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Genomes of the Hymenoptera

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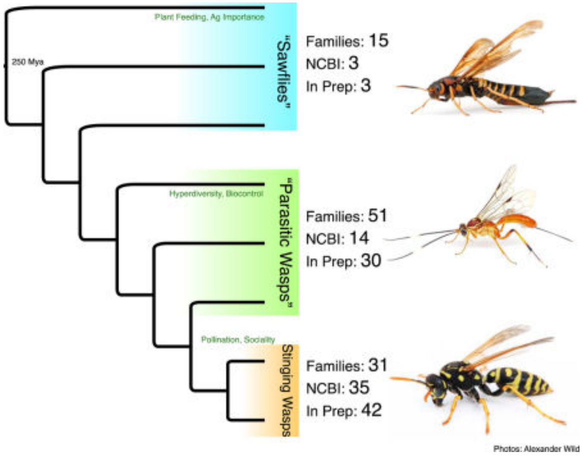
Abstract

Although Hymenoptera is the second-most sequenced arthropod order, with 52 publically archived genomes (71 with ants, reviewed elsewhere), these genomes do not capture the breadth of this very diverse order (Figure 1, Table 1). These sequenced genomes represent only 15 of the 97 extant families. Although at least 55 other genomes are in progress in an additional 11 families (see Table 2), stinging wasps represent 35 (67%) of the available and 42 (76%) of the in progress genomes. A more comprehensive catalogue of hymenopteran genomes is needed for research into the evolutionary processes underlying the expansive diversity in terms of ecology, behavior, and physiological traits within this group. Additional sequencing is needed to generate an assembly for even 0.05% of the estimated 1 million Hymenopteran species, with premier level assemblies for at least 0.1% of the >150,000 named species dispersed across the order. Given the haplodiploid sex determination in Hymenoptera, haploid male sequencing will help minimize genome assembly issues to enable higher quality genome assemblies.

Graphical abstract



Introduction

The order Hymenoptera with fossils dating back to the Triassic [1], is both ancient and hyper-diverse, with over 150,000 described and one million estimated species [2,3]. One of the "big four" insect orders, Hymenoptera comprise diverse species including sawflies and wood wasps ("Symphyta"), parasitoid wasps ("Parasitica"), and stinging wasps (Aculeata), which includes the ubiquitous and ecologically dominant ants, bees and social wasps. With an astonishing diversity of biologically interesting traits Hymenoptera have significant economic impact (e.g. biological control and pollination) and thus was one of the first insect orders to benefit from genome sequencing[4]. Despite additional genomes sequenced (Table 1) or in preparation (Figure 1, Table 2), genomic resources remain lacking for most major lineages, which comprise 28 superfamilies, 97 families, and 8,422 genera. Herein we discuss insights gained and opportunities for improvements for Hymenopteran genomics (noting that ants are reviewed separately).

State of Hymenopteran Genomic Resources

Features of Hymenopteran genomes

Hymenopteran genomes possess some notable and unique features. Hymenoptera are haplodiploid: unfertilized eggs produce haploid males and fertilized eggs produce diploid females [5]. Haplodiploidy engenders interesting biology related to sex determination[6], control of sex ratios, and relatedness[7], but is also useful for whole genome sequencing. Enough DNA can be extracted from a single large haploid male to provide material for whole genome sequencing without genetic variation (e.g. [8]). Another notable feature of some Hymenoptera is extremely high recombination rates, especially in social species such as the honey bee, where recombination rates are among the highest known for any organism[9].

Among sequenced examples, hymenopteran genomes are moderate in size (80% are between 180–340Mb) with a few exceptions [10–12]. Most possess 12,000–20,000 genes (note counts are highly annotation-pipeline and assembly contiguity dependent[13]), with a relatively low content of repetitive and transposable elements. One unusual feature is low

GC content, which ranges from 30–45% depending on the species[8]. Although the reason for low GC content is not yet understood, it may be related to GC-biased gene conversion and high recombination rates[14]. Due to their relatively small size and simple structure, Hymenopteran genomes are readily assembled and highly tractable for genome sequencing[15].

Genomes Generate Biological Understanding

The Hymenoptera include everything from herbivores to pollinators to predators to parasites, and the species filling each of these ecological roles are endowed with a complex set of physiological and behavioral adaptations. Genomic studies have informed applied questions related to pollinator health[16] and biological control using parasitoid wasps[17]. Comparative genomics approaches have unlocked some understanding of the molecular evolutionary basis for these adaptations, including the evolution of eusociality[8,12,18], social parasitism[19,20], venom function[19–22], and behavioral host specificity[23,24].

Potential Genomic Insights into Hymenoptera Biology

Pollinator health and management research has greatly benefited from the availability of reference genomes for many important pollinators (Table 1). Genomic approaches to pollinator health allow us to screen for disease, elucidate the effects of parasites, and investigate the immune response to environmental stressors and pathogens. Examples include developing new biomarkers of honey bee colony health [25–29], characterizing environmental stress responses and optimal developmental temperature regimes for the alfalfa leafcutting bee (an intensively managed solitary pollinator) [30,31] and developing other genomic and transcriptomic indicators of health in wild and managed pollinators[32–39]. Honey bee genomic nutrition research has been fruitful in generating insights into mechanisms of bee health [40–43]. Expanding this emerging field to native, unmanaged bees can provide a comparative perspective on how wild bee health is influenced by environmental diet restriction due to habitat loss[44]. This approach can also improve our understanding of innate and acquired immunity function among bees, which is critical for management and conservation efforts[45,46].

The vast majority of Hymenoptera species are parasitoids (green in Figure 1 and Table 2). The majority of insect species are attacked by at least one species of parasitic Hymenoptera[47–51], with complex and intimate host-parasitoid interactions [52] and narrow host ranges[53] which may drive ecological speciation[54,55]. Parasitoids are economically important as biological control agents of invasive pests, reducing pest abundance and impact, providing a safe, cost-effective alternative to insecticides [56], so understanding the genetic architecture and evolution of traits like climatic adaptation and host specificity is critical. Such research is revealing diverse mechanisms by which parasitoid wasps overcome the host immune system, including venoms, immunosuppressive factors such as polydnaviruses and virus-like particles, specialized embryonic cells (teratocytes), and larval secretions [57–59]. Parasitoids can also co-opt host endocrine systems, disrupting host development [60] or manipulating host behavior [61,62]. Recent findings have revealed evolutionary changes in some wasp lineages in association with microbes that affect the interactions with their host, suggesting much remains to be discovered. Turnover of integrated viral genomes within Braconidae and Ichnuemonidae wasp genomes are more complex than once anticipated [63–65]. Genomes in progress for three parasitoids with a common host have revealed that each has separate mechanisms to overcome host immunity and other defenses (M. Strand, personal communication) demonstrating that comparative genomics can reveal more information than phylogeny alone as illulstrated by the rich collection of research stemming from genomes in the genus *Nasonia* (Pteromalidae; [66]introduces the collection), though annotation of these genomes leveraged the extensive history of research on *Nasonia* genetics[67]. Comparable research on species from other families will be needed to fully realize the potential of genomics for parasitic Hymenoptera.

Mechanisms and evolution of social behavior are an emphasis of Hymenoptera genomic research. Aculeata are known for sophisticated social behavior within colonies of some ants, bees, and wasps, with eusociality arising multiple times within this clade[68,69]. Glimpses into the molecular basis for this cooperative lifestyle were among the most anticipated findings from the initial sequencing of the honey bee genome [4] while more recent comparative genomic approaches have placed these initial findings within a broader phylogenetic context[8,12,18]. Comparative methods are particularly useful for understanding the molecular basis for hymenopteran behavior given the impressive diversity of social niches[70,71]. Although social wasps have been a model lineage for understanding the evolution of sociality[72], there are currently only two published genomes for this group, both within the paper wasp genus *Polistes*[8,18].

While most of the focus of hymenopteran genomics has been on social evolution, the Hymenoptera offer many opportunities to further investigate the molecular basis for other aspects of development and animal behavior including maternal care, social parasitism, and foraging/hunting behavior. In some cases, the conceptual framework and predictions are already in place (e.g., social parasitism[73], development[74–79]), others can be enhanced by those generated for other taxonomic groups (e.g., venom evolution in snakes[80], genomic basis of diet shifts[81,82]).

Taxa that are underrepresented in genomics

Given the deep evolutionary distances between major hymenopteran families[83], selecting appropriate taxa for comparison presents a substantial challenge. Crown-group Hymenoptera originated 250–300 mya and spans evolutionary distances more than 3-fold those of modern birds[1,83,84]. Bees shared a common ancestor ~100 mya, and bees+apioid wasps diverged from ants ~145 mya, similar to the split between marsupial and placental mammals (>160 mya)[85]. Increasing the number of taxa sampled within each lineage, as well as the total number of lineages sampled will provide higher resolution to interpret genomic signatures of key phenotypes. In addition, we suggest specific groups that may be particularly appropriate for additional comparisons.

Expanding sampling of Hymenoptera genomes to include one or several genomes per family would provide a useful framework for future evolutionary studies within the order. Although significant recent progress has been made resolving higher-level phylogenetic relationships

[83,86–88], important uncertainties remain at the superfamily (Figure 1) and family levels, especially outside of the Aculeata. Having genomic data for all 97 families would help overcome common phylogenetic problems, such as insufficient data, incomplete lineages sorting, base composition bias, and long-branch attraction. Multiple carefully chosen representatives of each family would even further reduce issues related to poor taxon sampling[83]. While producing phylogenies with entire genomes is still too expensive for most multi-taxon studies, having a high quality genome for each family would enable more economical reduced-representation phylogenomics across more taxa [89,90]. Having a complete sampling of Hymenoptera genomes at the family level, would also provide a better evaluation of genome size variation and gene family evolution over the entire order. For developmental biology examinations, species should include samples that are readily available for experiments such as embryological and larval time series sampling for gene expression and localization.

Parasitoids are an immensely diverse group for those interested in biological control applications and evolutionary biology[91,92], however the genomes of only 14 species in five families have been published, with draft genomes of ~30 more species (one additional family) in progress (Figure 1, Table 1).

To study polyembryonic development[78], genomes from the four families have this trait and comparative genomics across these families would be informative. Two have been sequenced (Table 1, *M. cingulum* (Braconidae) and *C. floridanum* (Encyrtidae)); thus including at least one polyembryonic species from the Platygastridae and Dryinidae families is a priority that would fit in the 0.05% species sample. Because different families of parasitoids use different taxa of hosts with very different biologies, understanding mechanisms parasitoids use in overcoming host immunity and host choice will benefit by having genomes of at least one parasitoid species per family. Including additional samples to allow comparisons of parasitoids sharing the same host, such as *Drosophila*, and pairing with genomes of the hosts will greatly enable comparative studies across lineages and host/parasite interactions[93].

Comparative genomic approaches to understanding the evolution of eusociality will benefit from increasing the depth of coverage within key wasp and bee families, especially the Vespidae, Apidae and Halictidae. Each of these families includes a diversity of social lifestyles, along with closely related solitary individuals. In a few key lineages such as vespid wasps and carpenter bees (Apidae: Xylocopinae), there are also opportunities to compare genomes within lineages in which the entire spectrum of sociality occurs, from solitary to weakly social to highly eusocial[71]. These highly informative species, though underrepresented in previous genome sequencing efforts, have currently projects underway to fill these gaps, with eventual insight into the full spectrum of sociality evolution [94]. The sweat bees (Halictidae) are also particularly useful for social evolution comparative studies, representing at least two independent origins of eusociality, a dozen lineages that have reverted back to a solitary lifestyle[95–97], and with several species in the genera *Halictus*, *Lasioglossum*, and *Megalopta* with facultative expression of eusociality (where individuals or populations vary in solitarily or socially nesting). Understanding the genomic basis for *intra-specific* variation in social behavior can illuminate the evolutionary processes that may have been particularly important at the origins of eusociality. We propose including ten additional samples to enhance comparative genomics of social behavior corresponding to environmental factors, such as latitude or elevation[98–100], genetic influences [70] and *within* population variation due to foundress reproductive strategy[101] with dense sampling at fine phylogenetic scales.

Development of genomic resources for taxa from the non-social aculeate wasp families will provide a critical picture of the genomic substrate from which eusociality evolved, and additionally provide insight into the genomic signatures of other behavioral innovations, such as central place foraging (i.e., nesting), maternal care, and social parasitism. Particularly useful families include the spider wasps (Pompilidae), velvet ants (aka “cow killers”) (Mutillidae), thread-waisted wasps such as mud daubers (Sphecidae), and cicada killers and bee wolves (Crabronidae, including an independent origin of wasp eusociality). These groups are closely related to vespids and bees, and exhibit remarkable diversity in parental care, dietary breadth, parasitism, and venom function. Additionally, because wasp families are cosmopolitan and conspicuous, their genomes can be studied in the context of well-described behavior and natural history information.

Challenges

Several challenges may impede sequencing and assembly, as well as annotation, of the genomes of Hymenoptera including sample quantity, heterozygosity, and availability; functional interpretation, and unknowns. Though obtaining high quality DNA may be difficult because samples are lacking, (especially for parasitoids), for Chalcidoidea, the US National Science Foundation has funded a phylogenetics project that could make available high molecular weight DNA from 388 species in 294 genera in 24 families (John M. Heraty, personal communication). For bees, pinned specimens for many groups may be available from the U.S. National Pollinating Insect Collection at the USDA-ARS-PWA Pollinating Insect Research Unit. In addition, ARS scientists are routinely collecting new material in North America and could provide genome quality specimens (recently collected and identified) to interested collaborators for some families found in North America. Additionally, some available samples (also many parasitoids) are very small and yield ≤100 ng of DNA per wasp. Although enough DNA for short-read sequencing library preparation, extractions from many individuals are needed to provide sufficient DNA for long-read technologies and heterozygosity in these pooled samples contributes to assembly challenges. Theoretically this can be solved by inbreeding for multiple generations, however some species cannot be inbred (e.g. those with complementary sex determination, in which homozygosity causes mortality or sterile diploid males). Concerning annotation, genes that underlie interesting differences in biology often evolve rapidly, making it difficult to find homologs in species where gene functions are well known. Therefore there is a need for experimentally determined functions, (e.g. tissue specific expression and gene knockout/knockin). This is particularly true where differences in expression underlie differences in biology and distant actuators/enhancers and epigenetic modifications, may underlie differences in some key traits, (e.g. diapause differences among *Nasonia vitripennis* populations [102]). Finally, newly sequenced hymenopteran species may have genomic features that reduce genome assembly quality including large size, complex structure and high GC content.

Genome Quality and Cost Varies

Premier genomes are produced today using a combination of long-read sequencing and de novo contig assembly, long-range scaffolding with complementary technologies (Hi-C and BNG), and short-read base quality improvement. Such genomes are more contiguous, complete and correct than genomes generated with Sanger sequencing and while they cost many times less, they are still expensive compared to short read only assemblies. Short read only assemblies can have high fidelity despite short contigs, but the contigs are not as well scaffolded and the scaffolds contain many more gaps in the sequence than the premier assemblies. These short contig assemblies can be used for many comparative analyses to fill in missing branches in a phylogeny with less cost. We propose to combine these two types of assemblies in a strategic way to lessen the cost and optimize the utility of the data generated.

Other useful types of genomic data have been produced (ENCODE) or proposed (FAANG) to annotate other animals. At a minimum, long-read transcriptome data helps inform the order of exon containing contigs and itemize the variety of isoforms found in the organism and short-read RNAseq data can deeply sample expression data.

A Complete Catalogue is Possible

Although many strategies can be envisioned for future hymenopteran genomics, we suggest a three-pronged strategy focused on breadth, biology and diversity. Increasing the breadth of genome coverage across taxa of this hyper-diverse order will provide long-term scientific benefits, we propose obtaining high quality genomes from at least one representative of each family (81 samples). For the 15 families with more than 50 genera or more than 100 species we propose sampling an additional 0.05% of the species (27 samples, Table 2). For families of particular interest such as pollinators and parasitic wasps, we propose adding 42 species, bringing the total to 150 or 0.1% of the species. Premier genomes are less expensive than in the past, but still expensive so this may not be possible for all of these samples. Short read assemblies or 30× comparative mapping studies can be used to fill in the phylogenetic sampling with additional closely related species. Including transcript sequencing (with high quality long read data) is a cost effective adjunct to enhance the value of lower quality assemblies. With available samples, robust technologies and more reliable methods, this is a feasible task with the potential to impact studies for years into the future.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

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**of outstanding interest

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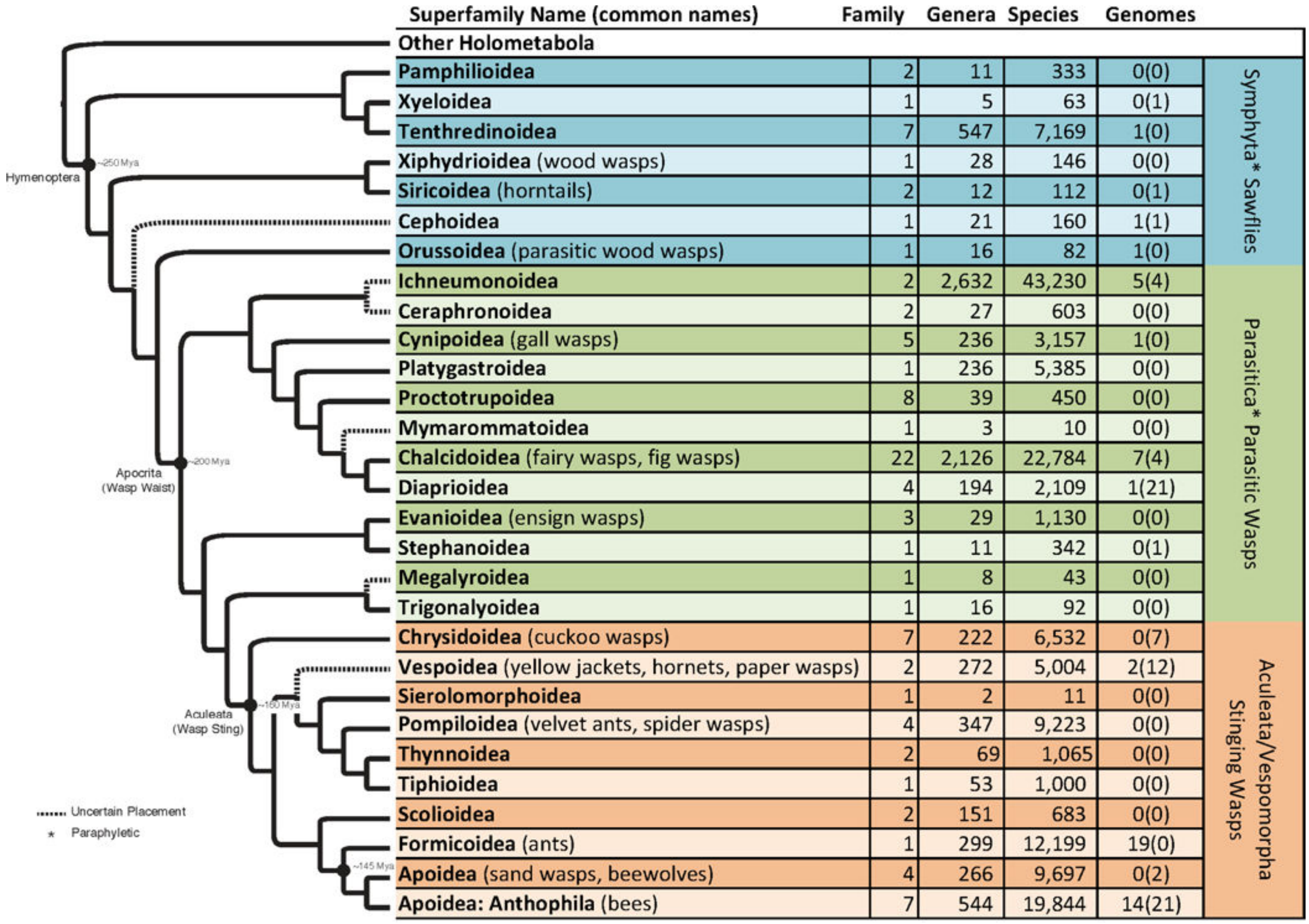
- Hyper-diverse Hymenoptera order includes parasitic and social insects
- Economically impactful for biological control and pollination
- Though second most sequenced order, still only 15% of families represented
- High quality genome assemblies are proposed for 150 Hymenopteran species
- With additional comparative genomes and transcriptomes to increase data breadth



Superfamily Name (common names)	Family	Genera	Species	Genomes
Other Holometabola				
Pamphilioidea	2	11	333	0(0)
Xyeloidea	1	5	63	0(1)
Tenthredinoidea	7	547	7,169	1(0)
Xiphydrioidea (wood wasps)	1	28	146	0(0)
Siricoidea (horntails)	2	12	112	0(1)
Cephoidea	1	21	160	1(1)
Orussoidea (parasitic wood wasps)	1	16	82	1(0)
Ichneumonoidea	2	2,632	43,230	5(4)
Ceraphronoidea	2	27	603	0(0)
Cynipoidea (gall wasps)	5	236	3,157	1(0)
Platygastroidea	1	236	5,385	0(0)
Proctotrupoidea	8	39	450	0(0)
Mymarommatoidea	1	3	10	0(0)
Chalcidoidea (fairy wasps, fig wasps)	22	2,126	22,784	7(4)
Diaprioidea	4	194	2,109	1(21)
Evanioidea (ensign wasps)	3	29	1,130	0(0)
Stephanoidea	1	11	342	0(1)
Megalyroidea	1	8	43	0(0)
Trigonalyoidea	1	16	92	0(0)
Chrysidoidea (cuckoo wasps)	7	222	6,532	0(7)
Vespoidea (yellow jackets, hornets, paper wasps)	2	272	5,004	2(12)
Sierolomorphoidea	1	2	11	0(0)
Pompiloidea (velvet ants, spider wasps)	4	347	9,223	0(0)
Thynnoidea	2	69	1,065	0(0)
Tiphioidea	1	53	1,000	0(0)
Scolioidea	2	151	683	0(0)
Formicoidea (ants)	1	299	12,199	19(0)
Apoidea (sand wasps, beewolves)	4	266	9,697	0(2)
Apoidea: Anthophila (bees)	7	544	19,844	14(21)

Figure 1. Hymenoptera phylogeny and genome assemblies

Phylogeny based upon[83,88], with dotted lines marking lineages of uncertain placement, branches not to scale (=cladogram). Major groups shown on right, individual superfamilies listed with columns indicating the numbers of Familes, Genera, Species, Genomes in NCBI (in Progress).

Table 1

Hymenoptera Genomes in INDC. Family Formicidae 19 genomes are omitted (reviewed elsewhere).

Family	Scientific Name	Representative Assembly	Reference
Agaonidae	Ceratosolen solmsi	GCF_000503995.1	[103]
Apidae	Apis cerana	GCF_001442555.1	[104]
Apidae	Apis dorsata	GCF_000469605.1	[105]
Apidae	Apis florea	GCF_000184785.2	*[12]
Apidae	Apis mellifera†	GCF_000002195.4	[4,13]
Apidae	Bombus impatiens†	GCF_000188095.1	[106]
Apidae	Bombus terrestris†	GCF_000214255.1	[106]
Apidae	Ceratina calcarata	GCF_001652005.1	[107]
Apidae	Eufriesea mexicana	GCF_001483705.1	[12]
Apidae	Euglossa dilemma	GCA_002201625.1	[10]
Apidae	Habropoda laboriosa†	GCF_001263275.1	[12]
Apidae	Melipona quadrifasciata	GCA_001276565.1	[12]
Braconidae	Cotesia vestalis	GCA_000956155.1	*[108]
Braconidae	Diachasma alloeum	GCF_001412515.1	[109]
Braconidae	Fopius arisanus	GCF_000806365.1	[17]
Braconidae	Macrocentrus cingulum	GCA_002156465.1	[110]
Braconidae	Microplitis demolitor	GCF_000572035.2	[65]
Cephidae	Cephus cinctus	GCF_000341935.1	[111]
Diprionidae	Neodiprion lecontei	GCF_001263575.1	[112]
Encyrtidae	Copidosoma floridanum	GCF_000648655.1	[113]
Figitidae	Leptopilina clavipes	GCA_001855655.1	[114]
Halictidae	Dufourea novaeangliae	GCF_001272555.1	[12]
Halictidae	Lasioglossum albipes	GCA_000346575.1	[115]
Megachilidae	Megachile rotundata†	GCF_000220905.1	[12]
Orussidae	Orussus abietinus	GCF_000612105.1	[116]
Pteromalidae	Nasonia giraulti	GCA_000004775.1	[117]
Pteromalidae	Nasonia longicornis	GCA_000004795.1	[117]
Pteromalidae	Nasonia vitripennis	GCF_000002325.3	[117]
Pteromalidae	Trichomalopsis sarcophagae	GCA_002249905.1	[22]
Tenthredinidae	Athalia rosae	GCF_000344095.1	[116]
Trichogrammatidae	Trichogramma pretiosum	GCF_000599845.1	[113]
Vespidae	Polistes canadensis	GCF_001313835.1	[18]
Vespidae	Polistes dominula	GCF_001465965.1	[8]

† Important polinators.

* Genome unpublished but included in collection.

Table 2

Hymenoptera Families with Genera and Species counts and Genomes in NCBI, otherwise published (Pub), in progress (Prog), and proposed here(Prop). Classification citations (Class) follow [2,3] with updates from [47,83,118]. Counts of genera and species are modified from [2] with richness sources cited (Rich).

			Genomes								
	Superfamily	**Family**	**Total**	**NCBI**	**Pub**	**Prog**	**Prop**	**Genera**	**Species**	**Rich**	**Class**
Aculeata/Vespomorpha	Thynnoidea	Chyphotidae	–	–	–	–	1	2	65	[119]	[118]
		Thynnidae	–	–	–	–	2	67	1,000	[120]	[118]
	Tiphioidea	Tiphiidae	–	–	–	–	2	53	1,000	[1]	[118]
	Pompiloidea	Pompilidae	–	–	–	–	3	125	4,855	[1]	[118]
		Mutillidae	–	–	–	–	2	200	4,252	[1]	[118]
		Sapygidae	–	–	–	–	1	12	66	[121]	[118]
		Myrmosidae	–	–	–	–	1	10	50	[120]	[118]
	Sierolomorphoidea	Sierolomorphidae	–	–	–	–	1	2	11	[122]	[83]
	Vespoidea	Rhopalosomatidae	–	–	–	–	1	4	72	[1]	[118]
		Vespidae	14	2	–	12	–	268	4,932	[1]	[118]
	Formicoidea	Formicidae	20	19	1	n/a	n/a	299	12,199	[123]	[118]
	Apoidea	Ampulicidae	1	–	–	1	–	6	200	[124]	[118]
		Heterogynaidae	–	–	–	–	1	1	8	[124]	[118]
		Sphecidae	–	–	–	–	1	17	716	[124]	[118]
		Crabronidae*	1	–	–	1	3	242	8,773	[124]	[118]
	Apoidea: Anthophila	Apidae	12	v11	–	1	–	209	5,749	[125]	[118]
		Andrenidae	1	–	–	1	1	77	2,917	[125]	[118]

Superfamily	Family	Genomes Total	NCBI	Pub	Prog	Prop	Genera	Species	Rich	Class
	Megachilidae	3	1	–	2	–	76	4,096	[125]	[118]
	Melittidae	–	–	–	–	1	15	187	[125]	[118]
	Halictidae	19	2		17	–	79	4,327	[125]	[118]
	Stenotritidae	–	–	–	–	1	2	21	[125]	[118]
	Colletidae	–	–	–	–	2	86	2,547	[125]	[118]
Scolioidea	Scoliidae	–	–	–	–	1	143	560	[1]	[118]
	Bradynobaenidae s.s.	–	–	–	–	1	8	123	[119]	[118]
Chrysidoidea	Bethylidae	1	–	–	1	1	84	2,340	[1]	[118]
	Chrysididae	6	–	–	6	–	81	2,500	[1]	[118]
	Dryinidae	–	–	–	–	2	41	1,605	[1]	[118]
	Embolemidae	–	–	–	–	1	2	39	[1]	[118]
	Plumariidae	–	–	–	–	1	7	22	[1]	[118]
	Sclerogibbidae	–	–	–	–	1	3	20	[1]	[118]
	Scolebythidae	–	–	–	–	1	4	6	[1]	[118]
Megalyroidea	Megalyridae	–	–	–	–	1	8	43	[2]	[3]
Trigonalyoidea	Trigonalidae	–	–	–	–	1	16	92	[2]	[3]
Evanioidea	Aulacidae	–	–	–	–	1	2	185	[2]	[3]
	Evaniidae	–	–	–	–	1	21	449	[2]	[3]
	Gasteruptiidae	–	–	–	–	1	6	496	[2]	[3]
Stephanoidea	Stephanidae	1	–	–	1	–	11	342	[2]	[3]

			Genomes								
	Superfamily	**Family**	**Total**	**NCBI**	**Pub**	**Prog**	**Prop**	**Genera**	**Species**	**Rich**	**Class**
		Eulophidae	1	–	–	1	2	334	4,969	[2]	[3]

[*] 20 are low coverage genomes.