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A NEW SPECIES OF *RHAGOLETIS* (DIPTERA, TEPHRITIDAE) FROM SWITZERLAND, WITH DISCUSSION OF ITS RELATIONSHIPS WITHIN THE GENUS

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A New Species of *Rhagoletis* (Diptera, Tephritidae) from Switzerland, with Discussion of its Relationships within the Genus. **Korneyev, S. V., Smith, J. J., Hulbert, D. L., Frey, J. E., Korneyev, V. A.** — *Rhagoletis merzi* sp. n., is described and illustrated based on specimens swept and reared from *Juniperus sabina* L. in Switzerland. A comparative review of Palaearctic species and a key to Palearctic and Nearctic species similar to *R. merzi* is provided. Based on DNA sequences from the COI, CAD, 28S, period, and AATS genes (4270 bp) of 92 isolates from two outgroup species (*Anastrepha ludens, Euphranta canadensis*), one species of *Carpomya* and 35 species representing most of species groups of *Rhagoletis*, a MrBayes analysis recovered a monophyletic lineage of *Juniper*-infesting species within a monophyletic cluster of *R. fausta, R. batava,* as well as the *suavis, cingulata, pomonella, tabellaria* and *juniperina* groups. The *juniperina* group includes both Nearctic (*R. juniperina* and undescribed forms) and Palaearctic species (*R. flavigenualis* and *R. merzi*). *Rhagoletis merzi* is more similar to the Nearctic *R. juniperina* in both morphological characters (wing pattern, occiput, mesonotum and legs coloration, shape of male surstyli) and molecular sequences than to the Palearctic *R. flavigenualis*.
Key words: phylogeny, multigene DNA analysis, juniper.

Introduction

The genus *Rhagoletis* Loew, 1862 belongs in the tribe Carpomyini and includes more than 75 described species of the true fruit flies occurring mostly in the Holarctic and Neotropical Regions and, to the lesser degree, in the Oriental Region (Smith & Bush, 1999; Korneyev & Korneyev, 2019). Many *Rhagoletis* species are economically important, including pests of apples, cherries, blueberries, and walnuts (Boller & Prokopy, 1976). Two pest species, *Rhagoletis cingulata* (Loew, 1862) (the eastern cherry fruit fly) and *R. completa* (Cresson, 1929) (the walnut husk fly) have been introduced from North America to Europe (Merz, 1991), and *R. cerasi* (Linnaeus, 1758) (the European cherry fruit fly) has recently been introduced to North America.

Larvae of most *Rhagoletis* species infest fleshy fruits of various angiosperm plants, except a few species whose larvae feed in gymnosperm fleshy cones or *galbuli* (commonly called "juniper berries"). *Rhagoletis* species are oligo- or monophagous, specialized frugivores, often infesting a single host species. Host plant specialization and fidelity are important aspects of *Rhagoletis* biology (Bush, 1966). Therefore, studying the patterns of host use and host shifts in *Rhagoletis* is an important part of fundamental evolutionary research and valuable from an economic perspective.

A host shift to an economically important crop from a native host has been documented for *Rhagoletis pomonella* (Walsh) from its native host plant *Crataegus* spp. (hawthorn) to introduced commercial apples (*Malus domestica*) in the last ~170 years (Walsh, 1867; Bush, 1969). Such host plant shifts in *Rhagoletis* have led to the formation of host races, the hypothesized initial stage of speciation-with-gene-flow, and have provided an opportunity to study the fundamental nature of population divergence and the formation of new species, especially in the *R. pomonella* species complex (Bush, 1969 and many other publications), which has become a textbook example of speciation in action (Schluter, 2000; Coyne & Orr, 2004; Nosil, 2012).

Rhagoletis species have been classified taxonomically into defined species groups beginning with the seminal work of Bush (1966), in which the *pomonella*, *tabellaria*, *suavis*, *cingulata* and *ribicola* species groups were proposed for classification of most North American *Rhagoletis* species based on analyses of their morphological characteristics. Analyses based on morphology (Jenkins, 1996), allozymes (Berlocher & Bush, 1982), morphology and mitochondrial DNA (Smith et al., 2006) further defined the species groups, but did not resolve relationships among these groups. The phylogenetic relationships among these five *Rhagoletis* species groups remained unresolved until Hamerlinck et al. (2016) demonstrated that the *pomonella* and *tabellaria* species groups are sister groups, and more recently Hulbert (2018) produced a more detailed and well supported phylogeny indicating the relationships among all five species groups.

Many of the Palearctic *Rhagoletis* species were grouped by Kandybina (1977) into the *cerasi*, *juniperina*, *alternata* and *meigenii* species groups, originally based on larval characters (she also provided refined diagnoses of the *suavis*, *cingulata*, and *pomonella* species groups); see Kandybina (1961, 1962, 1972), Kandybina & Richter (1976), and Richter & Kandybina (1997) for larval descriptions. These Palearctic *Rhagoletis* species were alternatively placed into the *cerasi*, *flavicincta*, *meigenii*, and *zernyi* species groups by Smith et al. (2006) based on mitochondrial COII and adult morphological characters.

The Palearctic *Rhagoletis* species (including those originally described in *Zonosema*, *Megarrhagoletis*, and *Microrhagoletis*, now considered synonyms of *Rhagoletis*) comprise more than 30 described taxa, most of which were reviewed and keyed by Rohdendorf (1961). Later, additional species were described by Jermy (1961), Kandybina (1972), Richter (1974), Kandybina & Richter (1976), Richter & Kandybina (1997), and Korneyev & Merz (1997). The Middle Asian, Far East Palearctic, and Oriental species of *Rhagoletis* and the closely related *Carpomya* were keyed by Korneyev & Merz (1997), Korneyev & Ovchinnikova (2004), Ito (2011), whereas Freidberg & Kugler (1989), Merz (1994), Korneyev (1997), and Mohamadzade Namin & Rasoulian (2009) treated the European, Middle Eastern, and Caucasian species. Korneyev et al. (2018 a) provided a key for the species of Europe, Asia Minor, Caucasus, and Near East, including Iran, along with references to each species, data on known host plants and distribution, as well as some taxonomic remarks. Recently, Korneyev & Korneyev (2019) provided a key to the Asian (except eastern) species.

Although not all non-Nearctic species were included, recent work using a Bayesian phylogenetic and Maximum Likelihood analysis based on DNA sequences at five loci (Hulbert, 2018) recovered a well-supported monophyletic group containing all of the Nearctic *Rhagoletis* species that belong to the five species groups named by Bush (1966), plus two unplaced Nearctic species (*R. fausta* and *R. juniperina*), as well as the Palearctic species *R. batava* and *R. flavigenualis* (Hulbert, 2018). Mitochondrial COII sequences had earlier suggested that *R. batava* and *R. flavigenualis* might have taxonomic affinity to the "core Nearctic taxa" (Smith et al., 2006). Additionally, Hulbert (2018) supported the monophyly of a group within this larger clade consisting of the two juniper-infesting species, the Nearctic *R. juniperina* Marcovitch and the Palearctic *R. flavigenualis* Hering. Thus, our working hypothesis is that all of the *Juniperus*-infesting species (*R. juniperina*, *R. flavigenualis*, *R mongolica* Kandybina, and *R. zernyi* Hering) comprise a monophyletic group, based on these initial DNA sequences and the very similar morphological characters and host plant preferences of these species. At this point in time, however, DNA sequences from *R. mongolica* and *R. zernyi* are lacking to test this hypothesis.

In this paper, we determined the position of a newly described species from Switzerland, *R. merzi* sp. n., and its relationships with the other *Rhagoletis* species. We provided comparison of its morphological characters with the species occurring in the Palaearctic Region, and DNA sequences at five genetic loci using a wide sample of other representatives of the genus.

Material and methods

The following acronyms refer to collections housing specimens:

MHNG: Muséum d'Histoire Naturelle, Geneva, Switzerland;
MSU: Michigan State University, East Lansing, MI, USA;
SIZK: I. I. Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, Kyiv, Ukraine;
SMNS: Staatliches Museum für Naturkunde Stuttgart, Germany.

Morphological terminology generally follows White et al. (1999) except for the wing venation, which follows Cumming & Wood (2017). Wing bands are labeled on figure 1 a. Measurements are given in mm. Body length of females includes the oviscape.

Genitalia were prepared for study using the following procedure: the abdomen was excised from a relaxed specimen, cleared in NaOH solution (10 %) for 2 hours at 90–95 °C, and then washed in distilled water. Genitalia were examined in a drop of glycerine on a microscope slide with a depression or under a glass cover slip. Detached parts are stored in polypropylene microvials containing glycerine pinned together with a specimen. Structures were measured with an ocular micrometer. Wing and habitus photographs were taken using a Canon PowerShot A640 camera connected to a Zeiss Stemi C-2000 (SIZK) microscope or using a Leica DFC 490 camera mounted on a Leica Z16 APO A microscope (MNKB). Photographs of genitalia were taken using a Nikon Coolpix P50 camera through the eyepiece of a Wild M11 light microscope. Digitized photographs were stacked using CombineZM® (Hadley, 2007) and Helicon Focus®. Some photos of *R. merzi* were taken at Michigan State University using a Visionary Digital Passport II system (Dun, Inc., Palmyra, Virginia, USA). Photographic stacks were taken with a Canon EOS 5D Mark II equipped with a 65 mm Canon Macro lens (Canon Inc., Tokyo, Japan) and Dynalite MH2015 Road Flash Heads (Dynalite Flash Equipment, Union, New Jersey, USA) mounted onto a Stack Shot Macro Rail system (Cognisys, Inc, Traverse City, Michigan, USA) and montaged in Helicon Focus 7.5.6 (Helicon Soft, Kharkiv, Ukraine). Postprocessing was performed with Adobe Photoshop v 19.1.9 (Adobe Inc., San Jose, California, USA).

DNA Isolation and PCR amplification, sequencing and editing

DNA extraction for all specimens except *R. merzi* sp. n. was done at Michigan State University, Department of Entomology in Smith's lab. DNA was extracted using the DNeasy Blood & Tissue Kit protocol (Qiagen, Valencia, CA). For most specimens a single leg or head was taken for analysis. Five loci, with total length of 4270 base pairs, previously shown to be useful in systematic analyses of insects, especially tephritids, were analyzed (Han et al., 2002; Hebert et al., 2004; Moulton & Wiegmann, 2004; Barr et al., 2005; Smith & Brown, 2008, Hamerlinck et al., 2016); see also Hulbert (2018: Table 2.2) for details.

The mitochondrial protein coding gene cytochrome oxidase I (COI) (684 bp), the nuclear protein coding carbamoyl-phosphate synthase (CPS) domain of carbamoyl-phosphate synthetase 2, aspartate transcarbamylase and dihydroorotase gene (CAD) (990 bp), the large subunit of the nuclear ribosomal gene (28S) (1359 bp), the nuclear protein coding period gene (614 bp) and the nuclear protein coding alanyl t-RNA synthetase gene (AATS) (623 bp) were the PCR-amplified regions.

Primers and thermocycler conditions used for each of the five genes amplified were listed by Hulbert (2018: Table 2.2). Amplifications of COI, period, and AATS employed a single primer pair. For 28S, two primer pairs were used to amplify two non-overlapping fragments separated by 58 bp (1445 bp total). For CAD, we used two primer pairs to amplify two overlapping fragments (1003 bp total).

Verification of successful amplification for all PCR products was confirmed electrophoretically via agarose gels (1 % w/v) prior to purification of PCR products using a QIAquick PCR Purification Kit (Qiagen, Valencia, CA) according to the manufacturer's specifications. Sanger sequencing was performed at the Michigan State University Research Technology Support Facility via BigDye Terminator Sequencing on an Applied Biosystems 3730xl DNA Analyzer (Foster City, CA, USA) using the PCR primers as sequencing primers.

All sequences were edited manually by visual comparison of the automatic base calls to the original electropherogram traces using MEGA (version 7.0.14) (Tamura et al., 2011) and deposited in GenBank (accession numbers MG825190-MG825320) (see Hulbert, 2018: Table 2.3) except for the new sequences obtained and uploaded in 2022 (table 1). Alignments of DNA sequences were constructed and edited in MEGA. We used the default parameters in MUSCLE (Edgar, 2004) as implemented in MEGA to align DNA sequences for all loci except 28S. For the 28S alignment, we used MAFFT with default parameters (Katoh et al., 2002).

The alignment is available as a supplementary file at https://doi.org/10.5281/zenodo.6111737.

The names of terminal taxa correspond to those in table 1 and Hulbert (2018: Table 2.3), except *R. bushi* Hulbert & Smith, 2018 sometimes mentioned as "buffaloberry_fly" by Hulbert (2018).

Sampling and DNA extraction of *Rhagoletis merzi* sp.n.

Infested fleshy cones of *Juniperus sabina* L. were sampled near Visperterminen, Switzerland in October 2016 by JJS. They were transferred to plastic boxes containing sterile sand to enable larvae to emerge from the fleshy cones and pupate. DNA of the pupae was extracted with the GenElute™ Mammalian Genomic DNA Miniprep Kit (Merck Sigma-Aldrich Chemie, Buchs, Switzerland) according to the manufacturer's recommendations.

Sequencing Library preparation and DNA sequencing

For library preparation, the Nextera® XT DNA Library Prep kit (Illumina, San Diego, CA, USA) was used with 1ng of DNA according to the manufacturer's recommendations. As the library was to be sequenced together with other samples on a MiSeq (Illumina, USA), the DNA had to be tagged by a barcoding PCR performed using primer pairs from the Nextera XT Index kit (Illumina, USA). The amplification reaction was conducted with the same reagents and the thermocycler was set to the following parameters: 95 °C for 3 min,

20 cycles of 95 °C (30 s), 55 °C (30 s), 72 °C (30 s), one additional step at 72 °C (5 min) and a final step at 4 °C until further processing.

Amplified products were cleaned with the protocol of the AMPure XP beads (Beckman-Coulter, Fullerton, CA, USA). The quality of the product was checked on a 1 % agarose gel and quantified on a Qubit 3.0 Fluorimeter (Thermo Fisher Scientific, Waltham, MA, USA) using the corresponding High-sensitivity dsDNA HS Assay Kit. The *Rhagoletis merzi* library was then pooled with the other samples prepared for this run in an equimolar way and loaded on a cartridge on the Illumina MiSeq sequencing system (Illumina, USA). MiSeq Reagent Kit V3 (2 × 300 bp) sequencing reagents (Illumina, USA) were used for this experiment together with 1 % of PhiX Control v.3 (Illumina, USA) spiking for quality control.

The collection and voucher information for the *Rhagoletis* and outgroup species sequenced are given in Hulbert (2018) except those given in the table 1 and the accession numbers in the table 2. We used the dataset of Hulbert (2018) in its entirety, adding to it three specimens of the new species *R. merzi*, and three specimens collected from *J. horizontalis* in 2015, which we designate as *R.* sp. nr. *juniperina* for the analyses here.

Phylogenetic analyses

We used a Bayesian framework for our phylogenetic analyses of the five-locus alignment. We predefined the following biologically relevant partitions in the alignments per the recommendation of the PARTITION-

Table 1. Specimen collection records (compatible with Table 2.1 in Hulbert, 2018)

Species group	No	Taxon	Locality	Host plant	Date	Collector
juniperina (= zernyi)	1	*R.* sp. ex *J. horizontalis* 15GHB2	Centerville Township, Michigan. USA 44.94, -85.81	Cupressaceae: *Juniperus horizontalis*	8.10.2015	J. J. Smith
juniperina (= zernyi)	2	*R.* sp. ex *J. horizontalis* 15gab3	Centerville Township, Michigan. USA 44.94, -85.81	Cupressaceae: *Juniperus horizontalis*	8.10.2015	J. J. Smith
juniperina (= zernyi)	3	*R.* sp. ex *J. horizontalis* 15BetsieA	Lake Township, Michigan. USA 44.69, -86.25	Cupressaceae: *Juniperus horizontalis*	8.10.2015	J. J. Smith
juniperina (= zernyi)	4	*R. merzi* sp. n. 2016 1	Switzerland, Valais, Visperterminen 46.262, 7.899	Cupressaceae: *Juniperus sabina*	17.10.2016	J. J. Smith
juniperina (= zernyi)	5	*R. merzi* sp. n. 2016 2	Switzerland, Valais, Visperterminen 46.262, 7.899	Cupressaceae: *Juniperus sabina*	17.10.2016	J. J. Smith
juniperina (= zernyi)	6	*R. merzi* sp. n. 2018 1	Switzerland, Valais, Visperterminen 46.262, 7.899	Cupressaceae: *Juniperus sabina*	17.10.2016	J. J. Smith

Table 2. GenBank accession numbers of the DNA sequences (compatible with Table 2.3 in Hulbert, 2018)

Taxon designation	COI	CAD	period	AATS	28S part A	28S part B
R. sp. ex *J. horizontalis* 15GHB2	OM541942	OM718809	OM718815	OM718821	OM569803	OM569801
R. sp. ex *J. horizontalis* 15gab3	OM541943	OM718810	OM718816	OM718822	OM569805	OM569802
R. sp. ex *J. horizontalis* 15BetsieA	OM541944	OM718811	OM718817	OM718823	OM569806	OM569803
R. merzi sp. n. 2016 1	OM632706	OM718812	OM718818	OM718824	OM649845	
R. merzi sp. n. 2016 2	OM632707	OM718813	OM718819	OM718825	OM649846	
R. merzi sp. n. 2018 1	OM632708	OM718814	OM718820	OM718826	OM649847	

FINDER software user-guide (Lanfear et al., 2017): 28S (fragments were concatenated and considered a single partition for phylogenetic analysis), and separate partitions for each nucleotide position (1st, 2nd, 3rd codon position) for COI, CAD, period and AATS. Next, we used PARTITIONFINDER v2.1.1 (Lanfear et al., 2017) to determine combinability of partitions and nucleotide substitution models. We then ran PARTITIONFINDER implementing PhyML (Guindon et al., 2010) with the "greedy" algorithm (Lanfear et al., 2012) using the corrected Akaike Information Criterion (AICc) to assess model and partition quality. We conducted runs of PARTITIONFINDER restricted to MRBAYES models.

The Bayesian analysis used four independent runs each with four Metropolis-coupled chains with default heating parameters (one cold and three heated) in MRBAYES. The chains were sampled once every thousand generations for 5 million generations and the first 25 % of samples were discarded as burn-in. All analyses converged to an average standard deviation of split frequencies below 0.02 (Ronquist et al., 2012).

A maximum-likelihood (ML) analysis was also perfo med in MEGA 11 (Tamura et al., 2021) using Tamura-Nei model (Nei & Kumar, 2000) with rates among sites Gamma distributed with invariant sites (G+I), NNI heuristic method, with the initial tree automatically made (NJ/BioNJ). The reliability of clustering patterns in the ML tree was determined by the bootstrap test (500 replications) in 4 threads.

Mesquite 3.20 (Maddison & Maddison, 2021) was used to visualize the phylogenetic trees and to estimate genetic distances using Kimura's two-parameter (K2P) model of nucleotide substitution.

Results

Rhagoletis Loew, 1862

Rhagoletis Loew, 1862 b: 44.

Type species: *Musca cerasi* Linnaeus, 1758 (by monotypy).
Zonosema Loew, 1862 b: 43.
Type species: *Tephritis alternata* Fallén, 1814 (by subsequent designation of Rondani, 1870: 6).
Microrrhagoletis Rohdendorf, 1961: 187.
Type species: *Microrrhagoletis samojlovitshae* Rohdendorf, 1961 (by original designation).
Megarrhagoletis Rohdendorf, 1961: 196.
Type species: *Megarrhagoletis magniterebra* Rohdendorf, 1961 (by original designation).

Diagnosis. Medium-sized (3.0–8.0 mm) fruit flies with 3 frontal and 2 (rarely 1) orbital setae, pale or dark postocellar seta, short head, first flagellomere usually with pointed apex (rarely rounded); thorax entirely orange to entirely black; postpronotal lobe usually pale yellow; scutellum orange to black with creamy white or yellow disc (black in *R. psalida*); surstylus of male with long and variously shaped, usually acute, posterior lobe; oviscape with T-shaped desclerotized posteromedial area ventrally; aculeus usually uniformly tapered apically. Third instar larva with variable number (from 3 to 20) of oral ridges and stomal sensory organ with or without preoral teeth.

Remarks. The morphological diagnosis of *Rhagoletis* almost entirely overlaps with that of *Carpomya*, which sometimes cannot be undoubtedly differentiated (except the mesonotum pattern and number of frontal setae; both variable). Current concepts of these genera need revision based on a sound multi-locus DNA reconstruction of phylogenetic relationships among the genera of Carpomyini.

Key to the *Rhagoletis* species similar to *R. merzi* sp. n.

This key includes *R. merzi* and the species similar to it, having a black body with postpronotal lobe and major part of scutellum yellow or white, the wing with 4 bands, of which the apical band is connected to the subapical band and separated from the apical wing margin by a crescentic marginal hyaline area: *Rhagoletis juniperina* Marcovitch, 1915, *R. zernyi* Hendel, 1927, *R. flavigenualis* Hering, 1958 (the *juniperina* group), *R. tabellaria* (Fitch, 1855), *R. persimilis* Bush, 1966, *R. electromorpha* Berlocher, 1982, *R. bushi* Hulbert et al., 2018 (*tabellaria* group), *R. ebbettsi* Bush, 1966, *R. ribicola* Doane, 1899 (*ribicola* group), and the following species unassigned to groups, *R. scutellata* Zia, 1938, *R. batava* Hering, 1958, *R. mongolica* Kandybina, 1972), and *R. bagheera* Richter & Kandybina, 1997.

1. Dark subbasal and discal bands widely connected in posterior part of wing (see Foote et al., 1993: figs 378–379). Nearctic Region only. ..... *tabellaria* group, part 2
— Dark subbasal and discal bands widely separated or connected by a pale grey, indistinctly darkened area (fig. 1). Palearctic and Nearctic Regions. 4
2. Apical crescentic hyaline area (cr) shorter, reaching at most to posterior 1/3 of costa in cell r_{4+5}; subapical band uniformly dark, crossvein dm-m pale emarginated (see: Foote et al., 1993: fig. 379). .... *R. electromorpha* Berlocher
— Apical crescentic hyaline area longer, reaching vein M_1; subapical band uniformly dark, crossvein dm-m not pale emarginated (see: Foote et al., 1993: 359). 3
3. Aculeus shorter than 0.7 mm. Larvae in fruits of *Cornus* (Cornaceae) and *Vaccinum* (Ericaceae). ....*R. tabellaria* (Fitch)
— Aculeus longer than 0.8 mm. Larvae in fruits of *Prosartes hookeri* (Liliaceae). .... *R. persimilis* Bush
4. Occiput completely yellow. Wing pattern usually yellowish brown, with bands laterally emarginated with brown (figs 1, a–b). Femora mostly or entirely yellow. Larvae in *Juniperus* fleshy cones. ....*juniperina* group, part 5

— Occiput with at least medial sclerite above occipital foramen, or often lateral of occipital suture black or brown. Wing pattern with blackish brown bands (figs 1, c–e). Femora coloration and host plants variable. 6
5. Discal and subapical bands widely connected at least in cell r_{2+3} (fig. 1, a). Spain. .....*R. zernyi* Hendel
— Discal and subapical bands entirely separated (fig. 1, b). Asia: Turkey, Caucasus, Iran, Middle Asia. .... *R. flavigenualis* Hering
6. Discal and subapical bands connected in cell r_{4+5} (see: Bush, 1966: fig. 200; Foote et al., 1993: fig. 381). USA: California..... *R. ebbettsi* Bush, 1966
— Discal and subapical bands widely isolated. 7
7. Femora yellow. 8
— At least mid and hind femora black. 9
8. Only dorsal third of occiput with dark transverse spot. Larvae in *Juniperus sabina*. Asia: Mongolia, (?) Kyrgyzstan. Genitalia not examined. ..... *R. mongolica* Kandybina
— Occiput with wide black horseshoe-shaped pattern reaching its lower half. Lateral surstylus with short posterior lobe. Spermatheca narrow and long, worm-like (see Bush, 1966: fig. 167). Larvae in *Ribes* spp. North America..... *R. ribicola* Doane
9. Occiput with wide black horseshoe-shaped pattern reaching its lower half. Lateral surstylus with long and narrow posterior lobe (fig. 2, a). Spermatheca rounded, small, < 0.05 mm in diameter, with neck longer than spermatheca itself (fig. 2, d). 10
— Occiput black only across upper 1/3. Lateral surstylus with short posterior lobe (fig. 2, c) (not known for *R. scutellata*). Spermatheca globose, larger, > 0.05 mm in diameter, with neck shorter than spermatheca itself (fig. 2 f) (not known in *R. scutellata*). Associated with *Juniperus* (host not known for *R. scutellata*). 12
10. Nearctic Region. Scutellum laterally and fore coxa usually black. Larvae in *Shepherdia argentea* (Pursh) Nutt. (Eleagnaceae). ..... *R. bushi* Hulbert & Smith
— Palearctic Region. Scutellum laterally and fore coxa usually yellow. Host plants different. 11
11. Smaller: wing length less than 2.8 mm (in ♂ 2.0–2.4, rarely up to 2.7 mm), in ♀ 2.2–2.5 mm). Larvae in *Rhamnus pallasii* (Rhamnaceae). Asia: Armenia, Georgia. ..... *R. bagheera* Richter & Kandybina
— Larger: wing length greater than 2.9 mm (in ♂ 3.0–3.6 mm, in ♀ 3.3–4.2 mm). Europe, Asia (Caucasus, Middle Asia, Siberia, China). Larvae in *Hippophae rhamnoides* L. (Elaeagnaceae). ..... *R. batava* Hering
12. Abdominal tergites 2–4 uniformly brown or black, without pale bands on posterior margins. Genital characters not examined. Host plants unknown. China (Gansu). ..... *R. scutellata* Zia
— Abdominal tergites 2–4 with pale bands on posterior margins. 13

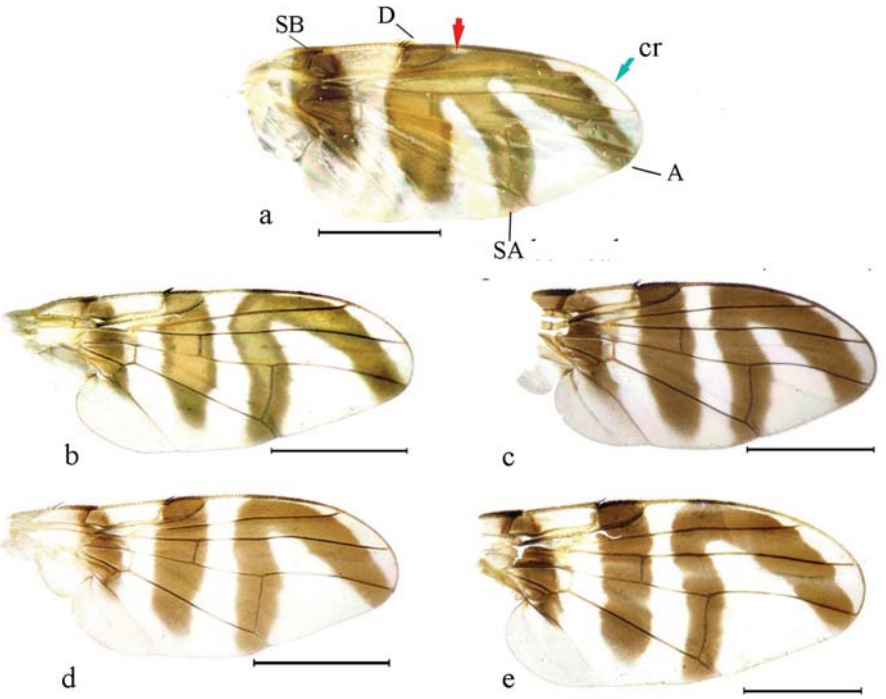

Fig. 1. Palearctic species of *Rhagoletis* species similar to *R. merzi*, wings: a — *R. zernyi*; b — *R. flavigenualis*; c — *R. merzi*, sp. n.; d — *R. bagheera*; e — *R. batava*. Bands are marked as follows: A — apical, D — discal, SA — subapical, SB — subbasal. Red arrow shows connection of D and SA; cyan arrow shows **cr** — crescentic hyaline area. Scale: 1 mm.

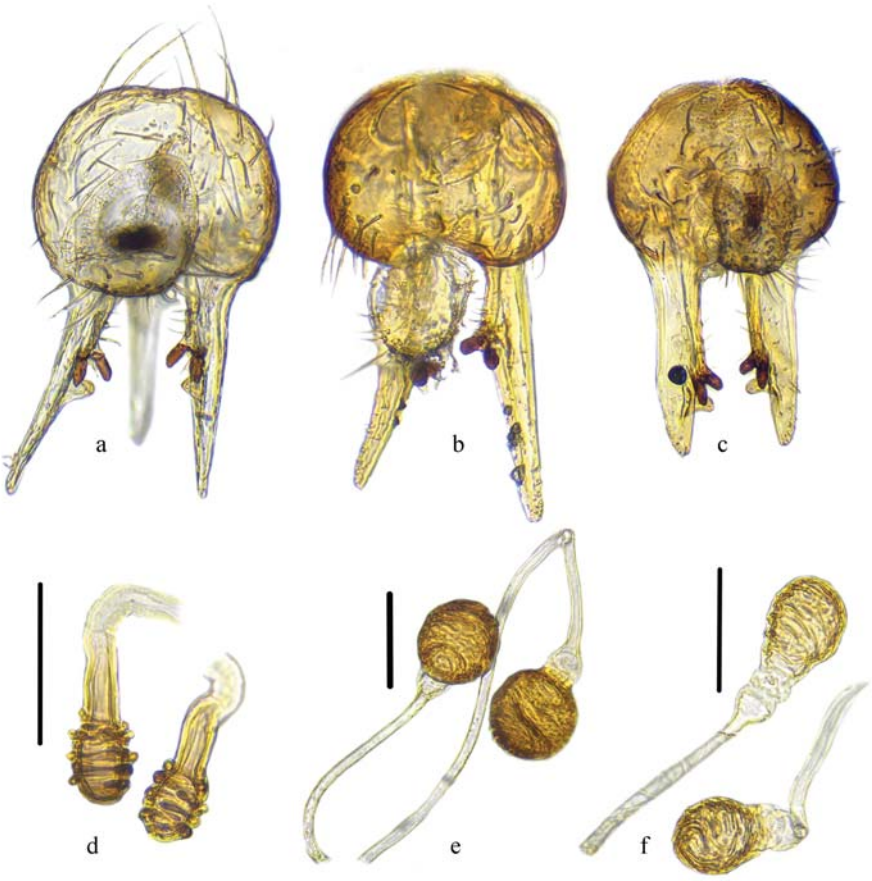

Fig. 2. Palearctic species of *Rhagoletis* species similar to *R. merzi*, epandrium and surstyli, posterior view (a–c) and spermatheca (d–f): a, d — *R. batava*; b, e — *R. flavigenualis*; c, f — *R. merzi* sp. n.

13. North America. Associated with various *Juniperus* spp. .... *R. juniperina* Marcovitch(possibly an assemblage of cryptic species)
— Europe: Switzerland. Associated with *Juniperus sabina*. ..... *R. merzi* sp. n.

Overview of Palearctic species similar to *R. merzi*

Rhagoletis bagheera Richter & Kandybina, 1997 (fig. 3)

Rhagoletis bagheera Richter & Kandybina, 1997: 915 (description, biology); Korneyev et al., 2018 a: 462 (key); Korneyev & Korneyev, 2019: 93 (key).

Type material. **Holotype** ♂: **Armenia**: "Erevan, ex fruits of *Rhamnus pallasii*, em. 28.VI.1971" (G. Ariutunan) (ZISP).

Paratypes. **Armenia**: Erevan, ex fruits of *Rhamnus pallasii*, em. 28.06.1971, 1 ♂, 1 ♀ (G. Arutiunan); Asni, Vedi Distr., 5.08.1965, 37 ♂, 20 ♀ (V. Richter), 1 ♂, 1 ♀, same labels (SIZK); **Georgia:** Vashlovan Nature Reserve, ex fruits of *Rhamnus pallasii*, 2 ♀, em. 24.06.1974 (I. Hodzevanishvili); idem, em. 4–18.05.1981 (I. Hodzhevanishvili) (ZISP).

Diagnosis. Head yellow, antenna and frontal vitta dark yellow; ventral half of median occipital sclerite and occiput lateral of it widely black or brown, widely yellow emarginated. Flagellomere 1 pointed apically. Scutum black, with 4 gray microtrichose vittae. Wing pattern with four brown bands, without intercalary band; apical band separated from costa by hyaline area in cells r_{2+3} and r_{4+5} (fig. 1, d). Femora dark brown to black. Abdomen black, tergites with yellow posterior margins. This species is similar to *R. batava* and *R. merzi* in general appearance and femora coloration, but is conspicuously smaller (body length = 2.7–2.9 mm and wing length = 2.2–2.36 mm for *R. bagheera*, > 3 mm in *R. batava* and

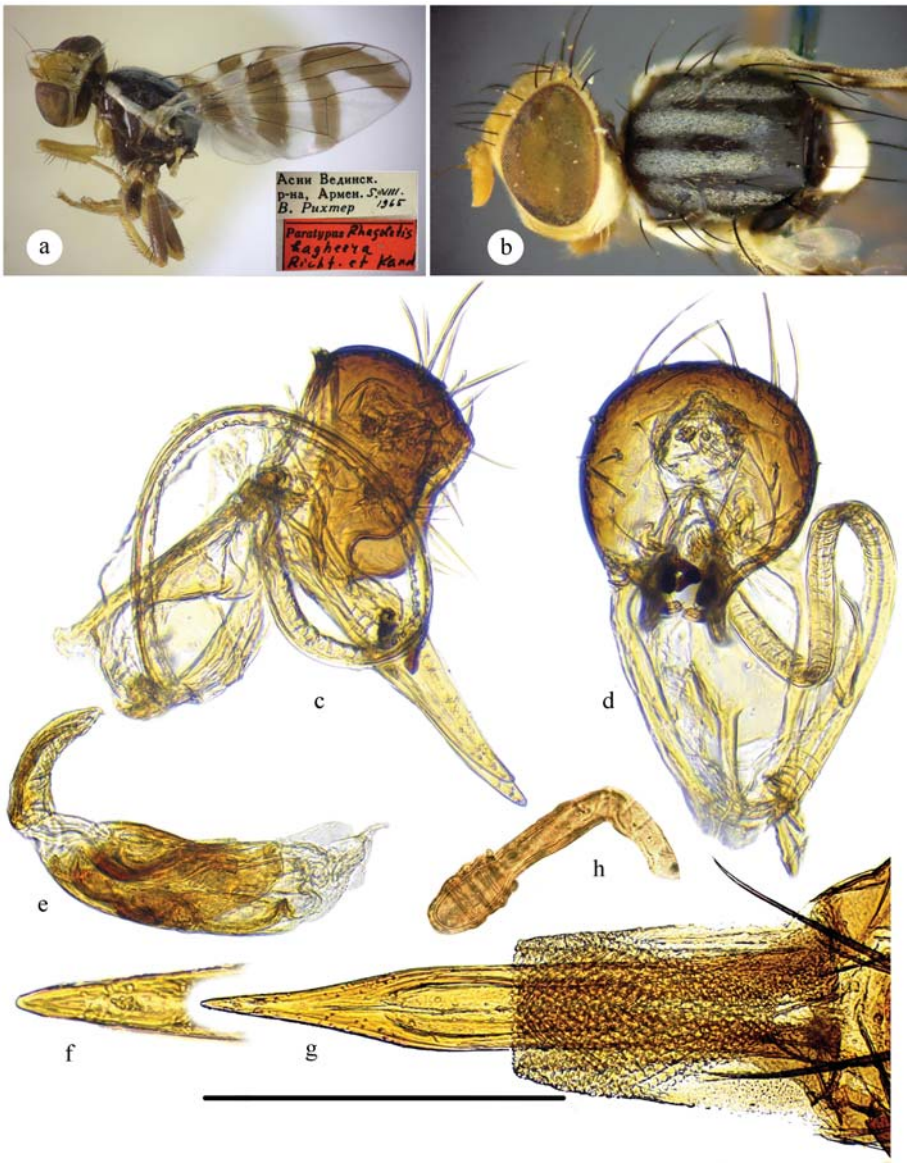

Fig. 3. *Rhagoletis bagheera* paratype male (a, c–e) and female (b, f–h): a — habitus left (abdomen dissected), b — same, dorsal; c, d — epandrium, hypandrium and surstyli (c — left, d — posterior), e — phallus glans; f — aculeus apex, g — ovipositor, h — spermatheca.

R. merzi) and has different host plants: *Rhamnus* (Rhamnaceae) for *R. bagheera*, and *Hippophae* (Elaeagnaceae) for *R. batava* and *Juniperus* (Cupressaceae) for *R. merzi*.

Measurements. Wing length ♂ = 2.0–2.4 mm; wing length ♀ = 2.2–2.5; costal cell length = 0.7; aculeus length = 0.71 mm; aculeus length / costal cell length = 1 (Richter & Kandybina, 1997).

Host plant. *Rhamnus pallasii* Fisch. & C.A. Mey (Richter & Kandybina, 1997).

Distribution. Armenia, Georgia.

Rhagoletis batava Hering, 1958 (fig. 4)

Rhagoletis batava Hering, 1958: 2 (description); Kandybina, 1977: 145 (larvae); Norrbom et al., 1999 (catalogue); Korneyev et al., 2018 a: 462, 2018 b: 43 (key; distribution); Korneyev & Korneyev, 2019: 93 (key).

Type material. **Holotype** ♀: **The Netherlands**: Terschelling I., Boschplaat (Theowald) (SMNS).

Non-type material. **Kyrgyzstan:** Tien Shan, 1500 m, "Pristan-Przewalsk", near Karakol (= Przewalsk), 42.5756° N, 78.3011° E, 28.07.1986, 4 ♂ (Korneyev); Karakol, on *Hippophae*, 15.08.1994, 1 ♀ (Korneyev); Terskei Alatau, Karakol ravin, h = 2050–2850 m, 42.4431° N, 78.4129° E, 12–13.08.1998, 3 ♂; 2 ♀ (Korneyev & Kameneva); Yssyk-Kol Region, Chong-Kyzyl-Suu, 42.250° N 78.130° E, 16–17.08.1998, 3 ♂, 1 ♀ (Korneyev & Kameneva); Alai , 45 km S of Kyzyl-Kiya, Kichik-Alai Ridge, Isfairam-Sai basin, Langar, h = 1800–1900 m, 39.8264° N, 72.1133° E, 30.07.1999, 4 ♂; 3 ♀ (Korneyev & Kameneva) (SIZK), idem, 3 ♂, 3 ♀ in alcohol (Korneyev & Kameneva) (MSU); **Russia:** Altay, Chikhachev Ridge, reared ex fruits *Hippophae rhamnoídes* 09.1966–17.03.1967, 3 ♂, 2 ♀ (Litvinchuk) (SIZK); **The Netherlands**: Hompelvoet Z.H. 10–18.07.2000, 2 ♂, 3 ♀ (B. V. Aartsen) (SIZK); **Tajikistan:** Peter First Range, 39.14382° N,71.56161° E, 3 km S Muk, 2320 m asl, swept from *Hippophae rhamnoides*, 26.07.2018, 3 ♂, 7 ♀; 39.07035° N,70.79778° E, Mirazyon, 1950 m asl, swept from *Hippophae rhamnoides*, 27.07.2018, 1 ♂; Turkestan Range, N slope, 39.520714° N, 68.925904° E, 25 km SE Dzharkutan, 2840 m asl, 6.08.2018, 3 ♀ (V. Korneyev) (SIZK).

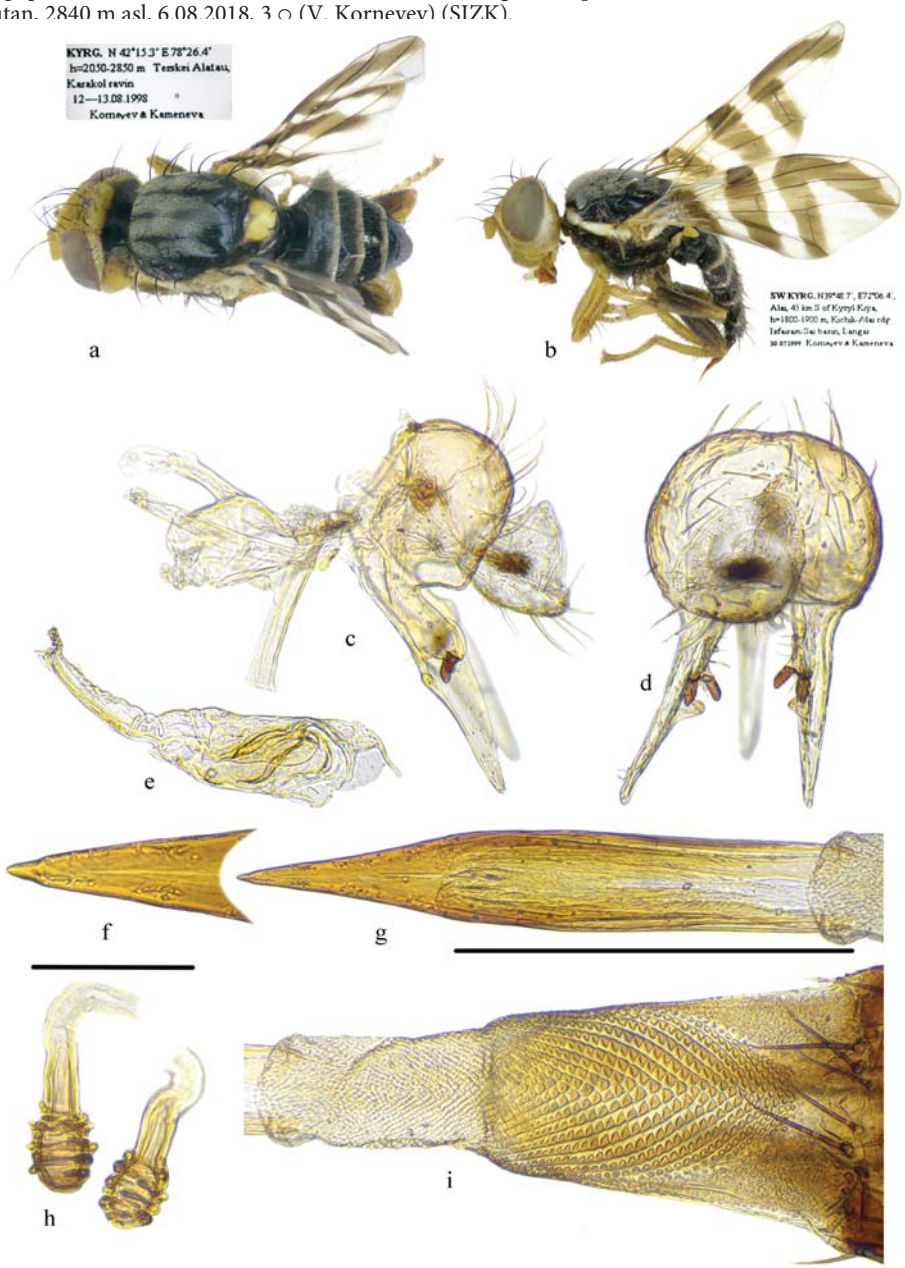

Fig. 4. *Rhagoletis batava* male (a, c–e) and female (b, f–j): a — habitus dorsal, b — same, left; c, d — epandrium, hypandrium and surstyli (c — left, d — posterior), e — phallus glans; f — aculeus apex, g — ovipositor, h — spermatheca; i — eversible membrane, ventral. Scale: f — 0.1 mm, g — 0.5 mm.

Diagnosis. *Rhagoletis batava* is similar to *R. bagheera* and *R. merzi* in general appearance and in having black femora, differing from *R. bagheera* by its larger size (wing length = or > 3 mm in *R. batava* vs. < 2.5 mm in *R. bagheera*) and from *R. merzi* by the conspicuously longer posterior lobe of the lateral surstylus (1.3 times as long as surstylus basal of prensisetae (fig. 4, d) vs. only 0.6–0.7 times as long as surstylus basal of prensisetae in *R. merzi* (fig. 8, b)) in the male and by spermatheca size and shape in the female (oval, 0.03 mm in diameter, and with the neck as long as the spermatheca in *R. batava* (fig. 4, i) vs. spherical, 0.09 mm in diameter, with the neck at most 0.8 times as long as the spermatheca itself in *R. merzi* (figs 2, f; 8 f)), as well as by the different host plants.

Measurements. Body length ♂ = 3.64 mm; body length ♀ = 3.9 mm; wing length ♂ = 3.0–3.6 (m = 3.38) mm; wing length ♀ = 3.3–4.2 (m = 3.8); costal cell length = 0.9; aculeus length = 0.78 mm; aculeus length /costal cell length = 0.9.

Host plant. *Hippophae rhamnoides* L. (Elaeagnaceae) (Kandybina, 1962).

Distribution. Europe (Korneyev et al., 2018 b); south of West and East Siberia; Middle Asia.

Rhagoletis flavigenualis Hering, 1958 (figs 5–6)

Rhagoletis zernyi: Zaitzev, 1947: 6 (misidentification; records from Georgia; host plants).
Rhagoletis flavigenualis Hering, 1958 (description); Rohdendorf, 1961 (key, description); Kandybina, 1977 (larva; distribution; host plants); Korneyev & Merz, 1997 (key, distribution); Norrbom et al., 1999 (catalogue); Gilasian & Merz, 2008; Mohamadzade & Rasoulian, 2009: 84; Korneyev et al., 2018 a: 466; 2018 b: 32 (key, distribution).

Type material. **Holotype** ♂: **Turkey**: S. Anatolia, Antalya-Kas, Katrandag, 1100 m (SMNS).
Non-type material. **Kazakhstan:** Aksu-Djabagly, on *Juniperus zeravshanica*, 17.08.1964, 2 ♂, 2 ♀;

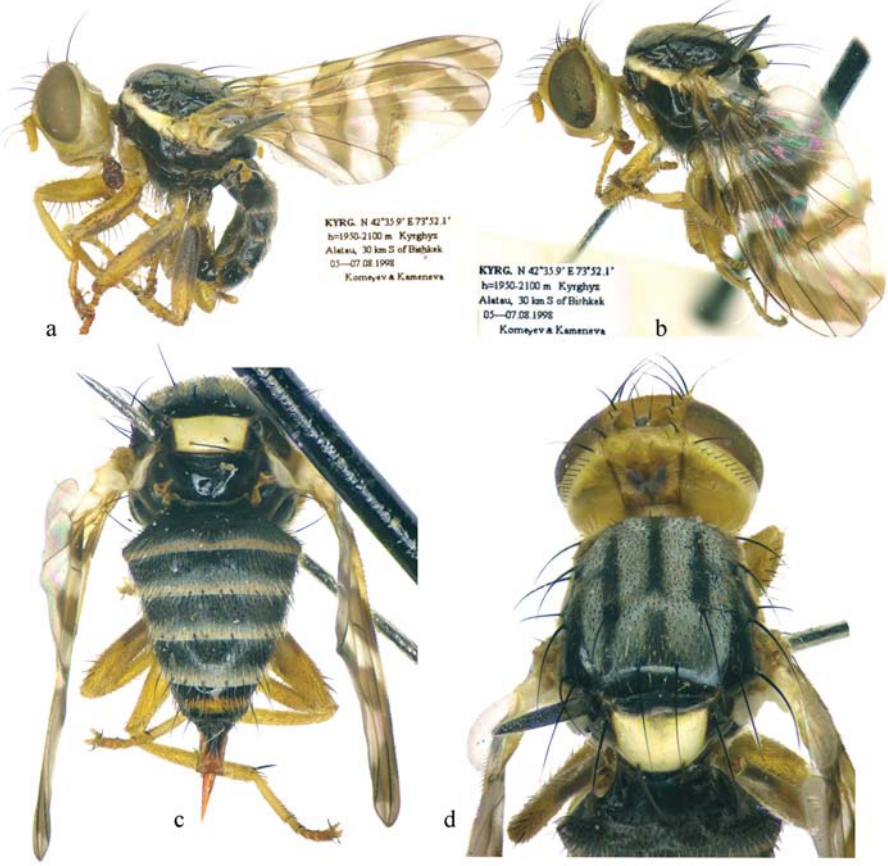

Fig. 5. *Rhagoletis flavigenualis* male (a) and female (b–e): a–b — habitus left, c — abdomen dorsal; d — occiput and mesonotum, posterodorsally.

15.09.1964 (Fisechko); **Kyrgyzstan:** Kyrghyz Alatau, 30 km S of Bishkek, 42°35.9′ N 73°52.1′ E, h = 1950–2100 m, 5–7.08.1998, 3 ♂, 1 ♀ (Korneyev & Kameneva) (SIZK); idem, 1 ♂, 1 ♀, in alcohol (MSU); Yssyk-Kol Region, Terskey Alatau, from *Juniperus sabina*, 5.08.1972 (Kandybina) (SIZK); **Tajikistan:** Ghissar Range, 2.5 km E Iskanderkul, 39.08530° N, 68.40226° E, 2360 m asl, swept from *Juniperus*, 7–8.07.2018, 3 ♂ (V. Korneyev) (SIZK); **Turkmenistan**: [Kopet-Dagh, between Firuza & state border], 23.09.1930, 1 ♀ (L. Bianchi) (SIZK).

Diagnosis. *Rhagoletis flavigenualis* can be differentiated from other species of the *Rhagoletis juniperina* group by having the medial occipital sclerite entirely yellow, entirely or predominantly yellow femora (at most hind femur brown basally), wing with basicostal cell clearly tinged with brown, wing bands partially yellowish-brown, with discal and subapical bands separated. *R. flavigenualis* is similar to *R. bagheera*, *R. batava*, *R. juniperina*, *R. mongolica*, and *R. merzi* in general appearance, differing from them also by having the occiput entirely yellow (or at most the occipital sutures tinged with brown) (*vs.* with the median occipital sclerite widely black at least on the ventral half in the other species); it also differs from the juniper-associated *R. juniperina* and *R. merzi* by having a conspicuously longer male posterior lobe of the lateral surstylus (1.3–1.5 times as long as surstylus basal of prensisetae (fig. 6, a) *vs*. 0.6–0.75 times as long as surstylus basal of prensisetae in *R. merzi* (fig. 8, b) and *R. juniperina* (Bush, 1966: fig. 83)). Abdomen black with posterior margins of tergites yellow. It is also similar to *Rhagoletis zernyi* in having the occiput and femora yellow and the wing bands partially yellowish-brown, differing from it by the entirely separated discal and subapical bands (in *R. zernyi*, the discal, subapical, and apical bands are connected at the anterior margin of the wing). Wing length 3.8–4.0 mm.

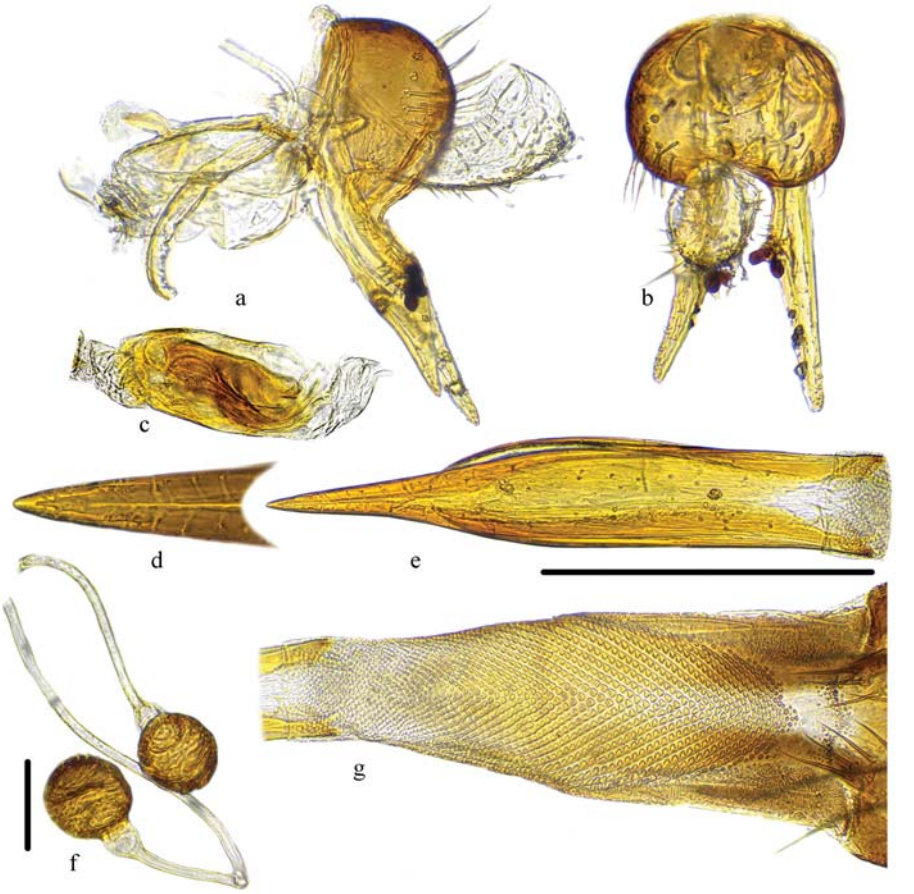

Fig. 6. *Rhagoletis flavigenualis* male (a–c) and female (d–g): a, b — epandrium, hypandrium and surstyli (a — left, b — posterior), c — phallus glans; d — aculeus apex, e — aculeus, f — spermatheca; g — eversible membrane, ventral. Scale: d, f — 0.1 mm, e, g — 0.5 mm.

Host plants. *Juniperus isophyllos* (as "*isocellos*") C. Koch; *J. foetidissima* Willd. (Zaitzev, 1947); *J. excelsa* M. Bieb., *J. seravschanica* Kom. (Kandybina, 1977).

Distribution. Georgia (Zaitzev, 1947: as "*R. zernyi*" — misidentification); Kazakhstan, Kyrgyzstan, Tajikistan, S Turkmenistan (Kandybina, 1977), Turkey, Iran (Gilasian & Merz, 2008; Mohamadzade Namin & Rasoulian, 2009).

Remarks. This species is widespread in the Asia Minor, Caucasus and Central Asia.

***Rhagoletis merzi* sp. n.** (figs 1, c; 7–8)

urn:lsid:zoobank.org:act:ADCCE1F4-7DB8-4EB6-9B5C-339A7F8F6ED9

Rhagoletis batava: Merz, 1994: 108 (misidentification);
Rhagoletis flavigenualis: V. Korneyev in: Merz, 2006: 8 (misidentification);
Rhagoletis sp. near *flavigenualis*: Korneyev et al., 2018 a: 466.

Type material. **Holotype** ♂: **Switzerland:** Visperterminen, VS, 1400 m, 26.07.1990 (Merz) (MNHG ENTO 00012822) (MHNG).

Paratypes: Switzerland: 1 ♀, Visperterminen, h = 1400 m, 17.07.1995 (Merz) (MNHG ENTO 00012824); Visperterminen, VS, 1400 m: 1 ♂, 18.07.1993 (Merz) (MNHG ENTO 0001825); 1 ♂, idem, 1520 m, 20.07.1993 Wald (Merz) (MNHG ENTO 0001828); 1 ♂, idem, 17.07.1995 (Merz) (MNHG ENTO 0001823); 1 ♂, Visperterminen, Kreuz, h = 1500 m, 21.07.2004 (Merz) (MNHG ENTO 0001827) (MHNG); Visperterminen, [Kreuz,] h = 1300–1900 m [swept from *Juniperus sabina*], 21.07.2004, 1 ♂, 1 ♀ (S. & V. Korneyev) (SIZK).

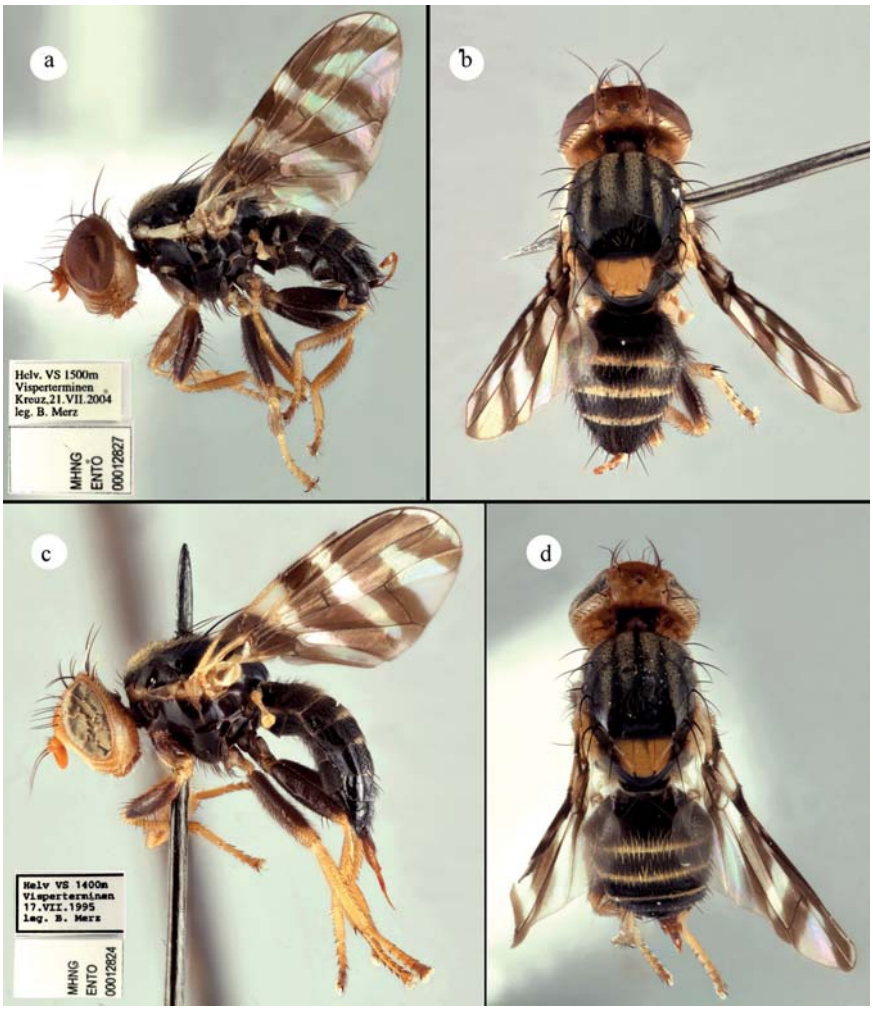

Fig. 7. *Rhagoletis merzi* sp. n. paratypes (MNHG): male (a–b) and female (c–d): a, c — habitus left, b, d — same, dorsal (photos by Bernard Landry).

Non-type specimens. **Switzerland:** Visperterminen, h = 1300–1900 m, reared from *Juniperus sabina* fleshy cones, 3 puparia [used for DNA extraction completely], 17.10.2016 (J. Smith).

Diagnosis. *Rhagoletis merzi* is similar to all other species having the wing pattern with four dark bands, apical band joined to subapical band and separated by a crescent hyaline area from the costal vein anteroapically. It is most similar to, and in fact to our knowledge morphologically indistinguishable from, the Nearctic *R. juniperina*. Both species have the occiput widely black or brown on the upper 1/3, wing bands uniformly brown to blackish, mid and hind femora black, male lateral surstylus with the posterior lobe relatively short, 0.6–0.75 times as long as surstylus basal of prensisetae (fig. 8, b), and female spermathecae large, 0.09 mm in diameter, with short neck (fig. 2, f). We recognize *R. merzi* as a distinct species from *R. juniperina* based on the significant genetic distance between their COI sequences (K2P = 0.071).

Rhagoletis merzi is also very similar to the Central Asian *R. mongolica* and *R. scutellata* (both known only from their holotypes, not examined for potential genitalic differences) in general appearance, including the wing pattern and having the occiput widely black on the upper 1/3. *Rhagoletis mongolica* is also associated with *J. sabina*, like *R. merzi*, whereas the host for *R. scutellata* is unknown. *Rhagoletis merzi* differs from *R. mongolica* by having black rather than yellow femora and from *R. scutellata* by abdominal tergites 2–4 having whitish or yellowish posterior margins and the basicostal cell brownish (in *R. scutellata*, basicostal cell entirely hyaline and abdominal tergites uniformly black or brown).

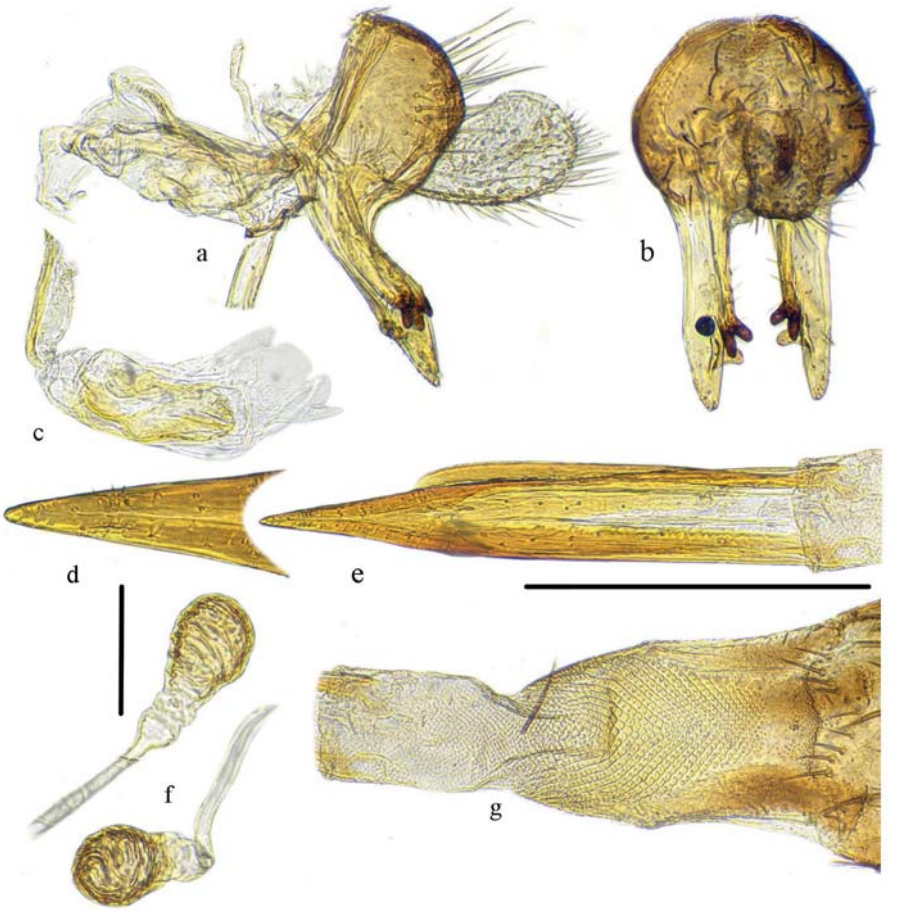

Fig. 8. *Rhagoletis merzi* sp. n. paratypes (SIZK): male (a–c) and female (d–g): a, b — epandrium, hypandrium and surstyli (a — left, b — posterior), c — phallus glans; d — aculeus apex, e — aculeus, f — spermatheca; g — eversible membrane, ventral. Scale: d, f — 0.1 mm, e, g — 0.5 mm.

This species readily differs from the West Palearctic *R. flavigenualis* and *R. zernyi* by having the widely black or brown median occipital sclerite, black mid and hind femora, and uniformly brown wing bands (in *R. flavigenualis* and *R. zernyi* median occipital sclerite and all femora uniformly yellow (very rarely only hind femur partly brown), and the wing bands at least partly yellow with brownish borders; *R. zernyi* differs also by having the discal and subapical bands widely fused). The genetic distance between *R. merzi* and *R. flavigenualis* is also significant (K2P = 0.063–0.066).

Rhagoletis merzi is similar to the Palearctic species *R. bagheera* and *R. batava*, and the Nearctic *R. bushi* in having the wing bands uniformly brown to blackish, and mid and hind femora black, differing from them by having the male lateral surstylus with the posterior lobe conspicuously shorter, 0.6–0.75 times as long as the surstylus basal of the prensisetae (fig. 8, b) vs. 1.3–1.4 times as long as the surstylus basal of the prensisetae in *R. bagheera* (fig. 3, c) and *R. batava* (fig. 6, a), and female spermathecae larger, 0.09 mm in diameter, with a short neck (fig. 2, f) vs. 0.02–0.03 mm in diameter, with the neck longer than the spermatheca itself in *R. bagheera* and *R. batava*. *Rhagoletis merzi* also has a different host plant, *Juniperus sabina* L., vs. *Hippophae rhamnoides* (Elaeagnaceae) for *R. batava* and *Rhamnus palasii* (Rhamnaceae) for *R. bagheera*. The genetic distance between *R. merzi* and *R. batava* is K2P = 0.064–0.068, and between *R. merzi* and *R. bushi* K2P = 0.078–0.079.

Description. *Head.* Orange-yellow, ocellar triangle, ventral part of median occipital sclerite and often occiput lateral of it black or brown. Antennal arista pubescent. Setae black except postocellar, posterior genal, and some occipital setae white. Paravertical seta short, about as long as black acuminate postocular setae. — *Thorax.* Scutum black, yellowish setulose, with microtrichia pattern with two pairs of partly fused matte grayish vittae separated by subshining darker areas. Postpronotal lobe and notopleural stripe creamy white to yellow; scutellum pale yellow, black on anterior margin dorsally and laterally. All thoracic setae black; basal scutellar seta inserted into black area. Halter yellow to creamy white. — *Legs.* Fore coxa yellow, mid and hind coxae black or brown; fore and mid trochanters yellow; hind trochanter brown or black; fore femur yellow anteroventrally, black posterodorsally; mid and hind femora black except apices yellow; hind femur somewhat thickened in male, with 2–3 longer subapical anterodorsal and 2–3 longer subapical anteroventral setae; tibiae and tarsi yellow (fig. 7). — *Wing* (fig. 1, c). 2.3 times as long as wide, with pattern consisting of basicostal cell with brownish tinge and four dark brown bands; subbasal band from humeral crossvein over basal half of costal cell through cells br, bm and cua (= anal cell auctt.) slightly into cell cup, discal band from pterostigma over crossvein r-m to posterior margin between veins M_4 (= CuA_1) and CuA + CuP (= CuA_1+A_1), subapical band from middle of cell r_1 over crossvein dm-m (= dm-cu) and apical band from middle of cell r_1 into apex of cell m_4; discal band separated from both subbasal and subapical bands (figs. 1, c; 7, a) or at most narrowly fused with subapical band at posterior margin (fig. 7, c); subapical and subapical bands fused in cells r_1 and r_{2+3}; apical band separated from costa between apex of cell r_1 and vein M_1; no intercalary band; vein R_{4+5} dorsally with 1 seta at node. — *Abdomen.* All segments mostly black, posterior margin of tergites 2–4 in male, and 2–5 in female narrowly creamy yellow (figs. 9, b, d). Oviscape shining black, as long as tergite 5; setae and setulae black. — *Genitalia.* Male. Epandrium black. Proctiger as long as epandrium (fig. 10, b). Surstylus dark yellow, lateral susrtylus with posterior lobe short, 0.6–0.75 times as long as surstylus basal of prensisetae (fig. 9, b). Phallus with moderately large glans (fig. 8, c) having membranous, narrow, finger-like apicodorsal process, large prepuce with smooth walls, and acrophallus with pair of semitubular filaments, very similar to that of *R. bagheera* (Richter & Kandybina, 1997: fig. 5), *R. flavigenualis* (fig. 6, c) and *R. juniperina* (Bush, 1966: fig. 125); preglans short and simple, without eversible caecum. Female. Eversible membrane with two pairs of taeniae 0.5 × as long as membrane itself, ventral side of membrane with scales of different size, medial ones larger than lateral ones and moderately pointed (fig. 9, g). Two globular spermathecae, 0.09 mm in diameter, with

long scale-like papillae on surface (fig. 9, f). Aculeus brown, 5.5 × as long as wide, with acute apex (figs. 9, d–e).

Measurements. Body length ♂ = 3.8–4.2 mm; wing length ♂ = 4.1–4.2 mm. Body length ♀ = 4.0–4.4 mm; wing length ♂ = 3.0, wing length ♀ = 3.6 mm, costal cell length = 0.9; aculeus length = 0.85 mm; aculeus length /costal cell length = 0.9.

Host plant. *Juniperus sabina* L. The pupae for DNA analysis were reared from the same plants and in the same locality as the type specimens were swept.

Distribution. Switzerland.

Etymology. This species is named in honor of the eminent Swiss dipterist Dr. Bernhard Merz, who collected most of the type specimens, in recognition of his contributions to the study of fruit flies.

Remarks. Kandybina (1977) reported specimens of "*R. mongolica*" with entirely black femora and partly black tibiae reared from *Juniperus sabina* in Kyrgyzstan, which need re-examination to determine whether they are conspecific with *R. merzi*.

Rhagoletis mongolica Kandybina, 1972

Kandybina, 1972: 913 (description), 1977 (larva; distribution; host plants; new records); Korneyev & Merz, 1997: 63 (key); Norrbom et al., 1999: 201 (catalogue); Korneyev & Ovchinnikova, 2004: 482 (key).

Comments. This species was originally described based on a single female and a third instar larva reared from *Juniperus sabina* L. in Mongolia (Kandybina, 1972). Later, the larva was redescribed based on material from the same host plant in Kyrgyzstan (Kandybina, 1977). The adult specimens from Kyrgyzstan were briefly described as having completely black femora and partly black tibiae; neither their male nor female genitalia have been described. We therefore consider *R. mongolica* to have entirely yellow femora as in the holotype, and the Kyrgyz specimens to be likely non-conspecific. The geographically "intermediate form" from Kyrgyzstan must be analyzed to clarify its taxonomic position and molecular differences from both *R. mongolica* and *R. merzi*.

Rhagoletis scutellata Zia, 1938

Zia *in*: Zia & Chen, 1938: 34 (description); Wang, 1998: 124 (redescription); Norrbom et al., 1999: 202 (catalogue); Korneyev & Ovchinnikova, 2004: 482 (key).

Remarks. This species is known from the holotype male from Gansu, China (IZAS), unavailable in this study. According to the original description, it possesses black femora, uniformly dark brown bands on the wing, and entirely black abdominal tergites; body length ♂ = 3.7; wing length ♂ = 4.0.

Additional study of the type and topotypic material from China, including morphology of the male and female genitalia, DNA sequences, and host plants, is needed.

Rhagoletis zernyi Hendel, 1927 (fig. 1, b)

Hendel, 1927: 76 (description, key); Merz & Blasco-Zumeta, 1995: 132 (host plant, distribution); Merz, 2001: 92 (checklist); Norrbom et al., 1999: 202 (catalogue); Korneyev et al., 2018 a: 468 (key, distribution).

Material. Spain: Monegros, Pina-de-Negro, 13.08.1992, 1 ♂ (Blasco-Zumeta) (Merz det., 1994) (SIZK).

Diagnosis. *Rhagoletis zernyi* can be differentiated from most species of *Rhagoletis* by the characters given for the *juniperina* group. It differs from the other species of that group by having yellow femora and the wing pattern with partially yellowish-brown discal and subapical bands that are broadly fused at anterior margin (other species have the wing pattern uniformly brown except *R. flavigenualis*, which has the discal and subapical bands separated (fig. 1, b)); male and female genitalia not examined. Abdomen black with posterior halves of tergites creamy or yellow. Body length 4.0–4.8 mm; wing length ♂ = 3.5–3.6 mm.

Distribution. Spain.
Host plants. *Juniperus thurifera* L. (Merz & Blasco-Zumeta, 1995).

Phylogenetic analysis

Hulbert's (2018) multigene molecular analysis grouped the included *Rhagoletis* species into ten lineages corresponding to 12 previously established species groups (*alternata, cerasi, meigenii, ferruginea, nova, striatella, juniperina, ribicola, cingulata, suavis, tabellaria,* and *pomonella*), which mainly correspond to the groups proposed by Bush (1966), Kandybina (1977), and Smith & Bush (1999) plus the unplaced *R. fausta* and *R. batava*.

Our analyses here is based on the 85 individuals from Hulbert (2018) plus three specimens of *R. merzi* and three specimens of *R.* sp. nr. *juniperina*, using the same 4270 bp from the COI, CAD, 28S, period, and AATS genes used in Hulbert (2018). The taxon sample includes two outgroup species (*Anastrepha ludens* and *Euphranta canadensis*), one species of *Carpomya* and 35 species representing most of the species groups of *Rhagoletis*.

The Bayesian analysis recovered a monophyletic cluster with high support, containing the *suavis, cingulata, pomonella, tabellaria*, and *juniperina* groups plus the unplaced species *R. fausta* and *R. batava* (fig. 9). All the juniper-associated species form a well-supported monophyletic lineage corresponding to the *juniperina* group within the clade described above. This includes both Nearctic (*R. juniperina* and undescribed species *R.* sp. nr. *juniperina*) and Palaearctic species (*R. flavigenualis* and *R. merzi*). It is interesting that *R. merzi* is more similar to the Nearctic taxa (*R. juniperina*, *R.* sp. near *juniperina*) in both morphological characters (wing pattern, occiput, mesonotum and leg coloration) and molecular sequences than to the Palearctic *R. flavigenualis*.

The Maximum Likelihood tree has a similar topology to that obtained with the Bayesian analysis, yet with some notable differences that mostly concern position of some basal groups (fig. 9). The *juniperina* group is recovered in the ML analysis with a bootstrap value of 58 and, within this group, *R. merzi* is nested within the North American lineage as sister to *R.* sp. near *juniperina* (bootstrap 75).

Conclusions

As a result of molecular and careful morphological study (including the structure of male and female genitalia), the population of fruit flies found to infest *Juniperus sabina* in the Swiss Alps, previously misidentified either as *R. batava* (Merz, 1994) or *R. flavigenualis* (V. Korneyev in: Merz, 2006) was found to represent a new species, *R. merzi*.

Rhagoletis merzi is a case of discovery of a previously unknown animal species in the very heart of Europe and in the part of the continent with the most thoroughly studied tephritid fauna. It remained dubiously identified for decades, though it differs morphologically from known west Palearctic species, and is genetically distinct from all other species of the genus.

Both morphological characteristics and DNA-based phylogenies show that *R. merz*i is related to three other juniper-infesting species of *Rhagoletis* from both the Nearctic and Palaearctic Regions: *R. juniperina*, *R. flavigenualis*, and *R. zernyi*.

Morphological characters can be used to diagnose *R. merzi* from some other juniper-infesting species. *Rhagoletis merzi* has a combination of black colored femora, round spermathecae and relatively short surstyli, strongly resembling the Nearctic *R. juniperina* and *R.* sp. near *juniperina*, but *R. merzi* is quite distant genetically from both of these species.

The new species has been already confused with *R. batava*, which feeds on sea buckthorn and has black femora as well. The use of a particular host plant can be a proxy for species identification in *Rhagoletis*, and is usually reliable in species identification within the genus, but caution must be exercised as there are rare exceptions where host-specific flies have been reared from 'non-natal' hosts that likely do not represent established populations (Bush, 1966; Yee & Goughnour, 2008; Hood et al., 2012; Yee et al., 2015).

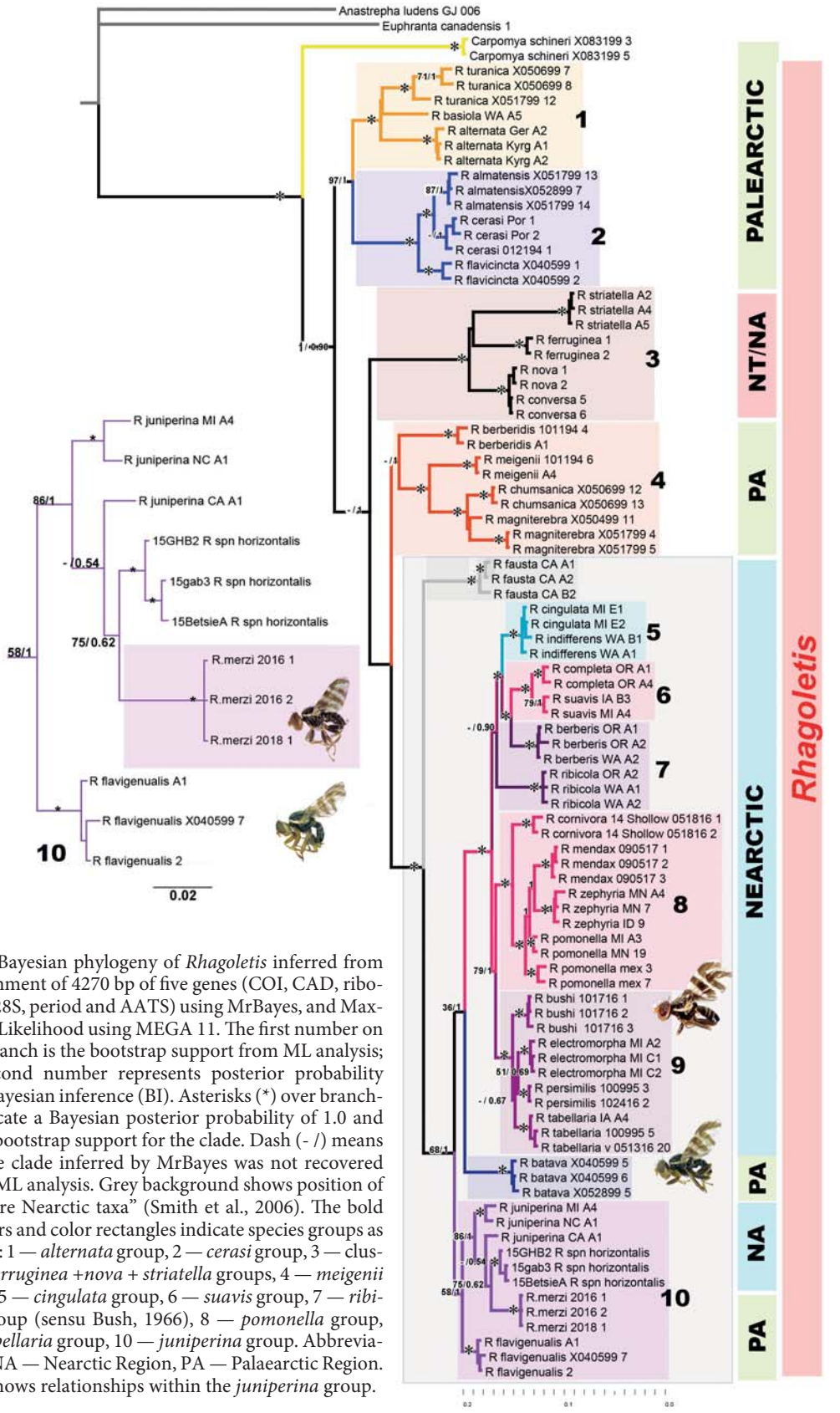

Fig. 9. Bayesian phylogeny of *Rhagoletis* inferred from an alignment of 4270 bp of five genes (COI, CAD, ribosomal 28S, period and AATS) using MrBayes, and Maximum-Likelihood using MEGA 11. The first number on each branch is the bootstrap support from ML analysis; the second number represents posterior probability from Bayesian inference (BI). Asterisks (*) over branches indicate a Bayesian posterior probability of 1.0 and 100 % bootstrap support for the clade. Dash (- /) means that the clade inferred by MrBayes was not recovered by the ML analysis. Grey background shows position of the "core Nearctic taxa" (Smith et al., 2006). The bold numbers and color rectangles indicate species groups as follows: 1 — *alternata* group, 2 — *cerasi* group, 3 — cluster of *ferruginea* +*nova* + *striatella* groups, 4 — *meigenii* group, 5 — *cingulata* group, 6 — *suavis* group, 7 — *ribicola* group (sensu Bush, 1966), 8 — *pomonella* group, 9 — *tabellaria* group, 10 — *juniperina* group. Abbreviations: NA — Nearctic Region, PA — Palaearctic Region. Inlay shows relationships within the *juniperina* group.

Unfortunately, we lack data about such peculiar species as *R. zernyi* and the morphologically similar species *R. scutellata* and *R. mongolica* from Central Asia, making the relationships of the Nearctic and Palearctic juniper-infesting *Rhagoletis* not fully resolved. Additional studies are needed to clarify the differences between *R. merzi* and *R. mongolica*, for which no molecular data are available. It will be important to obtain samples from the type locality of *R. mongolica* morphologically identical to its holotype, because the specimens infesting *Juniperus sabina* recorded by Kandybina (1977) from Kyrgyzstan as "*R. mongolica*" may be misidentified *R. merzi* as they differ from the *R. mongolica* holotype in the coloration details. These tasks are forthcoming, as are descriptions of a number of previously unknown new juniper-infesting species in North America (Hulbert et al., in prep.).

Rhagoletis merzi has a unique COI haplotype that shows essential differences from similar sequences from both the juniper-infesting *R. flavigenualis* (K2P = 0.063–0.066) and Nearctic *R juniperina* (K2P = 0.71), as well as from the superficially similar *R. batava* (K2P = 0.064–0.068).

Despite intensive studies in the genus *Rhagoletis*, mainly restricted to the pest and model species, the *Juniperus*-associated species remain one of the most poorly examined groups. Both sweeping and rearing from juniper fleshy cones often give very poor output; a full day of sweeping over juniper trees usually brings 1–2 specimens, and rearing, which is more productive, requires collecting cones during exact short time periods late in summer or in autumn.

Numerous superficially similar species associated with various hosts and differing by a few coloration and genitalic characters form a paraphyletic formation in the base of a monophyletic lineage represented mostly by Nearctic species. Both Bayesian and ML analyses show that the species of the *tabellaria* group, as well as *R. ribicola* and *R. batava*, do not form a monophyletic clade with the *juniperina* group (fig. 9) despite the strong morphological similarities of these flies. It is believed that the purely Nearctic species groups, such as the *pomonella, cingulata* and *suavis* groups are derivatives from the forms superficially similar to *R. juniperina*, *R. batava* or *R. ebbettsi*.

Authors' responsibilities

All authors collected material in the field. DLH, JEF, JJS and SVK extracted and sequenced DNA. All morphological dissections and descriptions, photographs, and trees were produced mostly by SVK and VAK, and analysis provided by DLH, SVK, JJS and VAK. The text was mostly written by DLH, SVK, VAK and JJS.

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