Far Eastern Entomologist

Дальневосточный энтомолог

Journal published by Far East Branch of the Russian Entomological Society and Laboratory of Entomology, Federal Scientific Center of the East Asia Terrestrial Biodiversity, Vladivostok

Number 529: 1-24 | ISSN 1026-051X (print edition) ISSN 2713-2196 (online edition) | August 2025

https://doi.org/10.25221/fee.529.1
https://elibrary.ru/vdhghk
https://zoobank.org/References/5F73B425-EDD4-4E4A-B133-1971756FFB36

SPECIES OF THE GENUS *APROCEROS* MALAISE, 1931 (HYMENOPTERA: ARGIDAE) OF THE RUSSIAN FAUNA: MOLECULAR GENOTYPING RESOLVES MORPHOLOGICAL PROBLEMS

S. A. Basov

Zoological Institute, Russian Academy of Sciences, 1 Universitetskaya Emb., St Petersburg 199034, Russia. E-mail: basov-sergej@mail.ru

Summary. Species of the small genus *Aproceros* Malaise in Russia are examined. Illustrated redescriptions of species, including detailed structures of the genitalia, are provided. Variability of the morphological characters and seasonal dimorphism are discussed. The taxonomic status of populations from different parts of the range, as well as the presence of various colour forms, are clarified based on molecular data including two mitochondrial and one nuclear genes. One species, *Aproceros hakusanus* Togashi, is excluded from the Russian fauna. The distributions of *A. leucopoda* Takeuchi and *A. pallidicornis* (Mocsáry) in Russia are clarified. An illustrated key to Russian species of the genus *Aproceros* and their forms is proposed, and the new data on the phenology of these species across different regions of Russia are provided.

Key words: Argidae, zigzag sawfly, variability, seasonal dimorphism, distribution, new records, Russia.

С. А. Басов. Виды рода *Aproceros* Malaise, 1931 (Hymenoptera: Argidae) фауны России: молекулярные исследования для решении морфологических проблем // Дальневосточный энтомолог. 2025. N 529. С. 1-24.

Резюме. Рассмотрены виды небольшого рода *Aproceros* Malaise фауны России. Даны иллюстрированные переописания видов, включающие строение генитального аппарата. Обсуждаются изменчивость морфологических признаков и сезонный диморфизм. На основе молекулярных данных уточнен таксономический статус популяций из разных частей ареала и их цветовых форм. Вид *A. hakusanus* Togashi, 1962 исключен из списка фауны пилильщиков России. Уточнено распространение *A. leucopoda* Takeuchi и *A. pallidicornis* (Mocsáry). Для российских видов рода *Aproceros* и их форм предложена иллюстрированная определительная таблица, а также рассмотрена фенология этих видов в различных регионах России.

INTRODUCTION

The sawfly of the genus *Aproceros* Malaise, 1931 (Hymenoptera: Argidae), mainly distributed across the eastern Palaearctic region, comprises ten described species (Taeger *et al*., 2010). The comparatively small species of this genus distinctly differ from other genera within the family Argidae. *Aproceros* sawflies are particularly widespread in Japan, China, and Korea, where their species diversity is distinctly high. However, only three its species have so far been recorded in Russia, *A. hakusanus* Togashi, 1962, *A. leucopoda* Takeuchi, 1939, and *A. pallidicornis* (Mocsáry, 1909) (Sundukov, 2017). The issue of accurately identifying these species and their taxonomy in the Russian fauna has not previously been examined in detail, mainly due to the scarcity of available collection material.

Interest to *Aproceros*, especially the so-called "zigzag sawfly" *A. leucopoda*, has increased enormously following its unexpected and rapid invasion of Europe in 2008 (Blank *et al*., 2010, 2014). This species causes outbreaks severely defoliating elms (*Ulmus* spp.) in southeastern Europe. The damage is inflicted by larvae feeding on elm foliage, creating distinctive zigzag-shaped patterns on leaves, which inspired its common English name. These characteristic feeding marks have been widely photographed and reported by citizen and scientists on platforms such as iNaturalist (https://www.inaturalist.org), greatly facilitating regular monitoring of the species' distribution and the discovery of new localities. *A. leucopoda* swiftly more likely was introduced to Europe through nursery stock intended for urban plantings, parks, and shelterbelts and then spread across Europe. It appeared in Russia after 2012 and subsequently expanding to south and central regions (Blank *et al*., 2010, 2014). Although its northernmost European occurrences now extend as far as Sweden and Finland, within Russia its established distribution currently remains confined to the Moscow region (Gninenko *et al*., 2013). The record of *A. leucopoda* in St. Petersburg (Shevchenko & Stcherbakova, 2020) is questionable and needs to be confirmed.

Unlike other *Aproceros* species, *A. leucopoda* exhibits obligate parthenogenesis (Blank *et al*., 2010). To date, no males of this species have been observed, either in natural populations or under laboratory conditions. In contrast, males of other species within the genus, such as *A. pallidicornis*, are frequently abundant in entomological collections and often outnumbering females. This parthenogenetic reproductive mode of life in *A. leucopoda* likely facilitated its rapid establishment and widespread dispersal in the new environments. Indeed, up to five generations per warm season have been documented (Mol & Vonk, 2015), with significant morphological and colouration variability noted among successive generations. This variability is consistent with observations reported for Sterictiphorinae sawflies in the genus *Aprosthema* Konow, 1899 (Vikberg, 2004).

Special attention should be given to the species *A. hakusanus*, as its record in Russia requires careful verification. Indeed, the original information about this species was itself treated as doubtful by its authors (Zhelochovtsev & Zinovjev, 1995). Since then, the species has been documented from Russia only once more (Sundukov, 2009), prompting a thorough re-examination of all available specimens. Outside Russia, confirmed records of *A. hakusanus* remain limited to the type locality in Japan, with no reliable sightings reported from neighboring countries (Togashi, 1968).

Our examination of collection specimens indicated unclear morphological boundaries among the three Russian *Aproceros* species. Many specimens from its native range identified as *A. leucopoda* deviate considerably in colouration from the original species description. Furthermore, certain European populations of *A. leucopoda* include specimens that resemble females of *A. pallidicornis* in several morphological traits, initially leading us to hypothesize a simultaneous invasion by these two species. Finally, the rare and poorly studied species *A. hakusanus* falls within the observed variability range of European *A. leucopoda*. These observations raise important questions about the taxonomic validity of various colour morphs and the potential existence of cryptic species. Morphological data alone proved insufficient to resolve these uncertainties; thus, we employed genetic markers, including two mitochondrial genes (COI, 16S rRNA) and one nuclear gene (28S rRNA), for the first time in the analysis of the three Russian *Aproceros* species.

MATERIAL AND METHODS

Sampling and specimen examination with light microscopy

Adult specimens of three *Aproceros* species, *A. hakusanus*, *A. leucopoda* and *A. pallidicornis*, were examined. Specimens were borrowed from the following collections: ZISP – Zoological Institute of the Russian Academy of Sciences, St. Petersburg; ZMMU – Zoological Museum of the Moscow State University, Moscow; FSCV – Federal Scientific Center of the East Asia Terrestrial Biodiversity (former Institute of Biology and Soil Science), Vladivostok; ISEA – Institute of Systematics and Ecology of Animals, Novosibirsk.

Specimen examination was performed under an Olympus SZ61 stereomicroscope. Colour photographs were taken with an Olympus SZX10 stereomicroscope coupled with an Olympus OM-D E-M1 camera. Image stacking was conducted with Helicon Focus 8.0.

General distribution data of the *Aproceros* species within Russia follow the "Annotated Catalogue of the Hymenoptera of Russia" (Sundukov, 2017). Some records are given for Russia based on photos from the website iNaturalist (iNaturalist, 2020) (https://www.inaturalist.org). Records of species distribution outside Russia were derived from ECatSym (2018). In the text, an asterisk (*) marks regions where species are recorded for the first time.

Scanning electron microscopy (SEM)

Selected anatomical structures from dissected *Aproceros* specimens were prepared for SEM imaging: right and left mandibles and lancet. After dissection in 70% ethanol, structures were dehydrated in 96% ethanol, mounted on aluminium stubs, and air-dried at room temperature for 24 hours. Mounted samples were sputter-coated with platinum using an Eiko IB5 sputter coater, then examined under a Quanta 250 scanning electron microscope at the Center of Collective Use "Taxon" (ZISP).

DNA extraction, amplification and sequencing

Total genomic DNA was extracted from 34 specimens (1 – *A. hakusanus,* 24 – *A. leucopoda,* 9 – *A. pallidicornis*) preserved either as dry material or in 70% ethanol. Each specimen was assigned a unique isolate identification code (ID), beginning with the prefix "S0" (e.g., S010). Whole legs and flight muscles were used as the extraction material. For the first subset of specimens, genomic DNA was extracted at the Center of Collective Use "Taxon" (ZISP) (http://www. ckp-rf.ru/ckp/3038/) using the DNA-Sorb-V extraction kit (AmpliSens, Russia) following the manufacturer's protocol, with a modification involving an extended overnight lysis incubation at 65°C to optimize DNA yield from insect tissue. Subsequent steps followed the manufacturer's extraction protocol. Extracted DNA was eluted in nuclease-free deionized water (Evrogen, Russia). DNA yield and purity were measured by spectrophotometry (Allsheng Nano 500, China). For the second subset of specimens, genomic DNA extractions were performed in the Ecology and Genetics Research Unit at the University of Oulu (Finland) using the DNeasy Blood & Tissue Kit (Qiagen) according to the manufacturer's protocol.

At ZISP, one polymerase chain reaction (PCR) was used to amplify three genetic markers: mitochondrial cytochrome oxidase I (COI), mitochondrial 16S rRNA, and nuclear 28S rRNA. COI (658bp) was amplified with the primer pair (Table 1) SymF5 and SymR3, 16S rRNA (385bp) with 16SBR_Hym and 16SAF_Hym, and 28S rRNA (611bp) with 28S_D2F v2 and 28S_D2Ra. Each 25 μL reaction contained 3 μL of template DNA, 200 μM of each dNTP (Evrogen, Russia), 0.5 μM of each primer, 0.25 μL of Taq DNA polymerase (Evrogen, Russia) or 0.5 μL of the 50X Encyclo polymerase mix (Evrogen, Russia) in the corresponding 10× buffer. Following successful amplification, PCR products were purified with CleanMag DNA PCR magnetic beads (Evrogen, Russia) to remove residual primers and unincorporated nucleotides. Purified PCR products were sequenced bidirectionally using both forward and reverse primers by Sanger sequencing at the Center of Collective Use "Taxon" (ZISP). Sequence reads were trimmed for quality and assembled into contigs using Geneious Prime 2024.0.3.

Table 1. Primers used for PCR

Primer	F/R	Sequence 5′–3′	Reference
COI (658bp)			
SymF5	F	ATGAATAAATGATTATTYTCWACWAATCAYAA	Prous *et al*., 2025
SymF5v2	F	ATGAATAAATGATTATTYTCWACWAAYCAYAA	Prous *et al*., 2025
SymF3v2	F	TTTTCWACWAAYCAYAAARAYATYGG	Prous *et al*., 2025
SymR3	R	TAAACTTCWGGRTGNCCAAARAATCA	Prous *et al*., 2025
C_LepFolF	F	ATTCAACCAATCATAAAGATATTGG	Hernández-Triana, 2014
C_LepFolR	R	TAAACTTCTGGATGTCCAAAAAATCA	Hernández-Triana, 2014
16S rRNA (385bp)			
16SA_Hym	F	TRACTGTRCAAAGGTAGC	Schulmeister, 2003
16SB_Hym	R	TTAATTCAACATCGAGGTCG	Schulmeister, 2003
28S rRNA (611bp)			
28S_D2F v2	F	CGGGTTGCTTGAGAGTG	This study
28S_D2Ra	R	CTCCTTGGTCCGTGTTTC	Schmidt, 2014

At the University of Oulu (Finland), COI was the sole marker sequenced for several specimens. Two PCR amplifications employed the QIAGEN Multiplex PCR Plus Kit together with primers SymF5v2, SymF3v2, and SymR3 (two forward primers to account for potential primer–template mismatches). Amplicons were sequenced with Oxford Nanopore R10.4.1 flow cells on MinION and the basecalled (using Dorado) fastq data was processed with the workflow described by Prous *et al*. (2025).

Finally, a single *A. hakusanus* specimen, was barcoded at the Canadian Center for DNA barcoding (CCDB), University of Guelph (Canada). The COI fragment was sequenced using the primer set C_LepFolF/C_LepFolR following the standard protocol (Waard *et al*., 2008).

All newly obtained sequences have been deposited in GenBank. COI sequences were successfully amplified from all 34 specimens (accession numbers: PV670410–PV670443). The 16S rRNA gene was sequenced from 13 specimens (accession numbers: PV686847–PV686859), and the 28S rRNA gene from 11 specimens (accession numbers: PV686870-PV686880); however, only nine specimens yielded sequences for all three loci. Detailed information on each specimen, including collection data and corresponding GenBank accession numbers, is provided in Table 2.

Table 2. Specimen data and complete list of sequences used in the molecular phylogenetic analysis

Isolate_ID	Species	Sex	Location	From	Generation	Body colour	Hind femora	COI NCBI_ID	16S NCBI_ID	28S NCBI_ID
S000	*A. hakusanus*	♀	Russia, Primorskiy Terr.	ZMMU	summer	black	pale	PV670410	X	X
S001	*A. pallidicornis*	♀	Russia, Primorskiy Terr.	ZISP	summer	black	pale	PV670435	X	X
S002	*A. leucopoda*	♀	Russia, Primorskiy Terr.	ZISP	summer	black	pale	PV670411	X	X
S003	*A. leucopoda*	♀	Russia, Primorskiy Terr.	ZISP	summer	black	pale	PV670412	X	X
S004	*A. pallidicornis*	♂	Russia, Primorskiy Terr.	ZISP	summer	black	dark	PV670436	X	X
S005	*A. pallidicornis*	♂	Russia, Primorskiy Terr.	ZISP	summer	black	dark	PV670443	PV686858	PV686879
S006	*A. pallidicornis*	♀	Russia, Primorskiy Terr.	ZISP	spring	black	dark	PV670437	X	X
S007	*A. leucopoda*	♀	Russia, Primorskiy Terr.	ZISP	summer	black	dark	PV670413	X	X
S008	*A. leucopoda*	♀	Austria, Traismauer	ZISP	summer	black	pale	PV670414	PV686847	PV686870
S009	*A. leucopoda*	♀	Russia, Belgorod Prov.	ZISP	summer	black	pale	PV670415	PV686848	X
S010	*A. leucopoda*	♀	Russia, Primorskiy Terr.	ZISP	summer	black	pale	PV670416	PV686849	PV686871
S012	*A. leucopoda*	♀	Russia, Rostov Prov.	ZISP	summer	red	pale	PV670417	PV686850	PV686872
S015	*A. pallidicornis*	♂	Russia, Primorskiy Terr.	ZISP	summer	black	dark	PV670438	X	X
S032	*A. leucopoda*	♀	Russia, Krasnodar Terr.	ZISP	spring	black	dark	PV670418	X	X
S035	*A. leucopoda*	♀	Russia, Khabarovsk Terr.	ISEA	spring	black	dark	PV670419	PV686851	PV686873
S036	*A. pallidicornis*	♀	Russia, Khabarovsk Terr.	ISEA	spring	black	dark	PV670439	PV686859	PV686880

Continue of Table 2

Isolate_ID	Species	Sex	Location	From	Generation	Body colour	Hind femora	COI NCBI_ID	16S NCBI_ID	28S NCBI_ID
S037	*A. leucopoda*	♀	Russia, Khabarovsk Terr.	ISEA	summer	black	pale	PV670420	PV686852	PV686874
S040	*A. leucopoda*	♀	Russia, Krasnodar Terr.	ZISP	spring	black	dark	PV670421	PV686853	PV686875
S041	*A. leucopoda*	♀	Russia, Krasnodar Terr.	ZISP	spring	black	dark	PV670422	X	PV686876
S042	*A. leucopoda*	♀	Russia, Primorskiy Terr.	ZISP	summer	black	dark	PV670423	X	PV686877
S044	*A. leucopoda*	♀	Russia, Primorskiy Terr.	ZISP	summer	black	pale	PV670424	PV686854	PV686878
S045	*A. leucopoda*	♀	Russia, Kemerov Prov.	ISEA	summer	black	pale	PV670425	PV686855	X
S046	*A. leucopoda*	♀	Russia, Krasnodar Terr.	ZISP	summer	black	pale	PV670426	X	X
S047	*A. leucopoda*	♀	Russia, Primorskiy Terr.	ZISP	spring	black	dark	PV670427	PV686856	X
S048	*A. leucopoda*	♀	Russia, Primorskiy Terr.	ZISP	summer	black	pale	PV670428	X	X
S051	*A. pallidicornis*	♀	Russia, Primorskiy Terr.	ZISP	summer	black	pale	PV670440	X	X
S052	*A. leucopoda*	♀	Russia, Rostov Prov.	ZISP	summer	red	pale	PV670429	X	X
S053	*A. leucopoda*	♀	Russia, Primorskiy Terr.	ZISP	summer	black	pale	PV670430	X	X
S056	*A. pallidicornis*	♀	Russia, Primorskiy Terr.	ZISP	summer	black	pale	PV670441	X	X
S058	*A. leucopoda*	♀	Russia, Krasnodar Terr.	ZISP	spring	black	pale	PV670431	X	X
S062	*A. leucopoda*	♀	Russia, Krasnodar Terr.	ZISP	spring	black	pale	PV670432	X	X
S063	*A. pallidicornis*	♂	Russia, Primorskiy Terr.	ZISP	summer	black	dark	PV670442	X	X
S072	*A. leucopoda*	♀	Russia, Voronezh Prov.	ZISP	summer	black	pale	PV670433	PV686857	X
S075	*A. leucopoda*	♀	Russia, Krasnodar Terr.	ZISP	spring	black	pale	PV670434	X	X

Phylogenetic analyses

To clarify the differences between *A. leucopoda* and *A. pallidicornis* species using molecular data, we conducted two partitioned phylogenetic analyses. First one was based on three genetic markers (COI, 16S rRNA, 28S rRNA) using nine specimens of *A. leucopoda* (2 specimens) and *A. pallidicornis* (7 specimens). Second one was based on COI sequences alone using 34 specimens of *A. leucopoda* (25 specimens) and *A. pallidicornis* (9 specimens). Two *Aprosthema* species were used as an outgroup (sequences from GenBank). DNA sequences were aligned using the MAFFT algorithm v7.450 (Katoh & Standley, 2013) in Geneious Prime 2024.0.3, with ambiguous regions manually excluded. Concatenation of individual alignments for partitioned analyses was performed using SequenceMatrix (Vaidya *et al*., 2011).

The best-fitting nucleotide substitution models were identified using jModelTest2 v.2.1.10 (Darriba *et al*., 2012) according to the Akaike Information Criterion (AIC). Selected substitution models were GTR+I for COI, GTR+G for 16S rRNA, and TIM1 for 28S rRNA. Phylogenetic trees were inferred using Maximum Likelihood (ML) implemented in IQ-TREE v.3.0.1 (Wong *et al*., 2025) and Bayesian inference (BI) implemented in MrBayes v.3.2.7a (Ronquist *et al*., 2012). The BI analyses consisted of four independent runs, each with four Markov chains, sampled every 100 generations. Runs were continued until the average standard deviation of split frequencies dropped below 0.01, with a minimum of 1,500,000 generations and a burn-in fraction of 25%. The 50% majority-rule consensus tree with posterior probabilities is presented. ML analyses included branch support assessments through SH-like approximate likelihood ratio tests (SH-aLRT; Guindon *et al*., 2010) and ultrafast bootstrap approximation (Hoang *et al*., 2018) with 1,000 replicates. Branch support values for BI and ML analyses follow the scheme of Prous *et al*. (2025). Trees were visualized using the Interactive Tree of Life v.6.9 online application (Letunic & Bork, 2021).

TAXONOMIC PART

Order Hymenoptera

Family Argidae

Subfamily Sterictiphorinae

Genus *Aproceros* Malaise, 1931

Aproceros Malaise, 1931: 152; Taeger *et al*., 2018.

Type species: *Aproceros umbricola* Malaise, 1931, by original designation.

DISTRIBUTION. East Palaearctic and Oriental regions; introduced to the West Palaearctic (Blank *et al*., 2014) and Nearctic (Martel *et al*., 2021).

HOST PLANT. Ulmaceae: *Ulmus glabra*, *U. laevis*, *U. minor*, *U. davidiana*, *U. pumila, U. japonica* etc.

Aproceros hakusanus Togashi, 1962

Aproceros hakusanus Togashi, 1962: 202; 1968: 232; Zhelochovtsev & Zinovjev, 1995: 401.

MATERIAL MISIDENTIFIED EXAMINED. **Russia**: *Primorskiy Terr.*: vicinity of Spassk[-Dal'niy], 29.VI.1961 (S000), A. Zhelochovtsev leg., 1♀ (ZMMU); Sikhote-Alin, Syahobe [Serebryanka] River basin, 24.VII.1936, K. Grunin leg., 1♀ (ZMMU) (A.N. Zhelochovtsev determination).

REDESCRIPTION. *Female* (after Togashi, 1962, only for principal characters). Body length 6.5 mm. Body black, shining; mouthparts yellowish; mandibles at apex red-brown; pronotum and most of mesothorax except posterior margin of scutellum pale brown; basal half of abdomen yellow-brown. Antennae brownish-black. Legs pale orange, fore and middle coxae and apices of hind tarsi darkened. Wings uniformly infuscated, forewings slightly stronger at base, veins and pterostigma dark brown. Head and thorax covered with greyish-white pubescence. Head from above transverse, strongly narrowed behind eyes; POL : OOL: OCL = 2 : 3 : 1. Supraclypeal area slightly convex, with a sharp median carina; anterior tentorial pit deep, connected with antennal foveae; median fovea punctiform, deep; malar space broad, about twice as long as antennal scape; anterior margin of clypeus nearly truncate. Antennae nearly as long as costa of fore wing. Median lobe of mesonotum (prescutum) with distinct median fold.

Male. Unknown.

DISTRIBUTION. Japan (Honshu). Record from Russia is misidefinition (see below for more details).

REMARKS. All the specimens we studied, identified earlier by Zhelochovtsev as *A. hakusanus*, should be considered light-coloured forms (Form B) of the summer generation of *A. leucopoda*, which is confirmed by molecular data. As result, I exclude *A. hakusanus* from the list of sawflies of Russia.

The type material of *A. hakusanus* was kept in Togashi's personal collection (Togashi, 1962), and after his death, the place of storage of the types is unknown and their re-study is now impossible. Perhaps the real range of this species (if it is valid taxon) is limited only to Japan, as the species is not recorded elsewhere outside the country. It is very possible that this taxon may be only a light-coloured form of one of the Japanese species. In favour of this is the light colouration of the body and the strongly constricted head behind the eyes. The unavailability of type specimens or any other specimens makes it impossible to verify the validity of the discussed species.

Many of the features specified by Togashi (1962) in the species description appear to be highly variable in the other two species we studied. Therefore, here we do not give upper the description suggested by Togashi in full, but only the most significant features of this species. The state of such a feature as the furrow of the medial lobe of the mesothorax is highly variable, although it has previously been widely used (Togashi, 1968) for species distinguishing.

Aproceros leucopoda **Takeuchi, 1939**
Figs 1A–I, 3A, D, 4D–K

Aproceros leucopoda Takeuchi, 1939: 415–416.

MATERIAL EXAMINED. **Austria**, Lower Austria, Traimauer, 48° 35'0N 15° 73'3E, VII.2013, E. Altenhofer leg., 6♀ (S008) (ZISP). **Russia**, *Belgorod Prov*., vicinity of Nagolnoe village, steppe, 14.VI.2008, D. Kasparyan leg., 1♀ (S009) (ZISP); *Rostov Prov*., Rassvet village, 2011, K. Artokhin leg., 4♀ (S012, S052) (ZISP); *Krasnodar Terr*.: without locality designation, 13.VI.2010, V. Shchurov leg., 1♀ (S046) (ZISP); tract Balka Krutaya, near the estuary of the Eya River, 11.IV.2016, V. Shchurov leg., 16♀ (S075, S058, S041, S032) (ZISP); vicinity of Kazachiy village, 12.IV.2023, V. Shchurov leg., 1♀ (S040) (ZISP); *Voronezh Prov*., 25 km NE of Voronezh, vicinity of Venevitinovo village, 9.VI.2023, D. Kirpach leg., 1♀ (S072) (ZISP), 1♀ (VSU); Voronezh, 28.VI.2023, O. Selivanova

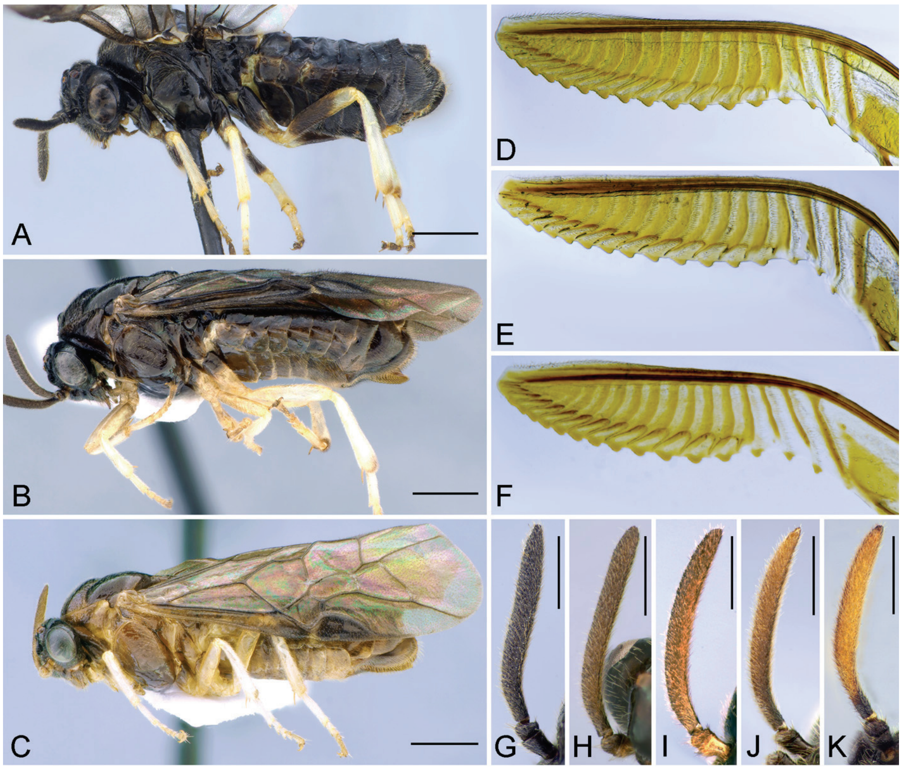

Fig. 1. *Aproceros* spp., females (Primorskiy Terr., Russia). A, D, G – *A. leucopoda* spring generation; B, E, H – *A. leucopoda*, summer generation, form A; C, F, I – *A. leucopoda* summer generation, form B; J–K – *A. pallidicornis*. Habitus, lateral view (A–C); lancet, lateral view (D–F); antenna, dorsal view (G–K); Scale bar: 1.0 mm (A–C), 0.5 mm (G–K).

leg., 1♀ (VSU); *Samara Prov.*, Zhiguli Natural Reserve, forest, Volga River, 2.VII. 2011, V. Chemyreva leg., 1♀ (ZISP); *Kemerovo Prov.*, vicinity of Novobachaty settlement, Bayatskie sopki, birch thicket, 23.VI.2015, A. Kostyunin leg., 1♀ (S045) (ISEA); *Khabarovsk Terr.*, vicinity of Khabarovsk, elm, 16.VIII.1964, P. Esipenko leg., 2♀ (ZISP), same locality, 14.VII.1964, 24.VII.1968 & 3.VIII.1972, A. Shtundyuk leg., 3♀ (ISEA); Bolshekhekhtsirskiy Natural Reserve, Cordon Bychikha, 26.V.2018, 28.V.2021 (S035) & 30.VI.2021 (S037), V. Dubatolov leg., 3♀ (ISEA); Anyuyskiy National Park, Cordon Nilo, 49°15'N 137°16'E, 24–25.VII. 2018, V. Dubatolov leg., 1♀ (ISEA); *Primorskiy Terr.*: 20 km S of Ussuriysk, Gornotayezhnaya Station, 31.VII & 4.VIII.1991, S. Belokobylskij leg., 5♀ (ZISP); Arsenyev, Sky-Base "Bodrost'", 26.V.2016, K. Kramp, M. Prous & A. Taeger leg., 1♀ (S047) (ZISP); Blue Ridge, 40 km S of Arsenyev, 1–4.VII.1999, V. Krivokhvatskiy & O. Ovchinnikova leg., 2♀ (ZISP); vicinity of Spassk-Dal'niy, 23.VII.1991,

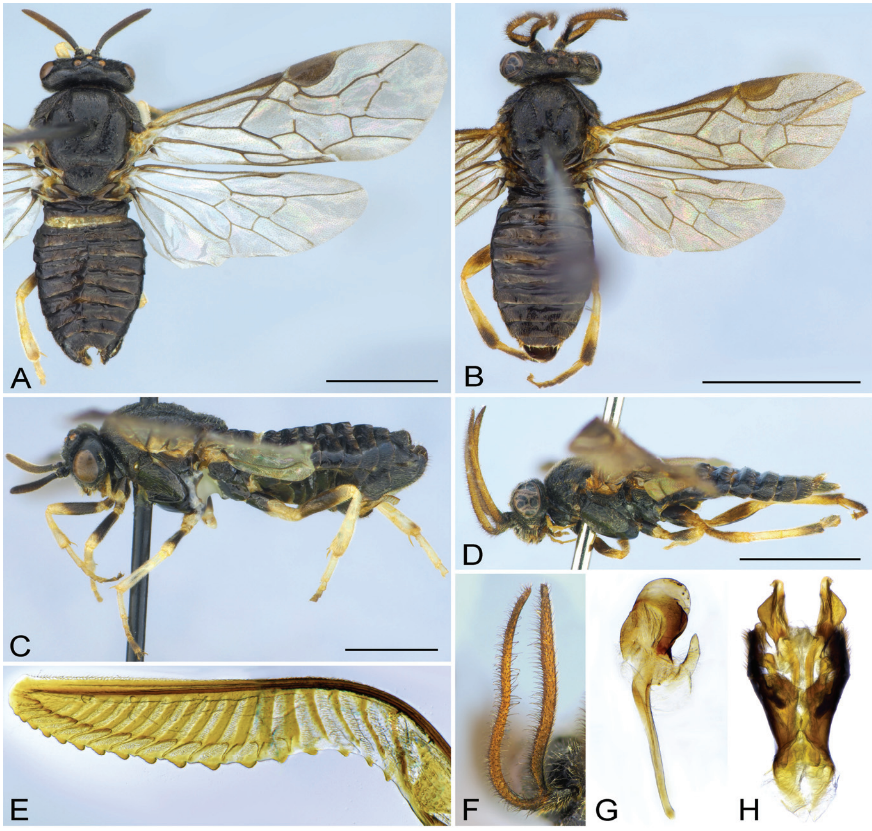

Fig. 2. *Aproceros pallidicornis* (Primorskiy Terr., Russia). A, C, E – female; B, D, F–H – male; habitus, dorsal view (A, B); habitus, lateral view (C, D); lancet, lateral view (E); antenna, dorsal view (F); penis valves, lateral view (G); genital capsule, dorsal view (H). Scale bar: 2.0 mm.

18.VII.1995, 8.VIII.1996, 22.VII.1998, 10.VII.2001, 26.VI.2003, & 20.VII.2006 (S010), S. Belokobylskij leg., 10♀ (ZISP), same locality, 26.VII.1985, D. Kasparyan leg., 1♀ (ZISP); Sudzukhinskiy (=Ussuriyskiy) Natural Reserve, 4.VIII.1972, V. Kuslitsky leg., 1♀ (ZISP); vicinity of Barabash-Levada, floodplain forest, 27.VI.1980, G. Krivolutskaya leg., 1♀ (ZISP); vicinity of Vityaz settlement, 4.VIII.1982, I. Kerzhner leg., 1♀ (ZISP); Ussuriyskiy Natural Reserve, Kamenushka–Kaymanovka, 31.VII.2008, A. Khalaim leg., 2♀ (S002) (ZISP); 10 km SW of Chernigovka, slopes with oak and pine, 26.VII.1996, S. Belokobylskij leg., 1♀ (ZISP); without locality designation, 30.VI & 22.VII.1960, Kolyvanova leg., 2♀ (ZMMU), 2♀ (FSCV); Partizansk, 3.VIII.1940, A. Romanov leg., 1♀ (ZMMU); "Kedrovaya Pad' " Natural Reserve, 9.V.1983, V. Zlobin leg. & 30.VIII.1995, S. Belokobylskij leg., 3♀ (ZISP); vicinity of Ryazanovka, 9.VII.1982, I. Kerzhner leg., 2♀ (ZISP); vicinity of Anisimovka, 28.V.1974, Berezantsev leg., 1♀ (ZISP); vicinity of Lazo village: 1–10.VII.2006, 6–10.VI.2008, 16–30.IV.2008 (S042), V. Shokhrin leg., 3♀ (ZISP); Lazovskiy Natural Reserve: cordon America 19–23.VI.05, V. Shokhrin leg., 1♀ (ZISP), Proselochnaya Bay, 25.VII.2008, Yu. Sundukov leg., 1♀ (S003) (ZISP); vicinity of Vladivostok, Sputnik, VII.2024, D. Ryaskin leg., 1♀ (ZISP); vicinity of Derchez village, floodplain of Bolshaya Usurka River, 7–15.VIII.2023, M. Sergeev leg., 1♀ (S044) (ZISP).

REDESCRIPTION. *Female* (after Takeuchi, 1939 with additions). Body length 5.8–6.9 mm. Body black, shining, without metallic lustre; labrum dark brown, mandibular apices brown, pronotum partly brownish. Antennae dark brown, scapus light. Legs white, coxae, trochanters and femora more or less yellowish, bases of coxae black, apex of hind tibia and all spurs darkened. Wings faintly evenly infuscated. Veins and pterostigma dark brown. Head entirely (OR distinctly) smooth, unpunctured, its width from above about 3.0 times medial length, strongly constricted behind eyes (dorsal view). Anterior margin of clypeus almost truncated. Supraclipeal area with sharp median keel. Median fossa weak. POL: OOL: OCL = 1.7 : 2 : 1. Malar space broad, its length approximately equal to length of scapus and pedicellum combined. Antennae short, approximately as long as width of head. Thorax smooth, but not strongly shining; median furrow of prescutum weak.

Variability.

Spring generation. Head behind eyes (dorsal view) weakly constricted or subparallel. Postocellular area clearly bounded by furrows. POL: OOL: OCL = 1 : 1.3 : 1. Body entirely black. Antennae black or brownish-black. Legs mostly white; coxae, bases or most part of fore and middle, but sometimes almost all femora except their apices black; apices of tarsi and hind tibiae often darkened.

Summer generation. Head behind eyes (dorsal view) subparallel or slightly expanded. Postocellular area clearly bounded by furrows. POL: OOL: OCL = 1.4 : 1.6 : 1. Due to the high variability of colouration of specimens of summer generations, we apply the concept of colour forms in this paper.

Form A. Body dark brown or black. Antenna completely black, rarely dark brown. Legs yellowish-white, less often fore and middle femora black at base.

Form B. Body entirely reddish or light brown. Head dark brown, rarely black. Mesonotum with variable dark pattern, often with dark brown spots on middle and lateral or only lateral lobes. Sometimes most of mesonotum dark brown. Tegulae and saw sheath brownish. All antennal segments reddish. Legs entirely white.

Male. Unknown. Probably an obligate parthenogenetic species.

DISTRIBUTION. Russia [Leningrad Prov. (this is doubtful record and require confirmation), Moscow Prov., *Belgorod Prov., Republic of Krym, Rostov Prov., Krasnodar Terr., Stavropol Terr., Voronezh Prov., Kabardino-Balkarian Republic, Republic of North Ossetia – Alania, Ulyanovsk Prov., *Saratov Prov. (iNaturalist, 2020), Samara Prov., Kemerovo Prov., *Khabarovsk Terr., Primorskiy Terr.], Austria, Belgium, Bosnia and Herzegovina, Bulgaria, Canada, China, Croatia, Czech Republic, Estonia, Germany, Hungary, Italy, Japan, Kazakhstan, Moldova, Poland, Netherlands, Romania, Serbia, Slovakia, Slovenia, Ukraine, USA, Yugoslavia.

REMARKS. The holotype of *A. leucopoda* (Fig. 9 in Blank *et al*., 2010) preserved at Entomological Laboratory, Graduate School of Life and Environmental Sciences, Osaka Prefecture University, Osaka, Japan.

The records of this species in the Leningrad Province (Shevchenko & Stcherbakova, 2020), mentioned as the most northern distribution in Russia (Kondratyeva *et al*., 2023), do not have precise indications and need to be verified. Single specimens were observed in St Petersburg park in 2017 on saplings of Resista-elm (*Ulmus resista*) imported from Germany, in the year of planting. Further monitoring was not carried out, and the planted trees died (L.N. Shcherbakova, personal communication). It remains unclear whether this species has survived in St Petersburg. No other information is available.

***Aproceros pallidicornis* (Mocsáry, 1909)**
Figs 2A–H, 3B–C, E–F, 4A–C

Aprosthema pallidicornis Mocsáry, 1909: 9.
Aproceros umbricola Malaise, 1931: 153.

MATERIAL EXAMINED. **Russia**, *Amur Prov*.: Samodon, 100 km W of Svobodnyi, 7.VIII.1959, A. Zinoviev leg., 1♂, 1♀ (ZISP); *Khabarovsk Terr*.: lower reaches of the Anyuy River, tributary of the lower Amur River, 30.VI.1910, V. Soldatov leg., 1♀ (ZISP); 20 km SE of Vyazemskiy, Sobolevo, 29.VII.1978, D. Kasparyan leg., 3♂ (ZISP); Khabarovsk, Arboretum: 25.VI & 20.VIII,1968, A. Shtundyuk leg., 2♂ (ISEA), 31.VII.1978, D. Kasparyan leg., 2♂ (ZISP); Shevki, 15 km S of Bikin, 2.VI.1983, A. Zinoviev leg., 1♂ (ZISP); Khehtsir, Osinovaya River, 7.VI.1983, D. Kasparyan leg., 1♂ (ZISP); vicinity of Vanino, 10.VIII.1976, Yu. Bodrova leg., 1♂ (FSCV); near Khabarovsk, Bolshekhekhtsirskiy Nature Reserve, vicinity of Bychikha cordon, 48.1713 N, 134.4950 E, 28.V.2021, V. Dubatolov leg., 1♀ (S036) (ISEA); *Primorskiy Terr*.: vicinity of Spassk-Dal'niy: 19.VIII.1987, 19.VII.1991, 5–12.VII & 13.VIII.1995, 21 & 31.VII, 4.VIII.1998, 8.VIII.1996 (S049, S051), 5–7.VIII.2019, 3.VII.2001 (S048, S056), 26–28.VI.2003, S. Belokobylskij leg., 19♂, 6♀ (ZISP), 10.VI & 8.VII.1961, A. Zhelokhovtsev leg., 1♂, 1♀

(ZMMU); 20 km S of Ussuriysk, Gornotayozhnaya station: 30.VII–8.VIII.1948, V. Gussakovskij leg., 2♂ (ZMMU), 20.VII.1981, D. Kasparyan leg., 1♂ (ZISP); vicinity of Ussuriysk, 1.VIII.1966, A. Kupyanskaya leg., 1♀ (ZMMU); Sikhote-Alin, 1.VIII.1936, V. Perelashina leg., 9♂ (ZMMU). Suvorovo village, 2–9.VII.1972, A. Ponomarenko leg., 26♂, 2♀ (ZMMU) (S059); 17.VII.1972, A. Ponomarenko, A. Rasnitsyn leg., 1♀ (ZMMU); Arsenyev, Sky-Base "Bodrost", 26.V.2016, K. Kramp, M. Prous, A. Taeger legs, 1♂ (ZISP); Zanadvorovka, 7.VI.1972, A. Ponomarenko, A. Rasnitsyn leg., 1♀ (ZMMU); 40 km NE of Spassk-Dal'niy, vicinity of Duchovskoe

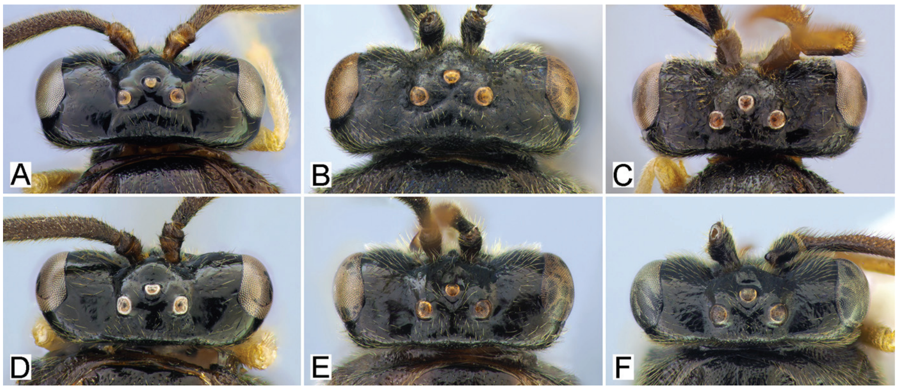

Fig. 3. *Aproceros* spp., head, dorsal view. A, D – *A. leucopoda* (Krasnodar Terr., Russia), females; B, C, E, F – *A. pallidicornis* (Primorskiy Terr., Russia), females (B, E) and males (C, F); spring generation (A–C); summer generation (D–F).

village, 1.VIII.1996, S. Belokobylskij leg., 1♀ (ZISP) (SEM0013); 20 km S of Spassk-Dal'niy, nr. Evseevka, 17.VII.1995, S. Belokobylskij leg., 1♂ (ZISP); Grodekovo, 5–15.VII.1965, D. Kasparyan leg., 1♂ (ISEA); Partizansk, 7.VII.1970, A. Shtundyuk leg., 1♂ (ISEA); vicinity of Vityaz settlement, 7–17.VIII.1982, I. Kerzhner leg., 2♂, 1♀ (ZISP); "Kedrovaya Pad' " Nature Reserve: 30.VIII.1995, S. Belokobylskij leg., 4♀ (ZISP), 13.VIII.2014, V. Chemyreva leg., 1♀ (S001); Ussuriyskiy Nature Reserve: 12.VIII.1986, V. Makarkin leg., 1♀ (FSCV), Kamenushka, 14.VII.1981, D. Kasparyan leg., 1♂ (ZISP), 2.V.1989, Sidorenko leg., 1♂ (FSCV), 25.V.2003, A. Lelei leg., 1♂ (FSCV), 31.VII.2008, A. Khalaim leg., 3♂ (S063) (ZISP), 23.V.2016, K. Kramp, M. Prous, A. Taeger leg., 1♂ (ZISP), Komarovka River valley: 3.VI.1989, Sidorenko leg., 1♀ (FSCV), 13–17.VII.1981, D. Kasparyan leg., 2♂, 1♀ (ZISP), cordon Staraya baza, 15–16.VII.1981, D. Kasparyan leg., 9♂ (ZISP), cordon Peishula, 30.VII.1972, V. Kuslitsky leg., 3♂ (ZISP); V. Chemyreva leg., 1♂ (S004); vicinity of Anisimovka: 21.VI.1975, Soboleva leg., 1♂ (FSCV), 11.VII.1977, Azarova leg., 1♀ (FSCV), 1.VIII.2022, P. Romantsov leg., 1♂ (ZISP); vicinity of Lazo, 26–29.V.2007, V. Shokhrin leg., 2♂ (ZISP); Vladivostok: 19.VII.1979, A. Zinoviev leg., 1♂ (ZISP), 8.VIII.1991 & 5.VII.2019 (S005), S. Belokobylskij leg, 2♂ (ZISP); Ryazanovka village, 9.VII.1982, I. Kerzhner leg., 1♀

(ZISP); 125 km SE of Dalnerechinsk, Pozhiga village, 19–22.VII.1983, D. Kasparyan leg., 5♂ (ZISP); Kishenevka village, 23–30.V.2008, V. Shokhin leg., 1♀ (S006) (ZISP); 24 km W Anuchino, 9.VII.1969, Tanaseichuk leg., 1♂ (ZISP); Lazovsky Nature Reserve, Korpad' cordon, 16–19.VII.2005, Yu. Sundukov, V. Shokhin legs, 1♂ (FSCV).

REDESCRIPTION. *Female.* Body length 5.4–5.7 mm. Body black, shining; mouthparts whitish; legs yellowish-white, coxae, most part of femora except apex black, apical segments of tarsi and hind tibiae often darkened. Flagellum orange or brown, often blackish at base and along posterior side. Basal halves of abdominal tergites mostly semi-transparent, sometimes whitish, membranous. Wings hyaline, veins and pterostigma dark brown, whitish at base. Pubescence of body silvery-white. Head mostly smooth, almost without punctures; frons and vertex convex, face very narrow, linear, with sharp keel; interantennal fovea small, rounded, placed above antennal sockets; clypeus flat, truncated along dorsal margin; malar space broad, almost equal to scapus and pedicellum combined. Sheath of saw simple, rounded in lateral view. Lancet as in *A. leucopoda*.

Variability.

Spring generation. Head behind eyes (dorsal view) weakly constricted or subparallel. Flagellum brownish-red. Body black. Legs yellowish-white, femora except apex black. POL: OOL: OCL = 1.2 : 1.5 : 1.0.

Summer generation. Head behind eyes (dorsal view) strongly constricted. Flagellum reddish. Body black or dark brown. Legs yellowish-white, fore and middle femora black at base, less often entirely white or with black markings on all femora. POL: OOL: OCL = 1.5 : 1.7 : 1.0.

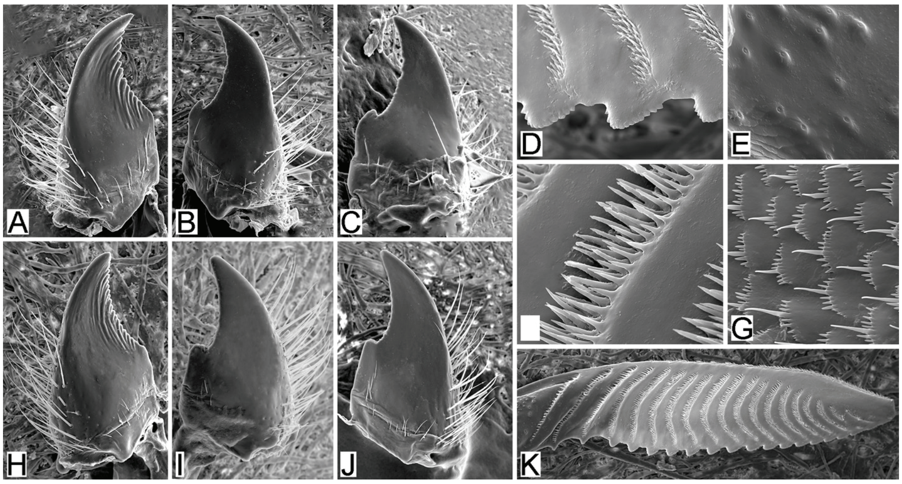

Fig. 4. *Aproceros* spp., females (Primorskiy Terr., Russia), summer generation. A–C – *A. pallidicornis*; D–K – *A. leucopoda*; left mandibles, frontal view (A, H); right mandibles, frontal view (B–C, I–J); median teeth of lancet, lateral view (D); radix pores of campaniform sensilla of lancet, lateral view (E); ctenidia of lancet, lateral view (F); pectines of inner aspect of the egg canal (G); lancet, lateral view (K). SEM micrograph.

Male (after Mocsáry, 1909 and Malaise, 1931; for additional information see Choi *et al*., 2015). Body length 4.0–4.5 mm. Body black, shining, smooth; mouth parts whitish; legs black, trochanters, knees, tibiae and tarsi dirty white, apices of hind tibia and surface of hind tarsi blackened; third antennal segment light brown, its base and two basal segments brownish-black; three basal tergites of abdomen translucent, whitish at base; wings uniformly infuscated, veins and pterostigma dark brown. Pubescence silvery-white. Frons in lateral view rounded, elevated; antennal furrows very broad and deep, lower part of face strongly impressed, frons between antennae linear. Clypeus truncated. POL: OOL: OCL = 0.9 : 1.4 : 1. Malar space broad. Head behind eyes (dorsal view) slightly narrowed.

DISTRIBUTION. Russia (Amur Prov., Khabarovsk and Primorskiy Terr.), South Korea (Choi *et al*., 2015), Japan, Iran (Chelav *et al*., 2008).

REMARKS. The number of males significantly higher than females in the collection materials. Probably males have mass flights (swarming). The original description of this species and its junior synonym, *Aproceros umbricola* Malaise, is given by authors for males. Here we give the description of the females on the basis of the examined material, the species identity of which is confirmed by molecular data.

A key to Russian species of the genus *Aproceros* and their forms

1. Males (only one species known in the Russian fauna) [body black, flagellum brownish-red, legs yellowish-white, most part of all femora and apex of hind tibiae black (Figs 2B–D, F)] …..………………………………..….... ***A. pallidicornis***

– Females 2

2. Head behind eyes in dorsal view weakly constricted or subparallel (Figs 3A–C). Flight period April-May (spring generation) 3

– Head behind eyes in dorsal view strongly constricted (Figs 3D–F). Flight period June-August (summer generation) 4

3. Flagellum black or dark brown (Fig. 1G). Body mostly black, rarely pronotum brownish. Legs yellowish-white, all or only fore and middle femora blackened, or rarely completely light (Fig. 3A). Inner tooth of right mandible weakly defined (Figs 4I–J) ..... ***A. leucopoda***

– Flagellum orange or brownish-red (Figs 1J–K). Body entirely black. Legs yellowish-white, most of all femora except their apices black (Figs 2A, C). Inner tooth of right mandible strongly pronounced (Figs 4B–C) .... ***A. pallidicornis***

4. Flagellum black or dark brown (Fig. 1B). Body dark brown. Legs yellowish-white, less often fore and middle femora darkened at base (Fig. 1H). [Inner tooth of right mandible weakly defined] (Forma A) ……………………………………................ ***A. leucopoda***

– Flagellum reddish (Figs 1I–K). Body and legs variable in colouration 5

5. All antennal segments reddish (Fig. 1I). Body entirely reddish, often with variable dark brown pattern on mesoscutum, head and saw sheath. Legs entirely yellowish-white (Fig. 1C). Inner tooth of right mandible weakly defined (Figs 4I–J) (Forma B) .... ***A. leucopoda***

– Only flagellum reddish (Figs 1J–K). Body entirely black or dark brown. Legs mostly yellowish-white, fore and middle femora black at base, less often entirely white or with black markings on all femora. Inner tooth of right mandible strongly pronounced (Figs 4B–C) …..……………………………………………..………………... ***A. pallidicornis***

PHYLOGENETIC TREES

In this study, we present the first sequencing data for COI, 16S rRNA, and 28S rRNA genes for *A. pallidicornis*, as well as 16S rRNA and 28S rRNA genes for Russian specimens of *A. leucopoda*. To evaluate species differentiation at the molecular level, we conducted a partitioned phylogenetic analysis using all three genetic markers from nine representative specimens. However, due to preservation issues, we were unable to obtain sequences for all three loci from every specimen. Both BI and ML analyses strongly support the monophyly of the *A. pallidicornis* and *A. leucopoda* clades (Fig. 5). Notably, within the *A. leucopoda* clade, populations from southern Russia and Khabarovsk form the distinct groups, each with moderate support (BS = 90).

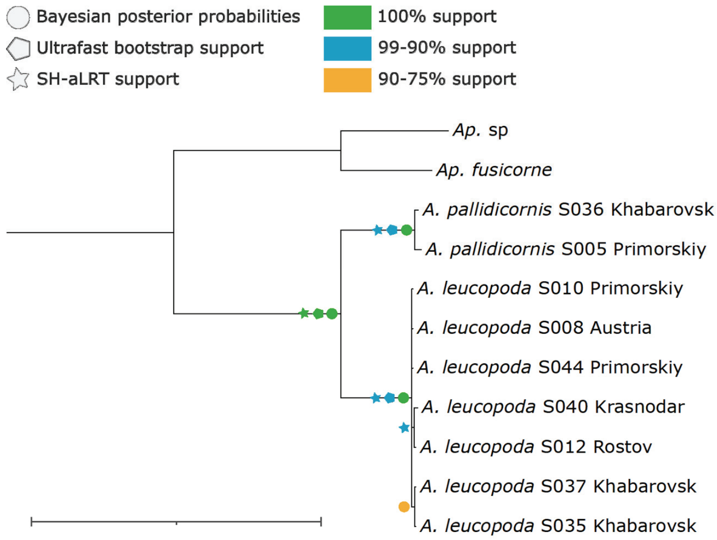

Fig. 5. Bayesian inference phylogenetic tree of *Aproceros pallidicornis* and *A. leucopoda* based on two mitochondrial (COI, 16S rRNA) and one nuclear (28S rRNA) genes. Specimens are labeled with their isolate identification codes (prefixed "S0"). Tree scale: 0.1 nucleotide substitutions per site.

Following genotyping specimens of *A. pallidicornis* and *A. leucopoda* at three molecular markers, we aimed to determine the correlation between individual colouration and species identity. In the COI-based analysis (Fig. 6), as well as in the complex COI/16S/28S analysis, specimens segregated into two clearly defined clades corresponding to the two species. The clade representing *A. pallidicornis* received stronger support in both BI (PP = 1) and ML (BS = 100) analyses compared to the *A. leucopoda* clade. In the resulting analysis, we see that samples of *A. leucopoda* from the native range (East Palaearctic) are almost genotypically identical to those

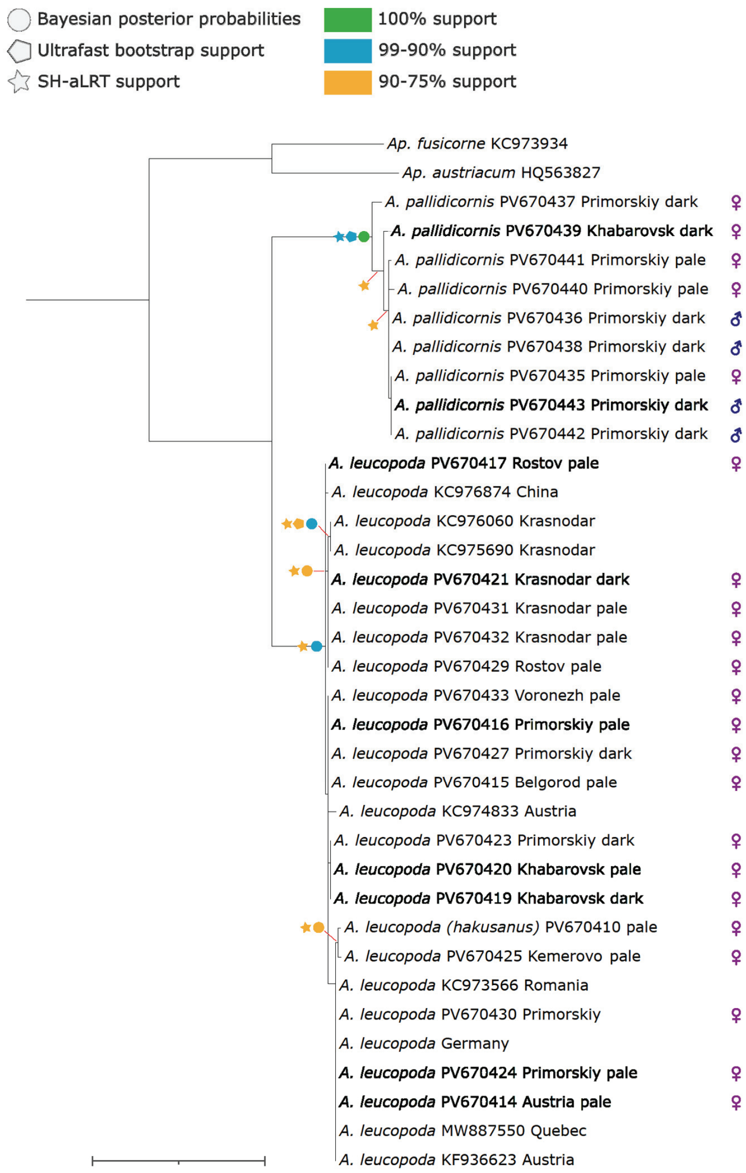

Fig. 6. Maximum likelihood phylogenetic tree of *Aproceros pallidicornis* and *A. leucopoda* based solely on the COI gene. For each sequence, the GenBank accession number and collection locality are indicated along side the species name. Sex and hind femora colouration phenotype are provided for specimens whose COI sequences were generated in this study. The colour of the hind femur, for the specimens studied, is shown at the end of each label. Sequences included in the partitioned analysis (Fig. 5) are highlighted in bold. Tree scale: 0.1 nucleotide substitutions per site.

from central Europe. This once again confirms the hypothesis of invasion of the species from East Asia (Blank *et al*., 2010). Parthenogenetic mode of reproduction favours low genetic variability of the studied loci, as a result polytomy on the tree remains partially unresolved.

Many individuals identified as *A. leucopoda* have colouration significantly deviating from the original description of the type species. Additionally, the specimen determinate by Zhelochovtsev as *A. hakusanus* was located within the *A. leucopoda* clade, forming a sister branch to a specimen from Kemerovo Province.

The colour of the hind femora was taken for verification as showing a wide range of variability. However, the assumption of the existence of cryptic species or local populations was not confirmed. Also, no correlation between phylogenetic relationships in populations and hind tibia colour was found.

PHENOLOGY

Aproceros leucopoda is widely known as an obligate parthenogenetic species. Parthenogenesis provides an accelerated life cycle, resulting in up to four (according to some reports, up to five–six: Mol & Vonk, 2015) generations per year. Adult life spans are 1–7 days, averaging about two days, and the whole cycle is less than 30 days (Blank *et al*., 2010).

In the European population (Hungary), the flight of *A. leucopoda* begins in mid-April, earlier than in the native range of Japan (Blank *et al*., 2010). However, our data show that in the conditions of the Russian Far East (Fig. 7), the flight period starts also in the mid-April, as well as in the south of the European part. The low number of specimens in the spring generation of the Far Eastern population is probably related only to the lack of material collected at this period, when the season has not yet arrived for many common groups.

Our data confirm the results of previous studies on the phenology of this species in the European part of Russia (Artokhin *et al*., 2012, Martynov *et al*., 2017). The flight of the overwintering generation begins in mid-April. The second and subsequent generations appear at the end of May, and according to the literature data adults are met until the beginning of September. Different developmental stages can be observed on trees at the same time. Because of this, a single long rise is formed on the graphs.

Comprehensive material from the Russian Far East allows us to analyze the phenology of the species in its native range for the first time. The wintering generation also appears from mid-April to May, and from the end of May to September a number of summer overlapping generations are formed. Even by the number of collected material, it is noticeable that due to several generations the number of adults increases considerably by August, but in September no adults were collected, while in Primorskiy Territory the warm season lasts till the end of September. It can be assumed that the species forms no more than four generations per year in the Far Eastern population.

The phenology of *A. pallidicornis* is discussed in detail for the first time. It is evident from our graph that the first females belonging to the hibernating generation are collected only in the end of May, which is much later than in *A. leucopoda*. We observe a significant increase in the number of collected material at the end of June, when the first summer generation of the species probably appears. The long period of adult activity indicates the possible development of the third generation, and multivoltine development of this species. In the spring generation the number of collected males is approximately equal to the number of females, but in the summer generation it exceeds it several times. The collected series of material allows us to suggest a mass flight of males (perhaps, swarming) during the summer period. In spite of frequent findings in August, adults are never found in September.

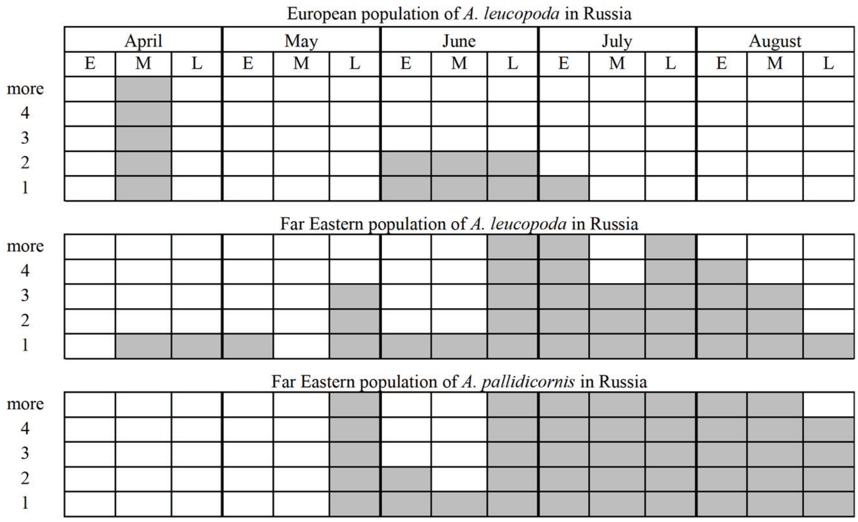

Fig. 7. Number of adults collected in the fields on the first ten days (E), second ten days (M) and the last ten or eleven days (L) of each month.

Thus, both species, in our opinion, develop as multivoltine species. *A. leucopoda* probably has up to four generations in both native and invasive parts of his habitats, while *A. pallidicornis* has only up to three generations. The flight of the overwintering generation in *A. leucopoda* begins earlier in both parts of the range than in *A. pallidicornis*. The activity of adults of both species sharply decreases by the end of August and is probably related to the phenology of the host plant.

DISCUSSION

The body colouration as well as the shape of the head, which were previously used by various authors (Takeuchi, 1939, Togashi, 1968) as diagnostic characters of species, cannot be considered sufficiently reliable. In subfamily Sterictiphorinae, it was already shown earlier on the species of genus *Aprosthema* (Vikberg, 2004).

The variability of colouration in the summer generation of *A. leucopoda* (forms A and B) exceeds that known for this and other genera of Sterictiphorinae. According to our observations, the colouration of the body is not associated with sexual, population or phenological factors. Besides thus, the cryptic species were not identified based on our molecular research either. We noted that in the summer generation in the European part of Russia, form B predominates, as already noted in the literature (Artokhin *et al*., 2012, Shchurov *et al*., 2012, Blummer, 2015), but in Europe and the Far Eastern population data mainly refer to form A. It was already described (Shchurov *et al*., 2012) that individuals with the colouration of the form B hatched from larvae of one generation in laboratory conditions in the Krasnodar Territory, and form A hatched from those sent to Moscow. These data prompted us to think about the exogenous nature of this phenomenon. The effect of temperature (especially at the pupal stage) on the colouration of insects is widely known for insects (Heal, 1989, Knapp & Nedvěd, 2013). It can be assumed that the ambient temperature can determine the colour patterns of the imago of *Aproceros leucopoda*. The south of the European part of Russia has the highest average annual temperatures in the summer months compared to the Far East or Central Europe, and this may be the main reason for the prevalence of the light-coloured form B here. These assumptions, however, require additional verification under laboratory conditions.

We made large series of microscopic examinations of ovipositors of females of both species from different forms, generations and localities. The results do not reveal reliable differences between the two species, neither in shape of lancet nor in the number of saw teeth (Figs 1D–F). Length and intensity of the middle furrow of the medial lobe of the mesonotum is also not a reliable diagnostic character and varies strongly among individuals.

The analysis of *A. leucopoda* haplotypes by COI showed low population diversity, which is probably related to the parthenogenetic mode of reproduction. As suggested earlier, the species probably invaded Europe from eastern Asia. The samples from central Europe belong to the same haplogroup as the Far Eastern population (our data). The lack of material from other East Asian countries makes it impossible to assess a more precise origin of the invasion. The Far Eastern population is quite homogeneous.

ACKNOWLEDGEMENTS

The author thanks to L.O. Poliushkevich (ZISP) and S.A. Belokobylskij (ZISP) for their help and valuable advice in writing the manuscript as well as to M. Prous (Tartu, Estonia) and M. Mutanen (Oulu, Finland) for help in sequencing part of the samples, and the staff of the Center of Collective Use "Taxon" (ZISP) for their research assistance. The author also thanks the researchers and curators of collections who provided materials for the present study: A. Taeger (Eberswalde, Germany), S.V. Vasilenko (ISEA), A.V. Antropov (ZMMU), A.S. Lelej (FSCV), Yu.N. Sundukov (Vladivostok, Russia), K.S. Artokhin (Rostov-on-Don, Russia), and V.I. Shchurov (Krasnodar, Russia).

REFERENCES

Artokhin, K.S., Ignatova, P.K. & Terskov, E.N. 2012. New insects including invasive species for the fauna of Rostov Region (Russia). *Caucasian Entomological Bulletin*, 8(2): 199–202. [In Russian] DOI: 10.23885/1814-3326-2012-8-2-199-202

Blank, S.M., Hara, H., Mikulas, J., Csoka, G., Ciornei, C., Constantineanu, R., Constantineanu, I., Roller, L., Altenhofer, E., Huflejt, T. & Vetek, G. 2010. *Aproceros leucopoda* (Hymenoptera: Argidae): An East Asian pest of elms (Ulmus spp.) invading Europe. *European Journal of entomology*, 107(3): 357–367. DOI: 10.14411/eje.2010.045

Blank, S.M., Köhler, T., Pfannenstill, T., Neuenfeldt, N., Zimmer, B., Jansen, E., Taeger, A. & Liston, A.D. 2014. Zig-zagging across Central Europe: recent range extension, dispersal speed and larval hosts of *Aproceros leucopoda* (Hymenoptera, Argidae) in Germany. *Journal of Hymenoptera Research*, 41: 57–74. DOI: 10.3897/jhr.41.8681

Choi, J.K., Lee, S.B., Wei, M. & Lee, J. W. 2015. Study on two genera, *Yasumatsua* Togashi and *Aproceros* Malaise (Hymenoptera: Argidae: Sterictiphorinae), from South Korea with description of a new species. *Entomological Research*, 45(6), 323–327.

Darriba, D., Taboada, G.L., Doallo, R. & Posada, D. 2011. ProtTest 3: fast selection of best-fit models of protein evolution. *Bioinformatics*, 27: 1164–1165. DOI: 10.1093/bioinformatics/btr088

deWaard, J.R., Ivanova, N.V., Hajibabaei, M. & Hebert, P.D.N. 2008. Assembling DNA barcodes: Analytical methods. *In:* Cristopher M. (Ed.). *Methods in Molecular Biology: Environmental Genetics*: 275–294. USA: Humana Press.

Gninenko, Yu.I., Gninenko, M.Yu. & Rakov, A.G. 2013. New discoveries of the elm zigzag sawfly in Russia. *Zashchita i Karantin Rastenii* [*Plant Protection and Quarantine*], 3: 40–41. [In Russian]

Guindon, S., Dufayard, J.-F., Lefort, V., Anisimova, M., Hordijk, W. & Gascuel, O. 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. *Systematic Biology*, 59: 307–321. DOI: 10.1093/sysbio/syq010

Heal, J.R. 1989. Variation and seasonal changes in hoverfly species: interactions between temperature, age and genotype. *Biological Journal of the Linnean Society*, 36(3): 251–269. DOI: 10.1111/j.1095-8312.1989.tb00493.x

Hernández-Triana, L.M., Prosser, S.W., Rodríguez-Perez, M.A., Chaverri, L.G., Hebert, P.D. & Ryan, G.T. 2014. Recovery of DNA barcodes from blackfly museum specimens (Diptera: Simuliidae) using primer sets that target a variety of sequence lengths. *Molecular Ecology Resources*, 14(3): 508–518. DOI: 10.1111/1755-0998.12208

Hoang, D.T., Chernomor, O., Von Haeseler, A., Minh, B.Q. & Vinh, L.S. 2018. UFBoot2: improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution*, 35: 518–522. DOI: 10.1093/molbev/msx281

iNaturalist. 2020. *iNaturalist*. USA. [online] https://www.inaturalist.org (accessed 11 April 2025).

Katoh, K. & Standley, D.M. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and* Evolution, 30(4): 772–780. DOI: 10.1093/molbev/mst010

Knapp, M. & Nedvěd, O. 2013. Gender and timing during ontogeny matter: effects of a temporary high temperature on survival, body size and colouration in *Harmonia axyridis*. *PLoS One*, 8(9): e74984. DOI: 10.1371/journal.pone.0074984

Kondratyeva, A.M., Rzhevsky, S.G., Aksenenko, E.V., Kirpach, D.A., & Kornev, I.I. 2023. Detection of a mass breeding site of the elm sawfly-zigzag *Aproceros leucopoda* Takeuchi, 1939 (Hymenoptera: Argidae) in Voronezh. *Samarskiy Nauchnyi Vestnik* [*Samara Journal of Science*], 12(3): 63–68. DOI: 10.55355/snv2023123108

Lafrenière, J. 2024. *Biologie et écologie de la tenthrède en zigzag de l'orme dans sa nouvelle aire de répartition au Québec et en Amérique du Nord*. Canada, Québec. 93 p.

Letunic, I. & Bork, P. 2021. Interactive Tree Of Life (iTOL) v5: an online tool for phylogenetic tree display and annotation. *Nucleic Acids Research*, 49: W293–W296. DOI: 10.1093/nar/gkab301

Malaise, R. 1931. Blattwespen aus Wladiwostok und anderen Teilen Ostasiens. *Entomologisk Tidskrift*, 52(2): 97–159.

Martel, V., Morin, O., Monckton, S.K., Eiseman, C.S., Béliveau, C., Cusson, M., & Blank, S.M. 2022. Elm zigzag sawfly, *Aproceros leucopoda* (Hymenoptera: Argidae), recorded for the first time in North America through community science. *The Canadian Entomologist*, 154(1): 1–18. DOI: 10.4039/tce.2021.44

Martynov, V.V., Nikulina, T.V. & Shokhin, I.V. 2017. Current distribution of invasive dendrophilous insects in the Rostov Province. *Subtropicheskoe i Dekorativnoe Tsvetovodstvo* [*Subtropical and Ornamental Gardening*], 63: 175–182. [In Russian]

Mol, A.W.M. & Vonk, D.H. 2015. De iepenzigzagbladwesp *Aproceros leucopoda* (Hymenoptera, Argidae), een invasieve exoot in Nederland. *Entomologische Berichten*, 75(2): 50–63.

Oten, K.L., Day, E., Dellinger, T., Disque, H.H., Barringer, L.E., Cancelliere, J., Somers, L. & Bertone, M.A. 2023. First records of elm zigzag sawfly (Hymenoptera: Argidae) in the United States. *Journal of Integrated Pest Management*, 14(1): 1–7. DOI: 10.1093/jipm/pmad009

Prous, M., Liston, A., Monckton, S.K., Kramp, K., Vårdal, H., Vikberg, V., Heibo, E. & Mutanen, M. 2025. West Palaearctic species of *Euura* Newman, 1837 (Hymenoptera, Tenthredinidae). *European Journal of Taxonomy*, 977: 1–377. DOI: 10.5852/ejt.2025.977.2799

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Hohna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61(3): 539–542. DOI: 10.1093/sysbio/sys029

Schmidt, S. & Walter, G.H. 2014. Young clades in an old family: major evolutionary transitions and diversification of the eucalypt-feeding pergid sawflies in Australia (Insecta, Hymenoptera, Pergidae). *Molecular Phylogenetics and Evolution*, 74: 111–121. DOI: 10.1016/j.ympev.2014.02.002

Schulmeister, S. 2003. Simultaneous analysis of basal Hymenoptera (Insecta): introducing robust-choice sensitivity analysis. *Biological Journal of the Linnean Society*, 79(2): 245–275. DOI: 10.1046/j.1095-8312.2003.00233.x

Shevchenko, S.V., Stcherbakova, L.N. Phylophagous arthropods on elms (Ulmus) in Saint Petersburg. *Dendrobiontnye bespozvonochnye zhivotnye i griby i ih rol v lesnykh ekosistemakh (XI Chteniya pamyati O.A. Kataeva): materialy vserossiiskoi konferentcii s mezhdunarodnym uchastiem (Sankt-Peterburg, 24–27 noyabrya 2012 g.)* [Dendrobiont invertebrate animals and fungi and their role in forest ecosystems (XI Readings in memory of O.A. Kataev): proceedings of the All-Russian conference with international participation (St. Petersburg, 24–27 November 2020)]: 359–360. [In Russian]

Sundukov, Yu.N. 2009. Order Hymenoptera. Symphyta. *In:* Storozhenko, S.Yu., Sundukov, Yu.N., Lelei, A.S. , Sidorenko, V.S., Proshchalykin, M.Yu., Kupyanskaya, A.N. (Eds). *Insects of Lazovsky Nature Reserve*: 212–220. Vladivostok: Dalnauka. [In Russian]

Taeger, A., Liston, A.D., Prous, M., Groll, E.K., Gehroldt, T. & Blank, S.M. 2018. *ECatSym – Electronic World Catalog of Symphyta (Insecta, Hymenoptera)*. Program version 5.0 (19 December 2018), data version 40 (23 September 2018). Senckenberg Deutsches Entomologisches Institut (SDEI), Müncheberg. [online] https://sdei.de/ecatsym/ (accessed 11 April 2025).

Takeuchi, K. 1939. A systematic study on the suborder Symphyta (Hymenoptera) of the Japanese Empire (II). *Tenthredo (Acta Entomologica)*, 2(4): 393–439.

Thomas, K.F., Wong, N.L.-T., Huaiyan, R., Hector, B., Andrew, J.R., Edward, S., Chris, B., Nicola, D.M., Nick, G., Matthew, W.H., Gavin, H., Rob, L. & Bui, Q.M. 2025. IQ-TREE 3: Phylogenomic Inference Software using Complex Evolutionary Models. [online] http://www.iqtree.org [updated 7 April 2025; viewed 11 April 2025] DOI: 10.32942/X2P62N

Togashi, I. 1962. Descriptions of new species of Symphyta (Hymenoptera) from Japan (1). *Kontyû*, 30: 202–204.

Togashi, I. 1968. Japanese sawflies of the subfamily Sterictiphorinae (Hym., Argidae). *Kontyû*, 36: 285–293.

Tsikas, A. & Karanikola, P. 2024. First record of the Zigzag elm sawfly *Aproceros leucopoda* (Hymenoptera: Argidae) in Greece. *Entomologia Hellenica*, 33(2): 70–77.

Vaidya, G., Lohman, D.J. & Meier, R. 2011. SequenceMatrix: concatenation software for the fast assembly of multi-gene datasets with character set and codon information. *Cladistics*, 27: 171–180. DOI: 10.1111/j.1096-0031.2010.00329.x

Vétek, G., Csávás, K., Fail, J. & Ladányi, M. 2022. Host plant range of *Aproceros leucopoda* is limited within Ulmaceae. *Agricultural and Forest Entomology*, 24(1): 1–7. DOI: 10.1111/afe.12463

Vikberg, V. 2004. Seasonal head dimorphism and taxonomy of some European species of *Aprosthema* (Hymenoptera: Symphyta: Argidae). *Beiträge zur Entomologie Contributions to Entomology*, 54(1): 107–125. DOI: 10.21248/contrib.entomol.54.1.107-125

Wong, T.K., Ly-Trong, N., Ren, H., Baños, H., Roger, A.J., Susko, E., Bielow, C., Maio N.D., Goldman, N., Hahn, M.W., Huttley, G., Lanfear, R. & Minh, B.Q. 2025. IQ-TREE 3: Phylogenomic Inference Software using Complex Evolutionary Models. [online] http://www.iqtree.org [updated 7 April 2025; viewed 11 April 2025] DOI: 10.32942/X2P62N

Zhelochovtsev, A.N. & Zinovjev, A.G. 1996. A list of the sawflies and horntails (Hymenoptera, Symphyta) of the fauna of Russia and adjacent territories. *Entomological Review*, 75: 58–80.

© **Far Eastern entomologist (Far East. entomol.)** Journal published since October 1994.

Address: Federal Scientific Center of the East Asia Terrestrial Biodiversity (former Institute of Biology and Soil Science), Far East Branch of the Russian Academy of Sciences, 690022, Vladivostok-22, Russia.

E-mail: storozhenko@biosoil.ru web-site: http://www.biosoil.ru/fee