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Genomes of Diptera Brian M Wiegmann¹ and Stephen Richards²

4 Diptera (true flies) are among the most diverse holometabolan

- 5 insect orders and were the first eukaryotic order to have a
- 6 representative genome fully sequenced. 110 fly species have
- 7 publically available genome assemblies and many hundreds of
- 8 population-level genomes have been generated in the model
- 9 organisms Drosophila melanogaster and the malaria mosquito
- 10 Anopheles gambiae. Comparative genomics carried out in a
- n phylogenetic context is illuminating many aspects of fly
- biology, providing unprecedented insight into variability in
- 13 genome structure, gene content, genetic mechanisms, and 14 rates and patterns of evolution in genes, populations, and
- rates and patterns of evolution in genes, populations, and
- 15 species. Despite the rich availability of genomic resources in
- 16 flies, there remain many fly lineages to which new genome
- sequencing efforts should be directed. Such efforts would be
- 18 most valuable in fly families or clades that exhibit multiple
- origins of key fly behaviors such as blood feeding, phytophagy,
- 20 parasitism, pollination, and mycophagy.

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32 Introduction

Diptera (true flies) are among the most diverse insect 33 orders, in both species (approx. 158 000 described species 34 in 180+ families), and in the diversity of their life histo-35 ries, behaviors, trophic habits, human impacts and mor-36 phological adaptations [1]. Because of the unquestioned 37 importance of Drosophila melanogaster as the premier 38 genetic model organism; the tremendous harm caused 39 to human health by vectoring disease (e.g., mosquitoes, 40 *tsetse*) and to agriculture as pests (e.g., Mediterranean fruit fly: Ceratitis capitata; Hessian fly: Mayetiola destructor; 41

42 sheep blow fly: *Lucilia sericata*), flies were among the first

animals to have a fully sequenced genome and, as an 43 order, include the largest number of insect species with 44 full and draft genomes currently completed and publicly 45 available (110 genomes). This number is growing as 46 deeper genomic sampling opens up phylogenetic com-47 parisons to provide frameworks for evaluating genetic 48 mechanisms and evolutionary processes at species-level 49 and population-level. The breadth of genomic sampling 50 is also increasing throughout the order into non-model 51 groups [2,3^{••}]. This wider taxonomic coverage is espe-52 cially valuable for increasing the evolutionary scope of 53 assessments outside of Drosophila and mosquitoes. Phy-54 logenetic comparisons both within and between fly fami-55 lies have led to landmark studies in gene regulation and 56 repair [4–7], development [8,9], neurobiology [10,11], sex 57 determination [12], insecticide resistance [13,14], trophic 58 specialization [15] and ecological adaptation [16–18], 59 among many others. Without doubt, fly science ---60 advanced by NextGen sequencing and the growth of 61 more complete genomic resources — has driven the 62 genomics revolution in insects. Here, we briefly summa-63 rize the taxonomic distribution of available dipteran 64 genomes, review some of the most exciting findings 65 generated by a 'comparative genomics' approach and 66 provide some broad guidelines for choosing additional 67 taxa to sequence in the new era of rapid, low cost, draft 68 genomes. 69

Diptera genomes – current status

Molecular, phylogenetic, and fossil evidence place the 71 origin of flies in the late Permian \sim 260 mya, beginning at 72 about the same time of the other major holometabolan 73 orders [19,20]. Their prodigious morphological and 74 genetic diversity and an episodic history of rapid diversi-75 fication have challenged efforts to fully resolve the fly tree 76 of life, but phylogenomic studies are providing a major 77 new source of evidence and the expansion of more deeply 78 sampled genomic resources are rapidly improving our 79 understanding of the fly tree [1,21]. Most recent studies 80 support classification of flies into five major infraorders, 81 Tipulomorpha, Culicomorpha, Psychodomorpha, Bibio-82 nomorpha, and Brachycera [1,19,22]. The Brachycera 83 (short-horned Diptera) with about 20 suprafamilial groups 84 and over 80 000 described species contains major radia-85 tions both among the early diverging, Lower Brachycera 86 lineages (180 mya) and in the schizophoran Cyclorrhapha 87 or 'higher flies' (65 mya). Schizophoran Cyclorrhapha are 88 diverse taxonomically and behaviorally, with over 78 fam-89 ilies and a wide range of habits including multiple inde-90 pendent origins of phytophagy, parasitoidism, mycoph-91 agy, mammal parasitism and myiasis, blood-feeding, and 92 the widespread larval feeding habit of saprophagy on all 93

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2 Insect genomics

manner of decaying organic substrates. Important polli-94 nators occur throughout the order and repeated close 95 associations with flowering plants seem to have been 96 an important driver of fly morphological-diversity, spe-97 cies-diversity, and ecological diversity [23–25]. Genomes 98 are now available in all five infraorders, but of the 99 110 genomes currently available across Diptera, most 100 of these are represented by the many closely related 101 species sampled in just two families: Culicidae (mosqui-102 toes, Culicomorpha; 27 genomes) and Drosophilidae 103 104 (Brachycera: Cyclorrhapha: Schizophora: Ephydroidea; 33 genomes) (Table 1). 105

Taxonomic coverage of genome sequences is increasing 106 across Diptera through new rapid sequencing technolo-107 gies, 'informed' informatics pipelines that capitalize on 108 the existing knowledge base, and concerted efforts to 109 well-studied expand resources for clades 110 2,3^{••},26[•],27,28^{••}]. Logically, the available assemblies 111 have been completed primarily in medically or agricul-112 turally important species where these data provide impor-113 tant information for vast research communities to facili-114 tate exploration of potential control mechanisms. This 115 includes genomes in multiple non-mosquito, blood-feed-116 ing disease vectors, including sand flies (three species, 117 Psychodidae), tsetse (six species; Glossinidae), and stable 118 fly (one species; Muscidae); and, in crop or fruit pests like 119 the wheat pest Hessian fly and 10 species of true fruit flies 120 (Tephritidae), or the blow flies, Lucilia sericata and Lucilia 121 *cuprina*, which are myasis-causing pests of sheep [29]. Vicoso and Bachtrog [3^{••}] and Dikow *et al.* [2] recently 122 123 expanded genomic knowledge in flies by adding draft genomes in 35 species distributed throughout the order 124 and notably increasing coverage for non-model flies in the 125 Lower Diptera and Lower Brachycera. 126

Characteristics of the fly genome 127

Fly genomes are highly variable in size when compared 128 throughout the order ranging from 89.58 Mb (Antarctic 129 midge, Belgica antarctica) to 1.18 Gb (horn fly, Haematobia 130 irritans) (Animal Genome Size Database, accessed 1/2/ 2018). Genome size can also vary significantly within a 131 family, ranging widely in sampled mosquitoes (210 Mb to 132 1.9 Gb) and 2-3-fold within the relatively small sized 133 genomes of Drosophilidae (117–386 Mb) [30]. Variation 134 in genome size is likely the result of large differences in 135 transposable element (TE) and other repetitive non-136 coding DNA [31,32]. Studies of genome architecture, 137 gene content, synteny, inversions, and the evolution of 138 non-coding elements are important areas of comparative 139 genomic study in flies [33-35]. Extraordinary coverage in 140 Drosophila has lead to groundbreaking work on how new genes are formed [36,37], how genes and genomic regions 141 interact and are regulated [38], and how genomic events 142 can shape organismal history [39,40]. Gene content is also 143 highly variable in flies. Drosophilids and mosquitos can 144 vary by 5000 genes with 13 920 genes estimated in

Drosophila melanogaster, and 18 955 in Culex quinquefasciatus, but the extremes are as few as 13 517 in Belgica antarctica [41[•]] and as many as 23 884 in the house fly, Musca domestica [42]. Despite this, the dynamics of gene family evolution are increasingly resolved through the 146 availability of species-level phylogenetic comparisons. 147 Major changes in copy number associated with physio-148 logical and behavioral adaptations have been demon-149 strated for P450s, chemoreceptors, and odorant binding 150 proteins, for example in the house fly, presumably due to 151 their trophic behaviors, exposure to insecticides, and 152 associations with animal pathogens [14]. Expansion and 153 contraction in the overall gene copy number has been 154 shown to be as much as $5 \times$ faster in Anopheles than in 155 Drosophila [43[•]]. The large number of high quality assemblies available for multiple species of mosquitoes and 156 Drosophila has also enabled the discovery, exploration and evolutionary analysis of small regulatory elements such as 157 microRNA [44,45], PIWI and Aubergine [46], and func-158 tional small reading frames (smORF) [47]. 159

Genomic sequencing for flies began in Cyclorrhapha with 160 the completion of Drosophila melanogaster [48] and in the 161 Culicomorpha with malaria mosquito, Anopheles gambiae 162 [49] and yellow fever mosquito *Aedes aegypti* [50]. These 163 genomes catalyzed the successful establishment and 164 growth of genome databases, annotation reference librar-165 ies, and analysis tools and pipelines; but also invigorated 166 large international research consortia that produced excel-167 lent assemblies for 12 Drosophila species [33] and 168 16 Anopheline mosquitoes [51]. For this reason, most 169 of our knowledge of fly genome variability comes at two 170 widely differing levels of divergence. Mosquitoes and 171 Drosophila shared a common ancestor approximately 240 mya [19] thereby representing one of the oldest splits 172 among extant fly lineages. Among Drosophila and Anoph-173 eles species, splits are likely to span divergences from only 0.24 mya to as many as 22-55 mya for sampled Drosophila 174 [52] and from 0.54 through 1.8-100 mya among anophe-175 lines [43[•]]. Genomic comparisons of mosquito and *Dro*-176 sophila, and between flies and other insect orders, reveal a marked genome-wide evolutionary rate acceleration in 177 Diptera [53], making flies a truly 'long-branched' taxon 178 relative to other insects. Mosquito/Drosophila compari-179 sons show that these two flies have diverged at a signifi-180 cantly greater rate from each other as can be seen in 181 comparisons among ancient diverging vertebrates 182 (450 mya) [54,55]. 183

The impact of phylogenetically-informed dipteran comparative genomics

Diptera provide some of the best examples available in 186 insects as to the power of comparative genomics to 187 advance understanding of ecological and evolutionary 188 patterns and mechanisms, adaptations and physiological 189 functions, and the linkage of genotype and phenotype. A 190 striking example is the identification of patterns of 191

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