

The genome of *Istocheta aldrichi* (Diptera: Tachinidae), a parasitoid of the Japanese beetle, *Popillia japonica* (Coleoptera: Scarabaeidae)

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Istocheta aldrichi Mesnil 1953 (Diptera: Tachinidae) is native to Japan and has recently become an important biological control agent of the Japanese beetle, *Popillia japonica* (Coleoptera: Scarabaeidae), a pest with >300 host plants, including roses, linden trees, and numerous agricultural crops. During the past decade, *I. aldrichi*'s range has greatly expanded across North America, particularly in Quebec and Ontario, Canada, and in the Midwest United States. In Minnesota, parasitism of Japanese beetles by *I. aldrichi* was documented in commercial apple orchards in 2021 and has since spread to multiple locations, highlighting its importance as a natural enemy. To facilitate research on *I. aldrichi* and other tachinid flies, we present a haploid reference genome generated from a single unsexed individual. The final genome assembly is 875.3 Mbp, contained in 1,041 scaffolds, with an N50 of 4.77 Mbp, and 99.5% complete Diptera BUSCOs present. We also present a complete mitogenome and use comparative genomics across 19 tachinid species to identify unique features of *I. aldrichi*. Specifically, we find that tachinids as a whole have undergone rapid copy number changes in 935 gene families, largely related to metabolism and morphogenesis. While many tachinid lineages have experienced contractions in gene families, *I. aldrichi* is characterized by a relatively high number of gene family expansions, many of which are predicted to function in metal ion transport. The *I. aldrichi* reference genome will further research opportunities on these parasitic flies, including their potential for biocontrol of *P. japonica*.

Keywords: parasitism; parasitic fly; biological control; tachinid; comparative genomics; genome assembly

Introduction

The parasitic fly, *Istocheta aldrichi* (Fig. 1a), is a member of the family Tachinidae: one of the largest families in the order Diptera (true flies) and the largest family of parasitoids outside of Hymenoptera (Stireman III et al. 2006, 2019). As is characteristic of parasitoids, tachinids complete their development as parasites in or on a host but are free-living as adults. The subfamily to which *I. aldrichi* belongs, Exoristinae, primarily consists of parasitoids of caterpillars (Stireman III et al. 2006). However, within the Exoristinae tribe Blondeliini, there have been a suite of shifts to diverse and distantly related orders of hosts (Stireman III et al. 2019). As a specialist parasitoid of the Japanese beetle (*Popillia japonica*, Coleoptera: Scarabaeidae), *I. aldrichi* is one such example. Compared to other tachinids with small eggs (microtype), *I. aldrichi* is known for its characteristic oviposition of large, macrotype, spherical white eggs placed on the pronotum ("back") of *P. japonica* (Fig. 1b) (Pelletier et al. 2023). Also known as the "Winsome fly," the species is oviparous, endoparasitic, and is known for superparasitism, where up to 8 eggs may be oviposited on a single beetle (Gagnon et al. 2023; Pelletier et al. 2023).

Popillia japonica is an invasive pest that was first detected in the United States in 1916 and can damage over 300 plants (Clausen et al. 1927; Shanovich et al. 2019). Since invading, the beetle has

spread throughout the eastern United States (Althoff and Rice 2022), with additional detections in several western states, and British Columbia, Canada—often prompting eradication efforts (Zhu et al. 2023; Makovetski and Abram 2024). Moreover, beginning in 2014, *P. japonica* was detected in Italy (Pavesi 2014; Gotta et al. 2023), with subsequent establishment in Switzerland (Graf et al. 2023). Early in the invasion process, eradication and crop protection relied heavily on pest trapping and insecticide use (Santoemma et al. 2021; Venette and Hutchison 2021). However, for long-term sustainability, biological control, including the conservation or release of natural enemies, continues to be one of the most promising alternatives to chemicals for managing *P. japonica* (Althoff and Rice 2022; Abram et al. 2024; Brodeur et al. 2024).

As part of a classical biocontrol program in the 1920s, *I. aldrichi* was identified in Japan and released in several northeastern US states for *P. japonica* control (Clausen et al. 1927; Fleming 1968). Among the many parasitoid species released against *P. japonica*, *I. aldrichi* was one of the primary agents that successfully established and became widespread (Clausen et al. 1927; Fleming 1968). The recent range expansion of *I. aldrichi* in North America also portends considerable biocontrol potential (Gagnon et al. 2023; Hutchison et al. 2024; Makovetski and Abram 2024). For example, in Quebec, Canada, total seasonal parasitism rates ranged from 3.2% to 27.3% across 8 locations (Gagnon et al. 2023).

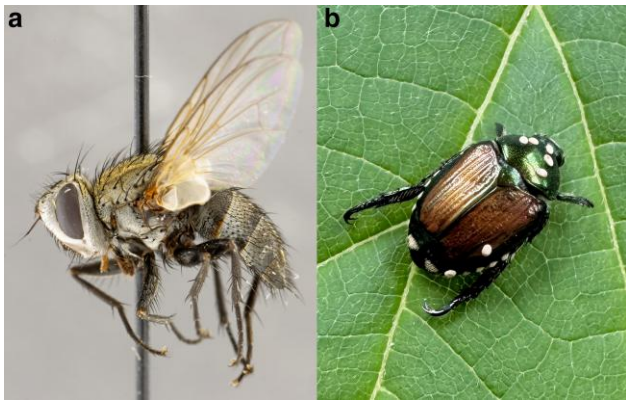


Fig. 1. *Istocheta aldrichi*. a) Female *I. aldrichi* (Canadian National Collection of Insects specimen ID CNC1711728). Image provided by the Canadian National Collection of Insects, Arachnids, and Nematodes (CNC), ©His Majesty The King in Right of Canada, as represented by the Minister of Agriculture and Agri-Food, licensed under the Open Government Licence—Canada. b) *I. aldrichi* eggs laid on the dorsum of its host, *Popillia japonica*. There are 5 eggs placed on the beetle's pronotum (the typical oviposition location), and 2 additional eggs present on the right elytra (considered “misplaced”). Photo credit and permissions: Ellie R. Hutchison Cervantes.

Furthermore, there is recent interest in introducing *I. aldrichi* to Europe for biological control of *P. japonica* (CABI 2021). *Istocheta aldrichi* exhibits several life history traits that are advantageous for biocontrol, including: (i) a tendency for high parasitism rates at low host densities, suggesting efficient searching behavior by females (Shanovich et al. 2021), (ii) rapid mortality of host beetles following egg hatch of the fly (death within 5 to 7 d), and (iii) that parasitized beetles stop feeding within 3 to 5 d of parasitization, which may help reduce defoliation and crop injury (Clausen et al. 1927; Brodeur et al. 2024; Hutchison et al. 2024). Additionally, Makovetski et al. (2025) recently examined thousands of crowd-sourced observations of parasitoid oviposition on Scarabaeidae species and concluded that the incidence of nontarget attacks by *I. aldrichi* is likely negligible as a risk to other Scarabaeidae species.

Here, we provide a reference genome for *I. aldrichi*: the first available for any species in the tribe Blondeliini. As *I. aldrichi* continues to expand in range across North America, the parasitoid offers many biocontrol attributes that should facilitate a growing impact on one of the most damaging invasive pests, *P. japonica*. The genome sequence will provide a research base to assist with (i) evaluating biological characteristics, such as overwintering ability and diapause biology, (ii) understanding the population genetics related to *I. aldrichi* establishment, (iii) generating tools for accurate identification and monitoring, and (iv) more broadly, improving our understanding of tachinid evolution.

Materials and methods

Species origin and sampling strategy

Istocheta aldrichi pupae were obtained from parasitized *P. japonica* beetles that had been field collected 14 d prior, from the foliage of wild grapes (*Vitis vinifera*), in Shoreview, Minnesota, United States (45.1321 N, −93.11875 W), July 20, 2024, following published sampling procedures (Gagnon and Giroux 2019; Shanovich et al. 2021). This is the peak period of *I. aldrichi* activity in southern Minnesota (Hutchison et al. 2024), when the beetles are abundant, and beetles with eggs on their pronota are common. As noted by Brodeur et al. (2024), no other tachinid species to date, with similar

oviposition behavior or egg shape, have been observed ovipositing on *P. japonica* adults in North America. Additionally, the high host specificity of *I. aldrichi* on *P. japonica* was recently supported (Makovetski et al. 2025). The species was also verified via the mitochondrial COX1 barcode (see below).

A cohort of 20 beetles, all having at least one characteristic *I. aldrichi* egg deposited on their pronota (Fig. 1b), were placed individually in 475 ml plastic, ventilated cups, at 22 °C and 16:8 (light:dark). Rearing cups were provisioned with fresh grape leaves for beetle nutrition (leaves changed daily), and moist filter paper for humidity. Although superparasitism (i.e. multiple parasitoid eggs deposited in or on a single host) by *I. aldrichi* is common, for the vast majority of cases, only one parasitoid larva successfully develops within the host's thorax/abdomen (Clausen et al. 1927; Pelletier et al. 2023). At 14 to 20 d post-collection, the *I. aldrichi* larvae had either exited the host cadaver to pupate or had pupated inside the host. Within 24 h after pupation, a total of 6 *I. aldrichi* pupae that had exited the host to pupate were collected and transferred to a −80 °C freezer prior to DNA extraction. A single random pupa of unknown sex was selected for sequencing.

Sequencing methods and sample preparation

We extracted DNA from a single pupa that had been rinsed with nuclease-free water using the Qiagen MagAttract kit following the manufacturer's protocols. DNA was concentrated to 25 µL using Sergi Lab Supplies magnetic beads and the PacBio SRE kit was used to deplete fragments shorter than 10 kb. The sample was barcoded, library prepped with the ONT SQK-NBD114.24 kit, and sequencing was performed on an Oxford Nanopore P2 Solo instrument on a single flowcell (v.10.4.1). Libraries were recovered, and flowcells were flushed with nuclease (EXP-WSH004 kit) prior to reloading every 24 h. Data were basecalled using dorado v.0.7.3 and basecalling model dna_r10.4.1_e8.2_400bps_sup@v5.0.0 (<https://github.com/nanoporetech/dorado>).

Nuclear genome assembly, curation, and quality control

Full details and code for all bioinformatics steps are available in Supplementary File 1. After sequencing, reads were further processed with “dorado correct” V.0.8.3 + 98456f7 (<https://github.com/nanoporetech/dorado>) and used for generating a primary assembly with Hifiasm v.0.19.9 (Cheng et al. 2021). The primary assembly was scaffolded using 3 rounds of ntLink v.1.3.11 (Coombe et al. 2023) with gap filling. Contamination screening and removal were performed with Blobools v1.1.1 (Challis et al. 2020) and both NCBI Foreign Contamination Screens: (i) FCS-adaptor to remove adaptor contamination, and (ii) the FCS-GX Genome Cross-Species Aligner (Astashyn et al. 2024) with the taxonomic ID NCBI:txid2500616 (*I. aldrichi*). Purge_dups v1.2.5 was used to remove redundant haplotigs and overlaps from the genome assembly (Guan et al. 2020). Genome completeness was assessed with Compleasm v0.2.6 (Huang and Li 2023), which scored assemblies against the Diptera_odb10 database of 3,285 benchmarking single-copy orthologs (BUSCOs) and Merqury v1.3 (Rhie et al. 2020).

Repeat assembly techniques

Repeat families were identified de novo using RepeatModeler v2.0.1 (Flynn et al. 2020). RepeatMasker v4.1.1 (Tarailo-Graovac and Chen 2009) was used to soft mask genomes with the de novo generated repeat libraries using slow search mode.

Table 1. Genomes used in comparative analyses.

Accession	Species	Clade ^a	Genome size (Mbp)	Host(s)	Completeness ^b
GCF_958450345.1	<i>Calliphora vicina</i>	Family Calliphoridae	706.5	N/A (Sivell 2024)	97.17
GCA_943735925.1	<i>Pollenia amentaria</i>	Family Polleniidae	1,270.7	N/A (Falk et al. 2023)	93.67
GCA_963932375.1	<i>Phania funesta</i>	Phasiinae	557.4	Shieldbugs (Hemiptera: Cydnidae) (Tschorsnig and Herting 1994; Nash and Falk 2024)	96.68
GCA_949628195.1	<i>Phasia obesa</i>	Phasiinae	876.8	Several families of Hemiptera (Falk et al. 2024)	94.22
GCA_030448955.1	<i>Trichopoda pennipes</i>	Phasiinae	670.3	Several families of Hemiptera (Bogale et al. 2023)	96.5
GCA_916610165.2	<i>Gymnosoma rotundatum</i>	Phasiinae	779.1	Hemiptera: Pentatomidae (Smith 2022)	95.61
GCA_937654795.1	<i>Cistogaster globosa</i>	Phasiinae	837.8	<i>Aelia</i> sp. (Hemiptera: Pentatomidae) (Falk and Lennon 2023)	95.53
GCA_947397855.1	<i>Thelaira solivaga</i>	Dexiinae	429.3	Lepidoptera: Erebididae (Falk and Smith 2023b)	97.72
GCA_963662145.1	<i>Sturmia bella</i>	Exoristinae	437.8	Nettle-feeding nymphalid butterflies (Falk et al. 2025)	95.46
GCA_932526305.1	<i>Epicampocera succincta</i>	Exoristinae	398.1	Several families of Lepidoptera (Falk and Raper 2023b)	97.51
GCA_963681545.1	<i>Germaria angustata</i>	Tachininae	586.5	<i>Euzophera alpherakyella</i> (Lepidoptera: Pyralidae) (Sivell et al. 2024b)	96.8
GCA_963924685.1	<i>Dexiosoma caninum</i>	Tachininae	517.1	Unknown. Other tribe Microphthalmini parasitize Melolonthinae (Coleoptera: Scarabaeidae) (Sivell et al. 2024a)	96.59
GCA_936439885.1	<i>Nowickia ferox</i>	Tachininae	670.7	<i>Apamea monoglypha</i> (Lepidoptera: Noctuidae) (Falk and Raper 2023a)	95.28
GCA_949987645.1	<i>Tachina grossa</i>	Tachininae	936.9	Lepidoptera: Lasiocampidae (Natural History Museum Genome Acquisition Lab et al. 2024)	93.79
GCA_944452675.1	<i>Tachina lurida</i>	Tachininae	899.2	Several families of Lepidoptera (Falk and Smith 2023a)	92.7
GCA_963402855.1	<i>Ormia ochracea</i>	Tachininae	330.9	Orthoptera: Gryllidae (Gray et al. 2019)	96.93
GCA_956483585.1	<i>Gymnocheta viridis</i>	Tachininae	600.3	Stem-boring Noctuids (Barclay et al. 2024)	96.01
GCA_947311025.1	<i>Lypha dubia</i>	Tachininae	645.0	Several families of Lepidoptera (Falk and Akinmusola 2024)	95.8
GCA_963675445.1	<i>Linnaemya vulpina</i>	Tachininae	554.0	Lepidoptera: Noctuidae (Sivell et al. 2024c)	96.32
GCA_951800035.1	<i>Linnaemya tessellans</i>	Tachininae	709.9	Assumed, Lepidoptera: Noctuidae (Falk and Smith 2024)	96.26

^a For tachinids, the subfamily is indicated. For the 2 outgroups, family is indicated.

^b Percentage of dipteran BUSCOs in the annotation determined to be complete by Compleasm. Full statistics are in Supplementary Table 2.

Gene finding methods

Gene prediction was performed with BRAKER v3.0.8 (Brůna et al. 2021) using soft-masked genomes against a curated protein database of Arthropoda proteins from OrthoDB (Kuznetsov et al. 2023). Gene function and domain annotation was performed by InterProScan v5.75-106.0 (Jones et al. 2014) and eggNOG-mapper v2.1.13 (Huerta-Cepas et al. 2019), utilizing the following databases: AntiFam v8.0, CDD v3.21, Coils v2.2.1, FunFam v4.3.0, Gene3D v4.3.0, Hamap v2025_01, MobiDBLite v4.0, NCBIfam v17.0, PANTHER v19.0, Pfam v37.4, PIRSF v3.10, PIRSR v2025_01, PRINTS v42.0, ProSitePatterns v2025_01, ProSiteProfiles v2025_01, SFLD v4, SMART v9.0, SUPERFAMILY v1.75, and eggNOG v5.0.2. Functional annotations and database references including gene ontology (GO) terms from the 2 programs were merged with the structural gene annotation from BRAKER to produce the final generic feature file.

Comparative genomics and gene family evolution

Genomes of 18 other tachinids plus 2 outgroups (from the families Polleniidae and Calliphoridae) were used in comparative analyses (Table 1). Genome assemblies were retrieved from NCBI, and each assembly was annotated following the same pipeline as described above for *I. aldrichi*, including de novo repeat identification and masking, and annotation with BRAKER. Completeness of each genome annotation was determined with Compleasm v0.2.6 (Huang and Li 2023), which scored annotations (longest transcript

variant protein sequences for each coding gene) against the Diptera_odb10 BUSCO database.

Orthologous groups of proteins (i.e. gene families) were clustered with OrthoFinder v2.5.4 (Emms and Kelly 2019), based on the longest transcript variant for each protein coding gene. The species tree generated by OrthoFinder was converted to an ultrametric tree via the chronos function in the ape package v5.8-1 (Paradis et al. 2019), and used in combination with the gene family counts to estimate significant gene family contractions and expansions across the phylogeny with CAFE v5.1 (Mendes et al. 2020). CafePlotter v0.2.0 (<https://github.com/moshi4/CafePlotter>) was used to extract gene families from the resulting CAFE output files.

To determine significant enrichments of GO terms within sets of genes or gene families, we followed previously developed methods (Lindsey et al. 2018). In brief, statistical testing was performed with BiNGO v 3.0.5 (Maere et al. 2005), implemented in Cytoscape v3.9.1 (Shannon et al. 2003), using hypergeometric tests and Benjamini & Hochberg FDR correction, at a corrected significance level of 0.05. The background set of GO terms differed depending on the comparison. For comparisons within one genome, the background included all genes in that genome. To test for GO term enrichment in a set of gene families, we first annotated all proteins used in orthogroup clustering with OrthoFinder via the EMBL web eggNOG mapper-2.1.12 (Huerta-Cepas et al. 2019) (<http://eggno-mapper.embl.de/>) to generate GO terms. Then, we created a custom background set of GO terms for each gene

Table 2. *Istocheta aldrichi* genome assembly and curation statistics.

Metric	Draft ^a	Final (contigs)	Final (scaffolds)
Sequences	2,297	1,063	1,041
Total assembly length (bp)	916,858,228	875,160,985	875,256,404
Min sequence length	5,340	5,340	5,340
Mean sequence length	399,155	823,293	840,784
Max sequence length	16,220,652	17,929,400	17,929,400
N50	3,182,884	4,766,515	4,769,057
L50	81	56	55
%GC	30.62	30.42	30.42
Compleasm ^b	Complete: 99.5%, 3,270 [Single copy: 97.96%, 3,218 Duplicated: 1.58%, 52] Fragmented: 0.06%, 2 Interrupted: 0.00%, 0 Missing: 0.40%, 13 Total searched: 3,285	Complete: 99.5%, 3,269 [Single copy: 98.33%, 3,230 Duplicated: 1.19%, 39] Fragmented: 0.09%, 3 Interrupted: 0.00%, 0 Missing: 0.40%, 13 Total searched: 3,285	

^a Draft assemblies are from HiFiasm, before ntLink and before purging contaminants.
^b Standard BUSCO annotation based on dipteran BUSCOs.

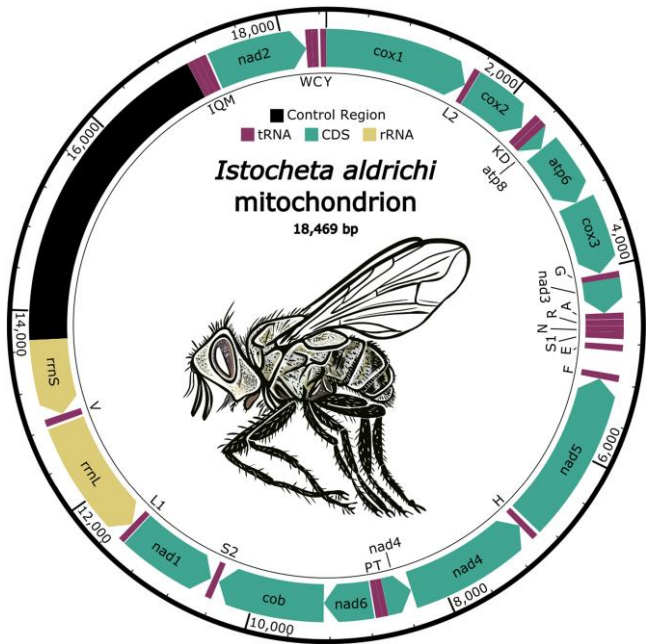


Fig. 2. *Istocheta aldrichi* mitochondrial genome. (*I. aldrichi* drawing: Melissa Schreiner, Colorado State University-Extension, Grand Junction, Colorado). The complete mitochondrial genome of *I. aldrichi*, with annotated rRNAs, tRNAs, coding sequences (CDS), and the predicted control region (defined based on relatives, Cameron 2014; Pei et al. 2024). tRNAs are indicated with single-letter IUPAC-IUB abbreviations corresponding to the amino acid. The mitochondrial genome and annotations are available at NCBI under accession number PX213662.

family, in which the GO terms included those represented by at least 40% of the genes in that family.

Mitochondrial genome

The mitochondrial genome was assembled using MitoHiFi v3.2.2 (Uliano-Silva et al. 2023) using the dorado-corrected reads as input, and the findMitoReference function by specifying the species *I. aldrichi* and min_length 14,000. The MitoHiFi assembled genome was circularized using Circlator v1.5.5 fixstart function (Hunt et al. 2015) and annotated using MITOS2 implemented on the Galaxy web server (Bernt et al. 2013; Donath et al. 2019). The resulting COX1 sequence was extracted and queried against the Barcode of Life Database (Ratnasingham and Hebert 2007)

(BOLD; <https://boldsystems.org/>) to further validate sample identity.

Results and discussion

Sequencing and assembly

We extracted high molecular weight DNA from a single *I. aldrichi* pupa and used Oxford Nanopore sequencing to generate a total of 10.6M reads totaling 49.9 Gbp with a read N50 of 11,980 bp (Supplementary Table 1). Error-corrected reads were then used to assemble a draft genome with Hifiasm. The draft genome of 916.9 Mbp was contained in 2,297 contigs with an N50 of 3.18 Mbp (Table 2). After scaffolding, decontamination, and purging haplotigs, the final genome assembly was 875.3 Mbp, contained in 1,041 scaffolds (1,063 contigs), with a scaffold N50 of 4.77 Mbp (Table 2, Supplementary File 3). The final genome assembly was relatively complete, with a 99.5% Compleasm score for dipteran BUSCOs. At 875.3 Mbp, *I. aldrichi* has the fourth largest genome of sequenced tachinid species ($n = 22$). Compared to similarly sized tachinid genomes (e.g. *Phasia obesa*, 876.8 Mbp, see Table 1), this assembly of *I. aldrichi* has fewer contigs (1,063 vs 3,378) and a larger contig N50 (4.77 Mbp vs 0.47 Mbp, respectively). While *I. aldrichi* has not been scaffolded onto chromosomes like many of the other tachinid genomes (including *P. obesa*, see references in Table 1), the *I. aldrichi* assembly here is nevertheless of high quality.

Mitochondrial genome

We assembled and annotated a complete 18,469 bp mitochondrial genome from *I. aldrichi*. We identified a complete gene set including small and large rRNAs, 22 tRNAs, and 13 protein coding genes (Fig. 2). The gene arrangement, like most other dipterans and tachinids, is the same as the ancestral insect mitochondrial genome (Cameron 2014; Pei et al. 2024). We cross-referenced the COX1 sequence from the mitochondrial genome assembly with the BOLD barcode database and determined that the mitogenome sequenced here was identical to published *I. aldrichi* barcodes at COX1 (sequences in BIN:ADE2384, see also Shanovich et al. (2021)).

Repeats

Greater than 70% of the *I. aldrichi* genome was derived from repetitive elements (Table 3). The majority of repeats, corresponding to

Table 3. Repetitive sequences in *Istocheta aldrichi*.

Name	Number	Length (bp)	Percent (%)
Retroelements	126,476	73,636,889	8.41
Penelope class	7,988	3,512,242	0.40
LINE class	92,362	45,926,233	5.25
L2/CR1/Rex	28,620	10,768,381	1.23
R1/LOA/Jockey	4091	2,630,147	0.30
R2/R4/NeSL	95	102,292	0.01
LTR class	34,114	27,710,656	3.17
BEL/Pao	6,335	5,393,792	0.62
Ty1/Copia	1,751	1,533,512	0.18
Gypsy/DIRS1	25,970	20,764,846	2.37
DNA transposons	197,900	87,342,017	9.98
hobo-Activator	57,782	17,658,477	2.02
Tc1-IS630-Pogo	73,612	33,272,189	3.80
Rolling-circles	171	42,189	0.00
Unclassified	1,900,031	442,956,545	50.61
Total interspersed repeats		603,935,451	69.01
Simple repeats	168,984	8,707,703	0.99
Low complexity	41,205	1,981,500	0.23
Bases masked ^a		614,668,413	70.23

^a Repetitive elements were identified with RepeatModeler, and masking was performed with RepeatMasker.

50.6% of the genome length, were unclassified, which is not atypical for nonmodel insect species (Petersen et al. 2019; Sproul et al. 2023). Retroelements and DNA transposons were the largest categories of identified elements, and accounted for 8.4% and 10% of the genome, respectively.

Gene finding

Structural annotation of the *I. aldrichi* genome characterized 32,005 mRNAs representing 28,569 genes (Table 4), which is only slightly above the average gene number for tachinids based on our annotations (mean = 25,816; Supplementary File 2). In contrast, the cricket parasitoid *Ormia ochracea* had the fewest genes ($n=14,670$), whereas *Cistogaster globosa*, a stinkbug specialist, was the most gene rich of the tachinids ($n=34,717$, Fig. 3b). Completeness metrics for the *I. aldrichi* annotation are high, with 94.24% complete dipteran BUSCOs present (Table 1). Annotation completeness was similarly high across the tachinid and outgroup species, with an average of 95.75% ($\pm 1.36\%$) of complete dipteran BUSCOs (Table 1, Supplementary Table 2). The lowest completeness score was for *Calliphora vicina* (93.67%). The duplicated score for the *I. aldrichi* annotation was 5.78%, which is consistent with others in the dataset (mean = 5.45% $\pm 0.32\%$, see Supplementary Table 2). Taken together, this is a robust dataset for inferring patterns of gene family evolution in this group.

A total of 27,877 *I. aldrichi* proteins were functionally annotated by eggNOG-mapper, with 2,559 annotated by eggNOG-mapper alone. Using InterProScan, 27,692 proteins were functionally annotated, with 2,374 characterized by InterProScan but not eggNOG-mapper. Finally, 25,318 proteins were functionally annotated by both programs. Results from both functional annotation programs were merged.

Comparative genomics of tachinids

We leveraged the published genomes of 18 additional tachinids and 2 outgroup species for comparative analyses (Table 1, Fig. 3). Phylogenetic reconstruction recapitulated most relationships that are well-supported by more in-depth analyses of Diptera and Tachinidae evolution (Stireman III et al. 2019; de Paula et al. 2024). Specifically, each tachinid subfamily was recovered as monophyletic, and the sister relationships of the

Table 4. *Istocheta aldrichi* genome annotation metrics.

Metric	Value
Number of genes	28,569
Number of mRNAs	32,005
Number of exons	97,869
Number of introns	65,966
Mean exons per mRNA	3
Total gene length	162,778,123 bp
Longest gene	224,090 bp
Mean gene length	5,698 bp
Longest CDS	66,945 bp
Mean CDS length	1,280 bp
Longest exon	32,355 bp
Mean exon length	427 bp
Compleasm ^a	Complete: 94.24%, 3,096 [Single copy: 88.46%, 2906 Duplicated: 5.78%, 190] Fragmented: 3.62%, 119 Interrupted: 0.00%, 0 Missing: 2.13%, 70 Total searched: 3,285

^a Standard BUSCO annotation based on dipteran BUSCOs.

subfamilies agreed with recently published phylogenies, except for the placement of the single representative species of Dexiinae, as this subfamily is generally accepted to be sister to Phasiinae (Stireman III et al. 2019; de Paula et al. 2024). *Istocheta aldrichi* was sister to the other 2 species within the Exoristinae (*Sturmia bella* + *Epicampocera succincta*), and Exoristinae was sister to Tachininae (Fig. 3).

Across the 21 genomes, 538,711 genes (96.4% of the total 558,763) were clustered into 24,885 gene families (Supplementary Tables 3 and 4). The largest gene family contained 1,305 genes, had between 1 and 208 paralogs per species, and was represented by all species except for *Sturmia bella*. A total of 8,935 gene families contained genes from all species, and of these, 5,707 gene families consisted entirely of single-copy genes. In total, 3,565 gene families (15,289 genes in total) contained genes exclusively derived from the same genome (i.e. species-specific families). A total of 9,001 gene families were present in all tachinid species, only one of which was also not present in both outgroups. The subfamily to which *I. aldrichi* belongs, Exoristinae, were uniquely missing 4 gene families that were present in all other species. All Exoristinae species also had genes in 33 gene families that were unique to the Exoristinae. Finally, for *I. aldrichi*, 97.5% of the 28,575 genes were assigned to gene families, and of these, there were 878 genes in 211 species-specific gene families. 702 *I. aldrichi* genes were defined as singletons, and there were 81 gene families that were uniquely lost in this lineage but present in all other species.

Curiously, one of the gene families missing in Exoristinae encoded for centromeric H3 (CENH3, “Cid” in *Drosophila melanogaster*, “CEN-P” in yeast). On further inspection, we determined that the Exoristinae CENH3 proteins were not missing, but instead clustered with canonical H3 variants of the other species due to their short N-terminus relative to the other tachinid CENH3 proteins. These Exoristinae proteins were clearly identifiable as centromeric H3 variants due to the Q69A and F85Y amino acid substitutions (relative to the highly conserved canonical H3), and a longer loop 1 region in the histone fold domain by one amino acid (Malik and Henikoff 2003; Drinnenberg et al. 2014). However, there did not appear to be any Exoristinae canonical H3 proteins present in that same gene family. Blastp searches against the annotated *I. aldrichi* proteome (query: *Drosophila melanogaster* H3, GenBank CAA32434.1) similarly did not recover any canonical H3 proteins,

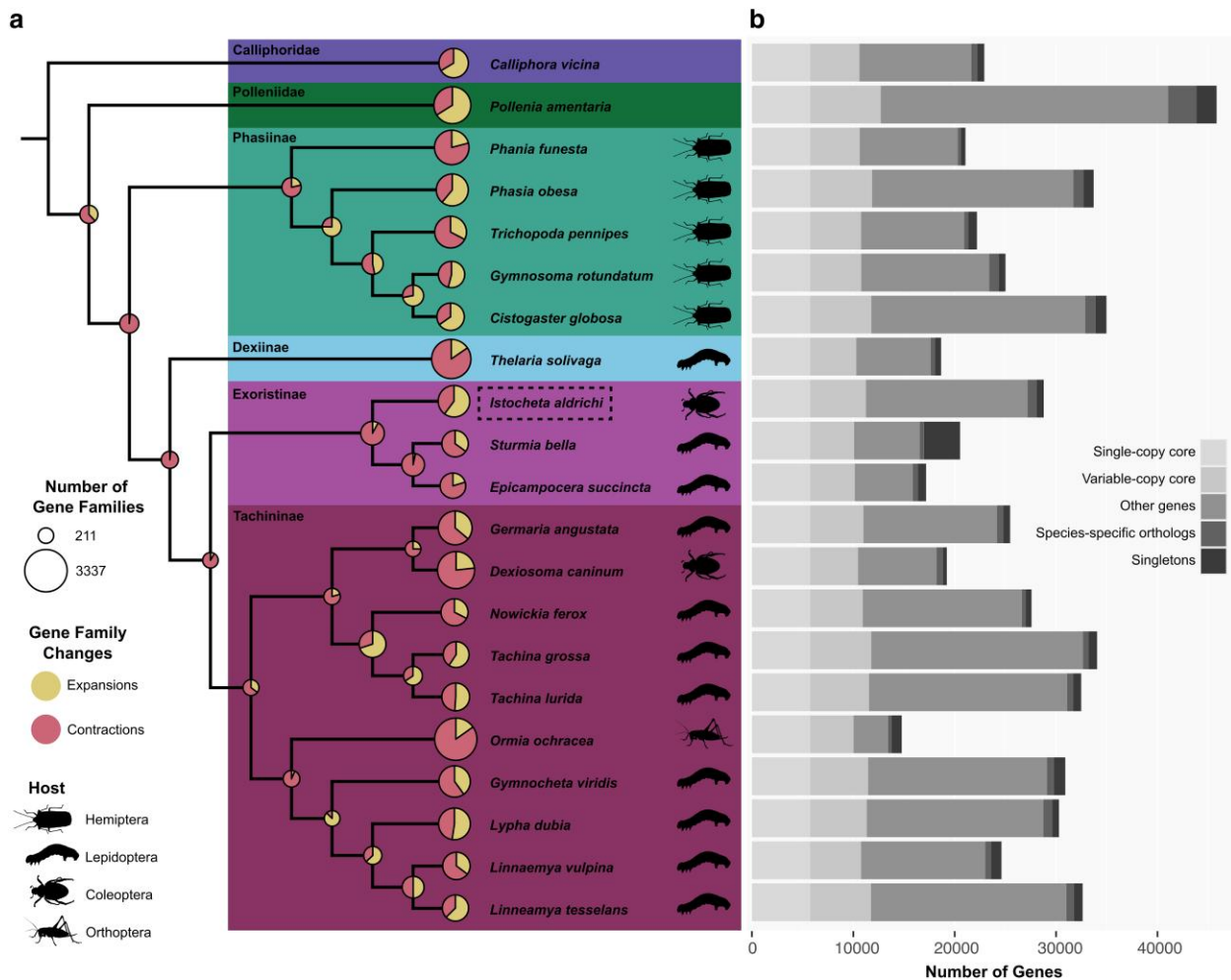


Fig. 3. Tachinid genome evolution. a) Phylogeny representing all Tachinidae subfamilies and select outgroups, showing superfamily wide gene family size changes and tachinid host associations. Circles at each node correspond to the total number of gene families that contracted or expanded in size. Colors within each circle indicate the proportion of those gene families that either expanded or contracted. *Istocheta aldrichi* is indicated with a dashed-line box. b) Stacked bar-chart reflecting the composition of genes associated with different levels of gene family conservation.

only CENH3. Finally, we determined that the H3 proteins were encoded in the genome, but they had undergone numerous duplications to the point that they had been masked during repetitive element analyses. Indeed, we identified 131 open reading frames across 5 contigs, which encoded for identical H3 proteins. While having numerous gene copies of histones is not unusual (Rooney et al. 2002), it seems the recent copy number expansion in this lineage is distinct from other clades in the family and also paired with a more divergent CENH3 N-terminus. Perhaps related to the signatures of histone evolution, the singleton genes unique to *I. aldrichi* were significantly enriched for 8 GO terms, 6 of which were related to mitosis and DNA repair (Fig. 4a, Supplementary Table 4), such as G2/M cell cycle checkpoints and double-stranded break repair and processing. In contrast to the *I. aldrichi* singletons, genes in *I. aldrichi*-specific gene families were significantly enriched for metabolic functions, especially those related to vitamin A, terpenoids, protein catabolism, mitochondrial biology, and the circulatory system (Fig. 4b, Supplementary Table 5).

Gene family size evolution

In addition to identifying gene families that had been completely gained or lost, we also identified gene families that underwent

changes in copy number at specific points across the phylogeny and characterized each one as either “expanding” (e.g. gaining paralogs) or “contracting” (e.g. losing paralogs) at a given node or leaf (Fig. 3a). First, we identified 935 gene families which experienced significant changes in the rate of gene gain and loss across the tachinid phylogeny. These families were significantly overrepresented for a suite of GO terms, largely involving metabolic functions and morphogenesis (Fig. 5a, Supplementary Table 6), which may relate to the evolution of parasitism in this group, especially in the context of host switches. We determined that at the root of Tachinidae, 618 gene families changed in size, and these were primarily contracting families ($n=607$). In fact, this node had the lowest percentage of expanding gene families (relative to all changing families at a node) across the phylogeny. The nodes representing the ancestors of each subfamily were also characterized by a relatively high level of gene family contractions (C) relative to expansions (E): Phasiinae [C:516, E:140], Dexiinae [C:2,535, E:462], Exoristinae [C:1,074, E:92], Tachininae [C:169, E:92]. In contrast, *I. aldrichi* had an especially high number of gene families that expanded in size on this branch ($n=1,261$); the second highest number across the extant species (second to *P. obesa*, $n=1,302$). An additional 833 gene families were

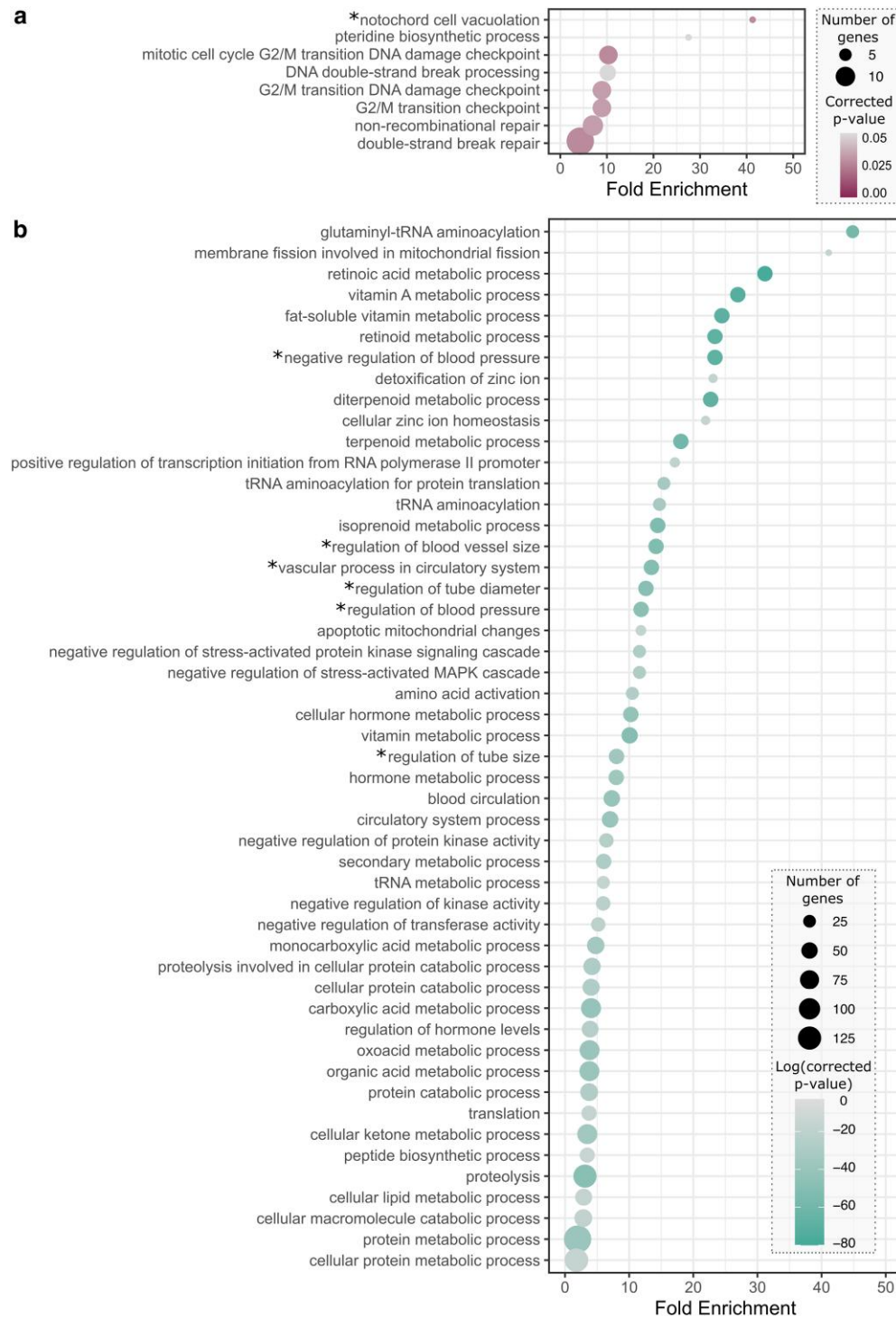


Fig. 4. Significantly overrepresented GO terms for genes unique to *Istocheta aldrichi*. a) Overrepresented GO terms for singleton genes unique to *I. aldrichi*. Full details can be found in [Supplementary Table 4](#). b) The top 50 most significant overrepresented GO terms for genes in *I. aldrichi*-specific gene families. Full details can be found in [Supplementary Table 5](#). The asterisks (*) denote GO terms with descriptions of vertebrate processes that do not occur in insects, but that involve conserved genes present in many metazoans.

determined to have contracted in the *I. aldrichi* lineage. *Istocheta aldrichi* was one of only 4 tachinid species where >60% of significant families underwent lineage-specific expansions (along with *P. obesa*, *Linnaemya tessellans*, and *C. globosa*). The gene families that increased in size on the *I. aldrichi* branch were significantly overrepresented for 5 GO terms (Fig. 5b, [Supplementary Table 7](#)), 4 of which were related to copper/metal ion transport.

The fifth overrepresented GO term was for RNA-dependent DNA replication, likely indicative of viral genes. Finally, gene families that contracted in size on the *I. aldrichi* branch were significantly overrepresented for 17 GO terms, all of which related to neurological processes such as sensory perception, mating/reproductive behavior, and cognition (Fig. 5c, [Supplementary Table 8](#)).

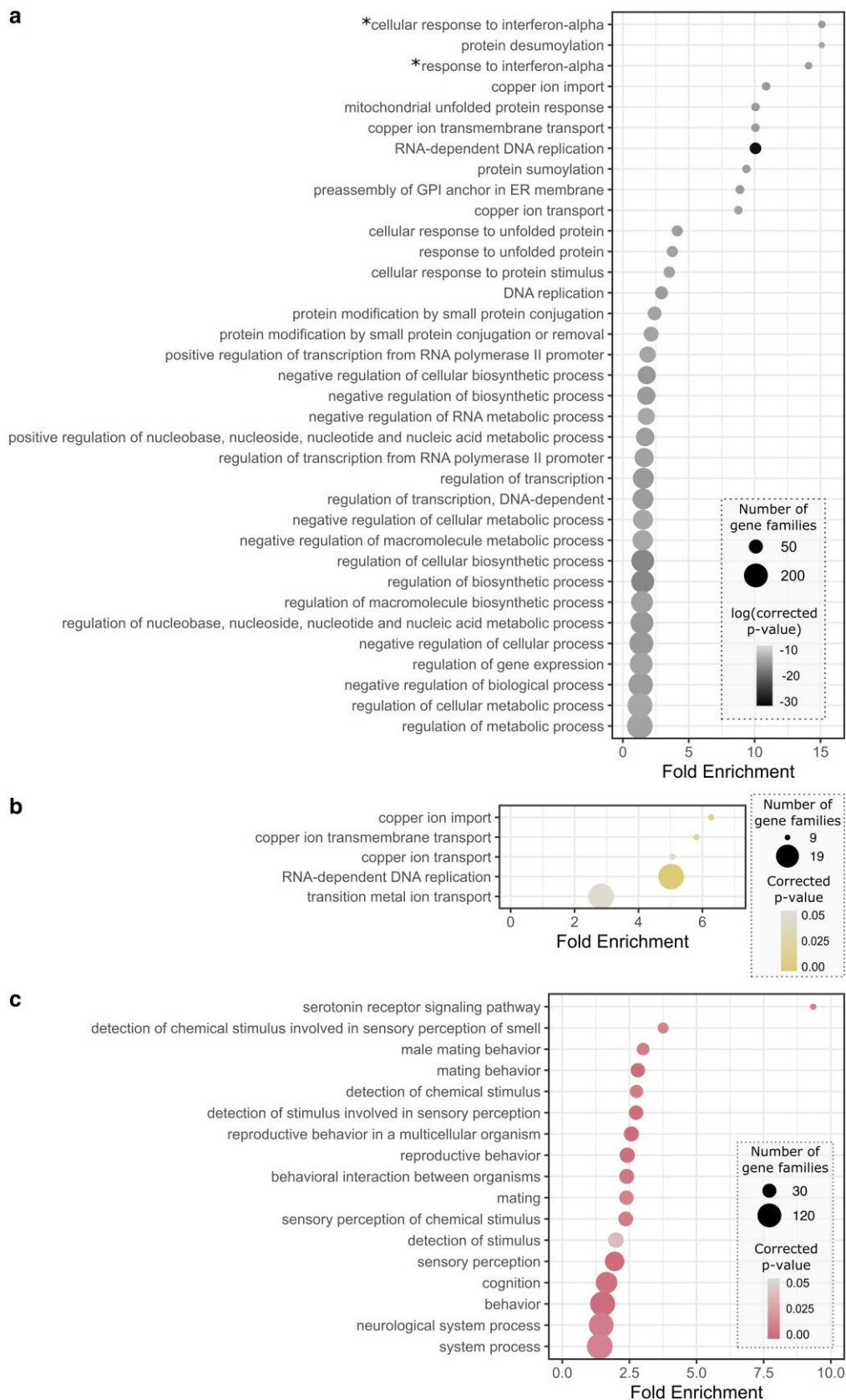


Fig. 5. Significantly overrepresented GO terms for dynamic gene families. a) Top 35 most significantly overrepresented GO terms for gene families with significant changes in the rate of gene gain and loss across the tachinid phylogeny. Full details can be found in [Supplementary Table 6](#). b) Overrepresented GO terms for gene families that increased in size on the *I. aldrichi* branch. Full details can be found in [Supplementary Table 7](#). c) Overrepresented GO terms for gene families that contracted in size on the *I. aldrichi* branch. Full details can be found in [Supplementary Table 8](#). The asterisks (*) denote GO terms with descriptions of vertebrate processes that do not occur in insects, but that involve conserved genes present in many metazoans.

Summary

The sequencing and analyses of the *I. aldrichi* genome presented herein represent the first available reference genome for the tribe Blondeliini, and the first functional genomic comparisons across the family Tachinidae, the second largest dipteran family in terms of numbers of species descriptions (Stireman III et al. 2019). For *I. aldrichi*, this will facilitate further research on the biological control of *P. japonica*. Of particular interest, this reference genome will support research on population genetics related to the recent spread of this fly. In addition to the importance of tachinids as biological control agents of many insect pests (Grenier 1988), their evolutionary history affords myriad opportunities to understand rapid speciation, parasitism, and major transitions between feeding ecologies and host associations (Stireman III et al. 2019). Indeed, others have estimated that Tachinidae may be one of the most rapidly diversifying lineages across all of metazoa (Scholl and Wiens 2016), and our work here provides a foundation to explore this diversity.

Data availability

The genome assembly and raw reads underlying this article are available at NCBI under the BioProject ID PRJNA1297203. The mitochondrial genome and annotations are available at NCBI under accession number PX213662. All code is available as an Rmarkdown file (Supplementary File 1). All Supplementary files are available at GSA FigShare (doi.org/10.25387/g3.30511283).

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Conflicts of interest

None declared.

Literature cited

Abram PK et al. 2024. Weighing consequences of action and inaction in invasive insect management. *One Earth*. 7:782–793. <https://doi.org/10.1016/j.oneear.2024.04.013>.

Althoff ER, Rice KB. 2022. Japanese beetle (Coleoptera: Scarabaeidae) invasion of North America: history, ecology, and management. *J Integr Pest Manag*. 13:2. <https://doi.org/10.1093/jipm/pmab043>.

Astashyn A et al. 2024. Rapid and sensitive detection of genome contamination at scale with FCS-GX. *Genome Biol*. 25:60. <https://doi.org/10.1186/s13059-024-03198-7>.

Barclay MVL, Falk S, Sivell O. 2024. The genome sequence of a tachinid fly, *Gymnocheta viridis* (Fallén, 1810). *Wellcome Open Res*. 9:714. <https://doi.org/10.12688/wellcomeopenres.23435.1>.

Bernt M et al. 2013. MITOS: improved de novo metazoan mitochondrial genome annotation. *Mol Phylogenet Evol*. 69:313–319. <https://doi.org/10.1016/j.ympev.2012.08.023>.

Bogale M et al. 2023. First description of the nuclear and mitochondrial genomes and associated host preference of *Trichopoda pennipes*, a parasitoid of *Nezara viridula*. *Genes (Basel)*. 14:1172. <https://doi.org/10.3390/genes14061172>.

Brodeur J, Doyon J, Abram PK, Parent J-P. 2024. *Popillia japonica* Newman, Japanese Beetle/Scarabée japonais (Coleoptera: Scarabaeidae). In: *Biological control programmes in Canada, 2013–2023*. CABI GB. p. 343–350.

Brůna T, Hoff KJ, Lomsadze A, Stanke M, Borodovsky M. 2021. BRAKER2: automatic eukaryotic genome annotation with GeneMark-EP+ and AUGUSTUS supported by a protein database. *NAR Genom Bioinform*. 3:lqaa108. <https://doi.org/10.1093/nargab/lqaa108>.

CABI. 2021. Classical biological control of Japanese beetle. Available online at: <https://www.cabi.org/projects/classical-biological-control-of-japanese-beetle/>.

Cameron SL. 2014. Insect mitochondrial genomics: implications for evolution and phylogeny. *Annu Rev Entomol*. 59:95–117. <https://doi.org/10.1146/annurev-ento-011613-162007>.

Challis R, Richards E, Rajan J, Cochrane G, Blaxter M. 2020. BlobToolKit—interactive quality assessment of genome assemblies. *G3 (Bethesda)*. 10:1361–1374. <https://doi.org/10.1534/g3.119.400908>.

Cheng H, Concepcion GT, Feng X, Zhang H, Li H. 2021. Haplotype-resolved de novo assembly using phased assembly graphs with hifiasm. *Nat Methods*. 18:170–175. <https://doi.org/10.1038/s41592-020-01056-5>.

Clausen CP, King JL, Teranishi C. 1927. The parasites of *Popillia japonica* in Japan and Chosen (Korea), and their introduction into the United States. US Department of Agriculture.

Coombe L, Warren RL, Wong J, Nikolic V, Birol I. 2023. ntLink: a tool-kit for de novo genome assembly scaffolding and mapping using long reads. *Curr Protoc*. 3:e733. <https://doi.org/10.1002/cpz1.733>.

de Paula LCB et al. 2024. Phylogenomic analysis of Tachinidae (Diptera: Calyptratae: Oestroidea): a transcriptomic approach to understanding the subfamily relationships. *Cladistics*. 40:64–81. <https://doi.org/10.1111/cla.12562>.

Donath A et al. 2019. Improved annotation of protein-coding genes boundaries in metazoan mitochondrial genomes. *Nucleic Acids Res*. 47:10543–10552. <https://doi.org/10.1093/nar/gkz833>.

Drinnenberg IA, deYoung D, Henikoff S, Malik HS. 2014. Recurrent loss of CenH3 is associated with independent transitions to holocentricity in insects. *Elife*. 3:e03676. <https://doi.org/10.7554/eLife.03676>.

Emms DM, Kelly S. 2019. OrthoFinder: phylogenetic orthology inference for comparative genomics. *Genome Biol*. 20:238. <https://doi.org/10.1186/s13059-019-1832-y>.

Falk S, Akinmusola R. 2024. The genome sequence of a tachinid fly, *Lypha dubia* Fallén, 1810. *Wellcome Open Res*. 9:8–564. <https://doi.org/10.12688/wellcomeopenres.21295.1>.

Falk S, Crowley L, Lewis O. 2025. The genome sequence of a tachinid fly, *Sturmia bella* (Meigen, 1824). *Wellcome Open Res*. 10:8–288. <https://doi.org/10.12688/wellcomeopenres.24253.1>.

Falk S, Lennon R. 2023. The genome sequence of a tachinid fly, *Cistogaster globosa* (Fabricius, 1775). *Wellcome Open Res*. 8:462. <https://doi.org/10.12688/wellcomeopenres.19924.1>.

Falk S, Mitchell R, Sivell O. 2023. The genome sequence of the black-bellied cluster fly, *Pollenia amentaria* (Scopoli, 1763). *Wellcome Open Res*. 8:466. <https://doi.org/10.12688/wellcomeopenres.19740.1>.

Falk S, Mitchell R, Smith MN, University of Oxford and Wytham Woods Genome Acquisition Lab. 2024. The genome sequence of

- a tachinid fly, *Phasia obesa* (Fabricius, 1798). Wellcome Open Res. 9:264. <https://doi.org/10.12688/wellcomeopenres.21577.1>.
- Falk S, Raper C. 2023a. The genome sequence of a tachinid fly, *Nowickia ferox* (Panzer, 1809). Wellcome Open Res. 8:275. <https://doi.org/10.12688/wellcomeopenres.19575.1>.
- Falk S, Raper C. 2023b. The genome sequence of the tachinid fly, *Epicampocera succincta* (Meigen, 1824). Wellcome Open Res. 8:276. <https://doi.org/10.12688/wellcomeopenres.19586.1>.
- Falk S, Smith MN. 2023a. The genome sequence of a tachinid fly, *Tachina lurida* (Fabricius, 1781). Wellcome Open Res. 8:288. <https://doi.org/10.12688/wellcomeopenres.19635.1>.
- Falk S, Smith MN. 2023b. The genome sequence of a tachinid fly, *Thelaira solivaga* (Harris, 1780). Wellcome Open Res. 8:564. <https://doi.org/10.12688/wellcomeopenres.19639.1>.
- Falk S, Smith MN. 2024. The genome sequence of a tachinid fly, *Linnaemya tessellans* (Robineau-Desvoidy, 1830). Wellcome Open Res. 9:243. <https://doi.org/10.12688/wellcomeopenres.21499.1>.
- Fleming WE. 1968. Biological control of the Japanese beetle. Technical Bulletin No. 1383. U.S. Department of Agriculture, Agricultural Research Service, Washington, D.C.
- Flynn JM et al. 2020. RepeatModeler2 for automated genomic discovery of transposable element families. Proc Natl Acad Sci U S A. 117:9451–9457. <https://doi.org/10.1073/pnas.1921046117>.
- Gagnon M-E, Doyon J, Legault S, Brodeur J. 2023. The establishment of the association between the Japanese beetle (Coleoptera: Scarabaeidae) and the parasitoid *Istocheta aldrichi* (Diptera: Tachinidae) in Québec, Canada. Can Entomol. 155:e32. <https://doi.org/10.4039/tce.2023.22>.
- Gagnon M-E, Giroux M. 2019. Records of the Japanese beetle and its parasitoid *Istocheta aldrichi* (Mesnil) (Diptera: Tachinidae) in Québec, Canada. The Tachinid Times. 32:53–55. [Accessed 2026 February 9]. <https://www.uoguelph.ca/nadsfly/Tach/WorldTachs/TTimes/Tach32.html>.
- Gotta P et al. 2023. *Popillia japonica*–Italian outbreak management. Front Insect Sci. 3:1175138. <https://doi.org/10.3389/finsc.2023.1175138>.
- Graf T, Scheibler F, Niklaus PA, Grabenweger G. 2023. From lab to field: biological control of the Japanese beetle with entomopathogenic fungi. Front Insect Sci. 3:1138427. <https://doi.org/10.3389/finsc.2023.1138427>.
- Gray DA, Kunerth HD, Zuk M, Cade WH, Balenger SL. 2019. Molecular biogeography and host relations of a parasitoid fly. Ecol Evol. 9:11476–11493. <https://doi.org/10.1002/ece3.5649>.
- Grenier S. 1988. Applied biological control with tachinid flies (Diptera, Tachinidae): a review. Anzeiger für Schädlingkunde, Pflanzenschutz. Umweltschutz. 61:49–56. <https://doi.org/10.1007/BF01906254>.
- Guan D et al. 2020. Identifying and removing haplotypic duplication in primary genome assemblies. Bioinformatics. 36:2896–2898. <https://doi.org/10.1093/bioinformatics/btaa025>.
- Huang N, Li H. 2023. Compleasm: a faster and more accurate reimplementation of BUSCO. Bioinformatics. 39:btad595. <https://doi.org/10.1093/bioinformatics/btad595>.
- Huerta-Cepas J et al. 2019. eggNOG 5.0: a hierarchical, functionally and phylogenetically annotated orthology resource based on 5090 organisms and 2502 viruses. Nucleic Acids Res. 47:D309–D314. <https://doi.org/10.1093/nar/gky1085>.
- Hunt M et al. 2015. Circlator: automated circularization of genome assemblies using long sequencing reads. Genome Biol. 16:294. <https://doi.org/10.1186/s13059-015-0849-0>.
- Hutchison W, Buchholz E, Meys E, Wold-Burkness S. 2024. The Winsome Fly, *Istocheta aldrichi*: a unique biocontrol agent for Japanese Beetle in Minnesota. Fruitedge. <https://fruitedge.umn.edu/winsome-fly-istocheta-aldrichi-unique-biocontrol-agent-japanese-beetle-minnesota>.
- Jones P et al. 2014. InterProScan 5: genome-scale protein function classification. Bioinformatics. 30:1236–1240. <https://doi.org/10.1093/bioinformatics/btu031>.
- Kuznetsov D et al. 2023. OrthoDB v11: annotation of orthologs in the widest sampling of organismal diversity. Nucleic Acids Res. 51:D445–D451. <https://doi.org/10.1093/nar/gkac998>.
- Lindsey ARI et al. 2018. Comparative genomics of the miniature wasp and pest control agent *Trichogramma pretiosum*. BMC Biol. 16:54. <https://doi.org/10.1186/s12915-018-0520-9>.
- Maere S, Heymans K, Kuiper M. 2005. BiNGO: a Cytoscape plugin to assess overrepresentation of gene ontology categories in biological networks. Bioinformatics. 21:3448–3449. <https://doi.org/10.1093/bioinformatics/bti551>.
- Makovetski V, Abram P. 2024. *Istocheta aldrichi* (Mesnil) makes its biological control debut in British Columbia, Canada. The Tachinid Times. 37:4–10. [Accessed 2026 February 9]. <https://www.uoguelph.ca/nadsfly/Tach/WorldTachs/TTimes/Tach37.html>.
- Makovetski V, Smith AB, Abram PK. 2025. Crowdsourced online data as evidence of absence of non-target effects from the century-old introduction of *Istocheta aldrichi* for biological control of *Popillia japonica* in North America. J Pest Sci (2004). 98:1451–1462. <https://doi.org/10.1007/s10340-025-01891-5>.
- Malik HS, Henikoff S. 2003. Phylogenomics of the nucleosome. Nat Struct Mol Biol. 10:882–891. <https://doi.org/10.1038/nsb996>.
- Mendes FK, Vanderpool D, Fulton B, Hahn MW. 2020. CAFE 5 models variation in evolutionary rates among gene families. Bioinformatics. 36:5516–5518. <https://doi.org/10.1093/bioinformatics/btaa1022>.
- Nash W, Falk S. 2024. The genome sequence of a tachinid fly, *Phania funesta* (Meigen, 1824). Wellcome Open Res. 9:713. <https://doi.org/10.12688/wellcomeopenres.23440.1>.
- Natural History Museum Genome Acquisition Lab, et al. 2024. The genome sequence of the giant tachinid fly, *Tachina grossa* (Linnaeus, 1758). Wellcome Open Res. 9:571. <https://doi.org/10.12688/wellcomeopenres.23102.1>.
- Paradis E, Blomberg S, Bolker B, Brown J, Claude J, Cuong HS, Desper R, Didier G. 2019. Analyses of phylogenetics and evolution, version 2.4: 47.
- Pavesi M. 2014. *Popillia japonica* specie aliena invasiva segnalata in Lombardia. L'informatore Agrario. 32:53–55. [Accessed 2026 February 9]. <https://gd.eppo.int/reporting/article-3272>.
- Pei W et al. 2024. Unusual rearrangements of mitogenomes in Diptera revealed by comparative analysis of 135 tachinid species (Insecta, Diptera, Tachinidae). Int J Biol Macromol. 258:128997. <https://doi.org/10.1016/j.ijbiomac.2023.128997>.
- Pelletier M, Legault S, Doyon J, Brodeur J. 2023. Where and why do females of the parasitic fly *Istocheta aldrichi* lay their eggs on the body of adult Japanese beetles? J Insect Behav. 36:308–317. <https://doi.org/10.1007/s10905-023-09841-8>.
- Petersen M et al. 2019. Diversity and evolution of the transposable element repertoire in arthropods with particular reference to insects. BMC Ecol Evol. 19:11. <https://doi.org/10.1186/s12862-018-1324-9>.
- Ratnasingham S, Hebert PD. 2007. BOLD: the barcode of life data system (<https://www.boldsystems.org/>). Mol Ecol Notes. 7:355–364. <https://doi.org/10.1111/j.1471-8286.2007.01678.x>.
- Rhie A, Walenz BP, Koren S, Phillippy AM. 2020. Merquy: reference-free quality, completeness, and phasing assessment for genome assemblies. Genome Biol. 21:245. <https://doi.org/10.1186/s13059-020-02134-9>.
- Rooney AP, Piontkivska H, Nei M. 2002. Molecular evolution of the non-tandemly repeated genes of the histone 3 multigene family.

- Mol Biol Evol. 19:68–75. <https://doi.org/10.1093/oxfordjournals.molbev.a003983>.
- Santoemma G et al. 2021. Chemical control of *Popillia japonica* adults on high-value crops and landscape plants of northern Italy. Crop Protection. 150:105808. <https://doi.org/10.1016/j.cropro.2021.105808>.
- Scholl JP, Wiens JJ. 2016. Diversification rates and species richness across the Tree of Life. Proc R Soc Lond B Biol Sci. 283:20161334. <https://doi.org/10.1098/rspb.2016.1334>.
- Shannon P et al. 2003. Cytoscape: a software environment for integrated models of biomolecular interaction networks. Genome Res. 13:2498–2504. <https://doi.org/10.1101/gr.1239303>.
- Shanovich HN, Dean AN, Koch RL, Hodgson EW. 2019. Biology and management of Japanese beetle (Coleoptera: Scarabaeidae) in corn and soybean. J Integr Pest Manag. 10:9. <https://doi.org/10.1093/jipm/pmz009>.
- Shanovich HN, Ribeiro AV, Koch RL. 2021. Seasonal abundance, defoliation, and parasitism of Japanese beetle (Coleoptera: Scarabaeidae) in two apple cultivars. J Econ Entomol. 114:811–817. <https://doi.org/10.1093/jee/toaa315>.
- Sivell O. 2024. The genome sequence of a bluebottle fly, *Calliphora vicina* Robineau-Desvoidy, 1830. Wellcome Open Res. 9:335. <https://doi.org/10.12688/wellcomeopenres.22469.1>.
- Sivell O, Mitchell R, Raper C. 2024a. The genome sequence of a tachinid fly, *Dexiosoma caninum* (Fabricius, 1781). Wellcome Open Res. 9:595. <https://doi.org/10.12688/wellcomeopenres.23193.1>.
- Sivell O, Mitchell R, Raper C. 2024b. The genome sequence of a tachinid fly, *Germaria angustata* (Zetterstedt, 1844). Wellcome Open Res. 9:578. <https://doi.org/10.12688/wellcomeopenres.23197.1>.
- Sivell O, Mitchell R, Raper C. 2024c. The genome sequence of a tachinid fly, *Linnaemya vulpina* (Fallén, 1810). Wellcome Open Res. 9:643. <https://doi.org/10.12688/wellcomeopenres.23296.1>.
- Smith M. 2022. The genome sequence of *Gymnosoma rotundatum* (Linnaeus, 1758), a parasitoid ladybird fly. Wellcome Open Res. 7:104. <https://doi.org/10.12688/wellcomeopenres.17782.1>.
- Sproul JS et al. 2023. Analyses of 600+ insect genomes reveal repetitive element dynamics and highlight biodiversity-scale repeat annotation challenges. Genome Res. 33:1708–1717. <https://doi.org/10.1101/gr.277387.122>.
- Stireman III JO, Cerretti P, O'Hara JE, Blaschke JD, Moulton JK. 2019. Molecular phylogeny and evolution of world Tachinidae (Diptera). Mol Phylogenet Evol. 139:106358. <https://doi.org/10.1016/j.ympev.2018.12.002>.
- Stireman III JO, O'Hara JE, Wood DM. 2006. Tachinidae: evolution, behavior, and ecology. Annu Rev Entomol. 51:525–555. <https://doi.org/10.1146/annurev.ento.51.110104.151133>.
- Tarailo-Graovac M, Chen N. 2009. Using RepeatMasker to identify repetitive elements in genomic sequences. Curr Protoc Bioinformatics. 25:4.10.1–4.10.14. <https://doi.org/10.1002/0471250953.bi0410s25>.
- Tschorsnig HP, Herting B. 1994. The Tachinids (Diptera: Tachinidae) of Central Europe: identification keys for the species and data on distribution and ecology. Stuttgarter Beiträge zur Naturkunde. Serie A, Biologie. 506:170–170.
- Uliano-Silva M et al. 2023. Mitohifi: a python pipeline for mitochondrial genome assembly from PacBio high fidelity reads. BMC Bioinformatics. 24:288. <https://doi.org/10.1186/s12859-023-05385-y>.
- Venette RC, Hutchison WD. 2021. Invasive insect species: global challenges, strategies & opportunities. Front Insect Sci. 1:650520. <https://doi.org/10.3389/fnsc.2021.650520>.
- Zhu G et al. 2023. Potential distribution and spread of Japanese beetle in Washington State. J Econ Entomol. 116:1458–1463. <https://doi.org/10.1093/jee/toad116>.

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