

First record of the invasive bark beetle Polygraphus proximus Blandford (Coleoptera: Curculionidae, Scolytinae) in the Republic of Kazakhstan

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The four-eyed fir bark beetle, Polygraphus proximus Blandford, 1894 (Coleoptera: Curculionidae, Scolytinae), is an aggressive invasive species originating from Far East. Over the past two decades, it distributed across Siberia, traversed the Urals and invaded some regions of the European part of Russia. In the secondary range, the pest kills heathy tree stands of Siberian fir, Abies sibirica Ledeb. (Pinaceae), both in native forests and man-made plantings, resulting in profound ecological and economic consequences. Here we report the first documented occurrence of this invasive pest in the Republic of Kazakhstan. Infested Siberian fir trees were discovered in the forest nearby Karaguzhikha village (East Kazakhstan Region), approximately 43 km away from Novoaleiskoye village (Altai Territory, Russia), where the pest was detected in 2016. The presence of trees colonized by the invasive pest and dead trees with specific symptoms in the examined forest stand suggest that P. proximus has likely been present in northeastern Kazakhstan for around a decade. The illustrations of affected habitat, male and female beetles and their morphological features are provided, and the early data on the damage caused by *P. proximus* and the potential for range expansions are discussed. The monitoring would be required to define the actual frontier of the pest distribution in Kazakhstan. Furthermore, it is imperative to alert the relevant authorities in Kazakhstan about the potential threat posed by this invasive tree-killer to native fir stands in the country.

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Keywords

Alien pest, four-eyed fir bark beetle, invasion, Siberian fir, damaged forest, northeastern Kazakhstan, first record

Introduction

The four-eyed fir bark beetle, *Polygraphus proximus* Blandford, 1894 (Coleoptera: Curculionidae, Scolytinae), is a coniferous pest species originating from the Russian Far East (Khabarovsk and Primorsky Territories, Sakhalin and the Kuril Islands), Japan, Northeast China, and Korea (Kurentsov 1941; Stark 1952; Krivolutskaya 1996). In its native range, it develops on Far Eastern firs *Abies nephrolepis* (Trautv. ex Maxim.) Maxim., *A. sachalinensis* F. Schmidt, *A. holophylla* Maxim., *A. mariesii* Mast., *A. homolepis* Siebold & Zucc., *A. veitchii* Lindley (Niijima 1941; Kurentsov 1941; Nobuchi 1966; Krivolutskaya 1996). Usually, it populates the trees weaken by abiotic and/or biotic factors (fire, pathogens, defoliating insects etc.), wind-fallen trees and cut logs (Kurentsov 1941; Nobuchi 1966). However, colonization of healthy trees in native range with subsequent mass mortality is not ruled out. For instance, in Japan the bark beetle caused mass decline of *A. sachalinensis* in 1970s (Koizumi 1977), whereas in 2018, it notably affected forest stands predominated by *A. veitchii* (Takagi et al. 2018).

For the first time outside of its native range, an outbreak of *P. proximus* was detected in Kemerovo Region (Western Siberia, Russia) in 2005 (Baranchikov et al. 2011a). However, the species was identified only in 2008, after its appearance in Tomsk Region (Baranchikov et al. 2011a; Krivets et al. 2015a). Since then, the pest was recorded across Siberia becoming the main factor of fir stands decline (Kerchev 2014a; Krivets et al. 2015a, 2015b, 2015c). By 2018 in Krasnoyarsk Territory (Central Siberia) alone, fir mortality associated with *P. proximus* occurred on the territory of 541,4 thousand ha, with a cascade of ecological and economic consequences (Pavlov et al. 2020). This invasive pest poses a significant threat to the survival of *A. sibirica*, given its distribution across the primary range of the host and the ability to kill fir trees before they reach reproductive stage (Gninenko 2012).

Abies sibirica was found to be highly susceptible to the new pest (Krivets et al. 2015a). In the trunks of this plant, the sclereids are situated less densely compared to that in the Far Eastern firs, making bark of the former species easy penetrable for *P. proximus* (Baranchikov et al. 2014a). Proceeding resin flow on Siberian fir trunks, occurring as the reaction to the continuous beetle attacks and colonization, significantly weakens the trees (Astrakhantseva et al. 2014). Moreover, Far Eastern phytopathogenic fungi *Grosmannia aoshimae* (Ohtaka et Masuya) Mas. et Yamaoka (Ophiostomataceae, Ascomycota), vectored by this bark beetle, which arrived with *P. proximus* to Siberia, deteriorates tree health accelerating forest decline (Pashenova et al. 2018).

Besides firs, in primary and secondary ranges the bark beetle can occasionally colonize coniferous species from other genera: *Picea, Pinus, Larix* and *Tsuga* (all from Pinaceae) (Niijima 1941; Nobuchi 1966; Kerchev 2014a; Krivets et al. 2015a). However, in mixed forests, it exhibits a preference for firs, *Abies* spp. (Niijima 1941; Kerchev 2014a; Krivets et al. 2015a).



In last years, the pest crossed the Ural Mountains and continued expanding its secondary range in the European part of Russia, providing spectacular tree decline in nature and man-made plantings (Chilakhsaeva 2008; Seraya et al. 2014; Dedyukhin, Titova 2021; Fir trees are being destroyed by the thousands 2023; Semenova 2023; The four-eyed fir bark beetle threatens... 2023). In 2012, *P. proximus* foci encompassing an area of 16,3 ha was identified in Altai Territory, whereas in 2013, the foci covering an area of 10,7 thousand ha was already documented in the Altai Republic (Inventory... 2022).

In early October 2016, Alexei A. Meshcherikov, a forest engineer from the Russian Centre of Forest Health (Pushkino, Moscow Region, Russia), discovered a foci of *P. proximus* in the forest nearby Novoaleiskoye village in Altai Territory (50°49'4"N 82°24'17"E), i.e. 5 km north from the state border of Russia with Kazakhstan. He traced the spread of the pest in Altai towards the border with Kazakhstan, and in spring 2017, in his letter to Yuri N. Baranchikov (the coauthor of the present paper), Meshcherikov mentioned about potential presence of the pest in fir stands at the source of Bulochniy Alley River situated near the border with Kazakhstan. Furthermore, he suggested that the pest might have already invaded the fir stands of the adjoining Uba River territory in northeastern Kazakhstan.

In 2021, *P. proximus* distributed across all districts of the Altai Territory, where *A. sibirica* is present, and subsequently a quarantine zone on this pest was established on the territory of more than 11 thousand ha (Altai... 2021).

The documentation of P. proximus spread on the territory of Altai and early observations of Meshcherikov altogether served for us as a motive to explore the northeastern territories of Kazakhstan adjoining Russia for the pest occurrence.

Materials and methods

In northeastern Kazakhstan, field work was carried out by Valentin V. Rudoi (the coauthor of this paper) in natural forest stands in two localities: (1) in the vicinity of the village of Karaguzhikha, Glubokovsky district (located in about 43 km from the Russian village Novoaleiskoye, Altai Territory, on a straight line) and (2) in the vicinity of the eco-village Chernaya Uba situated at the foot of Mount Lyamin Belok and Stanovoy Ridge (Ridder) (located in about 110 km from Novoaleiskoye) (Fig. 1). In the first locality, the survey were carried out on the area of 0.6 ha, in the second on an area of 0.16 ha, in the period of July 8-15, 2023.

The investigated biotopes were represented by black taiga forest predominated by *Abies sibirica*, with an admixture of *Betula pendula* Roth (Betulaceae) and *Populus tremula* L. (Salicaceae). The first visited forest stand (near Karaguzhikha) was situated on the northern slop, at the altitude of 514 m a.s.l.; the second (near Chernaya Uba) was located on the western slop (50°36'28"N 83°48'44"E) at the altitude of 860 m a.s.l.





Figure 1. The studied area in Kazakhstan in 2023. **(A-B)** the surveyed localities: **1** – the forest near Karaguzhikha village; **2** – the surroundings of Chernaya Uba eco-village. In the zoomed map **(B)**, Novoaleiskoye village (Altai Territory, Russia) nearby which Alexei A. Meshcherikov detected the foci of P. proximus in 2016 (see Introduction) is indicated by red point. **(C)** the biotope examined near Karaguzhikha, photo: V.V. Rudoi.

Overall, 164 fir trees were examined at the locality near Karaguzhikha (tree height 10-14 m, trunk diameter 10-22 cm). Their health category was accessed according to the classification given in Krivets et al. (2015a). In the vicinity of Chernaya Uba eco-village, 20 live fir trees and 14 windfallen trees (i.e. fallen approximately 1-3 years ago, in 2020-2022) were examined. The tree trunk diameter was estimated at a distance of about 1.5 m from forest floor. A visual inspection of trees and their trunks was carried out to document the overall tree statement, presence of red needles, drying branches, resin flow on the main trunk, the bark beetle exit holes etc. Number of exit holes was counted and accessed per dm², as per Krivets et al. (2015a). When the exit holes were detected, the bark pallets (10×20 cm) were dissected, opened trunk and bark pallets were inspected for the presence of the typical galleries, as well as larvae, pupae and imago, and remnants of beetles (i.e. their body parts: heads, abdomens, etc.). All bark beetle adults found in the galleries and their remnants were collected. They were placed in microtubes with a 95% alcohol solution for species identification and preservations for further DNA barcoding (the latter is in progress and will be present in a separate study). The insects and bark pallets are stored in the collection of Sukachev Institute of Forest (SIF) SB RAS (Krasnoyarsk, Russia); few bark pallets have been also deposited in the private collection of the second author.

Morphological identification of insects was done using the keys published in Stark (1952) and Krivolutskaya (1996). The tree damage symptoms were determined using the methodical book (Krivets et al. 2015a).



The map with sampled localities was produced using the online mapping software SimpleMappr (David 2010). The biotope, damaged trees, dissected tree trunks, the galleries and the insects were photographed using a digital camera on a Samsung Galaxy A50 smartphone (South Korea) and a Sony DSC-W830 digital camera (China). The photographs of localities were edited in Paint.net, a free (except for Microsoft Store) raster graphics editor for Windows NT based on NET Framework (Paint.NET 2004). Photographs of the beetles were taken with a Canon 50D camera with an MP-e65 lens. Photographs of maxilla, labium, proventriculus, and male genitalia were taken with a Zeiss Axio Scope A1 microscope. The photographs of insects were revised in Adobe Photoshop 24.0.1.

Result

Coleoptera: Curculionidae, Scolytinae

Polygraphus Erichson, 1836

Polygraphus proximus Blandford, 1894

Figs 2-5

Synonyms. Polygraphus magnus Murayama, 1956 (Wood 1992, p. 84), *P. laticollis* Eggers (Wood & Bright, 1992), *P. miser* Blandford, 1894, *P. nigricans* Kurentsov, 1948, *P. oblongus* Blandford, 1894 (Knizek 2011, p. 214), *P. abietis* Kurentsov, 1941 (Krivolutskaya 1996, p. 340; Mandelshtam 2013, p. 1), *P. horyurensis* Murayama, 1937 (Mandelshtam 2013, p. 1).

Material examined. The Republic of Kazakhstan, East Kazakhstan Region, Glubokovskiy district, nearby Karaguzhikha village, 50°45'49"N 83°01'30"E, 514 m, 08.07.2023, 3 bark pallets with characteristic galleries (dry collection), 2 beetles, 4 heads, 1 left and right corium, 3 abdomens and 3 pronotums (in 95% ethanol solution), deposited in SIF, Rudoi V.V. coll., Efremenko A.A. leg.

Diagnostic characters (Figs 2, 3). The beetles and the remnants (heads, abdomens etc.) of *P. proximus* were found under the bark of infested fir trees (*Abies sibirica*) nearby Karaguzhikha, northeastern Kazakhstan. No adults were located under the bark of fir trees near Chernaya Uba eco-village. Below the diagnostic characters of the genus and the species are summarized and the beetles and their features are illustrated in the original figures and drawing.

The characteristic features of the genus *Polygraphus* include the following: 1) elytral bases slightly emarginated at suture and scutellum obsolete, 2) pronotun unarmed by asperites, 3) eye entirely divided to two parts (Wood 1986). In Kazakhstan, two other closely related species, *Polygraphus poligraphus* (Linnaeus, 1758) and *P. punctifrons* Thomson, 1886 are present (Stark 1952). However, *P. proximus* can be distinguished from them by the antennal structure: 5-segmented antennal funicle (without pedicel) and vestiture on pronotum of fine, sparse hairs and elongate scales. In *P. poligraphus* and *P. punctifrons*, funucles are 4-segmented without pedicel and vestiture on pronotum of elongate scales only.

The adult of *P. proximus* is 2.50–3.50 mm long and 1.53–1.65 times as long as wide. Color dark brown to black, surface of pronotum and elytra with abundant pale and light brown hair and scales (Fig. 2 A, B). Frons of male and female dimorphic: in male with two central tubercles in level of upper eye margins, vestiture in central area of fine, sparse setae (Fig. 2A, D); in female without tubercles, surface with abundant longer setae (Fig. 2B, C, E). Antennae reddish brown, scape twice as long as funicle, pedicel scyphoid, antennal funicle five-segmented, segments equal in size, antennal club ovoid form with rounded apical margin. The length and form of club is variable (Fig. 2F). Maxilla with elongate subgaleal area, the galea and lacinia wide, with twelve obtuse spines (Fig 3A). Labium: mentum elongate and flat, without tuft of setae, the first segment of palpus with short pointed bristles (Fig. 3B). Pronotum dark brown, shining 0.73–0.77 times as long as wide,



surface without asperites punctured by numerous points, vestiture on pronotum of fine, sparse hairs and elongate scales. Scutellum obsolete. Elytra weakly shining, 1.51–1.54 times as long as wide. Elytral base weakly elevated with two rows of asperites, also sparse small asperites are present on intersriae of elytral disc. Declivity of elytra evenly rounded. Metepisternum, metaventrite and abdomen dark brown, dull. Vestiture consisting of fine short pale hairs. Legs reddish brown covered by pale setae.

Male genitalia (Fig. 3). The male aedeagus revealed normal proportions, tegmen open dorsally (Fig. 3D), penis apodemes (apophises) long, same with length of penis body (Fig. 3E). The spiculum is slightly curved, about as long as the penis including apodemes. Proventriculus: anterior plate distinctly emarginated in apical margin, usual to middle of anterior plate, inner lateral margins of the emargination bearing a row of some strongly curved teeth along margins (Fig. 3C), posterior plate slightly longer than the anterior, closing teeth extend middle of masticatory brush (Nobuchi 1969).



Figure 2. The adults of Polygraphus proximus. **(A, D)** male; **(B, C, E)** female; **(F)** antennae variability. Following characters are highlighted: tubercles (in male) vs. setae (in female) on frons; eyes divided to two parts (eye/2); five-segmented (5-s) funicle. Photos & drawing: A.V. Petrov.



Damage detection (Figs 4, 5). Nearby Karaguzhikha, following damage symptoms of *P. proximus* on fir trees were revealed: resin flow on fir trunks, round exit holes (2 mm in diameter) on trunks, two-armed horizontal mother galleries under the bark in phloem layer (exceptionally three-armed mother galleries having starlike pattern were also spotted), oval pupal chambers deepen in sapwood (Fig. 4).

Overall, 85 out of 164 trees (i.e. 52%) examined nearby Karaguzhikha had no noticeable external damage and looked healthy. They corresponded to the category I "healthy trees without attack attempts", as per classification in Krivets et al. (2015a). Nineteen trees (12%) had signs of attacks – fresh and/or old attempts of grinding into trunks (i.e. round entrance holes collapsed with resin drips; dried or relatively fresh drips). They corresponded to the category II-III (Krivets et al. 2015a), which could be here summarized as "weaken or significantly weaken, with attack attempts, but not colonized trees".





Figure 3. The internal sclerotized organs of Polygraphus proximus beetle. (A) maxilla, (B) labium, (C) proventriculus, (D-E) male genitalia (top and side views respectively). Photos: A.V. Petrov.

Other 42 trees (26%), with trunk diameter from 9 to 20 cm, had pronounced external damage signs



(resin flow on trunks, numerous exit holes). Their crowns had green needles (in some cases a bit paler green than in healthy tree); in few cases, sparse red needles were present on low branches (Fig. 4A). In some trees, low branches were dead (Fig. 4). By external appearance, such trees corresponded more to the category IV "colonized trees" (Krivets et al. 2015a). However, these trees had green needles across the whole crown, not largely red in the lower part of tree crowns as identified for this category in Krivets et al. (2015a). In fact, if the pest population is low, the needles on the infested trees can stay green for an extended period; in such case, the colonized trees with green crown should be classified to the category IV (Krivets: personal communication).



Figure 4. Damage symptoms of Polygraphus proximus on fir trees (Abies sibirica) nearby Karaguzhikha village (northeastern Kazakhstan), July 2023. (**A**) resin flow on the main trunk of fir tree; (**B**) mother galleries (MG2 – two-armed, MG3 – three-armed) and pupal chambers (PC) in sapwood; (**C**) the bark with exit holes; (**D**) prints of mother and larval galleries in the bark. Photos: V.V. Rudoi.



On 12 out of these 42 trees, the bark was opened and the typical mother galleries (mostly twoarmed) with larval tunnels and oval pupal champers were located in sapwood (and partially in the inner part of the bark pallets). The beetles and/or their remnants (see material examined) were found under the bark and in sapwood in seven out of 12 dissected tree. In 42 surveyed trees, the number of exit holes ranged from 7 to 24 per dm², with an average value of 13.6 ± 6 exit holes per dm². In general, such data indicate low density of *P. proximus* in the studied forest stand in Kazakhstan. Following Krivets et al. (2015a), the value below 20 exit holes/dm² means low density, 20,1-30 holes/dm² – average, > 30 holes/dm² – high density.

In the examined forest stand, no fir trees were assigned to the category V "freshly dead trees", with red crowns (i.e. red needles still attached to the branches). The remaining 18 trees (11%), with the trunks of a diameter 17–23 cm, were dead, but they were still standing trunks with easily detachable low branches, with multiple exit holes on the bark and partially loose bark on the main trunk (Fig. 5). They corresponded to the category VI "old dead trees" (Krivets et al. 2015c).

In the vicinity of Chernaya Uba, 20 fir trees (with green crowns) were examined on July 14, 2023, and no characteristic exit holes or other signs of *P. proximus* presence were detected on them. Additionally, 14 wind-fallen fir trees were surveyed. On one of them, which trunk carried the highest number of exit holes (i.e. 22 exit holes per dm²), the bark was dissected for examination of galleries. None of the examined galleries resembled to *P. proximus*. Overall, 26 beetles were collected from beneath the bark. All of them were all identified as *Dryocoetes hectographus* Reitter, 1913, a bark beetle species known for its association with firs and earlier recorded for Eastern Kazakhstan (Stark 1952; Kostin 1973; Knizek 2011).

Discussion

Since its first detection in Moscow Region in 2006 (Chilakhsaeva 2008), *P. proximus* has been consistently recorded in 14 administrative regions across both Asian and European parts of Russia over the past 17 years (Table 1). The early record of *P. proximus* from Leningrad Region (Mandelshtan, Popovichev 2000) was not included in the table, as it appeared to be questionable (Mandelshtam, Selikhovkin 2020; Selikhovkin et al. 2020).

The invasive pest continues extending its secondary range in Russia, causing huge damage to fir stands, with a cascade of ecological and economic consequences (Gninenko, Klyukin 2011; Mel'nik et al. 2018). In the European part of Russia, it presently occurs in Moscow Region, the Republics of Udmurtia and Tatarstan, and Perm Region (Rosselkhoznadzor for the Republic of Tatarstan... 2019; Baranchikov et al. 2020; Dedyukhin, Titova 2021; Gninenko et al. 2022; Semenova 2023) (Table 1). The records of new foci in this and other regions may yet emerge. Furthermore, our novel data indicates that the secondary range of the pest has extended beyond the border of Russia, and *P. proximus* is now present in Kazakhstan (Table 1). This invasive pest is considered a quarantine organism for Kazakhstan, and since 2015, it was included in the A1 list of quarantine species of the Republic of Kazakhstan (On approval of the list of quarantine objects... 2015).

N⁰	Region	Detection year	Reference			
RUSSIA						
Siberia						
1	Kemerovo Region	20051	Baranchikov, Krivets 2010; Gninenko, Klukin 2011			
2	Tomsk Region	2008	Krivets, Kerchev 2011			
3	Krasnoyarsk Territory	2009	Baranchikov at al. 2011a			
4	Altai Republic	2011	Baranchikov et al. 2011b			
5	Novosibirsk Region	2012	Krivets et al. 2014			
6	Altai Territory	2012	Krivets et al. 2013			
7	Khakassia Republic	2013	Baranchikov et al. 2013			



8	Irkutsk Region	2017	Bystrov, Antonov 2019			
9	Buryatia Republic	2021	Kerchev, Bykov 2023			
Ural						
10	Chelyabinsk Region	2022	Fir trees are being destroyed by the thousands 2023			
European part of Russia						
11	Moscow Region	2006	Chilakhsaeva 2008			
12	Udmurtia Republic	2019	Dedyukhin, Titova 2021			
13	Tatarstan Republic	2019	Rosselkhoznadzor for the Republic of Tatarstan 2019			
14	Perm Region	2022	Semenova 2023			
KAZAKHSTAN						
15	East Kazakhstan Region	2023	Kirichenko et al. 2023 (this article)			

 $\textbf{Table 1.} \textit{ The chronology of Polygraphus proximus detection in Russia and Kazakhstan^*}$

Early pest detection is a challenging task as there are currently no proven methods to identify the presence of *P. proximus* at early stage and detect tree infestation before the health of forest stands begins to deteriorate (Krivets et al. 2015c). It explains why in all cases in Russia and now in northeastern Kazakhstan this bark beetle was discovered already causing noticeable damage to fir stands. Ongoing efforts are being made to develop effective monitoring system (Gninenko et al. 2016; Krivets et al. 2018a) including pheromone monitoring (Viklund et al. 2022), but the timeline for the implementation of such systems remains uncertain.





Figure 5. Dead trees of Abies sibirica with loose bark and damage of Polygraphus proximus in the forest stand nearby Karaguzhikha village (northeastern Kazakhstan), July 2023. (**A**) dead trees with loose bark; (**B**, **C**) mother galleries (indicated by arrows) in sapwood; (**D**) exit holes in the bark. Photos: V.V. Rudoi.

The damage caused to firs by *P. proximus* documented in our study indicates that the pest has been present in northeastern Kazakhstan for at least a decade. However, to clarify its arrival time, additional research would be needed, in particular, the involvement of dendrochronological dating. For instance, in the beetle foci documented in 2009 in Krasnoyarsk Territory (Russia), by



implementing this dating approach, it was showed that the infested trees started dying in 1976, i.e. 34 years before the pest was documented in this locality (Baranchikov et al. 2014b). Remarkably, by 2011, this forest stand was wholly killed by the bark beetle (Baranchikov et al. 2014b). In Tomsk Region, where the decline of fir forest was initially documented in 2010–2011 (Baranchikov et al. 2011; Krivets et al. 2018b), dendrochronological dating has revealed that the infested trees started dying since the year 2000, suggesting that the pest arrived to region in about mid-1990s (Demidko 2014).

Overall, it takes about a decade from early infestation (and early tree mortality) to the whole tree stand decline in the pest foci. The analysis of satellite images obtained for the period for 2005–2014 for two *P. proximus* foci in Krasnoyarsk Territory showed that only 0.3% of trees died by the end of 2005, 17% of them declined five years later (in 2010), and 70% of trees died in eight years (in 2012), followed by the total tree stand collapse in 2014 (calculated based on data from Pavlov et al. 2020).

Considering the ability of *P. proximus* to infest healthy Siberian fir trees, it is likely to expect further spread of the pest on the territory of the European Russia and Kazakhstan. In Kazakhstan, apart from the Rudny Altai, *A. sibirica* grows in the Tarbagatay Range and the Jungar Alatau, and overall it accounts for 17% of all forests in the country (Gribanov et al. 1970). The expansion of *P. proximus* into these regions may have already occurred or could potentially happen in the near future.

Furthermore, this pest may penetrate the neighboring Central Asian countries, where potential host plants are present. The Semenov's fir (*Abies semenovii* B. Fedtsch), which is presently treated as a subspecies of *A. sibirica*, i.e. *A. sibirica* subsp. *semenovii* (B. Fedtsch.) (Farjon 2010), could potentially serve a new host for the pest. It grows in the western Tian Shan, the Zailiysky Alatau and the Talas Alatau in Kyrgyzstan (Gann 1970). According to molecular genetic data, *A. sibirica* and *A. sibirica* subsp. *semenovii* are clustered in one section, Pichta (Semerikova, Semerikov 2014a, 2014b), but by morphological features *A. sibirica* was treated under the section Balsamea (Farjon, Rushforth 1989). Despite the fact that this fir species has not been attacked by *P. proximus* in the collection of firs at the Main Botanical Garden of the Russian Academy of Sciences in Moscow (Seraya et al. 2014), it is premature to make conclusions regarding its resistance to the pest.

Polygraphus proximus has been included in the list of quarantine pests for EPPO (European and Mediterranean Plant Protection Organization) region countries (EPPO Global Database 2023). The European species of the section Abies, such as *Abies alba* Mill. and *A. nordmaniana* (Steven) Spach, are relatively resistant to the attacks of this pest as per observations in the Main Botanical Garden in Moscow (Seraya et al. 2014), as well as to its main phytopathogenic "companion", *G. aoshimae* (Baranchikov et al. 2018). In contrast to *A. sibirica*, these European fir species have thicker protective tissues and a higher degree of sclerification (Astrakhantseva et al. 2023). Other European fir species from this section, such as *A. cephalonica* Loudon, *A. nebrodensis* (Lojac.) Matte, *A. borisii-regis* Mattf, can also be resistant to the invader. The relict Mediterranean fir species, *A. pinsapo* Boiss. and *A. numidica* de Lannoy ex Carrière, belong to another section, Piceaster (Farjon 2010), and their resistance requires further study.

In is important to mention that besides firs, *P. proximus* is able to develop on other conifer species, including Scots pine (*Pinus sylvestris* L.), Siberian spruce (*Picea obovata* Ledeb.), Siberian pine (*Pinus sibirica* Du Tour), and Siberian larch (*Larix sibirica* Ledeb.) etc. (Kerchev 2012). The former plant species is also present in European countries. The potential to develop beneficial trophic associations by this invasive pest should be considered when assessing the risks of its distribution to new regions and countries.

Conclusions



Our first record of the invasive bark beetle *P. proximus* in Kazakhstan, where it was revealed already causing noticeable damage to fir forest, suggests that the pest has been present in the country for at least a decade. Its further spread on the territory of this republic is not ruled out. Therefore, it is crucial to promptly inform the relevant authorities in Kazakhstan about the potential threat posed by this invasive treekiller to forest health in the country. Furthermore, considerable attention should be directed towards monitoring the continuing spread of this pest in the European part of Russia and mitigating the risk of its invasion into Eastern Europe and further.

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References

Altai activists ask Rosselkhoznadzor "not to rashly cut down" polygraph-infested forests. Bankfaks, informatsione agentstvo. (accessed on: 2023-09) https://www.bankfax.ru/news/142431/ [In Russian]

Astrakhantseva NV, Pashenova NV, Pet'ko VM, Baranchikov YuN (2014) Reaction of trunk tissues of Siberian fir and Khingan fir to inoculation with the phytopathogenic fungus *Grosmannia aoshimae* (Ohtaka, Masuya et Yamaoka) Masuya et Yamaoka – the associate of the foureyed fir beetle. Proceedings of Saint Petersburg Forestry Academy (Izvestia Sankt-Peterburgskoj Isotehknicheskoj Akademii) 207: 142-153. [In Russian]

Astrakhantseva NV, Seraya LG, Pashenova NV, Kozhenkova AA, Baranchikov YuN (2023) Anatomical features of the bark as a factor of fir species resistance to infestation by the four-eyed fir bark beetle. Siberian Forestry Journal 5: 68–81. https://doi.org/10.1134/10.15372/SJFS20170101 [In Russian]

Baranchikov YuN, Astrakhantseva NV, Shchurov VI, Aleksandrova MS, Mukhina LN, Seraya LG, Pashenova NV (2014b) Phloem sclereids as a possible factor of fir resistance to invasive bark beetle attacks. Proceedings of the International Exhibition and Scientific Congress "Interexpo GEO-Siberia" 3 (2): 277–282. [In Russian]

Baranchikov YuN, Bibin AR, Demidko DA, Efremenko AA, Pashenova NV, Pertsovaya AA, Seraya LG (2018) Preliminary assessment of the resistance of fir species to the components of the invasive entomo-mycological complex. In: Musolin DL, Selikhovkin AV (Eds) Dendrobiotic invertebrates and fungi and their role in forest ecosystems. The Kataev Memorial Readings – X. Saint Petersburg State Forest Technical University, October 2018, Saint Petersburg, 4. [In Russian]

Baranchikov YuN, Demidko DA, Babichev NS, Petko VM (2013) Republic of Khakassia, then everywhere: the four-eyed fir bark beetle was found in another region of Siberia. In: Musolin DL, Selikhovkin AV (Eds) Dendrobiotic invertebrates and fungi and their role in forest ecosystems. The



Kataev Memorial Readings – VII. Saint Petersburg State Forest Technical University, November 2013, Saint Petersburg, 10. [In Russian]

Baranchikov YuN, Demidko DA, Laptev AV, Petko VM (2014a) The dynamics of Siberian fir trees decline in the outbreak of the four-eyed fir bark beetle. Moscow State Forest University Bulletin – Lesnoy Vestnik 18 (6): 132–138. [In Russian]

Baranchikov YuN, Krivets SA (2010) On professionalism in identifying insects: how the emergence of a new aggressive pest of fir in Siberia was overlooked. In: Anyushin VV (Ed.) XIV international scientific school-conference of students and young scientists "Ecology of Southern Siberia and adjacent territories". Abakan: Publishing house of the State Educational Institution of Higher Professional Education "Khakass State University named after N.F. Katanov", the proceedings 14 (1), 50-52. [In Russian]

Baranchikov YuN, Krivets SA, Petko VM, Kerchev IA, Mizeeva AS, Anisimov VA (2011b) In pursuit of the four-eyed fir bark beetle *Polygraphus proximus* Blandf. In: Anyushin VV (Ed.) XV international scientific school-conference of students and young scientists "Ecology of Southern Siberia and adjacent territories". Abakan: Publishing house of the State Educational Institution of Higher Professional Education "Khakass State University named after N.F. Katanov", the proceedings 15 (1): 52–54. [In Russian]

Baranchikov YuN, Petko VM, Astapenko SA, Akulov YeN, Krivets SA (2011a) The four-eyed fir bark beetle – a new aggressive pest of fir in Siberia. Moscow State Forest University Bulletin – Lesnoy Vestnik 4 (80): 78–81. [In Russian]

Baranchikov YuN, Seraya LG, Efremenko AA, Demidko DA (2020) There and back again: the Far Eastern invaders on fir and ash trees in Moscow. In: Musolin DL, Selikhovkin AV (Eds) Dendrobiotic invertebrates and fungi and their role in forest ecosystems. The Kataev Memorial Readings – XI. Saint Petersburg State Forest Technical University, November 2020, Saint Petersburg, 76–77. [In Russian]

Bystrov SO, Antonov IA (2019) First Record of the four-eyed fir bark beetle *Polygraphus proximus* Blandford, 1894 (Coleoptera, Curculionidae: Scolytinae) from Irkutsk Region, Russia. Entomological Review 99 (1): 54–55. https://doi.org/10.1134/S001387381901007X

Chilakhsaeva EA (2008) The first find of *Polygraphus proximus* Blandford, 1894 (Coleoptera, Scolytidae) in the Moscow region. Bulletin of the Moscow State Society of Natural Scientists. Department of Biology 113 (6): 39-42. [In Russian]

David P (2010) Shorthouse. SimpleMappr, an online tool to produce publication-quality point maps. (accessed on: 2023-08) www.simplemappr.net

Dedyukhin SV, Titova VV (2021) Finding of the bark beetle *Polygraphus proximus* Blandford, 1894 (Coleoptera, Curculionidae: Scolytinae) in Udmurtia. Russian Journal of Biological Invasions 2: 32–39. https://doi.org/10.35885/1996-1499-2021-14-2-32-39 [In Russian]

Demidko DA (2014) Dating of four-eyed fir bark beetle *Polygraphus proximus* Blandford (Coleoptera: Curculionidae: Scolytinae) invasion into Tomsk Rregion (Western Siberia). The Proceedings of Saint Petersburg Forestry Academy (Izvestia Sankt-Peterburgskoj Isotehknicheskoj Akademii) 207: 225–234. [In Russian]

EPPO Global Database (2023) *Polygraphus proximus* (POLGPR), Categorization. (accessed on: 2023-09) https://gd.eppo.int/taxon/POLGPR/categorization

Farjon A, Rushforth KD (1989) A classification of Abies Miller. (Pinaceae). Notes from the Royal



Botanic Garden, Edinburgh 46: 59–79.

Farjon AA (2010) Handbook of the World's Conifers. Brill Academic Publishers, Leiden, 1111 pp. https://doi.org/10.1163/9789047430629

Fir trees are being destroyed by the thousands. Visitors to the Taganay National Park are sounding the alarm due to mass decline of conifers. 74.RU Chelyabinskaya Oblast (accessed on: 2023-08) https://74.ru/text/ecology/2023/06/28/72434447/ [In Russian]

Gann PA (1970) Lesa Kirgizii. Lesa SSSR 5: 78-146. [In Russian]

Gninenko YI, Klyukin MS (2011) Ussuri bark beetle on the territory of Russia. Protection and quarantine of plants (Zashchita i karantin rastenij) 11: 32–34. [In Russian]

Gninenko YuI (2012) New invasive dendrophilous organisms – increasing importance for the country's forests. Ecological and economic consequences of dendrophilous insect invasions: All-Russian Federation conference with international participation (25-27. IX.2012, Krasnoyarsk, Russia). Forest Institute SB RAS, Krasnoyarsk, 12–15. [In Russian]

Gninenko YuI, Klyukin MS, Chilakhsaeva EA, Krivets SA, Kerchev IA, Bisirova EM, Demidko DA, Pashenova NV, Petko VM, Baranchikov YuN (2016) Recommendations for identifying, examining and localizing foci of the Ussuri polygraph in areas of invasion on the territory of the Russian Federation. VNIILM, Pushkino, 32 pp. [In Russian]

Gninenko YuI, Kozadayeva AA, Chilakhsayeva YeA (2022) Population of fir trees by the Ussuri polygraph in Moscow. New challenges – new research: collection of articles of the II International Scientific and Practical Conference (17.XI.2022, Petrozavodsk, Russia). ICNP New Science, Petrozavodsk, 72–77. [In Russian]

Gribanov LN, Lagov IA, Chaban PS (1970) Lesa Kazakhstana. Lesa SSSR 5: 5-77. [In Russian]

Inventory of stem pest foci in (2022) (accessed on: 2023-08) https://altay.rcfh.ru/presscenter/novost i/inventarizatsiya-ochagov-stvolovykh-vrediteley-v-2022-godu/16/12/2022 [In Russian]

Kerchev IA (2012) Experimental study of the possibility of the emergence of new trophic connections of four-eyed fir bark beetle *Polygraphus proximus* Blandf. (Coleoptera: Curculionidae, Scolytinae) in the West Siberian region. Vestnik Tomskogo Gosudarstvennogo Universiteta, Biologiya 3: 169–177. [In Russian]

Kerchev IA (2014a) Ecology of Four Eyed Fir Bark Beetle *Polygraphus proximus* Blandford (Coleoptera; Curculionidae, Scolytinae) in the West Siberian Region of Invasion. Russian Journal of Biological Invasions 5 (3): 176–185. https://doi.org/10.1134S2075111714030072

Kerchev I, Bykov R, Ilinsky Yu (2023) Expansion of the secondary range of *Polygraphus proximus* Blandford (Coleoptera; Curculionidae, Scolytinae): invasion of Khamar-Daban mountains (Republic of Buryatia). Acta Biologica Sibirica 9: 1–11. https://doi.org/10.5281/zenodo.7679805

Knížek M (2011) Scolytinae. In: Löbl I, Smetana A (Eds) Catalogue of Palaearctic Coleoptera. Apollo Books, Stenstrup 7: 204–251.

Koizumi C (1977) Beetle infestations associated with the cutting operations in the spruce-fir forests in Hokkaido. Bulletin of the Government Forest Experiment Station 297: 1–34. [In Japanese, English summary]

Kostin IA (1973) The dendrophagus beetles of Kazakhstan (Buprestidae, Carambycidae, Ipidae).



Publishing House of the Kazakh SSR, Alma-Ata, 287 pp. [In Russian]

Krivets SA, Baranchikov YuN, Pashenova NV, Bisirova EM, Kerchev IA, Petko VM, Pats YeN, Chernova NA (2013) The role of the invasive dendrophage *Polygraphus proximus* Blandf. in modern processes of degradation of fir forests in Southern Siberia. In: III International Conference "Biodiversity, environmental problems of the Altai Mountains and adjacent regions, present, past, future", Gorno-Altaisk, Russia, October 2013, RIO GAGU, Gorno-Altaisk, 262–266. [In Russian]

Krivets SA, Bisirova EM, Kerchev IA, Maslenok YeV, Nozdrenko YaV, Pats YeN (2014) The four-eyed fir bark beetleis a dangerous invasive pest of fir forests of the Novosibirsk region. In: X International scientific Congress: Interexpo-GEO-Siberia 2014 "Economic development of Siberia and the Far East", April 2014, Novosibirsk, Russia, SGGA, Novosibirsk 2: 240–244. [In Russian]

Krivets SA, Bisirova EM, Kerchev IA, Pats YE, Chernova NA (2015c) Transformation of taiga ecosystems in Western Siberia in invasion focus of four-eyed fir bark beetle *Polygraphus proximus* Blandford (Coleoptera: Curculionidae, Scolytinae). Russian Journal of Biological Invasions 8 (1): 41–63. https://doi.org/10.1134/S2075111715020058 [In Russian]

Krivets SA, Bisirova EM, Volkova ES, Debkov NM, Kerchev IA, Melnik M, Nikiforov AN, Chernova NA (2018a) Technology for monitoring fir forests in the four-eyed fir bark beetle invasion zone in Siberia. Toolkit. UMIUM, Tomsk, 74 pp. [In Russian]

Krivets SA, Kerchev IA (2011) The four-eyed fir bark beetle – a new dangerous pest of coniferous forests in the Tomsk region. In: VII International scientific Congress: GEO-Siberia-2011, April 2011, Novosibirsk, Russia, SGGA, Novosibirsk, 211–215. [In Russian]

Krivets SA, Kerchev IA, Bisirova EM, Debkov NM (2018b) Current distribution and the forecast expansion of four-eyed fir bark beetle *Polygraphus proximus* Blandford, 1894 invasive area in Tomskaya Oblast' (Western Siberia). Euroasian Entomological Journal 17(1): 53–60. [In Russian]

Krivets SA, Kerchev IA, Bisirova EM, Demidko DA, Pe'ko VM, Baranchikov YuN (2015b) Distribution of the four-eyed fir bark beetle *Polygraphus proximus* Blandf. (Coleoptera, Curculionidae: Scolytinae) in Siberia. Proceedings of Saint Petersburg Forestry Academy (Izvestia Sankt-Peterburgskoj Lesotehniceskoj Akademii) 211: 33-45. [In Russian]

Krivets SA, Kerchev IA, Bisirova EM, Pashenova NV, Demidko DA, Petko VM, Baranchikov YuN (2015a) The four-eyed fir bark beetle in the forests of Siberia (distribution, biology, ecology, identification and examination of damaged plantings): Methodological book. UMIUM, Krasnoyarsk, 48 pp. [In Russian]

Krivolutskaya GO (1996) Fam. Scolytidae – The bark beetles. In: Key for Identification of Insects of the Russian Far East 3 (3): 312–373. [In Russian]

Kurentsov AI (1941) Bark beetles of the Far East of the USSR. Publishing House of the USSR Academy of Sciences, Moscow, Leningrad, 234 pp. [In Russian]

Mandelshtam MY (2013) Annotated list of bark beetles (Scolytidae) of the fauna of Russia. (accessed on: 2023-08). http://www.zin.ru/Animalia/Coleoptera/rus/slrulist.htm [In Russian]

Mandelshtam MY, Selikhovkin AV (2020) Bark and ambrosia beetles (Coleoptera, Curculionidae: Scolytinae) of Northwest Russia: History of the study, composition and genesis of the fauna. Entomological Review 100: 800–826. https://doi.org/10.1134/S0013873820060093

Mandelshtam MYu, Popovichev BG (2000) Annotated list of bark beetles (Coleoptera, Scolytidae) of Leningrad Province. Entomological Review 80: 887–903.



Mel'nik MA, Volkova ES, Bisirova EM and Krivets SA (2018) Assessment of the ecological and economic damage to forest use caused by the invasion of the four-eyed bark beetle into dark coniferous ecosystems in Siberia. Proceedings of Saint Petersburg Forestry Academy (Izvestia Sankt-Peterburgskoj Lesotehniceskoj Akademii) 225: 58-75. https://doi.org/10.21266/2079-4304.2018.225.58-75 [In Russian]

Niijima Y (1941) Revision und neubeschreibung der Polygraphus-Arten (Coleoptera, Ipidae) in Japan. Insecta Matsumurana 15 (4): 123-135.

Nobuchi A (1966) Bark-beetles injurious to pine in Japan. Bulletin of the Government Forest Experiment Station 185: 1–50. [In Japanese with English summary]

Nobuchi A (1969) A comparative morphological study of the proventriculus in the adult of the superfamily Scolytoidea (Coleoptera). Bulletin of the Government Forest Experiment Station 224: 39–110.

On approval of the list of quarantine objects and alien species in relation to which plant quarantine measures are established and implemented, and the list of especially dangerous pests. Order of the Minister of Agriculture of the Republic of Kazakhstan dated March 30, 2015 No. 4-4/282. Registered with the Ministry of Justice of the Republic of Kazakhstan on July 23, 2015 No. 11739. 2025. Information and legal system of regulatory legal acts of the Republic of Kazakhstan (accessed on: 2023-10). https://adilet.zan.kz/rus/docs/V1500011739 [In Russian]

Paint.NET (2004) Raster graphics editor for Windows NT based on NET Framework. (accessed on: 2023-08) www.getpaint.net

Pashenova NV, Kononov AV, Ustyantsev KV, Blinov AG, Pertsovaya AA, Baranchikov YuN (2018) Ophiostomatoid fungi associated with the four-eyed fir bark beetle on the territory of Russia. Russian Journal of Biological Invasions 5 (9): 63–74. https://doi.org/10.1134/S2075111718010137

Pavlov IN, Litovka YA, Golubev DV, Astapenko SA, Chromogin PV, Usoltseva YV, Makolova PV, Petrenko SM (2020) Mass Reproduction of *Polygraphus proximus* Blandford in Fir Forests of Siberia Infected with Root and Stem Pathogens: Monitoring, Patterns, and Biological Control. Contemporary Problems of Ecology 13 (1): 71–84.

Rosselkhoznadzor for the Republic of Tatarstan. The Office of Rosselkhoznadzor for the Republic of Tatarstan has established a quarantine zone for the Ussuri polygraph (2019) (accessed on: 2023-08). https://shn.tatarstan.ru/index.htm/news/1576134.htm [In Russian]

Selikhovkin AV, Drenkhan R, Mandelshtam MYu, Musolin DL (2020) Invasions of insect pests and fungal pathogens of woody plants into the northwestern part of European Russia. Vestnik of Saint Petersburg University. Earth Sciences 65 (2): 263–283. https://doi.org/10.21638/spbu07.2020.203 [In Russian]

Semenova O (2023) In the Perm region, 17 hectares of forest will be cut down due to the invasion of the polygraph beetle. (accessed on: 2023-08) https://perm.aif.ru/society/details/v_permskom_krae_iz-za_nashestviya_zhuka-poligrafa_vyrubyat_17_ga_lesa [In Russian]

Semerikova SA, Semerikov VL (2014a) Molecular phylogenetic analysis of the genus *Abies* Mill. (Pinaceae) based on the nucleotide sequence of chloroplast DNA. Russian Journal of Genetics 50 (1): 7-19. https://doi.org/10.1134/S1022795414010104

Semerikova SA, Semerikov VL (2014b) Mitochondrial DNA variation and reticulate evolution of the genus *Abies*. Russian Journal of Genetics 50 (4): 366–377. https://doi.org/10.1134/S1022795414040139



Seraya LG, Pashenova NV, Mukhina LN, Dymovich AV, Aleksandrova MS, Baranchikov YuN (2014) Damage to species of the genus *Abies*Mill. in the collection of the Main Botanical Garden of the Russian Academy of Sciences by the four-eyed fir bark beetle *Polygraphus proximus* Bland. and its fungus associates. In: Proceedings of the All-Russian scientific conference with international participation dedicated to the 70th anniversary of the creation of the Institute of Forestry "Forest biogeocenoses of the boreal zone: geography, structure, functions, dynamics". Publishing House of the Siberian Branch of the Russian Academy of Sciences, Novosibirsk, 652–655. [In Russian]

Stark VN (1952) Fauna of the USSR. Coleoptera. Bark beetles. Publishing House of the USSR Academy of Sciences, Moscow, Leningrad 31, 462 pp. [In Russian]

Takagi E, Masaki D, Kanai R, Sato M, Kazunobu I (2018) Mass mortality of *Abies veitchii* caused by *Polygraphus proximus* associated with tree trunk diameter in Japan. Forest Ecology and Management 428: 14–19. https://doi.org/10.1016/j.foreco.2018.06.030

The four-eyed fir bark beetle threatens the Miass forests. First regional information agency (2023) (accessed on: 2023-08). https://www.1obl.ru/tv/vremya-novostey-miass/telefakt-ot-17-08-2023/ussuriyskiy-poligraf-ugrozhaet-miasskim-lesam/ [In Russian]

Viklund L, Baranchikov Y, Schroeder M, Efremenko A, Demidko D, Hedenström E (2022) Identification of sex-specific compounds in the invasive four-eyed fir bark beetle *Pol ygraphus proximus*. Chemoecology 32: 183–195. https://doi.org/10.1007/s00049-022-00377-5

Wood SL (1986) A reclassification of the genera of Scolytidae (Coleoptera), Great Basin Naturalist Mememoirs 10: 1-126.