1977; Mazur, 1979; Nikitsky, 1980; Kenis et al., 2004).

In Siberia, it was previously recorded on *Abies sibirica*, *Larix sibirica*, *Picea obovata*, *Pinus sibirica*, and *P. sylvestris* in the galleries of *Hylurgops palliatus*, *Ips sexdentatus*, *I. subelongatus*, *I. typographus*, *Orthotomicus proximus*, *Polygraphus proximus*, and *Tomicus piniperda*, feeding on their larvae and pupae (Kiseleva, 1946; Krivolutskaya, 1965; Kolomiets and Bogdanova, 1980; Krivets and Kerchev, 2016).

Plegaderus vulneratus (Panzer, 1797)

Material. Tomskii District, 18.5 km N of Petropavlovka, mixed coniferous forest, under dead bark of fallen *Pinus sibirica* processed by bark beetles, including *Ips amitinus*, 16.V.2022 (S.A. Krivets); Kurlek, Kedr research base, in gallery of *I. amitinus* under bark of *Pinus sibirica*, 1.VI.2020 (S.A. Krivets). 2 adults.

The species has a trans-Eurasian range and is distributed from taiga to forest-steppe. Its adults feed on eggs and young larvae, while its larvae destroy early instar larvae of the vast majority of common bark beetle species developing on conifers (Mamaev et al., 1977; Weslien, 1992; Schroeder and Weslien, 1994; Kenis et al., 2004).

In West Siberia, the species was previously found on *Abies sibirica*, *Larix sibirica*, *Picea obovata*, *Pinus sibirica*, and *P. sylvestris* in the galleries of *Dendroctonus micans*, *Ips acuminatus*, *I. duplicatus*, *I. sexdentatus*, *I. subelongatus*, *I. typographus*, *Orthotomicus proximus*, *O. suturalis*, *Polygraphus subopacus*, *P. proximus*, and *Tomicus piniperda* (Krivolutskaya, 1965; Kolomiets and Bogdanova, 1980; Krivets and Kerchev, 2016).

Family CLERIDAE

Thanasimus femoralis (Zetterstedt, 1828)
(= *Th. rufipes* Brahm.)

Material. Tomskii District, env. of Ipatovo, Luchanovo-Ipatovskii Siberian pine forest, 27–30.IV.2020; same locality, 4.VII.2021 (S.A. Krivets); Kurlek, Kedr research base, 6.VII.2020 (S.A. Krivets); env. of Bogashevo, Bogashevskii Siberian pine forest, 16.IV.2021 (I.A. Kerchev); env. of Nizhne-Sechenovo, Nizhne-Sechenovskii Siberian pine forest, 21.V.2021 (I.A. Kerchev). Larvae in galleries of *I. amitinus* under bark of *Pinus sibirica* and *Picea obovata*, 36 spms. Also adults identified by us from traps baited with *Ips typographus* pheromone, installed in *I. amitinus* outbreak foci in Belousovskii, Aksenovskii, Zorkaltsevskii, and Luchanovo-Ipatovskii Siberian pine forest, 27–30. IV.2020 (collected by colleagues from Tomsk Center for Forest Protection), 272 spms.

A Euro-Siberian forest species, an obligate predator of xylophagous beetles infesting conifers. Adults destroy bark beetles penetrating into the trees, while larvae destroy eggs, larvae, pupae, and young adults in bark beetle galleries, and also early instar larvae of longhorn and jewel beetles (Mamaev et al., 1977; Kolomiets and Bogdanova, 1980; Nikitsky, 1980; Weslien and Schroeder, 1999; Wermelinger, 2002; Kenis et al., 2004).

In West Siberia, the species was previously found on *Abies sibirica*, *Larix sibirica*, *Picea obovata*, *Pinus sibirica*, and *P. sylvestris* in the galleries of the bark beetles *Ips sexdentatus*, *I. subelongatus*, *I. typographus*, *Orthotomicus laricis*, *O. proximus*, *Polygraphus proximus*, and *Tomicus piniperda* (Kiseleva, 1946; Krivolutskaya, 1965; Kolomiets and Bogdanova, 1980; Krivets and Kerchev, 2016).

Family NITIDULIDAE

Epuraea dolosa Kirejtshuk, 1995

Material. Tomskii District, env. of Ipatovo, Luchanovo-Ipatovskii Siberian pine forest, 11.VI.2020; env. of Bogashevo, Bogashevskii Siberian pine forest, 16.IV.2021; env. of Aksenovo, Aksenovskii Siberian pine forest, 18.V.2021; env. of Zorkaltsevo, Zorkaltsevskii Siberian pine forest, 20.V.2021; env. of Nizhne-Sechenovo, Nizhne-Sechenovskii Siberian pine forest, 21.V.2021; Larinskii landscape sanctuary, 17.VI.2021; env. of Belousovo, Belousovskii Siberian pine forest, 15.VII.2021 (I.A. Kerchev). In galleries of *I. amitinus* under bark of *Pinus sibirica*, 32 adults, larvae in great numbers.

The species was previously known by occasional records from Norway and from Perm Territory of Russia

(Kirejtshuk, 1995). Here, it is recorded for the first time for Siberia.

Glischrochilus quadripunctatus (Linnaeus, 1758)

Material. Tomskii District, env. of Ipatovo, Luchanovo-Ipatovskii Siberian pine forest, 18.IX.2019 (I.A. Kerchev); env. of Aksenovo, Aksenovskii Siberian pine forest, 1.X.2020 (S.A. Krivets); env. of Bogashevo, Bogashevskii Siberian pine forest, 2.X.2020 (S.A. Krivets). A total of 19 adults in galleries of *I. amitinus* under bark of *Pinus sibirica*.

A forest species with a trans-Palaearctic range, often found under the bark of conifers, where it feeds on eggs, larvae, and pupae of xylophagous beetles including bark beetles (Nuorteva, 1956; Schroeder and Weslien, 1994; Kenis et al., 2004). According to Nikitsky (1980), this is a facultative predator, facultative saprophage, and mycetophage. Its larvae live under the bark and are saproxylophages with elements of necrophagy (Mamaev et al., 1977).

In West Siberia, the species was previously found on *Abies sibirica*, *Larix sibirica*, *Picea obovata*, *Pinus sibirica*, and *P. sylvestris*, and recorded as a predator of the bark beetles *Hylurgops palliatus*, *Ips sexdentatus*, *I. subelongatus*, *I. typographus*, *Polygraphus proximus*, and *Tomicus piniperda* (Kiseleva, 1946; Krivolutskaya, 1965; Kolomiets and Bogdanova, 1980; Krivets and Kerchev, 2016).

Family ZOPHERIDAE

Bitoma crenata (Fabricius, 1775)

Material. Tomskii District, 18.5 km N of Petropavlovka, mixed coniferous forest, under dead bark of fallen *Pinus sibirica* processed by bark beetles, including *Ips amitinus*, 16.V.2022 (S.A. Krivets, N.A. Smirnov), 2 adults.

A trans-Palaearctic forest species, occurring under the bark of dead coniferous and deciduous trees, both infested with bark beetles and intact ones. Kenis and co-authors (Kenis et al., 2004) listed this species as a predator of *Ips acuminatus* (Gyll.), *I. sexdentatus*, and *Tomicus* spp. with reference to Hérard and Mercadier (1996). In the opinion of many authors, the diet of this species is not exactly known; despite some evidence of predation, it can hardly be considered the main way of feeding (Mamaev et al., 1977; Kolomiets and Bogdanova, 1980; Nikitsky, 1980).

In West Siberia, the species was previously found under the bark of *Larix sibirica* and *Pinus sylvestris* in the galleries of *Ips acuminatus*, *I. sexdentatus*, *I. subelongatus*, *I. typographus*, and *Orthotomicus proximus* (Kolomiets and Bogdanova, 1980).

Family PYTHIDAE

Pytho depressus Linnaeus, 1767

Material. Tomskii District, 18.5 km N of Petropavlovka, mixed coniferous forest, under dead bark of fallen *Pinus sibirica* processed by bark beetles, including *Ips amitinus*, 16.V.2022 (S.A. Krivets), 1 larva; env. of Ipatovo, Luchanovo-Ipatovskii Siberian pine forest, in galleries of *I. amitinus* under bark of *Pinus sibirica*, 18.IX.2019; same locality, 30.IX.2020 (S.A. Krivets), 2 larvae.

The species is widespread in the forest zone of the Palaearctic and associated with various conifers (Mamaev et al., 1977; Schroeder and Weslien, 1994; Kenis et al., 2004). Mamaev and co-authors (Mamaev et al., 1977) described *P. depressus* as an omnivorous sapronecrophage with elements of predation. According to Nikitsky (1980), its early instar larvae are facultative predators that consume, besides detritus from the galleries and decomposing bark particles, also larvae and pupae of longhorn and bark beetles.

In West Siberia, its larvae were previously found under the bark of *Abies sibirica*, *Larix sibirica*, *Picea obovata*, *Pinus sibirica*, and *P. sylvestris* in the galleries of *Hylurgops palliatus*, *Ips acuminatus*, *I. sexdentatus*, *I. typographus*, *Orthotomicus proximus*, and *Polygraphus proximus* (Krivolutskaya, 1965; Kolomiets and Bogdanova, 1980; Krivets and Kerchev, 2016).

Family TENEBRIONIDAE

Corticeus fraxini (Kugelann, 1794)

Material. Tomskii District, env. of Ipatovo, Luchanovo-Ipatovskii Siberian pine forest, in galleries of *I. amitinus* under bark of *Pinus sibirica*, 9.VII.2020 (S.A. Krivets), 2 adults.

A forest species with a trans-Palaearctic range, developing in galleries of many bark beetles (Mamaev et al., 1977; Hérard and Mercadier, 1996; Kenis et al., 2004). Its adults feed on eggs, and its larvae consume larvae, pupae, and young beetles, as well as organic debris, detritus, and fungi in their galleries (Nikitsky, 1980).

In West Siberia, the species was previously recorded on *Abies sibirica*, *Picea obovata*, *Pinus sibirica*, and *P. sylvestris* in the galleries of *Hylurgops palliatus*, *Ips acuminatus*, *I. sexdentatus*, *I. typographus*, *Orthotomicus proximus*, *Pityogenes bidentatus*, *Polygraphus proximus*, and *Tomicus minor* (Kiseleva, 1946; Krivolutskaya, 1965; Kolomiets and Bogdanova, 1980; Krivets and Kerchev, 2016).

Corticeus linearis (Fabricius, 1790)

Material. Tomskii District, env. of Petukhovo, Petukhovskii Siberian pine forest, 11.VII.2019 (S.A. Krivets); env. of Aksenovo, Aksenovskii Siberian pine forest, 16.V.2022 (S.A. Krivets); Kurlek, Kedr research base, 1.VI.2020 (S.A. Krivets); env. of Ipatovo, Luchanovo-Ipatovskii Siberian pine forest, 17.VI.2020 (S.A. Krivets). A total of 10 adults in galleries of *I. amitinus* under bark of *Pinus sibirica*.

A widespread Palaearctic forest species, occurring on conifers in galleries of many bark beetles (Mamaev et al., 1977; Hérard and Mercadier, 1996; Kenis et al., 2004). It is ecologically close to the preceding species (Nikitsky, 1976, 1980).

In West Siberia, the species was previously recorded on *Abies sibirica*, *Larix sibirica*, *Picea obovata*, *Pinus sibirica*, *P. sylvestris* in the galleries of *Hylurgops palliatus*, *Ips acuminatus*, *I. sexdentatus*, *Orthotomicus proximus*, *Pityogenes bidentatus*, *P. chalcographus*, *P. quadridens* (Hart.), *Polygraphus proximus*, and *Tomicus minor* (Kiseleva, 1946; Krivolutskaya, 1965; Kolomiets and Bogdanova, 1980; Krivets and Kerchev, 2016).

Order DIPTERA

Family DOLICHOPODIDAE

Medetera excellens Frey, 1909

Material. Tomskii District, env. of Bogashevo, Bogashevskii Siberian pine forest, in gallery of *I. amitinus* under bark of *Pinus sibirica*, 2.X.2020 (S.A. Krivets), 1 larva.

A trans-Palaearctic forest species. Its larvae are obligate predators developing under the bark of conifers and feeding on larvae and pupae of bark beetles (Mamaev et al., 1977; Nikitsky, 1980; Weslien, 1992; Wermelinger, 2002; Kenis et al., 2004).

In West Siberia, the species was previously found on *Abies sibirica*, *Picea obovata*, and *Pinus sylvestris* in the galleries of the bark beetles *Dryocoetes hectographus* Rtt., *Orthotomicus proximus*, and *Polygraphus proximus* (Kolomiets and Bogdanova, 1973b; Krivosheina et al., 2018).

Medetera fasciata Frey, 1915

Material. Pervomaiskii District, env. of Tuendat, 26.VIII.2020 (N.A. Smirnov). Tomskii District, Kurlek, Kedr research base, 1.VI.2020 (S.A. Krivets); same locality, 1.VII.2020 (S.A. Krivets); env. of Ipatovo, Luchanovo-Ipatovskii Siberian pine forest, 28.IX.2020 (N.A. Smirnov); same locality, 11.VI–30.IX.2020 (S.A. Krivets). A total of 54 larvae in galleries of *I. amitinus* under bark of *Pinus sibirica* and *Pinus koraiensis*.

A Euro-Siberian forest species. Its larvae are obligate predators of bark beetles developing on conifers (Mamaev et al., 1977; Nikitsky, 1980).

In West Siberia, the species was previously found on *Pinus sylvestris* in the galleries of *Hylurgops palliatus*, *Ips acuminatus*, and *Pityogenes bidentatus* (Kolomiets and Bogdanova, 1980).

Medetera penicillata Negrobov, 1970

Material. Tomskii District, Kurlek, Kedr research base, 1.VI.2020 (S.A. Krivets); env. of Ipatovo, Luchanovo-Ipatovskii Siberian pine forest, 28.IX.2020 (N.A. Smirnov); Larinskii landscape sanctuary, 16.VI. 2021 (I.A. Kerchev). A total of 15 larvae in galleries of *I. amitinus* under bark of *Pinus sibirica*.

The species is known from the Russian Far East (Negrobov, 1970; Krivosheina, 1974) and from Japan (Negrobov and Naglis, 2016). Within its native range, its predatory larvae develop on *Pinus koraiensis* in the galleries of *Ips sexdentatus*, *Hylurgops interstitialis* Chap., *H. imitator* Rtt. (Mamaev et al., 1977), and on *Abies nephrolepis* (Trautv. ex Maxim.) Maxim. and *A. sachalinensis* (F. Schmidt) Mast. in the galleries of *Polygraphus proximus* (Krivets and Kerchev, 2016).

In Siberia, *M. penicillata* was first recorded in the early 2010s (Kerchev and Negrobov, 2012) as a predator of *Polygraphus proximus* in its invasive populations in fir forests, apparently after its introduction from the Far East along with this bark beetle (Kerchev, 2013). Currently, *M. penicillata* is widely distributed throughout the entire secondary range of *P. proximus* and is the most abundant entomophage of this host on *Abies sibirica.* The species was also found in the galleries of *Hylurgops palliatus* on the same plant species (Krivets and Kerchev, 2016) and in the galleries of *Dryocoetes autographus* and *D. hectographus* on *Picea obovata* (Krivosheina et al., 2018).

Medetera penicillata demonstrates a peculiar type of consortial relationship with *I. amitinus*, in which an invasive entomophage of Far Eastern origin that had previously reached high abundance in West Siberia was able to feed on a new invasive host of European origin.

Medetera pinicola Kowarz, 1877

Material. Tomskii District, Kurlek, Kedr research base, 1.VI.2020 (S.A. Krivets); env. of Aksenovo, Aksenovskii Siberian pine forest, 29.IX.2020 (N.A. Smirnov); env. of Ipatovo, Luchanovo-Ipatovskii Siberian pine forest, 18.IX.2019, 30.IX.2020 (S.A. Krivets); same locality, 28.IX.2020 (N.A. Smirnov). A total of 17 larvae in galleries of *I. amitinus* and *I. typographus* under bark of *Pinus sibirica*.

A Holarctic forest species, whose larvae are obligate predators of bark beetles on conifers (Mamaev et al., 1977; Nikitsky, 1980; Bickel, 1985; Wermelinger, 2002; Kenis et al., 2004; Krivosheina et al., 2018).

In West Siberia, the species was previously recorded on *Pinus sylvestris* in the colonies of *Orthotomicus proximus* and *Tomicus piniperda* (Kolomiets and Bogdanova, 1980) and on *Abies sibirica* in the galleries of the invasive bark beetle *Polygraphus proximus* (Krivosheina et al., 2018).

Medetera signaticornis Loew, 1857

Material. Tomskii District, Kurlek, Kedr research base, 7.VI–1.VII.2020 (S.A. Krivets); env. of Bogashevo, Bogashevskii Siberian pine forest, 2.X.2020 (S.A. Krivets). In galleries of *I. amitinus* under bark of *Pinus sibirica* and *P. koraiensis*, 4 larvae.

A Holarctic forest species, whose larvae are obligate predators of xylophages on conifers (Mamaev et al., 1977; Lieutier, 1979; Nikitsky, 1980; Bickel, 1985; Kenis et al., 2004; Krivosheina et al., 2018).

In West Siberia, the species was previously found on *Pinus sylvestris* in the galleries of *Ips sexdentatus* (Kolomiets and Bogdanova, 1980).

Medetera striata Parent, 1927

Material. Tomskii District, env. of Ipatovo, Luchanovo-Ipatovskii Siberian pine forest, 28.IX.2020 (N.A. Smirnov); same locality, 30.IX.2020 (S.A. Krivets). In galleries of *I. amitinus* under bark of *Pinus sibirica*, 3 larvae.

A Euro-Siberian species. Its larvae are predators of bark beetles on conifers (Nuorteva, 1956; Mamaev et al., 1977; Nikitsky, 1980; Kenis et al., 2004).

In West Siberia, the species was first recorded in 1965 on *Pinus sylvestris* in a colony of *Tomicus minor* (Kolomiets and Bogdanova, 1980).

Family XYLOPHAGIDAE

Xylophagus cinctus (De Geer, 1776)

Material. Tomskii District, env. of Ipatovo, Luchanovo-Ipatovskii Siberian pine forest, in gallery of *I. amitinus* under bark of *Pinus sibirica*, 18.IX.2019 (S.A. Krivets), 1 larva.

A Holarctic forest species developing under the bark of coniferous trees infested with various xylophilous insects. Early instar larvae usually feed as predators in the galleries of bark beetles, later instar larvae, in the tunnels of longhorn beetles and other insects with larger larvae developing under the bark (Nuorteva, 1956; Mamaev et al., 1977; Krivosheina et al., 2018).

In Siberia, the species occurs on all coniferous trees (*Abies sibirica*, *Larix sibirica*, *Picea obovata*, *Pinus sibirica*, and *P. sylvestris*), where is has been found in the galleries of *Dendroctonus micans*, *Ips subelongatus*, *I. typographus*, *Orthotomicus proximus*, and *Trypodendron lineatum* (Krivolutskaya, 1965; Kolomiets and Bogdanova, 1980). It was also recorded on *A. sibirica* trees co-infested with the invasive bark beetle *Polygraphus proximus* and the fir sawyer beetle *Monochamus urussovi* (Fisch.) (Krivets and Kerchev, 2016).

Family LONCHAEIDAE

Lonchaea collini Hackman, 1956

Material. Tomskii District, env. of Ipatovo, Luchanovo-Ipatovskii Siberian pine forest, in gallery of *I. amitinus* under bark of *Pinus sibirica*, 18.IX.2019 (S.A. Krivets), 1 larva.

The species is widespread in the forest zone of the Palaearctic. Its larvae are active predators feeding on larvae and pupae of xylophagous beetles that develop under the bark of coniferous trees (Morge, 1963; Mamaev et al., 1977; Nikitsky, 1980; Hérard and Mercadier, 1996; Kenis et al., 2004; Krivosheina et al., 2018).

In West Siberia, the species was previously found under the bark of *Larix sibirica*, *Picea obovata*, *Pinus sibirica*, and *P. sylvestris* in the galleries of *Dendroctonus micans*, *Hylurgops palliatus*, *Ips sexdentatus*, *I. subelongatus*, *I. typographus*, *Orthotomicus proximus*, *Tomicus minor*, and *T. piniperda* (Kolomiets and Bogdanova, 1980). It was also found in the galleries of *Polygraphus proximus* on *Abies sibirica* (Krivosheina et al., 2018).

Family STRATIOMYIDAE

Zabrachia minutissima (Zetterstedt, 1838)

Material. Tomskii District, env. of Ipatovo, Luchanovo-Ipatovskii Siberian pine forest, in galleries of *I. amitinus* on *Pinus sibirica*, 18.IX.2019, 30.IX.2020 (S.A. Krivets), 10 larvae.

A forest species with a trans-Palaearctic range. Its larvae co-occur with various bark beetles and other beetle species under the bark of coniferous trees (Mamaev et al., 1977; Nikitsky, 1980; Weslien and Schroeder, 1999; Kenis et al., 2004; Krivosheina et al., 2018).

Most of the available data suggest that this species is mainly necrophagous or necrosaprophagous (Krivosheina et al., 2018; Krivosheina and Kerchev, 2020). According to the observations of Mamaev (1972), larvae of *Z. minutissima* attack live larvae, mostly those of bark beetles, only in case of shortage of their usual food: dead xylophagous larvae and fungal mycelium. In the opinion of Nikitsky (1980), *Z. minutissima* is a broadly polyphagous species whose larvae can develop both as sapromycetophages and as facultative predators of bark beetles. Kolomiets and Bogdanova (1980) considered *Z. minutissima* a facultative predator of bark beetles, usually consuming weakened and dead larvae, pupae, and adults, but sometimes destroying healthy pupae and young beetles with weakly sclerotized integuments.

In Siberia, larvae of *Z. minutissima* were recorded under the bark of *Larix sibirica*, *Picea obovata*, *Pinus sibirica*, and *P. sylvestris* in the galleries of *Ips acuminatus*, *I. sexdentatus*, *I. subelongatus*, *I. typographus*, *Orthotomicus proximus*, and *Tomicus minor* (Krivolutskaya, 1965; Kolomiets and Bogdanova, 1980); they were also found in great numbers in abandoned galleries of *Polygraphus proximus* under the bark of *Abies sibirica* (Krivets and Kerchev, 2016).

Order HYMENOPTERA

Family PTEROMALIDAE

Dinotiscus eupterus (Walker, 1836)

Material. Tomskii District, env. of Belousovo, Belousovskii Siberian pine forest, 9.VII.2020 (I.A. Kerchev); env. of Ipatovo, Luchanovo-Ipatovskii Siberian pine forest and env. of Aksenovo; 29.IX.2020 (I.A. Kerchev); Larinskii landscape sanctuary, 17.VI.2021 (I.A. Kerchev). 8 adults reared from larvae parasitizing *I. amitinus* larvae under bark of *Pinus sibirica*.

A widespread Palaearctic species, introduced to New Zealand. Its larvae develop as ectoparasitoids of larvae of many bark beetle species infesting coniferous and deciduous trees (Nuorteva, 1957; Hedqvist, 1963; Mills, 1983; Noyes, 1998; Tselikh, 2010), including *I. amitinus* (Kenis et al., 2004).

In West Siberia, the species infests larvae of *Ips acuminatus*, *Orthotomicus proximus*, *Pityogenes bidentatus*, and *P. chalcographus* on *Pinus sylvestris*; *Dryocoetes baicalicus* Rtt. and *Scolytus morawitzi* Sem. on *Larix sibirica*; *Ips typographus* and *P. chalcographus* on *Picea obovata*; *Polygraphus proximus* on *Abies sibirica* (Kolomiets and Bogdanova, 1980; Krivets and Kerchev, 2016).

Rhopalicus tutela (Walker, 1836)

Material. Pervomaiskii District, env. of Tuendat, Siberian pine forest, 26.VIII.2020 (N.A. Smirnov). Tomskii District, env. of Petukhovo, Petukhovskii Sibe-

rian pine forest, 11.VII.2019 (N.A. Smirnov); env. of Ipatovo, Luchanovo-Ipatovskii Siberian pine forest and Belousovo, Belousovskii Siberian pine forest, 9.VII.2020 (I.A. Kerchev); env. of Aksenovo, Aksenovskii Siberian pine forest, 29.IX.2020 (I.A. Kerchev); env. of Bogashevo, Bogashevskii Siberian pine forest, 16.IV.2021 (I.A. Kerchev); env. of Zorkaltsevo, Zorkaltsevskii Siberian pine forest, 20.V.2021 (I.A. Kerchev). Kozhevnikovskii District, env. of Bazoi, Bazoiskii Siberian pine forest, 9.VIII.2020 (N.A. Smirnov). 19 adults reared from larvae and pupae collected in galleries of *I. amitinus* under bark of *Pinus sibirica*.

A widespread Palaearctic species, introduced to New Zealand, Canada, and the US (Peck, 1963; Noyes, 1998; Tselikh, 2010). It is a larval ectoparasitoid of many bark beetle species developing on coniferous and deciduous trees, including *I. amitinus* (Kenis et al., 2004). It was recorded in the largest outbreak focus of *I. amitinus* in Slovenia (Jurc and Bojović, 2006).

In West Siberia, the species was previously found under the bark of *Picea obovata*, *Pinus sibirica*, *P. sylvestris*, and the birch *Betula* sp. on the larvae of *Hylurgops palliatus*, *Ips acuminatus*, *I. sexdentatus*, *I. typographus*, *Tomicus minor*, and *Scolytus ratzeburgi* Jans. The species is ubiquitous and locally infests up to 15% of larvae in colonies of *I. sexdentatus* and up to 35% in those of *H. palliatus* (Kolomiets and Bogdanova, 1980).

Family BRACONIDAE

Ropalophorus clavicornis (Wesmael, 1835)

Material. Tomskii District, env. of Ipatovo, Luchanovo-Ipatovskii Siberian pine forest, 3 adults reared from *I. amitinus* beetles collected under bark of *Pinus sibirica* 17.IV.2020 (I.A. Kerchev). The presence of *R. clavicornis* was also detected by non-specific DNA amplification during analysis of an infested *I. amitinus* adult, performed by Yu.Yu. Ilinsky at the Laboratory of Molecular Genetics of Insects, Institute of Cytology and Genetics, Siberian Branch of the Russian Academy of Sciences.

The species is distributed in the forest zone of the Palaearctic. Its larvae develop as endoparasitoids of adult bark beetles *Ips amitinus*, *I. typographus*, and *Hylesinus fraxini* Pz. (Tobias, 1971; Kenis et al., 2004; Georgiev and Takov, 2005).

In West Siberia, the species is very rare; it was collected only once from the surface of *Picea obovata* logs infested with *I. typographus* (Kolomiets and Bogdanova, 1980).

DISCUSSION

The above list of insect species that are natural enemies of *I. amitinus* in Siberia was obtained during the first, short-term stage of a study of entomophages of this alien species, carried out in a limited area. Although this list cannot be considered complete, it allows us to give a preliminary characteristic of the complex of entomophages associated with *I. amitinus*. Among other things, such a characteristic is needed to organize further studies.

Analysis of the literature sources has shown that most of the predatory and parasitic insects feeding on *I. amitinus* within its secondary range are widespread representatives of the local fauna already known in West Siberia, which have established new trophic relationships with the invasive bark beetle. Of interest from the faunistic point of view are *Phloeonomus sjoebergi*, *Epuraea dolosa*, and *Ropalophorus clavicornis* found in the galleries of *I. amitinus*, since the two former species were previously unknown in Siberia, and *R. clavicornis* is a rare and little known species in the region. Certain ecological specificity is given to the complex of *I. amitinus* entomophages by *Medetera penicillata*, a predator of Far Eastern origin, which has apparently spread to Siberia together with *Polygraphus proximus* and currently acts as the principal regulator of its abundance in Siberian fir forests. It emerged that *M. penicillata* was able to easily switch to a new trophic object, namely *I. amitinus*.

Among the identified entomophages of *I. amitinus* in its invasion area, four trophic groups can be distinguished based on the regularity of their presence in the bark beetle galleries and the nature of their association with *I. amitinus* as prey or host. It should be noted that the available literature data are often ambiguous, since the trophic biology of xylophilic species in their natural habitats is difficult to characterize.

1. Obligate predators. 11 species: *Scoloposcelis pulchella*, *Nudobius lentus*, *Thanasimus femoralis*, *Medetera excellens*, *M. fasciata*, *M. penicillata*, *M. pinicola*, *M. signaticornis*, *M. striata*, *Xylophagus cinctus*, and

Lonchaea collini. Of these, *Th. femoralis* and *M. fasciata* were highly abundant during our research.

2. Facultative predators, combining zoophagy with other trophic variants. 15 species: *Tachyta nana*, *Homalota plana*, *Philonthus decorus*, *Phloeonomus sjoebergi*, *Placusa complanata*, *Cylister linearis*, *Paromalus parallelepipedus*, *Plegaderus vulneratus*, *Epuraea dolosa*, *Glischrochilus quadripunctatus*, *Pytho depressus*, *Corticeus fraxini*, *C. linearis*, *Zabrachia minutissima*, and (provisionally) *Bitoma crenata*. A number of species of this group can equally well be classified as facultative sapromycetophages. The rove beetle *Placusa complanata* was the most abundant species of this group in the galleries of *I. amitinus*.

3. Ectoparasitoids developing in larval hosts: *Dinotiscus eupterus* and *Rhopalicus tutela* (Pteromalidae).

4. Endoparasitoids developing in adult hosts: one species, *Ropalophorus clavicornis* (Braconidae).

The list of natural enemies of *I. amitinus* in its invasion areas will certainly be supplemented in the course of further detailed studies. For example, of 11 parasitoid species infesting the small spruce bark beetle in Europe (Kenis et al., 2004; Jurc and Bojović, 2006), 9 also occur in West Siberia. Besides *Dinotiscus eupterus*, *Rhopalicus tutela*, and *Ropalophorus clavicornis*, whose association with *I. amitinus* was confirmed by our material, these are *Coeloides bostrichorum* Gir., *Dendrosoter middendorfi* (Ratz.), *Roptrocerus mirus* (Walk.), *R. xylophagorum* (Ratz.), *Tomicobia seitneri* (Ruschka), and *Eurytoma arctica* Thoms. The list of *I. amitinus* entomophages may also be supplemented with some predators, especially those from the species-rich families Histeridae, Staphylinidae, Nitidulidae, Tenebrionidae, and Dolichopodidae.

The role of particular species and the whole complex of natural enemies in regulating the abundance of invasive *I. amitinus* populations will be assessed in further studies. Of particular interest in this respect is *Thanasimus femoralis*, one of the most effective predators that destroys bark beetles throughout the entire growing season, including both the adults penetrating into trees and the immature stages under the bark. High abundance of *Th. femoralis* in *I. amitinus* outbreak foci was revealed by an attempt to use traps baited with *I. typographus* pheromone to reduce the abundance of *I. amitinus*, undertaken by the Russian Forest Protection Center in 2020 in Tomsk and Kemerovo provinces. However, the pheromone trap method negatively affected the entomophage, which was captured in great numbers (Krivets, 2020). Therefore, the existing methods of forest protection should be improved to ensure preservation and use of beneficial insects in modern forestry.

CONCLUSIONS

The studies conducted in West Siberia has revealed 26 species of predatory insects and 3 species of parasitoids associated with the small spruce bark beetle *Ips amitinus*. All the predatory species are recorded here for the first time for this bark beetle, both in the invasion region and throughout its range.

The realized and potential abilities of the native fauna to produce a complex of entomophages associated with an invasive dendrophagous species have been studied. The trophic groups and common species of entomophages have been identified that should be studied as potential regulators of *I. amitinus* abundance and promising agents of biological protection of Siberian pine forests.

The species composition of the natural enemies of *I. amitinus* in its invasion areas in West Siberia has been determined, and information about entomophages of *I. amitinus* throughout its range has been significantly expanded and improved.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflict of interest.

Statement on the welfare of animals. All the applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All the procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

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