

Phylogeny of the genus *Tephritis* Latreille, 1804 (Diptera: Tephritidae)

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Abstract. The phylogenetic relationships of *Tephritis* Latreille, one of the largest genera of true fruit flies, are poorly understood due to the large number of species, lack of reliable morphological characters and difficulties in identification. In the present study we used two datasets to address these problems: one with 35 species of the genus *Tephritis* (28 from the Palearctic and seven from the Nearctic Region) and seven species from closely related genera of the tribe Tephritini (one species each of *Actinoptera* Rondani, *Capitites* Foote & Freidberg, *Euaresta* Loew, *Goniurellia* Hendel, *Trupanea* Schrank and two species of *Heringina* Aczél). For this dataset, we inferred the phylogenetic relationships using five genes (2914 bp): mitochondrial COI (687 bp), mitochondrial 16S rRNA (561 bp), and the nuclear genes Period (481 bp), AATS (444 bp), and the 28S rRNA (741 bp). The second dataset consisted of 64 species of the genus *Tephritis*, two species of *Heringina* and one *Capitites* as an outgroup and phylogenetic relationships were only inferred using COI (687 bp). The results of both analyses advance the understanding of species relationships, composition of species groups, and existing concepts of homology, relationships and divergence of the genus. Our results based on molecular phylogenetic relationships show that morphological characters are occasionally uninformative for delimiting monophyletic species groups; however, 10 species groups are moderately well supported based on their association with certain host plant taxa (genera, subtribes or tribes). Furthermore, we discuss monophyly of the genus *Tephritis*, and its relationships with the closely related genera *Heringina* and *Capitites*.

Key words. Diptera, Tephritidae, *Tephritis*, Asteraceae, species groups, host plants, phylogeny, distribution.

1. Introduction

The genus *Tephritis* Latreille 1804 is one of the largest genera of Tephritidae, with over 160 described species, mainly occurring in the Holarctic and, to a lesser degree, Afrotropical, Oriental, and Australasian Regions (NORRBOM et al. 1999), but entirely lacking in the Neotropical Region. Recently most of Australian species of *Tephritis* and *Campiglossa* were reassigned to the genus *Austrotephritis* (HANCOCK & DREW 2003). *Tephritis* species inhabit most climatic zones and altitudes from dry and hot semidesert to circumpolar tundra and alpine tundra in mountainous regions. Larvae of *Tephritis* species feed in flower heads of a wide range of Asteraceae of the tribes

Anthemideae, Astereae, Cardueae, Cichorieae, Inuleae, Senecioneae and Calenduleae, occasionally inducing non-lignified galls in flower heads, shoots and rosettes. Most *Tephritis* species are monophagous or stenophagous (feed on several species of the same genus: S. KORNEYEV 2016). *Tephritis* are potential control agents for invasive species of asteraceous plants, like species from *Cecidochares* Bezzi, *Chaetorellia* Hendel, *Mesoclanis* Munro, *Terellia* Robineau-Desvoidy, *Urophora* Robineau-Desvoidy (WHITE & ELSON-HARRIS 1992; FOOTE et al. 1993; EDWARDS et al. 2009; DAY et al. 2013; DAY et al. 2016; RANDALL et al. 2017; AIGBEDION-ATALOR et al. 2018). For

example, *T. neesii* (Meigen 1830) is considered as a potential biocontrol agent of Oxeye daisy, *Leucanthemum vulgare* Lam. (Asteraceae), but little is known about host-specificity (McCLAY et al. 2013). There are several examples of unsuccessful introduction: *T. dilacerata*, a Palearctic species, has been released in North America as the biocontrol agent for *Sonchus arvensis*, but population has not survived (FOOTE et al. 1993); *T. postica* was released in Australia in 1995 and 1997 but also has not established (TURNER 1996). For many *Tephritis* species, host plant relationships remain unknown.

Identification of *Tephritis* species is based on the keys by HENDEL (1927) and HERING (1944) or more recent keys for particular countries such as the ones by WHITE (1988) (Great Britain), FREIDBERG & KUGLER (1989) (Israel), FOOTE et al. (1993) (US & Canada), MERZ (1994) (Switzerland), V. KORNEYEV & OVCHINNIKOVA (2004) (Far East of Russia), and SMIT (2010) (The Netherlands). The genus is in need of thorough taxonomic revision, for there are still numerous undescribed species, and a number of names are likely synonyms. There is also a lack morphological information for inferring phylogenetic relationships in *Tephritis*, because the species have very little variation in the male genitalia while the same structures provide characters of phylogenetic significance in many other tephritid genera (V. KORNEYEV 1985, 1990; V. KORNEYEV & OVCHINNIKOVA 2004).

Only a few morphologically delimited (but not necessarily monophyletic) species groups have been recognized in the past: the *baccharis* group (JENKINS & TURNER 1989), the *leontodontis* and *hyoscyami* groups (MERZ 1995), the *maccus* group (V. KORNEYEV & DIRLBEK 2000), and the *pulchra* group (MERZ 1993; FREIDBERG & KÜTÜK 2002). Furthermore, a number of poorly morphologically differentiated “cryptic species” or “host races” are recognized in collections based on reared material from different plants, thus complicating the systematic understanding of the genus (S. Korneyev, personal observation). Association with certain plant taxa may be used as an informative character, but host plant associations remain unknown for many species. Therefore, a reconstruction of phylogenetic relationships with molecular characters is particularly attractive in *Tephritis*. Previously, sequences of *Tephritis* species were scarcely available, and collection material was too old or stored under inappropriate conditions for successful DNA extraction and sequencing.

A first step towards understanding the relationships was KORNEYEV'S (2016) phylogenetic analysis of the genus *Tephritis* based on morphological characters (52 species, 30 characters), host plant preferences (host plant tribe/genera used as character state for 52 species, 4 characters), and mitochondrial COI sequences (41 species, 271 specimens). The analysis was used to delimit preliminary species groups for *Tephritis*. Additional morphological studies of almost 9,000 *Tephritis* specimens representing more than 90 species from the Western Palearctic have served as a base to describe several new species and re-describe many little-known species (S. KORNEYEV 2013;

MOHAMADZADE & S. KORNEYEV 2012; S. KORNEYEV & MOHAMADZADE 2013; MOHAMADZADE et al. 2015; S. KORNEYEV et al. 2015a,b; MOHAMADZADE & S. KORNEYEV 2017; S. KORNEYEV & V. KORNEYEV 2019). These studies also included new host plant records, a review of the existing information, and a DNA barcoding analysis based on mitochondrial COI sequences, which yielded preliminary hypotheses about phylogenetic relationships within the genus. The present study is based on analyses which include additional genetic markers as well as new interpretation of their host plant associations and morphological characters in order to test the monophyly of the genus *Tephritis*, as well as delimitation of species groups proposed.

The most reliable data on *Tephritis* host plants were provided by MERZ (1994) based on his reared material. Other data were previously provided and summarized by FRAUENFELD (1857), FREIDBERG & KUGLER (1989), and V. KORNEYEV & KAMENEVA (1993) and many published records are compiled on the CoFFHI website (<https://coffhi.cphst.org/>), but these may represent unreliable records due to sweeping or rearing from samples contaminated by other plants, or misidentification of host plants. In any case, use of these data requires thorough reviews of these papers and subsequent critical analysis.

In the Palearctic Region, *Tephritis* species are associated with tribes of Asteraceae: Anthemideae, Astereae, Cardueae, Cichorieae, Gnaphalieae, Inuleae, Senecioideae, and Calenduleae. In some cases, both associations with certain host plant tribe or genus correlate with unique morphological characters (e.g., aculeus tip shape), which possibly support the monophyly of some species groups (for example, the *pulchra* group: see MERZ 1993; FREIDBERG & KÜTÜK 2002; and the *formosa* group: see S. KORNEYEV & V. KORNEYEV 2019). A major goal of the present study was the reconstruction of phylogenetic relationships within the genus *Tephritis* based both on molecular and morphological data. In addition to the COI barcode region, we sequenced four additional genetic markers (mitochondrial 16S and nuclear Period, AATS, and 28S).

The genus *Tephritis* belongs to the tribe Tephritini of the subfamily Tephritinae. The subfamily Tephritinae is a diverse taxon containing more than 200 genera and 1,950 species from all zoogeographical regions (NORRBOM et al. 1999). Its monophyly is supported both by morphology (V. KORNEYEV 1999) and molecular data (HAN et al. 2006). The tribe Tephritini contains almost 1000 described species of more than 80 genera including *Tephritis*, the largest of them. Many genera are similar to *Tephritis* in wing patterns and habitus. A phylogenetic analysis based on sequences of the 16S mitochondrial gene for 38 genera of different Tephritinae tribes (HAN et al. 2006) does not support the current tribal classification of the Tephritinae based on morphology; e.g., *Euaresta* and *Neotephritis*, which are morphologically similar to *Tephritis*, are not supported as closely related and are placed in a distant related group of Nearctic genera. On the other hand, HAN et al. (2006) proposed that *Tephritomyia* and *Trupanea*

are closely related to *Tephritis*. Additionally, relationships between several different *Tephritis* species were hypothesized for the first time as a large number of European fruit flies were barcoded (SMIT et al. 2013). For example, some of the morphologically defined species groups such as *pulchra* and *leontodontis* were supported, and *Heringina* Aczél appeared as an in-group within *Tephritis*, showing a possibility that *Heringina* might be an aberrant member of *Tephritis* or its sister-group (SMIT et al. 2013). Both studies provided a necessity to use *Euaresta*, *Actinoptera* Rondani, *Goniurellia* Hendel, *Trupanea*, *Capitites* Foote & Freidberg and *Heringina* as outgroup taxa for the present study.

2. Material and methods

Taxon sampling. Specimens were collected from May to October 2004–2017 in eastern Europe and Middle Asia (Severyn Korneyev and Valery Korneyev; deposited in I.I. Schmalhausen Institute of Zoology NAS of Ukraine, SIZK), in western and southern Europe and Israel (J. Smit; deposited in Naturalis Biodiversity Center, Leiden, The Netherlands, RMNH, except for one specimen collected by Allen Norrbom, now in SIZK collection), and in North America (Allen Norrbom and colleagues, material deposited in SIZK, with additional voucher specimens at National Museum of Natural History, Washington, DC, USA; and Dr. Martin Hauser and Dr. Steve Gaimari, material deposited in California Department of Food and Agriculture, Sacramento, California, USA, CSCA) (Table 3).

All material was stored in 96% ethanol at –18–20°C. DNA was extracted from more than 170 specimens. In the present study, for the COI analyses 67 specimens of different *Tephritis* species were used, while for the five-gene analysis used 35 specimens of the *Tephritis* species (28 from the Palaearctic Region and 7 from the Nearctic Region) and 7 species from the other genera of tribe Tephritini (one species each of *Actinoptera*, *Capitites*, *Euaresta*, *Goniurellia* and *Trupanea* and two species of *Heringina*) (Table 3). After testing primers and excluding samples that failed to extract or resulted in poor quality or limited DNA, we selected *Actinoptera*, *Capitites*, *Goniurellia*, *Heringina*, *Trupanea* for inclusion in the present study because of their different degrees of relatedness to *Tephritis*, and finally, *Euaresta aequalis* (Loew, 1862) was selected as the outgroup. The selection of the outgroup was based on the phylogenetic analysis of Tephritinae by HAN et al. (2006) as the distantly related representatives from the tribe Tephritini.

Abbreviations of depositories. CSCA – California State Collection of Arthropods, Plant Pest Diagnostics Center, California Department of Food and Agriculture, Sacramento, California, USA; RMNH – Naturalis Biodiversity Centre, Leiden, the Netherlands; SIZK – I.I. Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, Kyiv, Ukraine.

Microscopy. This work is partly based on morphological studies given in previous papers (S. KORNEYEV 2013; MOHAMADZADE et al. 2015; S. KORNEYEV et al. 2015a,b; S. KORNEYEV 2016; S. KORNEYEV & V. KORNEYEV 2019). Studied morphological characters show differences of wing patterns and aculeus among different species and are presented on the tree figures (Figs. 2, 3). Genitalia were prepared for study using the following procedure: the abdomen was excised from a relaxed

Table 1. Primer sequences.

Locus (size)	Primer pair	Primer sequence	Reference	Denaturation long (°C) (min:sec)	No. of cycles	Denaturation short (°C) (min:sec)	Annealing temp. (°C) (min:sec)	Extension time (°C) (min:sec)	Final ext. period (°C) (min:sec)
COI (687 bp)	LepF1 LepR1	5'-ATTCAACCAATCATAGAATAT-3' 5'-TAAACTTCTGGATGTCACAAA-3'	HEBERT et al. 2004	94°C, 5:00	34	94°C, 1:00	46°C, 1:30	72°C, 1:00	72°C, 5:00
16S (561 bp)	LR-N-13398 LR-J-12883	5'-CGCCTGTTTATCAAAAACAT-3' 5'-CTCCGGTTTGAACCTCAGATC-3'	HAN et al. 2006	95°C, 5:00	34	95°C, 0:30	50°C, 1:00	72°C, 1:00	72°C, 5:00
Period (481 bp)	Per2612Fdeg Per3105R	5'-ATTCTWTTGGARGGRGATGCC-3' 5'-AABGACATGGGTTGGTACATC-3'	BARR et al. 2005	95°C, 2:00	35	95°C, 0:30	57°C, 1:00	72°C, 1:00	72°C, 4:00
AAITS (444 bp)	M13A1x9ZF M13rA1x244R	5'-TGTAACACGACGCCAGTAYCAVCACNTTYTYGARATG-3' 5'-CAGGAAACAGCTATGACCATNCCRCARTCNATRTGYTT-3'	MORGULUS 2017 with modifications	95°C, 10:00	45	95°C, 0:30	50°C, 1:00	72°C, 1:00	72°C, 4:00
28S (1280 bp)	S28C (forward) S28E (forward) A28D (reverse) S28G (forward) A28F (reverse) A28HL (reverse)	5'-GTGCAAAATCGATTGTCAGAA-3' 5'-AGCAGGACGGTGGACATGGA-3' 5'-ACTTAAGCGCCATCCATTT-3' 5'-GAAAGTGGAGAAAGGGTTTGTG-3' 5'-TGGAACCGTATCCCTTCG-3' 5'-CTTACCTACATTATCTATCGACT-3'	HAN et al. 2002 with modifications	95°C, 5:00	35	95°C, 1:00	62.7°C, 1:00	72°C, 1:30	72°C, 5:00

Table 2. List of specimens and GenBank accession numbers.

Taxon	COI	16S	Period	AATS	28S
<i>Tephritis</i> cf. <i>dioscurea</i>	MN312021	MN331953	MN311979	MN394180	MN331891
<i>Tephritis multiguttata</i>	MN312022	MN331954	MN311980	MN394181	MN331892
<i>Tephritis</i> sp. nr. <i>tanaceti</i>	MN312023	MN331955	MN311981	MN394182	MN331893
<i>Tephritis araneosa</i>	MN312024	MN331956	MN311982	MN394183	MN331894
<i>Tephritis</i> cf. <i>ovatipennis</i>	MN312025	MN331957	MN311983	MN394184	MN331895
<i>Tephritis</i> spn. 1	MN312026	MN331958	MN311984	MN394185	MN331896
<i>Tephritis</i> spn. 2	MN312027	MN331959	MN311985	MN394186	MN331897
<i>Tephritis</i> spn. 4	MN312028	MN331960	MN311986	MN394187	MN331898
<i>Tephritis</i> spn. 3	MN312029	MN331961	MN311987	MN394188	MN331899
<i>Tephritis</i> cf. <i>tanaceti</i>	MN312030	MN331962	MN311988	MN394189	MN331900
<i>Tephritis</i> cf. <i>nigricauda</i>	MN312031	MN331963	MN311989	MN394190	MN331901
<i>Tephritis stigmatica</i>	MN312032	MN331964	MN311990	MN394191	MN331902
<i>Tephritis labecula</i>	MN312033	MN331965	MN311991	MN394192	MN331903
<i>Tephritis baccharis</i>	MN312034	MN331966	MN311992	MN394193	MN331904
<i>Tephritis arizonaensis</i>	MN312035	MN331967	MN311993	MN394194	MN331905
<i>Tephritis sahandi</i>	MN312036	MN331968	MN311994	MN394195	MN331906
<i>Tephritis hurvitzi</i>	MN312037	MN331969	MN311995	MN394196	MN331907
<i>Tephritis</i> cf. <i>conyzifoliae</i>	MN312038	MN331970	MN311996	MN394197	MN331908
<i>Tephritis</i> cf. <i>separata</i>	MN312039	MN331971	MN311997	MN394198	MN331909
<i>Tephritis kovalevi</i>	MN312040	MN331972	MN311998	MN394199	MN331910
<i>Tephritis youngiana</i>	MN312041	MN331973	MN311999	MN394200	MN331911
<i>Tephritis postica</i>	MN312042	MN331974	MN312000	MN394201	MN331912
<i>Tephritis cometa</i>	MN312043	MN331975	MN312001	MN394202	MN331913
<i>Tephritis conura</i>	MN312044	MN331976	MN312002	MN394203	MN331914
<i>Tephritis arsenii</i>	MN312045	MN331977	MN312003	MN394204	MN331915
<i>Tephritis kogardtauca</i>	MN312046	MN331978	MN312004	MN394205	MN331916
<i>Tephritis hyoscyami</i>	MN312047	MN331979	MN312005	MN394206	MN331917
<i>Tephritis</i> cf. <i>macculus</i>	MN312048	MN331980	MN312006	MN394207	MN331918
<i>Tephritis bardanae</i>	MN312049	MN331981	MN312007	MN394208	MN331919
<i>Tephritis tatarica</i>	MN312050	MN331982	MN312008	MN394209	MN331920
<i>Tephritis nozarii</i>	MN312051	MN331983	MN312009	MN394210	MN331921
<i>Tephritis oedipus</i>	MN312052	MN331984	MN312010	MN394211	MN331922
<i>Tephritis praecox</i>	MN312053	MN331985	MN312011	MN394212	MN331923
<i>Heringina arezoana</i>	MN312054	MN331986	MN312012	MN394213	MN331924
<i>Heringina guttata</i>	MN312055	MN331987	MN312013	MN394214	MN331925
<i>Tephritis neesii</i>	MN312056	MN331988	MN312014	MN394215	MN331926
<i>Tephritis</i> cf. <i>leavittensis</i>	MN312057	MN331989	MN312015	MN394216	MN331927
<i>Trupanea</i> cf. <i>jonesi</i>	MN312058	MN331990	MN312016	MN394217	MN331928
<i>Actinoptera discoidea</i>	MN312059	MN331991	MN312017	MN394218	MN331929
<i>Goniurellia tridens</i>	MN312060	MN331992	MN312018	MN394219	MN331930
<i>Capitites ramulosa</i>	MN312061	MN331993	MN312019	MN394220	MN331931
<i>Euaesta aequalis</i>	MN312062	MN331994	MN312020	MN394221	MN331932
<i>Tephritis dudichi</i>	MN312063				
<i>Tephritis angustipennis</i>	MN312064				
<i>Tephritis vespertina</i>	MN312065				
<i>Tephritis valida</i>	MN312066				
<i>Tephritis sauterina</i>	MN312067				
<i>Tephritis subpura</i>	MN312068				
<i>Tephritis alamutensis</i>	MN312069				
<i>Tephritis robusta</i>	MN312070				
<i>Tephritis crinita</i>	MN312071				
<i>Tephritis leontodontis</i>	MN312072				
<i>Tephritis matricariae</i>	MN312073				
<i>Tephritis arnicae</i>	MN312074				
<i>Tephritis formosa</i>	MN312075				
<i>Tephritis crepidis</i>	MN312076				
<i>Tephritis mutabilis</i>	MN312077				
<i>Tephritis</i> cf. <i>cameo</i>	MN312078				
<i>Tephritis divisa</i>	MN312079				
<i>Tephritis pallescens</i>	MN312080				

Table 2 continued.

Taxon	COI	16S	Period	AATS	28S
<i>Tephritis pulchra</i>	MN312081				
<i>Tephritis recurrens</i>	MN312082				
<i>Tephritis scorzonerae</i>	MN312083				
<i>Tephritis ruralis</i>	MN312084				
<i>Tephritis</i> cf. <i>gladius</i>	MN312085				
<i>Tephritis</i> cf. <i>admissa</i>	MN312086				
<i>Tephritis baccharis</i>	MN312087				
<i>Tephritis palmeri</i>	MN312088				
<i>Tephritis subpura</i>	MN312089				
<i>Tephritis signatipennis</i>	MN312090				
<i>Tephritis heliophila</i>	MN312091				

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 glycerin on a depression microscope slide, covered with a glass cover slip. Dissected structures are stored in polypropylene microvials containing glycerin pinned together with a specimen.

Photographs of genitalia were taken using a Nikon Coolpix P50 through the ocular of a Wild M11 light microscope; photographs of wing and habitus were taken using a Canon PowerShot A640 connected to a Zeiss Stemi C-2000 microscope. Digitized photographs were stacked using CombineZM® (HADLEY 2007). Specimens deposited in the collection of the Museum für Naturkunde Berlin were taken under supervision of Dr. Joachim Ziegler and Bernhard Schurian, and were stacked using Helicon Focus®. Pictures of all Nearctic specimens were taken at the National Museum of Natural History with the assistance of Dr. Allen Norrbom and Lucrecia Rodriguez using a Systematic Entomology Laboratory Visionary Digital camera system.

DNA isolation and PCR amplification. All DNA was extracted using the DNeasy Blood & Tissue Kit protocol (Qiagen, Valencia, CA). For most specimens, a single leg or head was removed, ground in a microcentrifuge tube with proteinase K and lysing buffer and then incubated for 12 hours. A non-destructive method was used for rare specimens: a whole abdomen was placed in the buffer and incubated for 12 hours. We PCR amplified each locus (COI, 16S, period, AATS, and 28S) using GotaqFlexi DNA polymerase (Promega, Madison, WI) in 25 µl reactions with the following concentrations of reagents: reaction buffer (5 mM), MgCl₂ (8 mM), dNTP (1.25 mM each), forward and reverse primers (1.25 mM each), DNA polymerase (0.25 mM), water (4.5 mM) and DNA template (3.5 mM). Primer sequences and PCR conditions for every gene were taken from literature sources and are listed in Table 1.

DNA sequencing and editing. DNA amplifications were performed in a 25-µL reaction volume using GoTaq® Flexi DNA Polymerase. PCR products (5 µL) were visualized on a 1% agarose gel using ethidium bromide. Amplified products (20 µL) were purified using QIAquick

PCR Purification Kit protocol (QIAGEN). Sanger sequencing was performed at the Michigan State University Research Technology Support Facility via Big-Dye Terminator Sequencing on an Applied Biosystems 3730xl DNA Analyzer (Foster City, CA, USA) using the PCR primers as sequencing primers. Sequences are deposited in GenBank (Table 2).

Phylogenetic analyses. The alignments of the protein-coding DNA were performed using MEGA 7 (KUMAR et al. 2016) using MUSCLE to align translated amino acids (EDGAR 2004). Non-coding rRNA genes (16S and 28S) were aligned using MAFFT (KATOHI et al. 2002). To find optimal partitioning schemes for the Bayesian and maximum likelihood analyses, we used PartitionFinder 2.1.1 (LANFPEAR et al. 2016) with the “greedy” search algorithm (LANFPEAR et al. 2012). Before running PartitionFinder the data were divided into 11 biologically relevant partitions, which included first, second and third nucleotide positions for each protein-coding gene (9 partitions) and two partitions for non-coding genes 16S and 28S. The following partitions were defined (with models): **GTR + I + G** for COI, Period (first positions) and 16S; **HKY + I + G** for 28S; **HKY + I** for COI (second positions); **GTR + G** for COI and Period (third positions); **HKY + G** for Period (second positions) and AATS (third positions); **K2P + G** for AATS (first positions); **F81** for AATS (second positions). Phylogenetic analyses using Bayesian inference were performed on the concatenated genetic dataset in MrBayes 3.2.6 (RONQUIST et al. 2012). The Bayesian analysis used four independent runs each with four Metropolis-coupled chains with default heating parameters (one cold and three heated). The chains were sampled once every thousand generations for 10 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 0.01 and all branch lengths and substitution model parameters had potential scale reduction factors less than 1.01 (RONQUIST et al. 2012). The Maximum Likelihood analysis was done in RAxML (STAMATAKIS et al. 2008) using the GTR+I+G model with the above partitioning scheme with 1000 bootstrap pseudoreplicates on the CIPRES online portal (MILLER et al. 2010).

Table 3. Material.

Sequence ID	Isolate	Organism	Host / reared or swept	Country: Location	Collection date	Collector	Lat.	Long.	Depository	Genes
T_cf_dioscorea_SW040722_CH	SW040722	<i>Tephritis</i> cf. <i>dioscorea</i>	<i>Achillea millefolium</i> (Anthemideae) / swept	Switzerland: Leuk, along road	22 July 2004	Allen Norrbom			SIZK	COI, 16S, Period, AATS, 28S
T_multiguttata_K14118_IR	K14118	<i>Tephritis multiguttata</i>	<i>Achillea</i> sp. (Anthemideae) / swept	Iran: Kurdistan, 5 km W Hossein Abad	13 June 2014	S. Korneyev & V. Korneyev	35.531111	47.206389	SIZK	COI, 16S, Period, AATS, 28S
T_sp_nr_tanacetii_K14025_IR	K14025	<i>Tephritis</i> sp. nr. <i>tanacetii</i>	<i>Tanacetum</i> sp. (Anthemideae) / swept	Iran: East Azerbaijan Province, nr Kaleybar	17 May 2014	S. Korneyev & V. Korneyev	38.852222	46.998333	SIZK	COI, 16S, Period, AATS, 28S
T_araneosa_AR170719_01m1_US	AR170719_01m1	<i>Tephritis araneosa</i>	unknown, possibly <i>Artemisia</i> sp. (Anthemideae) / swept	USA: Cochise Co., Carr Canyon, AR	19 July 2017	S. Lampert, M. Savaris, A. L. Norrbom & N.E. Woodley	31.42421	-110.29903	SIZK	COI, 16S, Period, AATS, 28S
T_cf_ovatipennis_US170524_04_US	US170524_04	<i>Tephritis</i> cf. <i>ovatipennis</i>	unknown, possibly <i>Corethrogyne</i> sp., <i>Eriogon</i> sp. (Astereae) / swept	USA: Summit and Wasatch Co., Uinta Mts. Kamas ESE 25 km; Hwy 150, UT	24 May 2017	S.M. Blank & K. Kramp	40.612	-110.962	CSCA	COI, 16S, Period, AATS, 28S
T_spn1_K170727_02m1_KG	K170727_02m1	<i>Tephritis</i> spn. 1	unknown / swept	Kyrgyzstan: Karakol gorge	27 July 2017	S. Korneyev & V. Korneyev	42.3805	78.4870	SIZK	COI, 16S, Period, AATS, 28S
T_spn2_K170708_14f1_KG	K170708_14f1	<i>Tephritis</i> spn. 2	<i>Artemisia</i> sp. (Anthemideae) / swept	Kyrgyzstan: Kashka-Suu ski resort	8 July 2017	S. Korneyev & V. Korneyev	42.644563	74.516080	SIZK	COI, 16S, Period, AATS, 28S
T_spn4_K170720_02f1_KG	K170720_02f1	<i>Tephritis</i> spn. 4	<i>Anthemis</i> sp. (Anthemideae) / swept	Kyrgyzstan: Karakol	20 July 2017	S. Korneyev & V. Korneyev	42.503818	78.403276	SIZK	COI, 16S, Period, AATS, 28S
T_spn3_K170803_06m1_KG	K170803_06m1	<i>Tephritis</i> spn. 3	<i>Pyrethrum</i> sp. (Anthemideae) / swept	Kyrgyzstan: Kashka-Suu ski resort	3 August 2017	S. Korneyev & V. Korneyev	42.644563	74.516080	SIZK	COI, 16S, Period, AATS, 28S
T_cf_tanacetii_U170618_04_UA	U170618_04	<i>Tephritis</i> cf. <i>tanacetii</i>	<i>Tanacetum vulgare</i> (Anthemideae) / swept	Ukraine: Irpin	18 June 2017	S. Korneyev & V. Korneyev	50.511901	30.261249	SIZK	COI, 16S, Period, AATS, 28S
T_cf_nigricauda_545642_FR	RMNH.INS.545642	<i>Tephritis</i> cf. <i>nigricauda</i>	<i>Anthemis arvensis</i> (Anthemideae) / swept	France: Pyrenees Orientales, Mont Louis, La Llagonne	20 June 2011	J.T. Smit	42.571917	2.110639	RMNH	COI, 16S, Period, AATS, 28S
T_stigmatica_AR170712_04m1_US	AR170712_04m1	<i>Tephritis stigmatica</i>	<i>Senecio</i> spp. (Senecioneae) / swept	USA: Coconino Co., Snowbowl, parking area, AR	12 July 2017	S. Lampert, M. Savaris & A.L. Norrbom	35.32944	-111.71139	SIZK	COI, 16S, Period, AATS, 28S
T_labecula_AR170712_01m1_US	AR170712_01m1	<i>Tephritis labecula</i>	<i>Chrysanthamnus nauseosus</i> (Astereae) / swept	USA: Coconino Co., Lake Mary Road (Rt. 3), AR	12 July 2017	S. Lampert, M. Savaris & A.L. Norrbom	35.13545	-111.63137	SIZK	COI, 16S, Period, AATS, 28S
T_baccharis_AR170720_01f1_US	AR170720_01f1	<i>Tephritis baccharis</i>	<i>Baccharis sarothroides</i> (Astereae) / swept	USA: Cochise Co., Paradise Road, wash along road, AR	20 July 2017	S. Lampert, M. Savaris & A.L. Norrbom	31.95976	-109.21239	SIZK	COI, 16S, Period, AATS, 28S
T_arizonaensis_AR170717_01f1_US	AR170717_01f1	<i>Tephritis arizonaensis</i>	<i>Baccharis salicifolia</i> (Astereae) / swept	USA: Greenlee Co., Rt. 191, AR	17 July 2017	S. Lampert, M. Savaris & A.L. Norrbom	33.1628	-109.36787	SIZK	COI, 16S, Period, AATS, 28S
T_sahandi_m1_K14058_IR	K14058	<i>Tephritis sahandi</i>	<i>Achillea chypsiolata</i> (Anthemideae) / swept	Iran: Kohgiluyeh and Boyer-Ahmad Province, near Sisakht	26 May 2017	S. Korneyev & V. Korneyev	30.874722	51.523889	SIZK	COI, 16S, Period, AATS, 28S
T_hurvitzi_K170717_02m1_KG	K170717_02m1	<i>Tephritis hurvitzi</i>	<i>Tragopogon longirostre</i> (Cichorieae) / swept	Kyrgyzstan: Kashka-Suu ski resort	17 July 2017	S. Korneyev & V. Korneyev	42.644563	74.516080	SIZK	COI, 16S, Period, AATS, 28S
T_cf_conyzifoliae_K170721_02m3_KG	K170721_02m3	<i>Tephritis</i> cf. <i>conyzifoliae</i>	<i>Crepis sibirica</i> (Cichorieae) / reared	Kyrgyzstan: Karakol gorge	21 July 2017	S. Korneyev & V. Korneyev	42.405358	78.458351	SIZK	COI, 16S, Period, AATS, 28S
T_cf_divisa_K16007_UA	K16007	<i>Tephritis</i> cf. <i>separata</i>	<i>Picris rigida</i> (Cichorieae) / swept	Ukraine: Ternopil region, near Synki	15 July 2017	S. Korneyev & V. Korneyev	48.602686	25.881431	SIZK	COI, 16S, Period, AATS, 28S

Table 3 continued.

Sequence ID	Isolate	Organism	Host / reared or swept	Country, Location	Collection date	Collector	Lat.	Long.	Depository	Genes
T_kovalevi_K170714_05m1_KG	K170714_05m1	<i>Tephritis kovalevi</i>	<i>Sonchus paluster</i> (Cichorieae) / reared	Kyrgyzstan: Boom gorge	14 July 2017	S. Korneyev & V. Korneyev	42.598036	75.809457	SIZK	COI, 16S, Period, AATS, 28S
T_sp5_K170714_02f1_KG	K170714_02f1	<i>Tephritis youngiana</i>	<i>Youngia</i> sp. (Cichorieae) / reared	Kyrgyzstan: Boom gorge	14 July 2017	S. Korneyev & V. Korneyev	42.598036	75.809457	SIZK	COI, 16S, Period, AATS, 28S
T_positica_K170707_31f2_KG	K170707_31f2	<i>Tephritis positica</i>	<i>Onopordium acanthium</i> (Cardueae) / reared	Kyrgyzstan: Chon Atyk, near Bishkek	7 July 2017	S. Korneyev & V. Korneyev	42.787072	74.572389	SIZK	COI, 16S, Period, AATS, 28S
T_cometa_K170731_03f1_KG	K170731_03f1	<i>Tephritis cometa</i>	<i>Cirsium</i> spp. (Cardueae) / swept	Kyrgyzstan: Karakol gorge	31 July 2017	S. Korneyev & V. Korneyev	42.392630	78.473630	SIZK	COI, 16S, Period, AATS, 28S
T_conura_K170723_01f1_KG	K170723_01f1	<i>Tephritis conura</i>	<i>Cirsium</i> spp. (Cardueae) / swept	Kyrgyzstan: Jeti-Oguz	23 July 2017	S. Korneyev & V. Korneyev	42.3448	78.2326	SIZK	COI, 16S, Period, AATS, 28S
T_arsenii_K14158_IR	K14158	<i>Tephritis arsenii</i>	<i>Dononium dolichotrichum</i> (Senecioneae) / reared	Iran: West Azerbaijan Province, near Turkish border, 10km west Zivoh	20 June 2017	S. Korneyev & V. Korneyev	37.133333	44.866667	SIZK	COI, 16S, Period, AATS, 28S
T_kogardtauca_K170707_21f1_KG	K170707_21f1	<i>Tephritis kogardtauca</i>	<i>Inula grandis</i> , f. <i>stenoalathia</i> (Inuleae) / reared	Kyrgyzstan: Chon Atyk, near Bishkek	7 July 2017	S. Korneyev & V. Korneyev	42.787072	74.572389	SIZK	COI, 16S, Period, AATS, 28S
T_hyoscyami_K170727_01m1_KG	K170727_01m1	<i>Tephritis hyoscyami</i>	<i>Carduus</i> spp. (Cardueae) / swept	Kyrgyzstan: Karakol gorge	27 July 2017	S. Korneyev & V. Korneyev	42.392630	78.473630	SIZK	COI, 16S, Period, AATS, 28S
T_of_maccus_K16001_f1_AF	K16001_f1	<i>Tephritis cf. maccus</i>	unknown / swept	Afghanistan: Berganghak	24 June 2016	Yu. Skryninik			SIZK	COI, 16S, Period, AATS, 28S
T_bardanae_K170717_04f1_KG	K170717_04f1	<i>Tephritis bardanae</i>	<i>Arctium</i> spp. (Cardueae) / swept	Kyrgyzstan: Kasha-Suu ski resort	17 July 2017	S. Korneyev & V. Korneyev	42.644563	74.516080	SIZK	COI, 16S, Period, AATS, 28S
T_tatarica_K170721_05f1_KG	K170721_05f1	<i>Tephritis tatarica</i>	<i>Alfredia nivea</i> (Cardueae) / reared	Kyrgyzstan: Karakol gorge	21 July 2017	S. Korneyev & V. Korneyev	42.405358	78.458351	SIZK	COI, 16S, Period, AATS, 28S
T_nozarii_K14057_IR	K14057	<i>Tephritis nozarii</i>	<i>Cirsium</i> sp. (Cardueae) / swept	Iran: Koghilyeh and Boyer-Ahmad Province, near Sisakht	26 May 2017	S. Korneyev & V. Korneyev	30.874722	51.523889	SIZK	COI, 16S, Period, AATS, 28S
T_oedipus_K170716_01m1_KG	K170716_01m1	<i>Tephritis oedipus</i>	<i>Lactuca tatarica</i> (Cichorieae) / swept	Kyrgyzstan: Orto-Tokoi	16 July 2017	S. Korneyev & V. Korneyev	42.29711	75.86995	SIZK	COI, 16S, Period, AATS, 28S
T_praecox_K14024_IR	K14024	<i>Tephritis praecox</i>	<i>Calendula arvensis</i> (Calenduleae) / swept	Iran: East Azerbaijan Province, nr Kaleybar	17 May 2014	S. Korneyev & V. Korneyev	38.852222	46.998333	SIZK	COI, 16S, Period, AATS, 28S
Heringina_arezana_K14122_IR	K14122	<i>Heringina arezana</i>	<i>Helichrysum</i> sp. (Gnaphaliteae) / swept	Iran: Kurdistan, Sanandaj, Abidar Mt	15 June 2014	S. Korneyev & V. Korneyev	35.314167	46.954722	SIZK	COI, 16S, Period, AATS, 28S
Heringina_guttata_U161001_UA	U161001	<i>Heringina guttata</i>	<i>Helichrysum arenarium</i> (Gnaphaliteae) / swept	Ukraine: Irpin	1 October 2016	S. Korneyev & V. Korneyev	50.507139	30.258750	SIZK	COI, 16S, Period, AATS, 28S
T_neesii_545553_f1_NL	RMINH.INS.545553	<i>Tephritis neesii</i>	<i>Leucanthemum vulgare</i> (Anthemideae) / swept	Netherlands: Ossendrecht, Stoppelbergen	15 Sep. 2011	J.T. Smit			RMINH	COI, 16S, Period, AATS, 28S
T_levittensis_US170520_01f1_US	US170520_01f1	<i>Tephritis cf. levittensis</i>	unknown, possibly <i>Arnica diversifolia</i> (Senecioneae) / swept	USA: Nye Co; White Pine Range; Hwy 6, NE	20 May 2017	S.M. Blank & K. Kramp	38.818	-115.351	CSCA	COI, 16S, Period, AATS, 28S
Trupanea_cf_jonesi_US170601_03_US	US170601_03	<i>Trupanea cf. jonesi</i>	many different Asteraceae / swept	USA: Lander Co; Desatoya Mts; Austin SW 59 km; Hwy 722, NE	1 June 2017	B.E. Altenhofer & S.M. Blank	39.341	-117.127	CSCA	COI, 16S, Period, AATS, 28S
Actinoptera_discoida_K170707_28_KG	K170707_28	<i>Actinoptera discoida</i>	<i>Helichrysum</i> sp. (Gnaphaliteae) / swept	Kyrgyzstan: Chon Atyk, near Bishkek	7 July 2017	S. Korneyev & V. Korneyev	42.787072	74.572389	SIZK	COI, 16S, Period, AATS, 28S
Goniurella_tridens_K170707_02_KG	K170707_02	<i>Goniurella tridens</i>	<i>Inula macrophylla</i> (Inuleae) / swept	Kyrgyzstan: Chon Atyk, near Bishkek	7 July 2017	S. Korneyev & V. Korneyev	42.787072	74.572389	SIZK	COI, 16S, Period, AATS, 28S
Capitites_ramulosa_20120524_IL	20120524	<i>Capitites ramulosa</i>	<i>Phagnalon rupestre</i> (Gnaphaliteae) / swept	Israel: Har (Mt.) Hermon	24 May 2012	J.T. Smit	33.294667	35.759417	RMINH	COI, 16S, Period, AATS, 28S

Table 3 continued.

Sequence ID	Isolate	Organism	Host / reared or swept	Country: Location	Collection date	Collector	Lat.	Long.	Depository	Genes
<i>Euresta aequalis</i> _US170827_01_US	US170827_01	<i>Euresta aequalis</i>	<i>Xanthium strumarium</i> (Heliantheae) / swept	USA: Putah Creek, CA	27 August 2017	S. Korneyev	38.514	-122.077	SIZK	COI, 16S, Period, AATS, 28S
<i>T. dudichi</i> _30103325_RMNH_INS_544815	30103325_RMNH_INS_544815	<i>Tephritis dudichi</i>	<i>Telekia speciosa</i> (Inuleae) / reared	Ukraine: Transcarpathian reg. Carpathian Mts. Kuziy Massif	20 July 2011	S. & V. Korneyev	47.933	24.116	RMNH	COI
<i>T. angustipennis</i> _30103291_RMNH_545637	30103291_RMNH_545637	<i>Tephritis angustipennis</i>	<i>Achillea ptarmica</i> (Anthemideae) / swept	France: Pyrenees Orientales, Mont Louis, La Llagonne	20 June 2011	J.T. Smit	42.572	2.111	RMNH	COI
<i>T. vespertina</i> _30103355_RMNH_544845	30103355_RMNH_544845	<i>Tephritis vespertina</i>	<i>Hypochoeris radicata</i> (Cichorieae) / swept	Italy		P. van Helldingen & J.T. Smit			RMNH	COI
<i>T. valida</i> _4007592937_RMNH_556413	4007592937_RMNH_556413	<i>Tephritis valida</i>	<i>Inula helenium</i> (Inuleae) / swept	Russia: North Caucasus, Karachay-Cherkess Republic, Teberda, southern part of town	27 July 2013	S. & V. Korneyev	43.413	41.731	RMNH	COI
<i>T. sauterina</i> _4007592956_RMNH_556394	4007592956_RMNH_556394	<i>Tephritis sauterina</i>	<i>Aster alpinus</i> (Astereae) / reared	Russia: North Caucasus, Karachay-Cherkess Republic, Teberda, Khatipara Mt.	13 August 2013	S. & V. Korneyev	43.433	41.700	RMNH	COI
<i>T. subpura</i> _ML170719_01m1	ML170719_01m1	<i>Tephritis subpura</i>	<i>Baccharis</i> sp. (Astereae) / swept	USA: Maryland: Sandy Point Park, Route 50 ramp area, sweeping	30 Sep 2017	Allen Norrboom	39.018	-76.408	SIZK	COI
<i>T. alamutensis</i> _Iran_K14108	K14108	<i>Tephritis alamutensis</i>	<i>Cousinia</i> sp. cf. <i>umbrosa</i> (Cardueae) / swept	Iran: Dazvin, Alamut castle	9 June 2014	S. & V. Korneyev	36.445	50.583	SIZK	COI
<i>T. robusta</i> _Iran_K14192	K14192	<i>Tephritis robusta</i>	<i>Cousinia</i> sp. (Cardueae) / swept	Iran: Sarein, Vargehsaran	3 July 2014	S. & V. Korneyev	38.183	47.981	SIZK	COI
<i>T. crinita</i> _Afgan_K16003_f1	K16003_f1	<i>Tephritis crinita</i>	unknown / swept	Afghanistan: Bande Amir	29 June 2016	Yu. Skrylnik			SIZK	COI
<i>T. leontodontis</i> _0330Tepleo	RMNH.INS.252292	<i>Tephritis leontodontis</i>	<i>Leontodon autumnalis</i> , <i>L. helveticus</i> , <i>L. hispidus</i> (Cichorieae) / swept	Spain: País Vasco, Guipúzcoa, San Sebastián, Igeldo	17 June 2009	J.T. Smit	43.299833	-2.061056	RMNH	COI
<i>T. matricariae</i> _f1_Netherlands_555073	RMNH.INS.555073	<i>Tephritis matricariae</i>	<i>Crepis foetida</i> (Cichorieae) / swept	Netherlands: Colmiont, Wrakelberg	30 June 2012	John Smit			RMNH	COI
<i>T. arnicae</i> _m1_Ukraine_544816	RMNH.INS.544816	<i>Tephritis arnicae</i>	<i>Doronicum austriacum</i> (Senecioneae) / reared	Ukraine: Carpathians, Hoverla	17 July 2011	S. & V. Korneyev			RMNH	COI
<i>T. formosa</i> _0071	RMNH.INS.252033	<i>Tephritis formosa</i>	<i>Sanctus asper</i> , <i>S. oleraceus</i> (Cichorieae) / swept	Greece: Beabies	16-22 June 2008	G. Ramel			RMNH	COI
<i>T. crepidis</i> _30103300_RMNH_545646	30103300_RMNH_545646	<i>Tephritis crepidis</i>	<i>Crepis biennis</i> , <i>C. blattarioides</i> (Cichorieae) / swept	The Netherlands, Rhemen, Blauwe Kamer	13 June 2011	D. Belgers & J.T. Smit			RMNH	COI
<i>T. mutabilis</i> _0067	RMNH.INS.252029	<i>Tephritis mutabilis</i>	<i>Leontodon hispidus</i> (Cichorieae) / swept	Greece: Elodia	25 Feb - 2 Mar 2008	G. Ramel	38.750469	20.722714	RMNH	COI
<i>T. cf. cameo</i> _Iran_K14061	K14061	<i>Tephritis cf. cameo</i>	<i>Cousinia</i> sp. (Cardueae) / swept	Iran: Pass near Sasakht	26 May 2014	S. & V. Korneyev	30.8747	51.5238	SIZK	COI
<i>T. divisa</i> _0237	RMNH.INS.252199	<i>Tephritis divisa</i>	<i>Picris echinoides</i> (Cichorieae) / swept	Spain: País Vasco, Alava, Vitoria-Gasteiz, Etxebarri-Urtupia	28 May 2009	J.T. Smit	42.872700	-2.516914	RMNH	COI
<i>T. pallescens</i> _K16005_m1_Afgan	K16005_m1_Afgan	<i>Tephritis pallescens</i>	unknown / swept	Afghanistan: Bande Amir	17 June 2016	Yu. Skrylnik			SIZK	COI
<i>T. pulchra</i> _252111_Spain	RMNH.INS.252111	<i>Tephritis pulchra</i>	<i>Scarzonera laciniata</i> (Cichorieae) / swept	Spain: Aragón, Huesca, Almuédvar, S Embalse Sotonera	23 May 2009	John Smit	42.191667	-0.761	RMNH	COI
<i>T. recurrens</i> _252345_Serbia	RMNH.INS.252345	<i>Tephritis recurrens</i>	<i>Scarzonera</i> sp. (Cichorieae) / swept	Serbia: Nis, Suva Planina, Jelasnicka, Klisura	24 June 2009	John Smit	43.364722	22.098056	RMNH	COI

Table 3 continued.

Sequence ID	Isolate	Organism	Host / reared or swept	Country: Location	Collection date	Collector	Lat.	Long.	Depository	Genes
T_ruralis_U170402_01_Irpin_Ukr	U170402_01_Irpin_Ukr	<i>Tephritis ruralis</i>	<i>Hieracium lactuella</i> , <i>H. pilosella</i> (Cichorieae) / swept	Ukraine: Kyiv region, Irpin meadow	12 April 2017	V. Korneyev	50.511901	30.261249	RMINH	COI
T_cf_gladius_K16004_f1_Afghan2	K16004_f1	<i>Tephritis cf. gladius</i>	unknown / swept	Afghanistan: Bande Amir	29 June 2016	Yu. Skrylnik			SIZK	COI
T_cf_admissa_K170707_29f1	K170707-29	<i>Tephritis cf. admissa</i>	<i>Cousinia tianschanica</i> (Cardueae) / swept	Kyrgyzstan: Chon Aryk, near Bishkek	7 July 2017	S. & V. Korneyev	42.787072	74.572389	SIZK	COI
T_baccharis_US170831_07m1	US170831_07m1	<i>Tephritis baccharis</i>	<i>Baccharis salicifolia</i> (Asteraceae) / swept	USA: Los Angeles, Natural History Museum of L. A. County, garden	31 July 2017	S. Korneyev, B. Brown, L. Gonsales & G.A. Kunn	34.017	-118.288	SIZK	COI
T_palmeri_US170831_01f1	US170831_01f1	<i>Tephritis palmeri</i>	<i>Baccharis neglecta</i> , <i>B. halimifolia</i> (Asteraceae) / swept	USA: Los Angeles, Natural History Museum of L. A. County, garden	31 July 2017	S. Korneyev, B. Brown, L. Gonsales & G.A. Kunn	34.017	-118.288	SIZK	COI
T_subpura_TX110426_01f1	TX110426_01f1	<i>Tephritis subpura</i>	<i>Baccharis glomeruliflora</i> , <i>B. halimifolia</i> (Asteraceae) / swept	USA: Texas: Houston	11 April 2017	J.D. Lopez			SIZK	COI
T_signatipennis_AR170726_01f1	AR170726_01f1	<i>Tephritis signatipennis</i>	<i>Machaeranthera canescens</i> (Asteraceae) / swept	USA: Arizona: Pima Co., Mount Lemmon, Alder Campground, WP 325	26 July 2017	S. Lampert, M. Savaris & A.L. Norrbom	32.43562	-110.75173	SIZK	COI
T_heliophila_0361Tephel	RMINH_INS.252323	<i>Tephritis heliophila</i>	<i>Tragopogon dubius</i> (Cichorieae) / swept	Serbia: Beigrade, Doliblati sands, tweede stop	22 June 2009	J.T. Smit	44.851167	21.285306	RMINH	COI

Outgroup taxa. Species of the genera assigned to the “Higher Tephritinae” (sensu V. KORNEYEV 1999) (*Euaerea*, *Actinoptera*, *Capitites*, *Goniurellia*, *Trupanea*), or *Tephritis* group of genera (sensu MERZ 1999) (*Actinoptera*, *Capitites*, *Goniurellia*, *Trupanea*) or the “groups 1–2” (sensu HAN et al. 2006) (*Euaerea*, *Goniurellia*, *Trupanea*) have been included into analysis as outgroups, along with *Heringina*, which was tested as a possible ingroup member of *Tephritis*.

Systematics of Asteraceae. The system used herein is based on the tribal classification by FUNK et al. (2009). The genus *Doronicum*, which is considered a genus incertae sedis basal to the tribe Senecioneae (FUNK et al. 2009) is provisionally considered to be a member of that tribe.

3. Results and discussion

3.1. Molecular analysis

For the concatenated dataset of the five genes, phylogenetic topology obtained with Bayesian inference is shown in Figure 1. The clade containing *Tephritis*, *Capitites*, *Heringina*, and *T. praecox* (the *Tephritis* aggregation lineage) was moderately supported in the Maximum Likelihood analyses (ML, bootstrap support = 70), but very strongly supported as a monophyletic clade in the BI tree (BPP, Bayesian posterior probability = 1). In the ML analyses genus *Capitites* is placed within *Tephritis*, however, in the BI analyses it appears as the sister-group to the monophyletic group containing *Tephritis* s.str., *Heringina*, *T. praecox*, *T. oedipus*, and *T. maccus*, with strong support (BPP = 0.95). This corresponds well with the preliminary results of the morphology-based phylogenetic analysis of S. KORNEYEV (2016) in which *Capitites* is the sister-group to the monophyletic *Tephritis* s.str. + *Heringina* + *T. praecox* clade.

Within the *Tephritis* lineage, four major monophyletic clades (I–IV in Fig. 1) are recognized. Clade I is represented by three morphologically distinct *Tephritis* species plus *Heringina*, which in addition share no obvious host-plant preferences, being associated with the **Gnaphalieae** (*Heringina*), **Calenduleae** (*T. praecox*) or **Cichorieae** (*T. oedipus* and presumably *T. maccus*). These species have mostly Mediterranean / Near East distribution (except *Heringina guttata*, which has expanded its range on sandy dunes northwards to southern Sweden in the postglacial time). The species in Clade II do not seem to share any obvious morphological synapomorphies and are diverse in their wing patterns; most of them infest host plants of the tribe **Cardueae**, except for *T. kogardtauca* and *T. arsenii*, which infest members of the tribes **Inuleae** and **Senecioneae**. Clade III (BPP = 1) contains four morphologically diverse species, but they share host plants

Table 4. *Tephritis* species groups and lineages. — **Abbreviations:** PA – Palearctic region; NEA – Nearctic region.

Clade	Species Group	Species (for bold selected species sequences are given in this article)	Host plant species	Host Plant Tribe	Source	Character Evidence	Region	
I	maccus group	<i>T. azari</i> Mohamadzade & Korneyev, 2012	unknown		MOHAMADZADE et al. 2015	Morphology	PA	
		<i>T. gharajii</i> Mohamadzade & S. Korneyev, 2015	unknown		MOHAMADZADE et al. 2015	Morphology	PA	
		<i>T. maccus</i> Hering, 1937	swept from <i>Lactuca scariola</i>	Cichorieae	MOHAMADZADE et al. 2015	Morphology, COI; Period; AATS; 28S	PA	
		<i>T. urelliosomima</i> Korneyev, Diribek, 2000	unknown		MOHAMADZADE et al. 2015	Morphology	PA	
		<i>T. sophus</i> Gentilini & V. Korneyev, 2006 †	unknown		MOHAMADZADE et al. 2015	Morphology	PA	
	I	<i>T. oedipus</i> Hendel, 1927	<i>Lactuca tatarica</i>	<i>Lactuca tatarica</i>	Cichorieae	KORNEYEV & KARYUK 2009	Morphology, host, COI; 16S; Period; AATS; 28S	PA
			<i>T. praecox</i> (Loew, 1844)	<i>Calendula arvensis</i> , <i>C. incana</i> , <i>C. maderensis</i>	Calenduleae	MERZ 1994; SMIT 2006	Morphology, host, COI; 16S; Period; AATS; 28S	PA
			<i>Heringina guttata</i> (Fallen, 1814)	<i>Helichrysum arenarium</i>	Gnaphalieae	MOHAMADZADE & KORNEYEV 2015	Morphology, host, COI; 16S; Period; AATS; 28S	PA
			<i>H. arezoana</i> Mohamadzade & Korneyev, 2015	<i>Helichrysum arenarium</i>	Gnaphalieae	MOHAMADZADE & KORNEYEV 2015	Morphology, host, COI; 16S; Period; AATS; 28S	PA
			<i>T. posifica</i> (Loew, 1844)	<i>Onopordum</i> spp.	Cardueae	MERZ 1994	Morphology, host, COI; 16S; Period; AATS; 28S	PA
II	hyoscyami group	<i>T. acanthiophilopsis</i> Hering, 1938	<i>Cirsium canum</i> , <i>C. libanoticum</i> , <i>C. sorocephalum</i>	Cardueae	MERZ 1994; KARIMPOUR 2011; KORNEYEV 2016	Morphology, host	PA	
		<i>T. cometa</i> (Loew, 1840)	<i>Cirsium anvense</i> , <i>C. palustre</i> , <i>C. vulgare</i>	Cardueae	MERZ 1994	Morphology, host, COI; 16S; Period; AATS; 28S	PA	
		<i>T. erdemlii</i> Kütük, 2008	<i>Cirsium vulgare</i>	Cardueae	KÜTÜK 2008	Morphology, host	PA	
		<i>T. umbrosa</i> Diribek & Diribek, 1968	unknown			Morphology	PA	
		<i>T. longicauda</i> Sueyoshi, 1998	<i>Cirsium purpuratum</i>	Cardueae	SUEYOSHI 1998	Morphology, host	PA	
		<i>T. hendeliana</i> Hering, 1944	<i>Carduus nutans</i> , <i>C. thoenmeri</i>	Cardueae	MERZ 1994; KORNEYEV & KAMENEVA 1992	Morphology, host, COI	PA	
		<i>T. hyoscyami</i> (Linnaeus, 1758)	<i>Carduus acanthoides</i> , <i>C. crispus</i> , <i>C. defloratus</i>	Cardueae	MERZ 1994	Morphology, host, COI; 16S; Period; AATS; 28S	PA	
		<i>T. conura</i> (Loew, 1844)	<i>Cirsium palustre</i> , <i>C. spinosissimum</i> , <i>C. polycanthum</i>	Cardueae	MERZ 1994; KORNEYEV & KAMENEVA 1993	Morphology, host, COI; 16S; Period; AATS; 28S	PA	
		<i>T. anthrax</i> Korneyev & Evstigneev, 2019	<i>Cirsium obvallatum</i>	Cardueae	KORNEYEV & EVSTIGNEEV 2019	Morphology, host	PA	
		<i>T. carduelis</i> Hardy, 1974	<i>Carduus edelbergii</i>	Cardueae	HARDY 1974	Morphology, host	PA	
II	arnicae group	<i>T. atocoptera</i> Agarwal & Kapoor, 1988	<i>Carduus onopordioides</i>	Cardueae	AGARWAL & KAPOOR 1988	Morphology, host	OR	
		<i>T. arnicae</i> (Linnaeus, 1758)	<i>Arnica montana</i> , <i>Doronicum austriacum</i> , <i>D. grandiflorum</i> , <i>D. hungaricum</i>	Senecioneae	KORNEYEV et al. 2015	Morphology, host, COI	PA	
		<i>T. arsenii</i> Korneyev, Khaganinia, Mohamadzade, Zarghani 2015	<i>Doronicum dolichotrichum</i>	Senecioneae	KORNEYEV et al. 2015	Morphology, host, COI; 16S; Period; AATS; 28S	PA	
		<i>T. dudichi</i> Aczél, 1939	<i>Inula grandiflora</i> , <i>I. hirta</i> , <i>Telexia speciosa</i>	Inuleae	KORNEYEV 2016; MERZ 1994; MERZ 1992	Morphology, host, COI	PA	
		<i>T. kogardtauca</i> Hering, 1944	<i>Inula grandis</i> , <i>I. stenocalathia</i>	Inuleae	KORNEYEV, Karimpour & MOHAMADZADE 2015	Morphology, host, COI; 16S; Period; AATS; 28S	PA	
		<i>T. valida</i> (Loew, 1858)	<i>Inula helenium</i>	Inuleae	KORNEYEV et al. 2016	Morphology, host, COI	PA	
		<i>T. afrostriata</i> Korneyev, 2013	unknown		KORNEYEV 2013	Morphology	PA	
		<i>T. alamutensis</i> Mohamadzade & Korneyev, 2017	<i>Cousinia</i> sp. cf. <i>umbrosa</i>	Cardueae	MOHAMADZADE & KORNEYEV 2017	Morphology, host, COI	PA	

Table 4 continued.

Clade	Species Group	Species (for bold selected species sequences are given in this article)	Host plant species	Host Plant Tribe	Source	Character Evidence	Region
II	bardanae group (b. g.)	<i>T. bardanae</i> (Schränk, 1803)	<i>Arctium lappa</i> , <i>A. minus</i> , <i>A. nemorosum</i> , <i>A. tomentosum</i>	Cardueae	WHITE 1988; MERZ 1994	Morphology, host, C01; 16S; Period; AATS; 28S	PA
		<i>T. ghissarica</i> Kornejev & Kornejev, 2019	<i>Cousinia</i> sp.	Cardueae	KORNEYEV & KORNEYEV 2019	Morphology, host	PA
		<i>T. kyrgyzica</i> Kornejev & Kornejev, 2019	<i>Cousinia</i> sp.	Cardueae	KORNEYEV & KORNEYEV 2019	Morphology, host	PA
		<i>T. tridentata</i> Kornejev & Mohamadzaade, 2013	<i>Jurinea baissinensis</i>	Cardueae	KORNEYEV & MOHAMADZADE 2013	Morphology, host	PA
		<i>T. zernyi</i> Hendl, 1927	<i>Arctium minus</i>	Cardueae	MERZ 1994	Morphology, host	PA
		<i>T. admissa</i> Hering, 1961	<i>Cousinia tienshanica</i>	Cardueae	KORNEYEV 2013	Morphology, host, C01	PA
		<i>T. angulatofasciata</i> Portschiński, 1892	<i>Cousinia</i> sp.	Cardueae	KORNEYEV 2013	Morphology, host	PA
		<i>T. carneae</i> Kornejev, 2013	<i>Cousinia</i> sp.	Cardueae	KORNEYEV 2013	Morphology, host, C01	PA
		<i>T. gladius</i> Kornejev, 2013	<i>Cousinia calathidial</i>	Cardueae	KORNEYEV 2013	Morphology, host, C01	PA
		<i>T. ochroptera</i> Kornejev, 2013	<i>Cousinia refracta</i>	Cardueae	KORNEYEV 2013	Morphology, host	PA
		<i>T. robusta</i> Kornejev, 2013	<i>Cousinia</i> sp.	Cardueae	KORNEYEV 2013	Morphology, host, C01	PA
		<i>T. tatarica</i> Portschiński, 1892	<i>Alfredia nivea</i> , <i>Ancathia igniaria</i>	Cardueae	KORNEYEV 2013; SHCHERBAKOV 2013	Morphology, host, C01; 16S; Period; AATS; 28S	PA
		<i>T. pallascens</i> Hering, 1961	unknown		KORNEYEV 2016	Morphology, host, C01	PA
		<i>T. nozarii</i> Mohamadzaade, 2011	<i>Cirsium</i> sp.	Cardueae	MOHAMADZADE 2012	Morphology, host, C01; 16S; Period; AATS; 28S	PA
		III	leontodontis group	<i>T. conyzifoliae</i> Merz, 1992	<i>Crepis conyzifolia</i> , <i>C. sibirica</i>	Cichorieae	MERZ 1994; SHCHERBAKOV 2001
<i>T. crepidis</i> Hendl, 1927	<i>Crepis biennis</i> , <i>C. blattarioides</i>			Cichorieae	MERZ 1992b, 1994	Morphology, host, C01	PA
<i>T. divisa</i> Rondani, 1871	<i>Picris echinoides</i>			Cichorieae	MERZ 1994	Morphology, host, C01; 16S; Period; AATS; 28S	PA
<i>T. fallax</i> (Loew, 1844)	<i>Leontodon hispidus</i>			Cichorieae	MERZ 1994	Morphology, host	PA
<i>T. leontodontis</i> (De Geer, 1776)	<i>Leontodon autumnalis</i> , <i>L. helveticus</i> , <i>L. hispidus</i>			Cichorieae	MERZ 1994	Morphology, host, C01	PA
<i>T. mariannae</i> Merz, 1992	<i>Leontodon hispidus</i>			Cichorieae	MERZ 1994	Morphology, host	PA
<i>T. matricariae</i> (Loew, 1844)	<i>Crepis foetida</i>			Cichorieae	MERZ 1994	Morphology, host, C01	PA
<i>T. mutabilis</i> Merz, 1992	<i>Leontodon hispidus</i>			Cichorieae	MERZ 1994	Morphology, host, C01	PA
<i>T. separata</i> Rondani, 1871	<i>Picris hieracioides</i>			Cichorieae	MERZ 1994	Morphology, host, C01	PA
<i>T. simplex</i> (Loew, 1844)	<i>Crepis albidia</i>			Cichorieae	MERZ 1994	Morphology, host	PA
<i>T. truncata</i> (Loew, 1844)	<i>Leontodon crispus</i> , <i>L. incanus</i> , <i>L. tenuiflorus</i>			Cichorieae	MERZ 1994	Morphology, host	PA
<i>T. vespertina</i> (Loew, 1844)	<i>Hypochaeris radicata</i>			Cichorieae	MERZ 1994	Morphology, host, C01	PA
<i>T. dilacerata</i> (Loew, 1846)	<i>Sonchus olerensis</i>			Cichorieae	MERZ 1994	Morphology, host	PA
<i>T. formosa</i> (Loew, 1844)	<i>Sonchus asper</i> , <i>S. oleraceus</i>			Cichorieae	MERZ 1994	Morphology, host, C01	PA
III	formosa group			<i>T. kovalovi</i> Kornejev & Kameneva, 1990	<i>Sonchus paluster</i>	Cichorieae	KORNEYEV & KAMENEVA 1990
		<i>T. sanchina</i> Hering, 1937	<i>Sonchus uliginosus</i>	Cichorieae	HERING 1937	Morphology, host	PA
		<i>T. theryi</i> Ségué, 1930	unknown		KORNEYEV 2016	Morphology	PA
		<i>T. youngiana</i> Kornejev & Kornejev 2019	<i>Youngia</i> sp.	Cichorieae	KORNEYEV & KORNEYEV 2019	Morphology, host, C01; 16S; Period; AATS; 28S	PA
		<i>T. ruralis</i> (Loew, 1844)	<i>Hieracium lactuella</i> , <i>H. pilosella</i>	Cichorieae	MERZ 1994	Morphology, host, C01	PA

Table 4 continued.

Clade	Species Group	Species (for bold selected species sequences are given in this article)	Host plant species	Host Plant Tribe	Source	Character Evidence	Region
IV	pulchra group	<i>T. carmen</i> Hering, 1937	<i>Scorzonera hispanica</i>	Cichorieae	MERZ 1994	Morphology, host	PA
		<i>T. crinita</i> Hering, 1961	unknown	Cichorieae	KORNEYEV 2016	Morphology, COI	PA
		<i>T. heliophila</i> Hendel, 1927	<i>Tragopogon dubius</i>	Cichorieae	MERZ 1994	Morphology, host, COI	PA
		<i>T. hurvitzii</i> Freidberg, 1981	<i>Tragopogon longirostre</i>	Cichorieae	FREIDBERG & KUGLER 1989	Morphology, host, COI; 16S; Period; AATS; 28S	PA
		<i>T. merzi</i> Freidberg & Kütük, 2002	<i>Scorzonera kotschyi</i>	Cichorieae	FREIDBERG & KÜTÜK 2002	Morphology, host	PA
		<i>T. pulchra</i> (Loew, 1844)	<i>Scorzonera laciniata</i>	Cichorieae	MERZ 1994	Morphology, host, COI	PA
		<i>T. recurvens</i> Loew, 1869	<i>Scorzonera</i> sp.	Cichorieae	FREIDBERG & KÜTÜK 2002	Morphology, host, COI	PA
		<i>T. scorzonerae</i> Merz, 1993	<i>Scorzonera hirsuta</i>	Cichorieae	MERZ 1994	Morphology, host, COI	PA
		<i>T. arizonensis</i> Quisenberry, 1951	<i>Baccharis serotnoides</i>	Astereae	JENKINS & TURNER 1989	Morphology, host, COI; 16S; Period; AATS; 28S	NEA
		<i>T. baccharis</i> (Coquillett, 1894)	<i>Baccharis salicifolia</i>	Astereae	JENKINS & TURNER 1989	Morphology, host, COI; 16S; Period; AATS; 28S	NEA
IV	baccharis group	<i>T. californica</i> Doane, 1899	<i>Baccharis pilularis</i>	Astereae	JENKINS & TURNER 1989	Morphology, host	NEA
		<i>T. palmeri</i> Jenkins, 1989	<i>Baccharis neglecta</i> , <i>B. halimifolia</i>	Astereae	JENKINS & TURNER 1989	Morphology, host, COI	NEA
		<i>T. rufipennis</i> Doane, 1899	unknown	Astereae	JENKINS & TURNER 1989	Morphology	NEA
		<i>T. subpura</i> (Johnson, 1909)	<i>Baccharis glomeruliflora</i> , <i>B. halimifolia</i>	Astereae	JENKINS & TURNER 1989	Morphology, host, COI	NEA
		<i>T. labeacula</i> Foote, 1959	<i>Ericameria nauseosa</i>	Astereae	FOOTE et al. 1993	Morphology, host, COI; 16S; Period; AATS; 28S	NEA
		<i>T. stigmatica</i> (Coquillett, 1899)	<i>Astereae</i> spp., <i>Senecio</i> spp.	Astereae; Senecioneae	FOOTE et al. 1993	Morphology, host, COI; 16S; Period; AATS; 28S	NEA
		<i>T. angustipennis</i> (Loew, 1844)	<i>Achillea ptarmica</i>	Anthemideae	MERZ 1994	Morphology, host, COI	PA; NEA
		<i>T. bimaculata</i> Freidberg, 1981	unknown	Anthemideae	FREIDBERG & KUGLER 1989	Morphology	PA
		<i>T. brachyura</i> Loew, 1869	<i>Artemisia rufifolia</i>	Anthemideae	KORNEYEV & KAMENEVA 1993; collections	Morphology, host	PA
		<i>T. dioscorea</i> (Loew, 1856)	<i>Achillea millefolium</i>	Anthemideae	MERZ 1994	Morphology, host, COI; 16S; Period; AATS; 28S	PA
IV	angustipennis group	<i>T. hungarica</i> Hering, 1937	unknown	Anthemideae	KORNEYEV 2016	Morphology	PA
		<i>T. jabeliae</i> Freidberg, 1981	<i>Pyrethrum santolinoides</i>	Anthemideae	FREIDBERG & KUGLER 1989	Morphology, host	PA
		<i>T. luteipes</i> Merz, 1992	<i>Artemisia thuscula</i>	Anthemideae	MERZ 1992a	Morphology, host	PA
		<i>T. mesopotamica</i> Korneyev & Diribek, 2000	unknown	Anthemideae	KORNEYEV 2016	Morphology	PA
		<i>T. multiguttata</i> (Becker, 1913)	<i>Achillea</i> sp.	Anthemideae	KORNEYEV 2016	Morphology, host, COI; 16S; Period; AATS; 28S	PA
		<i>T. nebulosa</i> (Becker, 1908)	unknown	Anthemideae	MERZ 1994	Morphology	PA
		<i>T. neesii</i> (Meigen, 1830)	<i>Leucanthemum vulgare</i>	Anthemideae	MERZ 1994	Host, COI; 16S; Period; AATS; 28S	PA
		<i>T. nigricauda</i> (Loew, 1856)	<i>Anthemis anensis</i>	Anthemideae	MERZ 1994	Morphology, host, COI; 16S; Period; AATS; 28S	PA
		<i>T. rydeni</i> Hering, 1956	unknown	Anthemideae	KORNEYEV 2016	Morphology	PA
		<i>T. sahandi</i> Mohamadzade et al., 2011	<i>Achillea clypeolata</i>	Anthemideae	KHAGHANINIA et al. 2011	Host, COI; 16S; Period; AATS; 28S	PA
<i>T. spreta</i> (Loew, 1861)	unknown	Anthemideae	KORNEYEV 2016	Morphology	PA		
<i>T. stictica</i> Loew, 1862	<i>Oenanthe maritima</i>	Anthemideae	FREIDBERG & KUGLER 1989	Morphology, host	PA		

Table 4 continued.

Clade	Species Group	Species (for bold selected species sequences are given in this article)	Host plant species	Host Plant Tribe	Source	Character Evidence	Region	
IV	angustipennis group	<i>T. tanacetii</i> Hering, 1956	<i>Tanacetum vulgare</i> ; <i>T. corymbosum</i>	Anthemideae	MERZ 1994	Morphology, host, COI; 16S; Period; AATS; 28S	PA	
		<i>T. variata</i> (Becker, 1908)	unknown				Morphology	PA
		<i>T. volkovitskii</i> (Richter, 1995)	unknown					PA
		<i>T. santolinae</i> Hering, 1934	<i>Santolina chamaecyparissius</i>	Anthemideae	KORNEYEV 2016	Morphology, host		PA
		<i>T. araneosa</i> (Coquillett, 1894)	<i>Artemisia</i> sp.	Anthemideae	FOOTE et al. 1993	Morphology, COI; 16S; Period; AATS; 28S		NEA
		<i>T. candidipennis</i> Foote, 1960	<i>Tanacetum</i> spp.	Anthemideae	FOOTE et al. 1993	Morphology		NEA
		<i>T. ovatifennis</i> Foote, 1960	<i>Erigeron</i> spp.	Astereae	FOOTE et al. 1993	Morphology, COI; 16S; Period; AATS; 28S		NEA
		<i>T. leavittensis</i> Blanc, 1979	<i>Arnica</i> spp.	Senecioneae	FOOTE et al. 1993	Morphology, COI; 16S; Period; AATS; 28S		NEA
		<i>T. signatipennis</i> Foote, 1960	<i>Eurybia integrifolia</i> , <i>Machaeranthera aquaeifolia</i> , <i>M. canescens</i>	Astereae	FOOTE et al. 1993	Morphology		NEA
		<i>T. sp.1</i>	unknown				Morphology, host, COI; 16S; Period; AATS; 28S	PA
		<i>T. sp.2</i>	<i>Artemisia</i> sp.	Anthemideae	KORNEYEV collected in 2017	Morphology, host, COI; 16S; Period; AATS; 28S		PA
		<i>T. sp.3</i>	<i>Pyrethrum</i> sp.	Anthemideae	KORNEYEV collected in 2017	Morphology, host, COI; 16S; Period; AATS; 28S		PA
		<i>T. sp.4</i>	<i>Anthemis</i> sp.	Anthemideae	KORNEYEV collected in 2017	Morphology, host, COI; 16S; Period; AATS; 28S		PA
			<i>Aster</i> sp.	Astereae	KORNEYEV 2016	Morphology, host		PA
			<i>T. sauterina</i> Merz, 1994	<i>Aster alpinus</i>	Astereae	MERZ 1994	Morphology, host, COI	PA

in the tribe **Cichorieae**. Morphologically diverse members of Clade IV (BPP = 0.84) are associated with the tribes **Anthemideae** and **Astereae**, occurring in the Palaearctic and Nearctic Regions, except for *T. stigmatica*, associated with a few species of **Astereae** but primarily **Senecioneae**, and *T. hurvitzii*, which is the sister to the remainder of the clade, and represents a group of species strictly associated with host plants of the genera *Tragopogon* and *Scorzonera* (tribe **Cichorieae**).

For the dataset based on COI, phylogenetic topology obtained with Bayesian inference is shown in Figure 2, representing 64 species of the genus *Tephritis*, which is largely congruent with the phylogenetic tree based on the five-genes dataset.

Based on combined morphological characters, host plant preferences, and molecular data of both datasets (five genes and COI), Table 4 provides a species group classification for 106 described *Tephritis* species, including the 35 species used in the five-gene phylogenetic analyses and 64 used in the COI analysis. The other 38 species are placed to the groups based on morphological similarity to some of the group members or both morphological and host similarity and with the species placed in the group based on molecular analyses. Ten recognized groups of species are discussed under each of the four clades defined in the five-gene analysis.

3.2. Discussion, clades and species group recognition

3.2.1. Overview

In this study, we present phylogenetic analyses of the genus *Tephritis* inferred from two mitochondrial and three nuclear gene sequences from specimens collected in Europe, Middle East, and North America. Morphologically, the genus *Tephritis* is a homogenous, which impedes with carrying out a phylogenetic analysis based on morphological characters. For example, the male genitalia, which usually serve as a source of a good number of phylogenetically meaningful characters, are almost identical. On the other hand, body and wing coloration and patterns used for species identification are very variable and seem to be subject to frequent homoplasy.

The most widely-used morphological characters that are used to group *Tephritis* species are modifications of the aculeus shape: *leonodontis* with the deep apical notch (MERZ

1992, 1993, 1995); *pulchra* with preapical steps (FREIDBERG & KÜTÜK 2002); *formosa* with rounded blunt apex (S. KORNEYEV & V. KORNEYEV 2019); *maccus* with aculeus moderately broad and sharply tapered subapically to a short narrow apex (MOHAMADZADE et al. 2015). The monophyly of each of the above species groups based on characters not occurring elsewhere in the *Tephritis* group of genera and thus considered synapomorphies is strongly supported by their host-plant relationships, belonging to the same genus or tribe of Asteraceae, in contrast to range of wing-pattern types, which varies widely (see FREIDBERG & KÜTÜK 2002 as an example).

As has been previously shown for the Carpomyini fruit flies, the morphological and molecular phylogenies are often incongruent (SMITH et al. 2006). Thus, the morphological characters are sometimes misleading when trying to identify monophyletic groups of species, which are extremely diverse in the body coloration and wing patterns. On the other hand, the species groups within *Tephritis* are moderately supported by the association with certain host plant taxa (genera, subtribes or tribes). It corresponds well with the hypothesis that the early evolutionary events in such groups were the shifting to another, often distantly related but common and abundant host plant from an extinct host (compare with the *Rhagoletis* groups of species well supported by the host plants and molecular phylogeny vs. morphology (SMITH et al. 2006) and that ecological factors involving adaptations to and isolation of populations on certain host plants have played an important role in many cases as geographic isolation (BUSH 1969, 1992) in the evolution of frugivorous tephritids.

The five-gene molecular phylogenetic analysis shows the genus *Tephritis* (along with the species assigned to the nominal genus *Heringina* as part of the in-group) to be monophyletic (BPP=0.95). It forms a monophyletic lineage with *Trupanea*, *Goniurellia*, and *Capitites* (BPP=0.99), which corresponds to the *Tephritis* group of genera (sensu MERZ 1999); the genus *Capitites* appears here as a sister-group of the *Tephritis* (Fig. 1). This corroborates results obtained in the COI-based analysis with a wider set of taxa and partly by the morphological data (S. KORNEYEV 2016 and unpublished data).

However, in some analyses, the position of *Capitites* differs alternatively being the sister-group of the *Acanthiophilus*–*Trupanea*–*Tephritomyia* lineage (MORGULIS 2017) or of *Acanthiophilus*–*Trupanea*–*Tephritomyia*–*Tephritis* (Han, pers. comm.). Based on these results, the genus *Tephritis* can be defined as a monophyletic clade within the *Tephritis* group of genera (MERZ 1999) of the tribe Tephritini and a group of species with two pairs of frontal setae (synapomorphy (SA) of the genus), two pairs of orbital setae (symplesiomorphy (SP)), and two pairs of scutellar setae (SP), short spatulate labellum (SP), wing apex with 3 large hyaline spots separated by two dark radiate bars (“apical fork”; SP; secondarily modified in several terminal lineages); male genitalia with phallus glans widely membranous in apical half and lacking the acrophallus (SA of the *Tephritis* group of genera), membranous part of the glans mod-

erately short (not transformed into a long trunk-like membranous tube) (SP) and sclerotized basal part of the glans uniformly smooth and having neither spines, nor sclerotized appendages, nor other sclerotized sculpture (SP) (in contrast to *Dectodesis* Munro, *Austrotephritis* Hancock & Drew, *Acanthiophilus* Becker, *Trupanea*, *Euarestoides* Benjamin, *Hyalotephritis* Freidberg, and *Goniurellia*, which usually have spinulose appendages in the basal sinus of the glans). Such a definition covers the species currently not included in *Tephritis*: *Heringina guttata*, *H. arezoana*, and *Multireticula perspicillata* (Bezzi 1924), that differ only in a few characters, possibly autapomorphies, which do not contradict their possible inclusion into *Tephritis* (broad, widely dark patterned wing; occasionally setulose dorsal surface of vein R₄₊₅; partly shining or mainly yellow, black spotted abdominal tergites).

We consider them belonging in the *Tephritis* lineage as a monophyletic taxon supported both by at least a single morphological synapomorphy (2 frontal setae vs. 3 frontal setae in most genera in the *Tephritis* group), in addition to support via molecular-based phylogenetic analysis. However, formally this inclusion is to be a part of a wider forthcoming taxonomic revision.

As has been previously noted (S. KORNEYEV 2013; S. KORNEYEV & V. KORNEYEV 2019), some large complexes of species with significant characters useful for identification (e.g., the “apical fork” modified into a dark apical crossband, mushroom-like spot or two apical spots separated from remaining dark pattern) are clearly polyphyletic as shown by the current molecular-based analysis.

The species groups with monophyly supported by modifications of the aculeus tip shape are the ***leontodontis***, ***pulchra***, ***formosa*** and ***maccus*** groups, as noted above. About 1/3 of the described *Tephritis* species are not placed in any of the species groups discussed above (Table 4).

Along with that, the phylogenetic analysis based on molecular data reveals several additional monophyletic species groups based on specialization for certain host plant taxa. It concerns the *angustipennis*, *arnicae* and *valida* species groups (Fig. 1), and certain lineages in the *angustipennis* and *hyoscyami* groups strictly associated with closely related plant taxa.

3.2.2. Clade I (Fig. 1): *Heringina* and *maccus* group

Each of the three lineages represented in Clade I (Fig. 1) differ greatly from each other as well as from other species of *Tephritis*, in their wing patterns (*Heringina*, *T. maccus*), aculeus shape (*Heringina*, *T. maccus*, *T. oedipus*) or phallus glans sclerotization (*T. praecox*). Monophyly of the clade is poorly supported and needs additional investigation.

The subclade containing *Heringina* and *T. praecox* is fairly supported (BPP = 0.89) and includes two taxa morphologically different from each other and the remaining species of *Tephritis*. The nominal genus *Heringina*, with two species, represents a lineage of rhizome-bud feeding

species (V. KORNEYEV et al. 2020, in prep.) associated with *Helichrysum* (tribe **Gnaphalieae**), whereas *T. praecox* is known to have flower head feeding maggots reared from *Calendula* (tribe **Calenduleae**), a tribe closely related to **Gnaphalieae**. According to RENNWALD et al. (2015), there are repeating references to *Filago* (**Gnaphalieae**) as its additional host plant; these references can be traced down to J. MIK (1880), HENDEL (1927), MIHÁLYI (1960) unconfirmed and either based on misidentification of an undescribed species or represent a real record from an alternative host plant.

The subclade containing *T. oedipus* and *T. maccus* has moderately high support (BPP = 0.91). The **maccus group** is clearly monophyletic and supported by a unique morphological synapomorphy (aculeus moderately broad and sharply tapered subapically to a short narrow apex: Fig. 3B) it was defined in KORNEYEV & DIRLBEK (2001). The group is represented in the five gene phylogeny by *T. maccus* alone. It has a total of four extant species: *T. azari* Mohanadzade & Korneyev, 2012, *T. gharalii* Mohanadzade & Korneyev, 2015, *T. maccus* Hering, 1937, and *T. urelliosomima* Korneyev & Dirlbek, 2001; plus one extinct fossil species, *T. sophus* Gentilini & Korneyev, 2006 (upper Miocene; the only fossil record of *Tephritis* (GENTILINI et al. 2006)). Detailed information about the group morphology and distribution is given in MOHAMADZADE & S. KORNEYEV (2012) and MOHAMADZADE et al. (2015). No data on the host plants of the species of the **maccus group** are known, except a sample of *T. sp. cf. maccus* swept in a stand of *Lactuca scariola*, its possible host plant. As the larvae of *T. oedipus* feed in flower heads of *Lactuca tatarica* (tribe **Cichorieae**), these data could support a common plant genus for the *T. oedipus* + *T. maccus* lineage and their sister-group relationship.

Tephritis praecox, *T. oedipus*, *T. maccus* group spp. and *Heringina* spp. have aberrant wing patterns, aculeus shape and / or sclerotization of phallus glans compared to the rest of *Tephritis* species, and thus each can be considered to be its sister-group, but neither the morphological data, nor molecular phylogeny do not resolve polytomies neither for separation them to genus-group taxa, nor for lumping them (including synonymization of *Heringina* and *Tephritis*).

3.2.3. Clade II (Fig. 1): *hyoscyami*, *arnicae*, *valida*, and *bardanae* groups

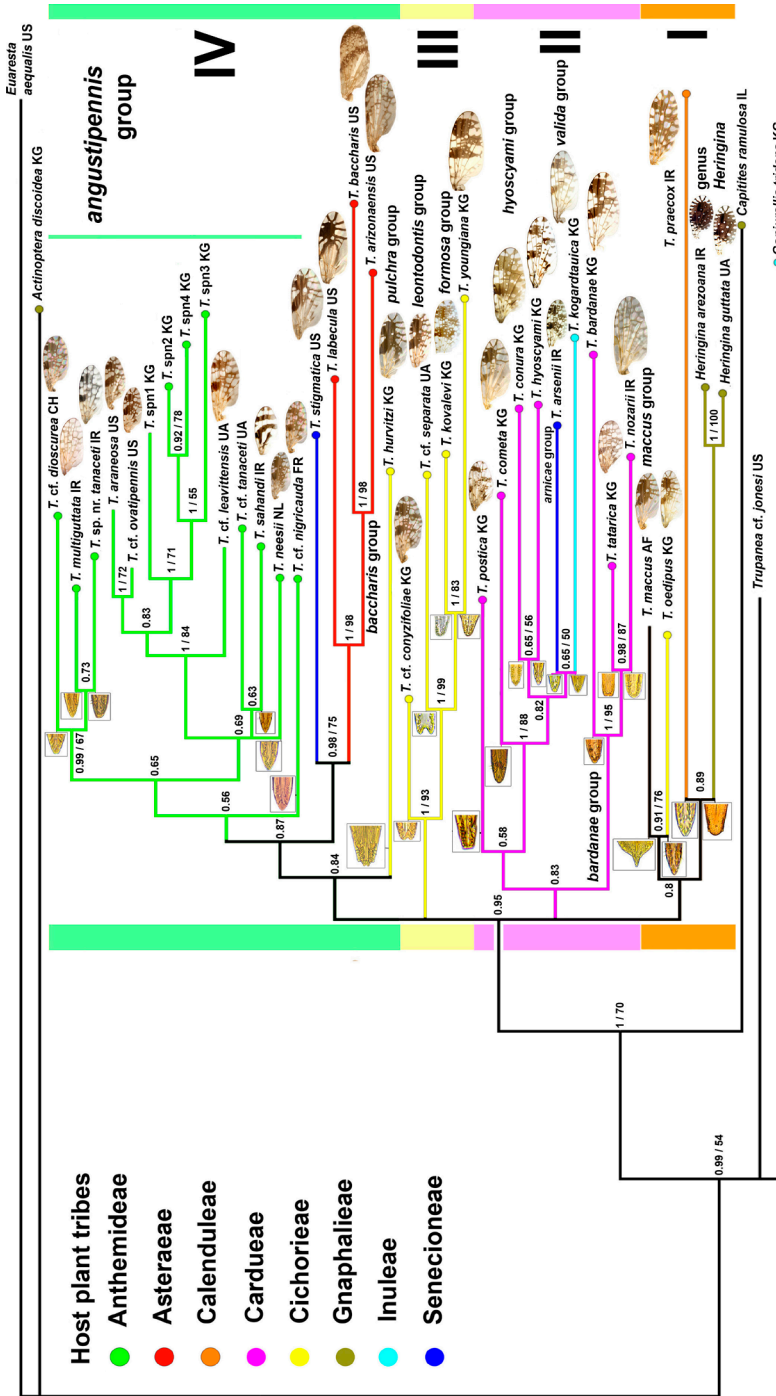
Clade II corresponds to the **hyoscyami species group** (sensu MERZ 1995). The original definition was based on two characters believed to be synapomorphies: oviscape basally white setulose and “wing pattern with two narrow rays along the apical portion of veins r_{4+5} and m_{1+2} , giving a starshaped appearance”. He noticed that this group may be further divided into two monophyletic subgroups, each with two species-groups (MERZ 1995). The morphology-based monophyly of this group has not been ever demonstrated (the first character is present in most outgroups and the second is hardly applicable to

all the diversity of wing patterns). In molecular-based phylogenies, this lineage has the weakest support of the four clades defined within *Tephritis* in the molecular phylogeny (BPP = 0.83). Most species within Clade II are associated with thistles (tribe **Cardueae**) showing no morphological synapomorphies. Clade II includes two well-supported monophyletic subclades within.

The **first subclade** includes *Cirsium*- and *Carduus*-associated species along with two species with non-*Cardueae* hosts. The **Cardueae** associated species: *T. cometa*, *T. conura*, and *T. hyoscyami* share no morphological synapomorphies; each of these lineages represents several morphs or host races currently considered conspecific, but showing very small differences in their mitochondrial COI sequences: 1) *T. cometa* + *T. acanthiophilopsis* lineage; 2) *T. conura* + unnamed host races (SEITZ & KOMMA 1984; ROMSTOCK & ARNOLD 1987; DIEGISSER 2005); 3) *T. hyoscyami* + *T. hendeliana*. We consider these three lineages corresponding to the **hyoscyami species group** sensu MERZ (1995). Additional species closely related to them, similar morphologically and also associated with *Cirsium* and *Carduus*, namely *T. anthrax*, *T. atocoptera*, *T. campana*, *T. cardualis*, *T. erdemlii*, and *T. umbrosa* are to be included in this group (S. KORNEYEV & EVSTIGNEEV 2019). *T. longicauda* Sueyoshi feeding in *Cirsium* flower heads in the Eastern Palearctics show “intermediate” characters of *T. cometa* and *T. conura* (V. KORNEYEV 1995; V. KORNEYEV & OVCHINNIKOVA 2004) and may also belong in this group.

Both the **hyoscyami species group** and the **first subclade** appear to be paraphyletic, for the next two, “non-thistle”, groups are nested within them. 1) *Tephritis kogardtauca*, *T. valida*, and *T. dudichi* closely related according to the COI tree (Fig. 2), as well as 2 undescribed new species, all feeding in flower heads of Inuleae, and form the **valida group**. 2) *Tephritis arsenii* and *T. arnicae* infesting **Senecioneae** plants form the **arnicae group** (supported by the COI tree, Fig. 2). Species of both groups share the wide, subrectangular spots at apices of veins R_{4+5} and M_{1+2} , usually separated from the dark wing pattern, with each other and *T. hyoscyami* + *T. hendeliana* species that may also support their closer relationships. Five-loci analysis reveals possible monophyly of the *T. kogardtauca* + *T. arsenii* lineage, but its support is low (BPP = 0.65) and dubious. Moreover, in the COI analysis, the **arnicae group** appears to be related much closer to *T. ruralis*, the species showing strong morphological resemblance with *T. arsenii* and *T. arnicae*, but feeding in the Cychorieae.

Monophyly of the **second subclade** of Clade II (*T. bardanae* + *T. tatarica* + *T. nozarii* and their closest relatives) was revealed by both analyses to include species very diverse morphologically but mostly associated with *Cousinia*, a vast paraphyletic genus with burdocks (*Arctium*) nested within it. Monophyly of the **bardanae group** defined herein and corresponding to this lineage is supported by the results of the COI-based phylogenetic analysis to include *T. bardanae* and *T. alamutensis* sister taxa in the COI tree (with morphologically similar



↑ Fig. 1. Phylogram based on data from two mitochondrial genes (COI, 16S) and three nuclear genes (ribosomal 28S, protein coding Period and AATS) as recovered by Bayesian inference and Maximum Likelihood. Support values are recorded on each node as Bayesian posterior probability and maximum likelihood bootstrap percentages PP/BP. Roman numerals indicate major clades discussed in the text. Host plant associations are given as colored circles. — *Abbreviations* of Countries: AF – Afghanistan; CH – Confoederatio Helvetica (Switzerland); FR – France; IR – Iran; KG – Kyrgyzstan; NL – The Netherlands; UA – Ukraine; US – United States; AZ – Arizona; CA – California; MD – Maryland; TX – Texas.

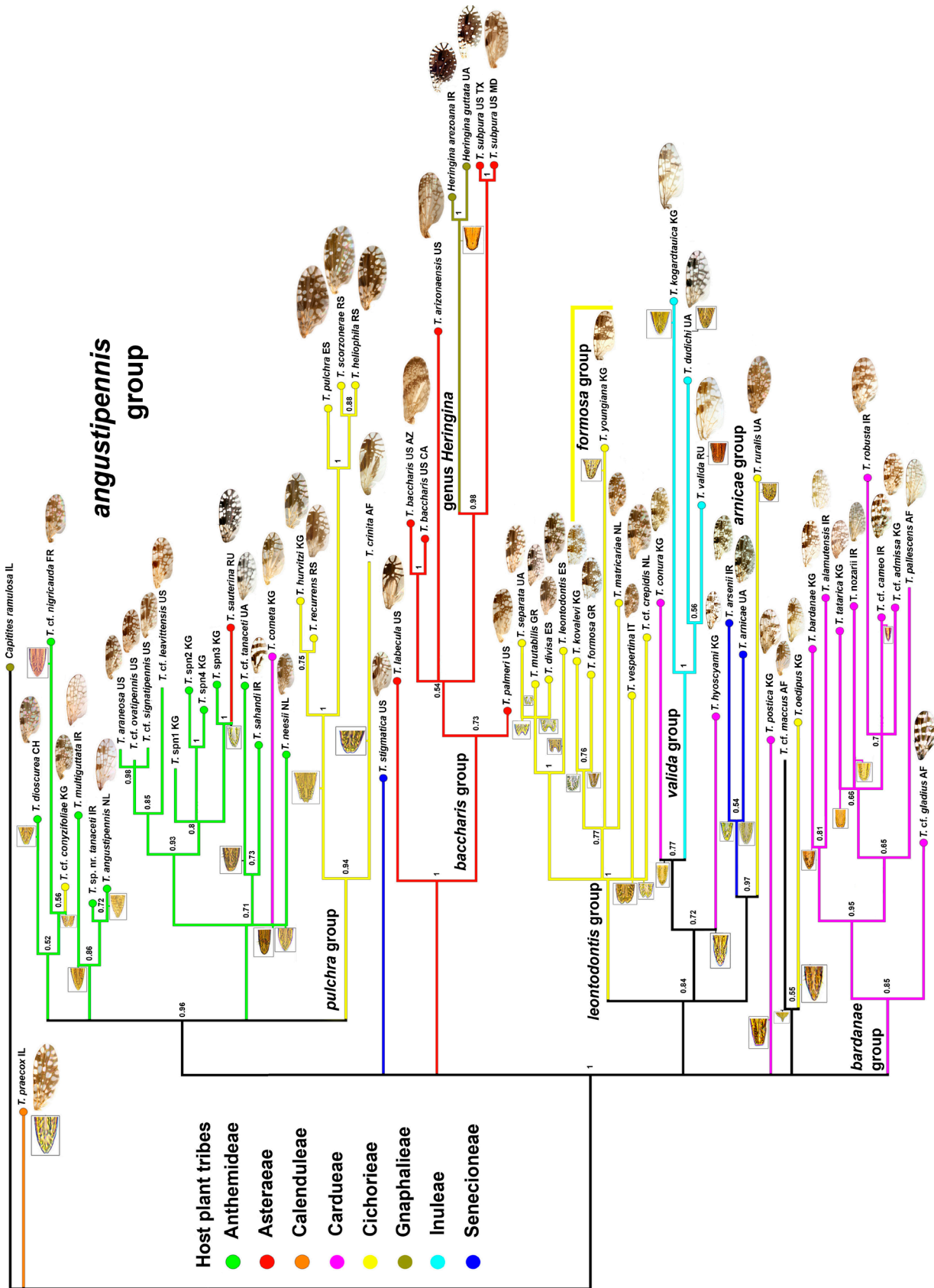
↓ Fig. 2. Phylogram based on data from one mitochondrial gene COI as recovered by Bayesian inference. Support values are recorded on each node as Bayesian posterior probability PP. Host plant associations are given as colored circles. — *Abbreviations* of Countries and States: AF – Afghanistan; CH – Confoederatio Helvetica (Switzerland); ES – Spain; FR – France; GR – Greece; IL – Israel; IR – Iran; IT – Italy; KG – Kyrgyzstan; NL – The Netherlands; RU – Russia; RS – Serbia; UA – Ukraine; US – United States; AZ – Arizona; CA – California; MD – Maryland; TX – Texas.

T. zernyi, *T. ghissarica* Korneyev & Korneyev, *T. kyrgyzica* Korneyev & Korneyev, *T. ochracea*, and *T. afrostriata*). The **bardanae group** also includes *T. tatarica* and morphologically similar related species: *T. admissa*, *T. cameo*, *T. gladius*, and *T. robusta*, which infest *Cousinia* and share a synapomorphy: a short apical crossband on the wing apex, which does not occur in the outgroups (S. KORNEYEV 2013).

On the COI tree, the lineage corresponding to the latter assemblage also includes *T. pallescens* and *T. nozarii*, the two species with a very different, pale grid-like wing patterns; their topological position inside the lineage is poorly supported (BPP of lineages inside < 0.7), vague,

and hardly contradicting their possible basal position (Fig. 2). Their host-plant associations are unknown; at most *T. nozarii* was reported to be swept from *Cirsium* (MOHAMADZADE 2012), which is not necessarily its host plant. On the five-gene tree *T. nozarii*, forms a monophyletic lineage with *T. tatarica* (BPP=0.98).

The last ungrouped species also belonging in the Clade II, is *T. postica*, which appears in an unresolved basal polytomy in the COI-based phylogram and a sister taxon to the **hyoscyami species group** but with a low support). It is associated with various species of the genus *Onopordum* (Cardueae), which also supports its placement in the Clade II.



Judging from the host-plant preferences alone or also from the wing pattern, *T. tridentata* S. Korneyev et Mohamadzade Namin, 2013, an unplaced species associated with *Jurinea* (Cardueae) and having the spots at apices

of veins R_{4+5} and M_{1+2} , isolated from the remaining dark wing pattern, may also belong to this clade; as soon as no DNA sequences are available, we place it here provisionally.

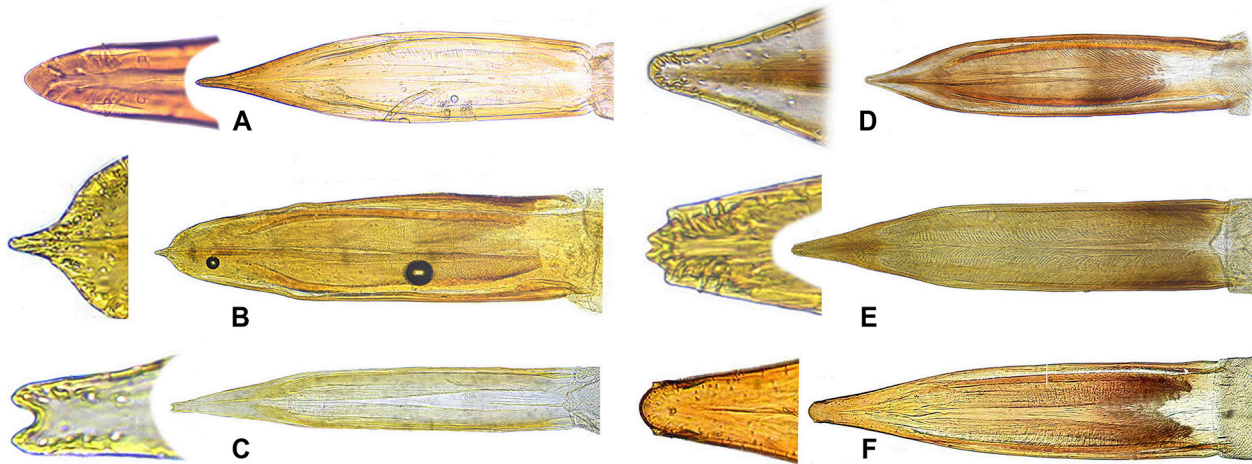


Fig. 3. Morphological synapomorphies of *Tephritis* species groups (modifications of the aculeus tip shape). **A:** common aculeus shape for *Tephritis* (*T. nigricauda*); **B:** *maccus* group: aculeus sharply tapered subapically to a short narrow apex (*T. maccus*); **C:** *leontodontis* group: notched tip of the aculeus (*T. separata*); **D:** *formosa* group: aculeus subapically poorly sclerotized and apically narrowed and rounded (*T. formosa*); **E:** *pulchra* group: aculeus with pair of subapical steps (*T. hurvitzi*); **F:** *Heringina*: aculeus tip rounded with pair of steps on sides (*H. guttata*).

3.2.4. Clade III (Fig. 1): *leontodontis* and *formosa* groups

This clade has a high support in the five-gene tree (BPP = 1), but the species included here share no synapomorphies. They all are associated with host plants of the tribe **Cichorieae** (mainly *Sonchus*, *Crepis*, *Picris* or closely related genera). The four species included in the five gene analysis represent two species groups with high support (BPP = 1) also in the COI analysis.

MERZ (1995) defined the **leontodontis group** as having aculeus apically not evenly rounded (with steps or indentations, both states absent in the other *Tephritis* or in the outgroups). This multistate character cannot be considered a single synapomorphy; instead, the aculeus tip shape provides several modifications as synapomorphies of more restricted lineages considered below.

The **leontodontis group**, as defined here, includes *T. crepidis*, *T. conyzifoliae*, *T. leontodontis*, *T. divisa*, *T. separata*, *T. matricariae* (Loew), *T. mutabilis* and based on morphological data and host-plant preferences, also *T. mariannae*, *T. simplex* (Loew), and *T. truncata*. These species share at least one morphological synapomorphy not occurring elsewhere in the *Tephritis* group of genera, the deeply notched tip of the aculeus (Fig. 3C) (MERZ 1995) and the group is strongly supported (BP=1) in the COI analysis (Fig. 2). In the five-locus analysis, the **leontodontis group** is represented by *T. conyzifoliae* and *T. separata*, supporting its close relationship to the following group (Fig. 2).

Position of *T. frauenfeldi* Hendel, which has the wing pattern very similar to *T. leontodontis*, and the aculeus with shallow apical notch, but associated with *Jurinea* (Cardueae), remains unclear, as no DNA sequences are available.

The **formosa group**, as defined here, includes five or six species with at least one synapomorphy: the subapically poorly sclerotized (not occurring elsewhere in the

Tephritis group of genera) and apically narrowed and rounded aculeus (Fig. 3D). *T. dilacerata*, *T. formosa*, *T. kovalevi*, and *T. sonchina* have the oviscape entirely covered by brown setulae, whereas *T. youngiana* Korneyev & Korneyev, 2019 has a white-setulose oviscape and is believed to be the sister-group to the other four species, which also share association with flower heads of *Sonchus*, whereas *T. youngiana* is associated with *Youngia* (sometimes considered a synonym of *Crepis*). Monophyly of *T. formosa* + *T. kovalevi* + *T. youngiana* lineage is partly supported by the COI analysis (Fig. 2; BI = 0.77), with unresolved basal polytomy, which involves also morphologically different *T. matricariae* (Loew), here placed to the **leontodontis group**. The **formosa group** provisionally includes a strictly endemic, little-known *T. theryi* Séguy from Morocco, which is believed to be closely related to *T. formosa*.

3.2.5. Clade IV (Fig. 1): *pulchra*, *baccharis* and *angustipennis* groups

This clade has moderate support (BPP = 0.84) and contains two major lineages, which correspond to the groups considered below.

The **pulchra group** (MERZ 1993; FREIDBERG & KÜTÜK 2002) corresponds to the *T. hurvitzi* lineage in this analysis. It has been established based on two morphological synapomorphies (oviscape with brown setulae only; aculeus with pair of subapical steps, both states not occurring elsewhere in the *Tephritis* group of genera (Fig. 3E) and includes *T. recurrens*, *T. hurvitzi*, *T. heliophila*, *T. pulchra*, *T. scorzonerae*, and *T. crinita* (a monophyletic clade supported by a neighbour-joining analysis based on COI (SMIT et al. 2013), the COI analysis in this study (BI 0.94) (Fig. 2), and morphology: aculeus tip shape), and also *T. carmen* and *T. merzi*. All the species except *T. crinita* (whose biology is unknown) induce communal flowerhead or stem galls

in closely related *Scorzonera* and *Tragopogon* plants (tribe **Cichorieae**).

The other subclade has moderately high support (BPP = 0.87), containing a number of poorly supported lineages, represented by species associated mainly with the tribes **Anthemideae** and **Astereae**.

The **baccharis group** defined by JENKINS & TURNER (1989) is represented in this study by four morphologically diverse species (forming a well-supported subclade (BPP = 0.98) in the Nearctic Region. This group includes *T. arizonaensis*, *T. baccharis*, *T. californica*, *T. palmeri*, *T. rufipennis*, and *T. subpura* (JENKINS & TURNER 1989). It is apparently a strictly monophyletic group represented by the species are associated with hosts in the genus *Baccharis* (tribe **Astereae**) and restricted in distribution to the Nearctic Region, but having no obvious synapomorphies. The COI-based analysis (Fig. 2) shows that the lineage represented by *T. arizonaensis* and *T. baccharis* also includes closely related *T. palmeri* and *T. subpura*; of them, *T. arizonaensis*, *T. californica*, and *T. palmeri* have an extremely short and wide “apical fork” in the wing pattern, *T. baccharis* and *T. rufipennis* possess a further modified “apical dark”, but the wing pattern in *T. subpura* has a wing pattern with more typical apical fork. Species in this group sometimes have additional white frontal setae. The sister-lineage for the **baccharis group** is the Nearctic *T. labecula*, feeding in *Ericameria* (also the tribe **Astereae**), but having a wing pattern strongly resembling those of *T. crinita*, *T. hurvitzii* and *T. merzi* of the **pulchra group**. Furthermore, *T. stigmatica*, sister to the rest of the species in the **baccharis group**+ *labecula* lineage, has a similar wing pattern with a distinct stellate pattern connected to the pterostigma by a broad band, and feeds in the flower head or stem galls of various *Senecio* (tribe **Senecioneae**) (NOVAK et al. 1967; GOEDEN 1988).

In the COI analysis, this lineage unexpectedly contains *Heringina* with two species of predominantly Palaearctic Middle East distribution and non-related hosts, which looks extremely unlike and resulted from the method error.

The remaining species in Clade IV in the 5 gene analysis form the **angustipennis group** (defined here), which comprises mainly smaller species (WL = 2.7–4.0 mm) associated with plants of the tribes **Anthemideae**, **Astereae**, and occasionally **Senecioneae**. Species in this group have similar grid-like wing patterns having two, three, or one large, often subrectangular hyaline spots in cells r_1 , r_{2+3} and r_{4+5} . Monophyly of this clade has very low support on the five gene tree (BPP = 0.56), but the morphology and host plant preferences support this theory of close relationship. In the COI-based analysis it shows paraphyly, with the **pulchra group** nested in it, and an unresolved basal polytomy.

The species associated with various *Achillea*, *Tanacetum* and possibly *Artemisia* (tribe **Anthemideae**) here considered **angustipennis group** with *T. angustipennis*, *T. hungarica*, *T. rydeni*, *T. nebulosa*, *T. brachyura*, *T. dioscorea*, *T. tanacetii*, and *T. multiguttata*, show no evident morphological synapomorphies, except possibly

small size (see above), short aculeus and the cell r_1 with 2 hyaline spots. Among all the species of the genus, *T. angustipennis* has a circumboreal distribution from Europe through Siberia to Alaska, Canada, and south to Colorado in the USA (FOOTE et al. 1993).

In the five-gene analysis, this group is represented by the three latter species, which form a monophyletic subclade (BPP = 0.99), but the other species also associated with *Achillea* and closely related *Tanacetum*, as *T. sp. nr. tanacetii* and *T. sahandi*, both are not pulled in this lineage, staying in an basal set of taxa with low support or “almost unresolved basal polytomy”.

Another part of this group also includes the species either morphologically similar or poorly recognizable from *T. nigricauda* or associated with *Leucanthemum* and related genera of the **Anthemideae**. In the five-gene and COI-based analyses they are represented by *T. sp. nr. nigricauda* and three additional undetermined species mentioned by SMIT et al. (2013). These species usually have a wide medial dark bar in cell cua , wide spots at the apices of veins R_{4+5} and M_{1+2} usually fused with each other and the remaining dark pattern, and a moderately short oviscap (at most as long as the 3 posteriormost exposed abdominal tergites). Additionally, *T. bimaculata*, *T. spreata*, *T. jabeliae*, and *T. mesopotamica* may also belong here. Despite their strong morphological similarity, species of this group show considerable genetic diversity, even falling into different lineages and giving the appearance of paraphyly of the group.

The position of *T. neesii*, which also feeds in *Leucanthemum*, appears to be basal to this and the following lineage (SMIT et al. 2013; S. Korneyev unpublished data).

A clade which includes *T. araneosa*, *T. leavittensis*, and *T. ovatipennis* from the Nearctic Region and at least four undescribed new species from the Central Asian mountains of the Palaearctic Region appears, on the contrary, to be strictly monophyletic, mostly **Astereae**-associated and nested among the **Anthemideae**-associated species. Two of the undescribed species were swept from **Astereae** (*Aster*, *Erigeron*, *Chrysothamnus*) at 2500–3500 m a.s.l. They mostly share blackish leg coloration, dark wing pattern, short oblique hyaline crossband distal to vein R_1 apex, shining black tergite 6 and oviscap of female covered entirely by black setulae. However, none of these characters occurs in all the species and thus can be considered a synapomorphy to determine this group as a whole. We tentatively place other species into this group based on their morphological similarity, their host association, or on COI molecular data, including the Nearctic *T. candidipennis* and *T. signatipennis*, and possibly also the Palaearctic *T. corolla* and *T. sauterina*, the latter species infesting flower heads of *Aster alpinus* (tribe **Astereae**).

The poor resolution and high polytomy in this clade requires further studies and explanation. We can speculate if it may reflect rather recent evolutionary events, such as a rapid radiation following Pleistocene glaciation. This hypothesis is indirectly supported by the fact that Clade IV is the only part of the genus that has sub-

clades of either Holarctic or strictly Nearctic distribution, which could be formed by Trans-Beringean migration of ancestral populations.

3.2.6. *Tephritis* incertae sedis

Most species of *Tephritis* in the analysis are here assigned to ten species groups: *angustipennis*, *arnicae*, *baccharis*, *bardanae*, *formosa*, *hyoscyami*, *leontodontis*, *maccus*, *pulchra*, and *valida*. However, several remain unplaced: *T. labecula*, *T. postica*, *T. stigmatica*, *T. oedipus*, *T. praecox*. Similarly, the species here assigned to *Heringina* are not forming a sister group to *Tephritis* and future studies have to consider whether *Tephritis* and *Heringina* are synonyms. These studies should also include *Austrotephritis*, *Capitites*, *Dectodesis*, *Heringina* and address the status of *Tephritis praecox*. About 70 species remain poorly known or unavailable for study and have neither been analyzed nor placed into the any of species groups discussed here.

4. Conclusions

One hundred and six species of the genus *Tephritis* are placed in ten species groups (Table 4), based on morphological, ecological or molecular features, whereas the remaining species (about 70) have not been placed into the any of species groups yet, as they remain poorly known or unavailable for study. Future efforts will focus on increasing sampling density, and obtaining representative specimens from geographically distant and biologically different populations and species. With these in hand, molecular phylogenetic analysis in the context of morphology and host plant use should clarify hitherto unresolved issues of the taxonomy of the genus *Tephritis* and related taxa such as *Austrotephritis*, *Capitites*, *Dectodesis*, *Heringina* and the status of *Tephritis praecox*.

5. Acknowledgements

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Authors' contributions

All work in molecular lab was done by S. Korneyev under supervision and support of J. Smith and with assistance of D. Hulbert. DNA was extracted from specimens collected in 2004–2017. Most of the specimens were collected in Eastern Europe and Middle Asia (S. Korneyev and V. Korneyev), Western, Southern Europe and Israel (J. Smit). Material from North America is kindly provided by A. Norrbom and S. Gaimari. Analysis was done by S. Korneyev under supervision of D. Hulbert, article was written by S. Korneyev and significantly improved by all coauthors.

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File 1: korneyev&al-tephrisphylogeny-asp2020-electronic-supplement1 — Nexus file with COI, Period, AATS, 16S and 28S sequences for 5 gene tree shown on Fig. 1.

File 2: korneyev&al-tephrisphylogeny-asp2020-electronic-supplement2 — Nexus file with COI sequences for COI tree shown on Fig. 2.