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Meiotic recombination is a key event of sexual reproduction in higher eukaryotes that shuffles allele combinations and promotes accurate segregation of chromosomes. The rate of meiotic recombination varies within and across species. All studied insects that show advanced eusociality have shown exceptional rates of meiotic recombination suggesting its role in the evolution of eusociality. Eusociality has evolved independently mostly in two insect orders: Hymneoptera (bees, wasps, and ants) and Blattodea (termites). The notion of high recombination rates is based on just eight estimates of recombination rate from eusocial Hymenoptera (four of which are from a single genus) representing a lack of breadth of data in eusocial insects. To overcome this limitation, this dissertation presents recombination rate estimates from three unexplored species representing the taxa of stingless bees and termites. The results confirm the association of high recombination rates and eusociality but suggest eusocial Hymenoptera generally exhibit higher recombination rates than eusocial Blattodea. The dissertation also reports unusual linkage patterns in male termites that suggest the possibility of an unconventional mechanism of genomic exchange in termites. Overall, this dissertation helps in increasing the breadth of available recombination rate data and strengthen the support for the hypothesis that advanced social evolution in insects invariably selects for high recombination rates.

GENOMIC ANALYSIS OF MEIOTIC RECOMBINATION IN SOCIAL INSECTS

by

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DEDICATION

Dedicated to my late father, Shri H.L. Waiker, who taught me the value of education and always encouraged me to think big.

APPROVAL PAGE

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I: GENERAL INTRODUCTION

Meiotic recombination

Meiosis is a key event of sexual reproduction in higher eukaryotes and thought to be a major innovation of eukaryotic life on the earth (Maynard Smith, 1978). It is a special mode of cell division that makes haploid gametes from a diploid cell. During this process, maternal and paternal chromosomes exchange their genetic material through meiotic recombination (Eichenlaub-Ritter, 2014). Recombination during meiosis is one of the defining features of sexual reproduction, creating new allelic combinations that did not exist on the same chromosome. From an evolutionary point of view, meiotic recombination helps mitigate a phenomenon called 'Hill-Robertson interference.' It is when advantageous alleles at different loci arise on a different background a competition occurs between them that inhibits adaptation. Recombination prevents this competition by bringing advantageous alleles to a common background and facilitating adaptation (Hill & Robertson, 1966). Furthermore, the advantageous allele might be linked to a deleterious allele that can reduce the efficacy of selection on the advantageous allele. In this case, recombination can break the association between advantageous and deleterious alleles (Ritz et al., 2017). Recombination can also purge deleterious mutation from natural populations that accumulate in organisms with limited recombination (termed as Muller's ratchet) (Felsenstein, 1974; Muller, 1964). Recombination can have deleterious effects on the fitness of organisms as well. For example, recombination can break the association in populations where beneficial alleles are present on the same haplotype resulting in lower progeny fitness (Otto & Lenormand, 2002).

In general, meiotic recombination influences the variability of content and structure in the eukaryotic genome and thus contributes to the evolution of eukaryotes (Stapley et al., 2017). The persistence and pervasiveness of recombination is explained by its ability to improve the efficacy

of selection via generation of haplotypic variations (Burt, 2000). The paradoxical role of meiotic recombination (generating new genetic combination making it a rapid source of genetic variability and reducing the fitness of a population by breaking up the favorable combination of alleles) is central to the evolution of sex (Otto, 2009) and speciation when there is gene flow (Felsenstein, 1981). In other words, the conditions that facilitate the formation of new species with gene flow are the same as those that impede the evolution of sex. Despite the absence of a unified evolutionary explanation for the importance of meiosis and recombination, it is ubiquitous in all eukaryotes (Hofstatter & Lahr, 2019; Speijer et al., 2015). The extensive research in meiotic recombination has enhanced our understanding of this process. However, several puzzles related to its mechanism, features, species or sex differences, and evolutionary benefits are yet to be solved (Lenormand et al., 2016).

Recombination is characterized cytologically by counting the number of chiasmata or by estimating frequency on a population of meiotic products between observable sets of markers on the genome (discussed in the next section). Mechanistically, meiosis involves one round of DNA replication and two rounds of cell division, thus halving the generated cells' genomic content. In the process of meiosis, the homologous chromosome pairs and undergo recombination (Kohl & Sekelsky, 2013). The recombination process is not just thought to be essential to increase genetic diversity but also provides a physical connection to the homologous chromosome and ensures faithful segregation (Capilla et al., 2016). At least one crossover per chromosome pair is necessary (termed as the ‘obligate crossover’), which puts a lower bound on the amount of recombination that occurs in most organisms (G. H. Jones & Franklin, 2006; S. Wang et al., 2015). In 1964, Robin Holliday described the mechanism of recombination in fungi (Holliday, 1964) which became the basis of a generally accepted model of recombination in eukaryotes. The process begins with

deliberate double-strand breaks (DSBs) on the genome. DSBs can compromise genome integrity if not repaired (Hochwagen & Amon, 2006) and therefore they are restricted in the process of meiosis both temporally (during prophase I) (Keeney et al., 2014) and spatially (in euchromatin regions preferentially in chromatin loops (Brachet et al., 2012) and specialized regions called 'hotspots' in many species) (de Massy, 2013). The DSBs can either be repaired via synthesis-dependent strand annealing (SDSA), resulting in the transfer of a short DNA segment called gene conversion (GC) (McMahill et al., 2007). The alternate route of repair consists of reciprocal strand exchange called double Holliday junction (dHJ), in which the two strands of homologous duplexes swap pairing partners across a short region. The DNA resolvases then cleave these junctions to reestablish the two separate duplexes. The gene conversion outcomes in this resolution could be a non-crossover (NCO) or a crossover (CO) depending upon how resolvase nicked strands (Allers & Lichten, 2001; Kohl & Sekelsky, 2013). DSBs in heterochromatin regions such as centromere can be resolved with an NCO rather than a CO (Brachet et al., 2012) affecting the rate of recombination (see next section). The relative ratio of CO to NCO varies among species, and the mechanism behind this variation is unknown (Singh, 2012). Both of these outcomes are accompanied by a short gene conversion sequence that fills in the DSB on one homologous chromosome with the sequence from the other homolog. The region exchanged by COs can extend up to several megabases, while region associated with NCO gene conversion have been estimated to span ~50-1000 bp (Baudat et al., 2010; Jeffreys & May, 2004). Due to technical limitations, detecting NCO events is challenging, while the CO events have much larger genomic region and are detectable (Gay et al., 2007). The distribution of DSBs and the ratio of CO to NCO also depends on the genomic architecture and recombination-specific proteins (discussed in the next section), which can affect the recombination rate.

Variation in meiotic recombination rates

Recombination maps are the primary source to quantify meiotic recombination, which is based on the probability of recombination events between known markers along the genome (Jones et al., 1997). It is a correlation of recombination distance (in centimorgan or cM) between marker pairs and respective physical distance, in the number of base pairs (in bp or Mb). The unit cM denotes the expected number of crossovers between two markers in 100 meioses (Haldane, 1919). Differences in recombination rate (usually expressed in cM/Mb) determine the amount of genetic variation within a population and the rate at which new combinations of alleles are introduced in the population (Smukowski & Noor, 2011). This measure of recombination rate is an average likelihood of recombining from sampling a population and does not represent the level of recombination in a single gametocyte cell. The rate of recombination varies substantially among species, among individuals, between sexes, and among different parts of the genome (Lynch, 2006; Wilfert et al., 2007). These variations are not well understood, and it has been suggested that different taxa-specific mechanisms may control recombination frequency and landscape, and a unified explanation is still lacking (Stapley et al., 2017).

A closer look at different scales is needed to understand some of these variations. At the species level, sex differences have been observed in many organisms (Hedrick, 2007). In some species, the absence of recombination has been observed in one sex (called Achiasmate species). For example, males in *Drosophila* and females in *Bombyx* are achiasmatic (Haldane, 1922). The lower autosomal recombination rate in the heterogametic sex may reflect a pleiotropic consequence of selection against recombination between the sex chromosomes (Satomura et al., 2019) while it has also been suggested that no recombination in the heterogametic sex reflects selection to maintain recombination on the X or Z chromosomes in the homogametic sex

(Lenormand & Dutheil, 2005). Species with recombination in both sexes (called heterochiasmate species) can show a range of the ratio of female to male recombination (Lenormand & Dutheil, 2005). For example, in atlantic salmon, the rate of recombination ratio is 8.26 times higher in females than males (Moen et al., 2004) whereas it is only 0.7 in Japanese flounder (Castaño-Sánchez et al., 2010). Additionally, sex differences in recombination may be more local such as human males exhibit higher recombination at telomeric regions while females show higher recombination near centromere (Kong et al., 2002). Females in some mammals have longer bivalents (less compact chromatin) which facilitates DSBs to resolve as CO and thus can explain some sex differences in recombination rates (Petkov et al., 2007; Talbert & Henikoff, 2010). An evolutionary explanation for sex differences in recombination rates in heterochiasmate species is thought to be due to the haploid selection, i.e., the sex with more intense haploid selection should have a lower recombination rate because it minimizes the recombination load (Lenormand, n.d.). At the chromosomal scale, a minimum number of crossovers must be achieved for proper segregation (Fledel-Alon et al., 2009). The haploid number and length of the chromosome can thus affect the recombination rate; for example, many birds with numerous short chromosomes tend to have high recombination to ensure proper disjunction (Groenen et al., 2009). The recombination rate also varies along the chromosome: higher towards distal ends while low around centromere, again for proper segregation (Ellermeier et al., 2010). Furthermore, crossover at one chromosome location prevents another crossover from occurring nearby, a phenomenon known as crossover interference (Hillers, 2004). Crossover interference is important in proper chromosomal segregation and limits mutational cost due to DSBs (Otto & Payseur, 2019). Chromosomal inversions suppress recombination and even can suppress completely with a series of overlapping inversions along a chromosome because inversions cause problems with pairing and segregation

(Hoffmann & Rieseberg, 2008; Kirkpatrick & Barton, 2006). Sex chromosomes show reduced or no recombination primarily to facilitate sex determination (Furman et al., 2020). At molecular and genomic scale, while the core meiotic recombination machinery is mostly conserved among different organisms (Villeneuve & Hillers, 2001); studies suggest that species-specific gene expression (Petit et al., 2017; Ziolkowski et al., 2017) and genome architecture (Brachet et al., 2012; T. V. Kent et al., 2017; Lynch, 2006; Tiley & Burleigh, 2015) are major contributing factors in the variation of recombination rate. Additionally, several features have been positively associated with recombination, such as GC content, gene density, simple repeats, transposable elements, and several sequence motifs (Smukowski & Noor, 2011). Large-scale DNA rearrangements have been documented to inhibit recombination, the reason of which is thought to be an ecological adaptation in certain plants (Fang et al., 2012; Lowry & Willis, 2010). Genomes are usually differentiated into gene-rich euchromatin and repeat-rich heterochromatin, with the latter often found around centromere and associated with suppression of recombination (Lawrence et al., 2017). GC-rich areas on genomes have been reported to have more recombination motifs (Bessoltane et al., 2012) and thus GC content can explain some of the recombination rate variations. Although, evidence suggests recombination drives GC content evolution in many species (Mugal et al., 2015) through GC-biased gene conversion (gBGC) (Pessia et al., 2012). gBGC is considered a non-adaptive process that favors G and C allele transmission during recombination repair (Duret & Galtier, 2009). The gBGC-driven base composition evolution is considered universal; however, eukaryotes and prokaryotes present conflicting views- the eukaryotes genomic GC content increase notably in regions subjected to frequent recombination, but it is not observed to the same extent in prokaryotic genomes (Bobay & Ochman, 2017; Bohlin & Pettersson, 2019). Genome-wide methylation at CpG sites, including methylation of

transposable elements, suppress recombination (Zemach et al., 2010). Some cis-acting modifiers (caused by polymorphisms at the site of recombination or on the same chromosome) and trans-acting modifiers (polymorphic loci encoding diffusible molecules that modulate recombination on same or different chromosomes) also control recombination (Lawrence et al., 2017). Moreover, the overlap of both modifiers can modulate recombination, such as trans-acting binding protein PRDM9 in conjunction with specific cis-motifs attract recombination machinery (Myers et al., 2010) by methylating proximal nucleosomes and recruits meiotic DSBs (Powers et al., 2016). Furthermore, PRDM9 has also been shown to drive DSB formation in human and mice affecting the distribution of recombination hotspots across genome (Baudat et al., 2010). Recombination hotspots are common in birds and mammals but fruit flies and nematodes do not have distinct hotspots (Smukowski & Noor, 2011). Maps of quantitative trait loci (QTL) have revealed roles of some sequence variants in modulating recombination rate (Johnston et al., 2016; Kadri et al., 2016; Sandor et al., 2012) with some variants have even shown sex-specific effects of recombination in humans (Kong et al., 2014). Finally, Recombination rate estimates have become more precise and method progress has enabled new fine scale genome studies (Comeron et al., 2012).

Among all studied organisms so far, protozoa and fungi show the highest rates of recombination (Wilfert et al., 2007). These organisms are often characterized by parasitic lifestyle, small genome, and an extended haploid and asexual phase during their life cycle. Parasites can adapt high recombination rate in response to host-induced selection in an arms race scenario of coevolution (termed “the Red Queen Hypothesis”) (Bell, 1982; Salathé et al., 2008). While high recombination in genomic regions of hosts have been observed (Kerstes et al., 2012; Kovalchuk et al., 2003), the high recombination rate is more pronounced in parasites with small physical genome sizes. Furthermore, presence of asexual phase in these organisms may

experience higher Hill-Robertson Interference (Hill & Robertson, 1968) and select for higher rates of recombination (Otto & Barton, 2001). In higher eukaryotes, social hymenopterans such as bees, ants, and wasps show high rates of recombination (Wilfert et al., 2007). Despite being a key component in the evolution of sexual reproduction, the evolution and maintenance of the variation in recombination rates across species are poorly understood (Henderson & Bomblies, 2021). Further fine-scale genomic studies in greater range of species are needed to understand these variations in detail.

Eusociality in insects

A species is considered 'social' in which organisms interacts with other members of same species. Eusociality is the highest level of organization in sociality which is defined by three fundamental traits namely, (a) cooperative brood care, (b) generation overlap and (c) differentiation of castes within the same colony (Michener, 1969; Wilson, 1971). The castes in eusocial animals are specialized behavioral groups which usually divides individuals to perform reproductive and non-reproductive duties. Eusociality exist in certain insects, crustaceans and mammals however mostly observed and studied in Hymenoptera (ants, bees and wasps) and Blattodea (termites).

Eusocial insects live in a complex society with a few reproductive members and large numbers of sterile workers (Korb, 2008). Eusocial insects show high degree of altruism where one or a few individuals produce all offspring while others commit themselves to sterility. Altruism is a cooperative behavior that is argued to be selected against because it reduce the fitness of performer relative to selfish individuals that do not perform the behavior (West et al., 2007). Kin selection theory is the most popular explanation for altruism in eusocial insects (Anderson, 1984; Queller & Strassmann, 1998). The basic empirical prediction of kin selection theory is the social

behavior should correlate with genetic relatedness (Eberhard, 1975). In general, it has been hypothesized that social organisms may have an evolutionary benefits to help each other if they share genes and the benefit proportional to the relatedness. This inclusive fitness theory (as termed by Hamilton) explains how selection works when individuals not only affect their own but also the fitness of relatives – a general expansion of Darwin's natural selection theory. Inclusive fitness theory (or kin selection theory) in eusocial insects predicts if the fitness effect is greater than zero then altruism will be favored (Hamilton, 1964a, 1964b). It was mathematically expressed as rb-c > 0, where c is the fitness cost to the altruist, b is fitness benefits to recipient of altruistic act and r is the genetic relatedness between them (Charnov, 1977). It is worth to note that kin selection is not restricted to altruism: rb (indirect fitness) and -c (direct fitness) may be applied to any social behavior (Gardner et al., 2011). Moreover, kin selection operates in organisms other than social insects and have been tested successfully in wide range of taxa (Bourke, 2011).

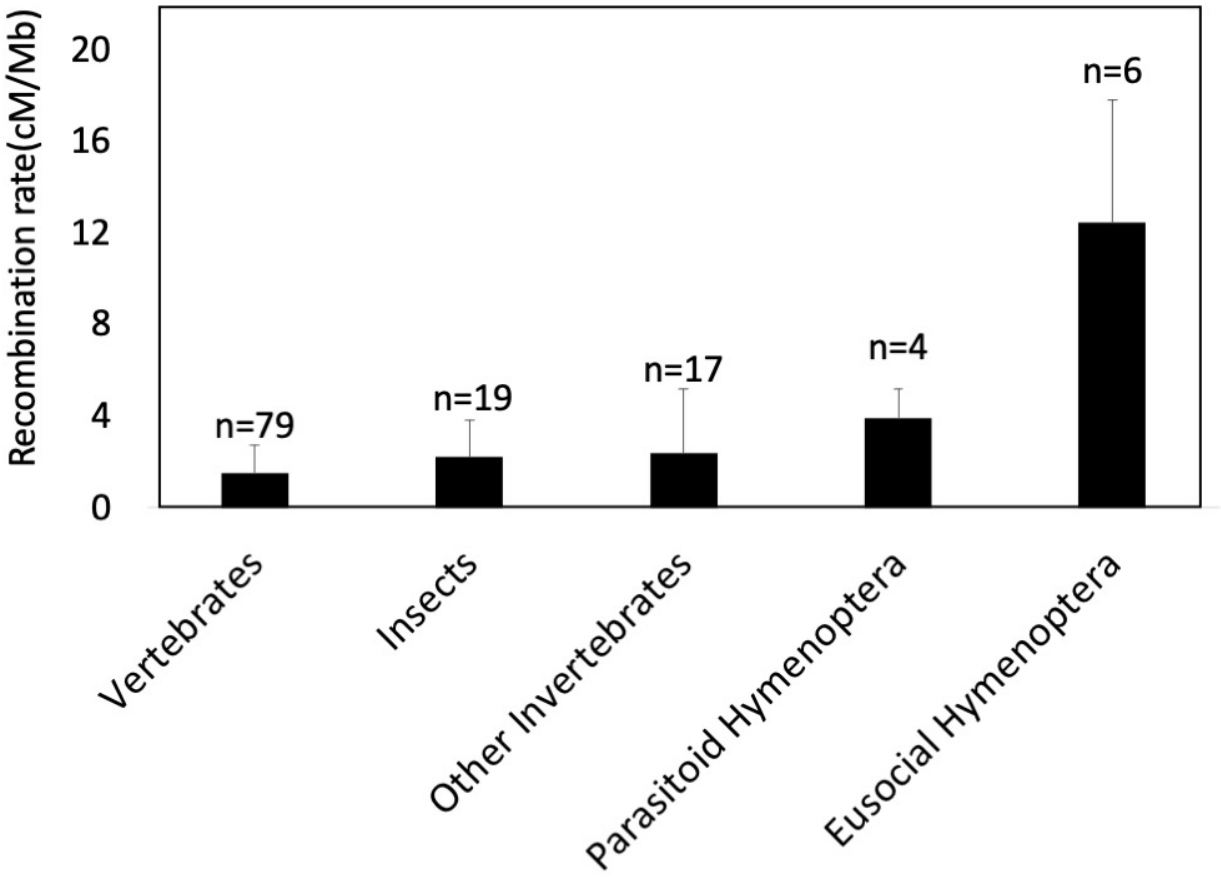
Evolution of eusociality in Hymenoptera has been proposed as a consequence of their sex-determination system of haplodiploidy in which males develop from unfertilized eggs and are haploid and females develop from fertilized eggs and are diploid (Hamilton, 1964a, 1964b). With haplodiploidy, sisters from singly-mated mothers, on average, share 75% of their genes whereas mother always share 50% of genes with her offspring. As a consequence, sisters will propagate their own genes by helping mother raise more sisters (reproductive altruism) than raise their own offspring. However, haplodiploidy explanation cannot be applied to explain eusociality in diplodiploid eusocial Isoptera (termites) for which alternative genetic explanations such as chromosomal linkage hypothesis and sex-ratio bias hypothesis have been proposed (Kobayashi et al., 2013; Thorne, 1997). The chromosomal linkage hypothesis suggest much of termite genome is sex-linked which makes sisters related above 50% and brothers related above 50% but

brother-sister relatedness less than 50% (Thorne, 1997). Sex-ratio bias hypothesis suggest that kin selection can result in sex ratio bias in when sex-asymmetric inbreeding occurs in an Asymmetric queen succession (AQS) termite colony (Kobayashi et al., 2013). Ecological factors such as symbiont hypothesis suggest with each molt, termites lose the lining of hindgut and subsequent bacteria and protozoa that colonize the gut for cellulose digestion. The need for recolonization of gut with microbes predisposed termites towards a eusociality (Thorne, 1997). Several hypotheses have been discussed for evolution of eusociality but support for a unified explanation that can be applied to both haplodiploid eusocial hymenoptera and diploid eusocial blattodea is still lacking.

Meiotic recombination rates in eusocial insects

Eusocial hymenopterans have shown exceptionally high rates of meiotic recombination compared to other eukaryotes (**Figure I-1 and Appendix A**) while no recombination information is available in eusocial blattodeans so far.

Figure I-1: Recombination rates of different animal groups (Data: Appendix A). Eusocial Hymenoptera group has shown exceptionally higher recombination rates compared to other groups.



This high rate of recombination has been suggested to be a property of eusociality (H. Liu et al., 2015) and has not been found in solitary insects (J. C. Jones et al., 2019). Although, some nonsocial insects such as *Drosophila pseudoobscura* also exhibit high recombination rate (McGaugh et al., 2012) and has been used to test variation in recombination rates between closely related species (Smukowski & Noor, 2011). It suggests a possibility that elevated recombination rates have arisen due to natural selection connected to eusociality. The cause for such an increase in this group of organisms is not known yet, and several hypotheses have also been proposed to explain this high recombination such as due to high chromosome number (Sherman, 1979); compensatory increase due to male haploidy (Hunt & Page, 1995); to stabilize homologous chromosome pairs (Baker et al., 1976); to reduce interindividual variance (Gadau et al., 2000); and

to increase genotypic diversity in complex insect society (Sirvio et al., 2006). However, none of these hypotheses are fully adequate to explain this phenomenon of high recombination (Gadau et al., 2000; C. F. Kent & Zayed, 2013). At present, all the theories that have been put forward explaining high recombination in eusocial insects can be principally categorized into three sets of arguments: first set is based on a short-term evolutionary advantage of recombination by increasing genotypic diversity to facilitate division of labor, colony fitness and disease resistance– the genotypic diversity hypothesis (Wilfert et al., 2007). Genetic diversity arguments have also been proposed to explain multiple mating by females (polyandry) in social Hymenoptera (Crozier & Fjerdingstad, 2001) and supported by numerous empirical studies (Mattila & Seeley, 2007; Tarpy & Seeley, 2006). However, modeling indicates that polyandry leads to a much stronger increase in offspring genetic diversity than any recombination effect and therefore it has been argued that increased recombination is unlikely to have evolved by selection on colony genetic diversity (Rueppell et al., 2012). Second set of argument is based on the idea that increased recombination rates have been selected for to facilitate evolutionary innovations in worker caste by alleviating negative effects of reproductive skew and small effective population size – social innovation hypothesis (C. F. Kent & Zayed, 2013). This hypothesis suggest that high recombination may facilitate the divergence of queen and worker phenotypes, especially when worker- and queen-selected genes are physically close (C. F. Kent & Zayed, 2013). Correlations between recombination rate and the location of genes that are important for caste-specific functions support this argument (C. F. Kent et al., 2012; H. Liu et al., 2015). This benefit can drive the higher recombination in honey bees (and potentially other eusocial insects) after eusociality evolves. However, these correlations have also been found in a solitary bee, *Megachile rotundata* (J. C. Jones et al., 2019) and inconsistent results have been found even in the same species *Apis mellifera*

(Wallberg et al., 2015), making this argument contentious. Furthermore, it is unknown whether the high rates in worker genes is connected to evolution of eusociality or ancestral orthologs of these genes already had high rates prior to the evolution of eusociality. The third argument suggest higher recombination rates has potential to reduce kin conflict by reducing variation in relatedness between workers (Sherman, 1979; Templeton, 1979) and selfish genetic elements (Haig & Grafen, 1991) in social insects – the reduction of genetic conflict hypothesis. The lack of a clear correlation between chromosome number and eusociality (L. Ross et al., 2015) argues against this hypothesis, but selfish genetic elements enabled by reduced recombination certainly exist in the form of "social chromosomes" (J. Wang et al., 2013) in genetically heterogeneous social insect societies. Thus, more empirical data are needed to evaluate the validity of these theoretical arguments and to fully understand the implications of high recombination on eusociality.

As explained in previous sections, the selection is more effective when the fates of alleles at different loci are uncoupled by recombination, but this general explanation does not explain why such increased recombination should be observed in social insects and not in other organisms. One possible explanation could be the low effective population size of social insects as the majority of the individuals are sterile workers (Wilson, 1971). In such small effective population, the genetic drift is at maximum generating linkage disequilibrium that has adverse effects on the multilocus selection (Glémin, 2003) because it will cause advantageous alleles to be found more often on different chromosomes than on the same chromosome, reducing the efficiency of natural selection. These effects can be counterbalanced by the adaptation of elevated recombination (Otto & Barton, 2001). Although eusocial benefits have been claimed as a result of high recombination, data on social insects are heavily biased towards selected species of eusocial. The understanding of relationship of eusociality in insects and meiotic recombination is limited by small number of

social (and related nonsocial) insect species for which recombination rate data is known. Eusociality is key feature of all termites and have been repeatedly evolved in Hymenoptera (Hughes, Oldroyd, et al., 2008; Legendre & Condamine, 2018). Recombination rate estimates from species from a range of independent origins would strengthen the notion that high recombination is consistently associated with eusociality. Currently, no recombination data are available from Meliponini tribe (Stingless bees) of Hymenoptera which makes up most specious tribe in Apinae (Michener, 2013). Meliponini is consist of more than 500 species of stingless bees with an independent evolutionary origin of eusociality (Cameron, 1993; Hedtke et al., 2013). Additionally, no recombination information is available from Isoptera (social Blattodeans) which consist of more than 3000 eusocial termite species (Krishna et al., 2013b, 2013c) and evolved 50 million years before eusocial Hymenoptera (Bourguignon et al., 2015). Based on previous observations on social insects, it is intuitive that these eusocial species may also show high rates of recombination, but it is important to note that these insects exhibit striking biological differences such as genetics and lifestyle. The social insect genomes studied so far are relatively small and compact (in terms of DNA sequence length) while genomes of termite and stingless bee are relatively large (Gregory, 2021). Being distant in phylogeny, there are several genetic and physiological differences between Hymenoptera and Isoptera (K. J. Howard & Thorne, 2010). Hymenoptera exhibit haplodiploid genetic system while termites are the only diploid eusocial group of insects (Choe & Crespi, 1997).

Sexual reproduction is the rule in most of the social insects however facultative use of asexual reproduction such as parthenogenesis has been shown in some ants and termites of independent phylogenetic origin (Wenseleers & Van Oystaeyen, 2011). The relationship between parthenogenesis and recombination has not been studied well (Lenormand, n.d.) although

parthenogenetic animals would increase Hill-Robertson Interference and should select for higher rates of recombination. This prediction has been supported by limited data (Stapley et al., 2017). Parthenogenesis could either be arrhenotokous, meaning haploid individuals are parthenogenetically or thelytokous where diploid individuals develop from unfertilized eggs (Klowden, 2007). While no reports are available on the correlation of recombination to arrhenotokous parthenogenesis, the recombination in thelytokous parthenogenesis seems to be reduced such as in *Apis mellifera capensis* pseudo-queens (Baudry et al., 2004) or completely absent such as in *Daphnia magna* (Hebert & Ward, 1972). *R. speratus* has facultative parthenogenesis in which new queens in the colony are produced thelytokously, whereas workers and primary reproductive are produced through sexual reproduction (Matsuura et al., 2009). Furthermore, when comparing the recombination rates between male and female of the same species, the sex difference cannot be ignored. It has been reported in multiple species and known as Haldane-Huxley rule, which states that lack of recombination or achiasmy occurs in heterogametic sex of a dioecious species. However, achiasmy is considered rare or unknown in the taxa with parthenogenetic reproduction (Lenormand & Dutheil, 2005). Due to haplodiploidy in eusocial hymenopterans, the recombination maps were only limited to females in case of eusocial insects, but the diplo-diploid termites provide an opportunity to construct recombination maps for both sexes.

This dissertation aims to increase the breadth of meiotic recombination rate data for eusocial insects while testing the hypothesis of elevated recombination rates at the same time. Chapter II and Chapter III describe new recombination maps for one stingless bee species (*Frieseomelitta varia*) and two species of subterranean termites (*Reticulitermes flavipes* and *Reticulitermes speratus*). Chapter II can provide estimate on a monandrous species and compare

the results with available polyandrous data where we are predicting that monandrous eusocial species exhibit higher recombination rates than their polyandrous counterparts if recombination is selected to increase intra-colonial genetic diversity. Chapter III can provide insights on impact of parthenogenesis on recombination by comparing a species that show no parthenogenesis (*R. flavipes*) to a closely related species that exhibit facultative parthenogenesis (*R. speratus*) where we are predicting *R.speratus* to exhibit higher recombination rate than *R. flavipes* based on the prediction. Chapter III will also compare the sex effects of termite, which will be the first study to report sex-differences in recombination rates in any social insect.

CHAPTER II: RECOMBINATION MAPPING OF THE BRAZILIAN STINGLESS BEE FRIESEOMELITTA VARIA CONFIRMS HIGH RECOMBINATION RATES IN SOCIAL HYMENOPTERA

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Background

Meiotic recombination is a universal process in sexual organisms that facilitates accurate segregation of chromosomes, which is achieved by the physical connection between homologous chromosomes. This connection depends on the formation of at least one reciprocal exchange between homologous chromosomes, a crossover (Mercier et al., 2015). In most eukaryotes, these crossover events occur once or twice per chromosome pair during meiosis (Fernandes et al., 2018). The narrow range is presumably a consequence of a rather invariant selection for a minimal number of crossovers that are required to avoid aneuploidy while minimizing the risk of genomic instability or other deleterious effects of recombination (Ritz et al., 2017). However, recombination also allows for a reciprocal exchange of genetic material, facilitating adaptive evolution (Hartfield & Keightley, 2012). Explanations of these evolutionary benefits include the reduction of Hill-Robertson interference (Hill & Robertson, 1966), the “Red Queen” hypothesis (Hamilton et al., 1990), and avoidance of Muller’s rachet (Kondrashov, 1982). The process of meiotic recombination increases the efficiency of natural selection by shuffling allele combinations in offspring and can create a greater genotypic variation that selection can act upon

(Capilla et al., 2016). Based on these evolutionary arguments, the recombination rate is predicted to vary more widely than what is structurally required. Accordingly, recombination rate varies significantly across species, populations, and individuals (Comeron et al., 2012; Hunter et al., 2016; Kawakami et al., 2017), in addition to local variation within genomes (Stapley et al., 2017). Some of this variation can be linked to directional selection and environmental fluctuation, while some may be non-adaptive, and yet other variation may be reported due to measurement errors (Becks & Agrawal, 2010; Carja et al., 2014; Ross-Ibarra, 2004; Smukowski & Noor, 2011; Stapley et al., 2017).

The high recombination rates of social Hymenoptera present a prominent case of recombination rates that are above the minimally required crossover numbers to guarantee proper chromosome segregation (Beye et al., 2006; Rueppell et al., 2016; Shi et al., 2013; Sirvio et al., 2006; Sirviö, Johnston, et al., 2011; Wilfert et al., 2007). Reports of high recombination rates in all studied social hymenopteran species – four honey bees, two ants, one wasp, and one bumblebee – support this notion when compared to the lower recombination rates of solitary hymenopterans (J. C. Jones et al., 2019; Wilfert et al., 2007). Social evolution in the order Hymenoptera has led repeatedly to highly complex societies with reproductive division of labor, cooperative brood care, and overlapping generations (Crespi & Yanega, 1995). Social insects vary in social complexity (Choe & Crespi, 1997), and the level of social complexity may be related to recombination rate (Sirviö, Johnston, et al., 2011; Stolle et al., 2011).

Current hypotheses to explain the high recombination rates of social insects can be principally divided into several arguments. The first set is based on a short-term evolutionary advantage of recombination by increasing genotypic diversity to enhance disease resistance, division of labor, or potentially other factors (J. C. Jones et al., 2019; Sirvio et al., 2006; Wilfert

et al., 2007). Genetic diversity arguments have also been proposed to explain multiple mating by females (polyandry) in social Hymenoptera (Crozier & Fjerdingstad, 2001) and supported by numerous empirical studies (Mattila & Seeley, 2007; Tarpy & Seeley, 2006). However, modeling indicates that polyandry leads to a much stronger increase in offspring genetic diversity than any recombination effect and therefore it has been argued that increased recombination is unlikely to have evolved by selection on colony genetic diversity (Rueppell et al., 2012). The second argument is based on the idea that increased recombination rates have been selected for to facilitate the rapid, independent evolution of caste-specific genes in social insects and allow the evolution of caste differences (C. F. Kent et al., 2012): High recombination may facilitate the divergence of queen and worker phenotypes, especially when worker- and queen- selected genes are physically close (C. F. Kent & Zayed, 2013). Correlations between recombination rate and the location of genes that are important for caste-specific functions support this argument (C. F. Kent & Zayed, 2013; H. Liu et al., 2015). However, these correlations have not been consistently found even in the same species *Apis mellifera* (Wallberg et al., 2015), making this argument contentious (J. C. Jones et al., 2019). A third argument, the potential for high genomic recombination to reduce the potential for kin conflict (Sherman, 1979; Templeton, 1979) and selfish genetic elements (Haig & Grafen, 1991) in social insects, is also plausible. The lack of a clear correlation between chromosome number and sociality (L. Ross et al., 2015) argues against this "reduction of genetic conflict" hypothesis, but selfish genetic elements enabled by reduced recombination certainly exist in the form of "social chromosomes" in genetically heterogeneous social insect societies (J. Wang et al., 2013). Thus, more empirical data are needed to evaluate the validity of these theoretical arguments.

In addition to their high genomic recombination rates, the socially complex ant, wasp, and honey bee species share important sociobiological features (Sirviö, Pamilo, et al., 2011). All of these species are polyandrous even though monandry was the ancestral state in each clade (Hughes, Oldroyd, et al., 2008). While polyandry may indicate selection for genetic diversity within colonies, recombination and polyandry may both increase genotypic diversity. Thus, we are predicting that monandrous species with advanced eusociality exhibit higher recombination rates than comparable polyandrous species if recombination is selected to increase intra-colonial genetic diversity. However, this prediction has not yet been tested. Furthermore, colonies of all investigated species contain only one reproductive queen, which is physically diverged from the worker castes. Nevertheless, workers have retained a functional ovary in all these species, indicating that queen-worker divergence is not as complete as in species with completely sterile workers. Based on a stronger divergent selection between worker- and queen-specific genes in species with complete worker sterility, such species are predicted to exhibit particularly high recombination rates based on the second of the above hypotheses.

An important taxon of social insects that has not yet been investigated regarding genomic recombination rates is the stingless bees (Meliponini), which make up the most specious tribe in the Apinae (Danforth et al., 2013). Stingless bees exhibit advanced eusociality and include several species that are essential pollinators in tropical ecosystems (Michener, 2013). The pantropical distribution of stingless bees suggests that their origin dates back to the ancient Gondwana supercontinent more than 100 million years ago (de Camargo & de Menezes Pedro, 1992). Despite their ecological relevance and biodiversity of about 600 described species in 60 genera, stingless bees remain understudied in all aspects, including their social behavior and genomic features (Hrncir et al., 2016; Rasmussen & Cameron, 2009), such as recombination.

This deficit contrasts particularly with honey bees, which only represent one genus of ten species that evolved during the past 25 million years (Cridland et al., 2017). Multiple studies within and across species of honey bees document their exceptional recombination rates, ranging from 17.4 - 37.0 centimorgan (cM) per megabase (Mb) (Beye et al., 2006; DeLory et al., 2020; H. Liu et al., 2015; C. R. Ross et al., 2015; Rueppell et al., 2016; Shi et al., 2013). Stingless bees have presumably diverged from honey bees over 80 million years ago, and it is unclear how social their common ancestor was (Danforth et al., 2013). Stingless bees rival honey bees in social complexity, are predominantly monandrous, and can have completely sterile workers (Boleli et al., 1999; Luna-Lucena et al., 2019; J. M. Peters et al., 1999; Vollet-Neto et al., 2018). Thus, based on both, genotypic diversity and caste divergence model, they are predicted to exhibit even higher recombination rates than honey bees. Stingless bees are also the most important missing taxon to assess the link between eusociality and high recombination rates in the Hymenoptera.

Frieseomelitta varia (Lepeletier, 1836) is a Neotropical, medium-sized species of stingless bee that occurs in several parts of Brazil (Moure et al., 1999). Living in large colonies with one monandrous queen, F. varia workers are completely sterile with heavily modified and non-functional ovaries (Boleli et al., 1999). The genome of *F. varia* has been sequenced and assembled (de Paula Freitas et al., 2020). Hence, we chose F. varia to construct a high-quality recombination map using SNP markers, benefitting from recent advances in sequencing technology and the large number of haploid sons produced by a single female in this species.

Results

The sequencing of genomic DNA of 180 *F. varia* males from a single mother resulted in highly variable numbers of high-quality reads ranging from 60,427 to 48,610,455 (mean: 13,428,476 ± 10,517,236 SD). A draft genome sequence for this mapping population was created

from two individuals with highest read counts. These data from two individuals proved sufficient for a 301 Mbp assembly with an average GC content of 37% (Table II-1). This assembly was used as a direct reference for SNP calling to only discover the SNPs that were segregating in our mapping population. However, for downstream analyses the published, more contiguous genome Fvar_1.2 (de Paula Freitas et al., 2020) was used. On average, 81% (±0.03% SD) of the reads from each sample aligned to this reference (Table II-S1), and 9514 SNP markers were extracted after preliminary quality filtering.

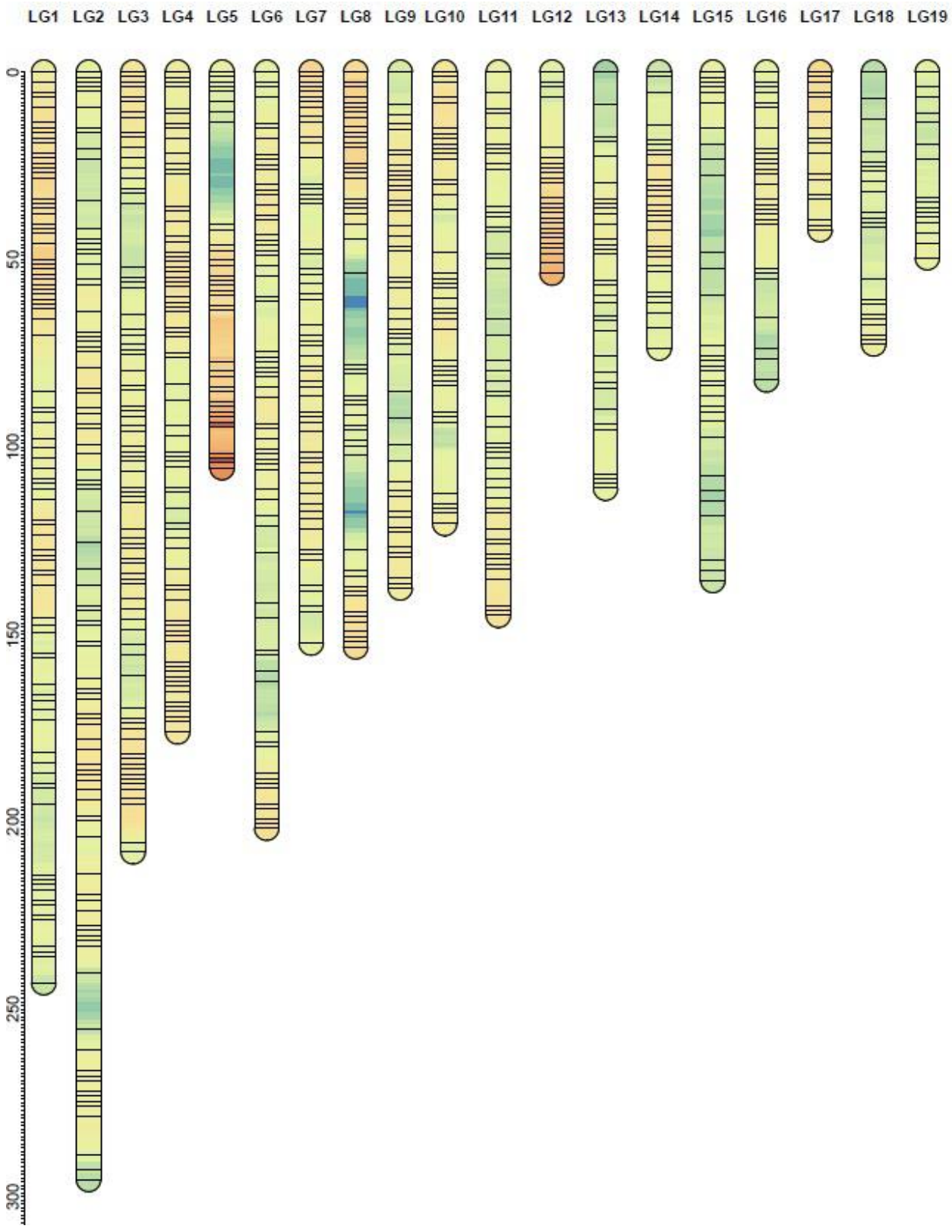
Table II-1: Genome assembly of Friseomelitta varia used in this study for SNP calling (Sequences deposited in NCBI BioProject accession number PRJNA668370)

Statistics	Value
# scaffolds	102310
Maximum Scaffold length	250.165 KB
Number of scaffolds >50 KB	556
N/L50	4687/16.294 KB
N/L90	25945/1.141 KB
GC (%)	36.93
Total genome length	301.35 MB

After filtering the original set of 9514 markers as described in methods, 1023 unique SNP markers were included in constructing the initial linkage map. The resulting map contained 20 linkage groups ranging from 49.5 cM to 242.9 cM, totaling 2573.2 cM. Post-hoc addition of previously excluded markers joined ends of two linkage groups but did not close any remaining linkage gaps (> 20cM). The final map of F. varia comprised 1417 high-quality SNP markers

assembled into 19 linkage groups (Figure II-1). Thus, the map is containing 4 extra linkage groups compared to 15 previously reported chromosomes (Kerr & da Silveira, 1972). The final map length was 2557.9 cM with linkage groups ranging from 42.0 cM to 295.4 cM. The average marker density was 0.55 markers per cM. The highest density was observed for group 12 (one marker every 1.03 cM), whereas group 15 had the lowest density (one marker every 3.31 cM) (Table II-2). Based on a physical genome size of 275 Mb (de Paula Freitas et al., 2020), the genetic map length resulted in a minimum estimate of 9.3 cM/Mb for the genome-wide recombination rate of *F. varia*.

Figure II-1: **Linkage map of F. varia. The final genetic length of the map was 2558 cM, which consisted of 19 linkage groups ranging from 42 cM to 295 cM. The linkage groups are sorted according to descending marker numbers from 158 markers in LG1 to 18 markers in LG19. Further efforts to end-join any of these linkage groups failed. Each horizontal black line indicates an SNP marker, and their vertical position indicates recombination distances among markers. The color depicts approximate marker density within linkage groups. For complete plot with marker labels and positions please refer Figure II-S1.**


LG1
LG2
LG3
LG4
LG5
LG6
LG7
LG8
LG9
LG10
LG11
LG12
LG13
LG14
LG15
LG16
LG17
LG18
LG19
0
50
100
150
200
250
300

The location of 99.1% of the mapped SNPs was identified in Fvar_1.2 based on best nBLAST results (Table II-S2). The SNP sequences mapped to 563 unique scaffolds (25.9% of all scaffolds) with a combined length of 204.8 Mb, representing 74.5 % of the total genome (Table II-2). Scaffolds that were covered by our linkage map were much larger (median length = 260348 bp) than scaffolds that were not represented (median = 4141 bp). The alignment of scaffolds to our linkage map uniquely mapped 451 scaffolds to our 21 linkage groups while 112 scaffolds mapped to multiple linkage groups (Figure II-2 and Figure II-S1). Based on the overall genome coverage of 74.5 %, the maximum estimate for the genome-wide recombination rate of *F. varia* equals 12.5 cM/Mb (2558 cM / 275 Mb * 0.745). On the basis of the length of the matching scaffolds, the average recombination rate for each linkage group was calculated, ranging from 9.6 to 17.5 cM/Mb (Table 2). A negative relationship between the average recombination rate of linkage groups and their physical length was observed, but this was not significant (Spearman's correlation, R= -0.38, n = 19, p-value= 0.11; Figure II-S2).

Table II-2: Summary of linkage groups of the *Frieseomelitta varia* map

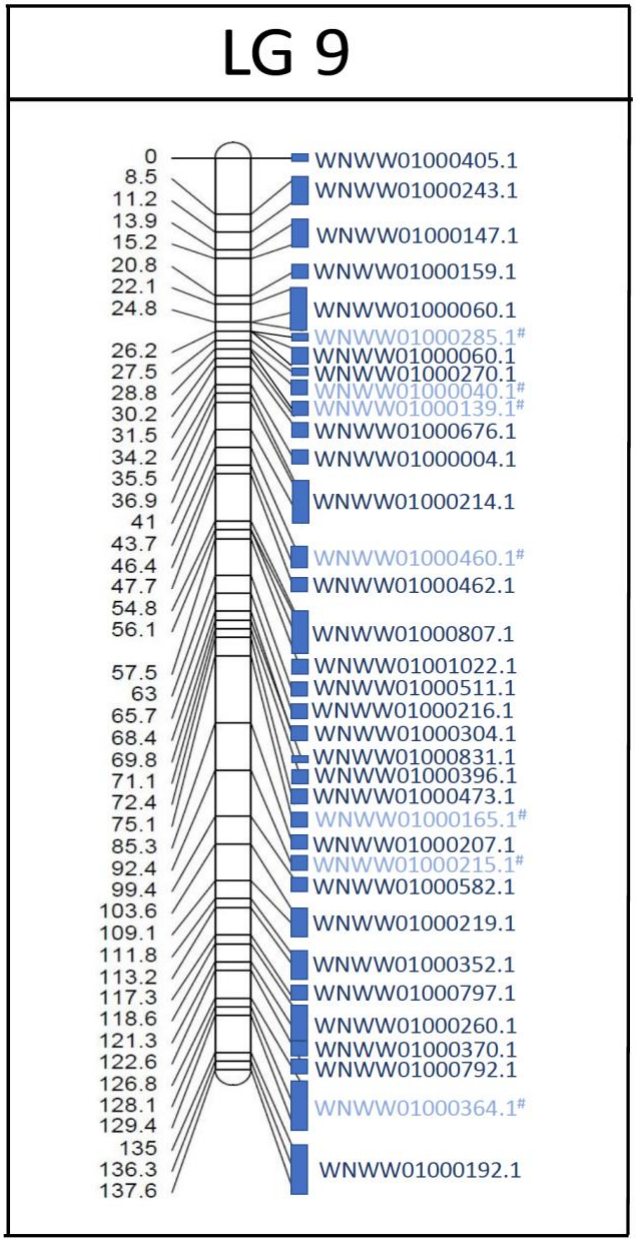
Linkage Group	Length (in cM)	Marker number	Marker density (Avg. cM distance between two consecutive markers)	# matched scaffolds	Combined scaffold length (in Mb)	Average LG rec. rate (LGRR) (in cM/Mb)
1	242.85	158	1.54	50	19.49	12.46
2	295.44	141	2.1	64	20.10	14.70
3	208.04	120	1.74	49	17.97	11.58

4	175.95	113	1.56	47	18.37	9.58
5	105.55	101	1.05	33	6.87	15.37
6	201.73	100	2.02	44	14.74	13.69
7	152.31	91	1.67	41	14.31	10.65
8	153.26	86	1.78	31	13.96	10.98
9	137.55	74	1.86	27	12.80	10.75
10	120.38	74	1.63	31	8.19	14.69
11	144.90	65	2.23	28	13.01	11.13
12	53.62	52	1.03	17	5.00	10.72
13	110.98	45	2.47	21	10.41	10.66
14	73.63	43	1.71	14	4.31	17.09
15	135.58	41	3.31	17	7.76	17.47
16	82.09	36	2.28	15	6.04	13.59
17	42.02	34	1.24	11	2.53	16.59
18	72.55	25	2.9	11	4.34	16.73
19	49.49	18	2.75	12	4.62	10.71
All	**2557.92**[$]	**1417**[$]	**1.81**[*]	**563**[$]	**204.82**[$]	**12.49**[*]

[$] Sum

[*] Weighted average

Figure II-2: Example of genomic scaffold alignment to the linkage map of F. varia. Most of the genome scaffolds (Fvar_1.2) matched to sequences associated with SNPs of a single linkage group and had no match with other groups (indicated by dark blue text). However, some scaffolds matched to more than one linkage group (highlighted in light blue text color and #). Blue boxes represent the approximate size of the matching scaffolds.



Discussion

Genome-wide recombination rates in social Hymenoptera are among the highest known in the Metazoa, but the molecular and evolutionary causes for this phenomenon remain unclear. Here, we present an additional case of high recombination in the highly social stingless bee Frieseomelitta varia, representing the diverse and important tribe Meliponini. This result

represents a significant expansion of the correlation between advanced sociality and elevated recombination rates because stingless bees have diverged from honey bees over 80 million year s ago (Cridland et al., 2017; Danforth et al., 2013). In addition to its taxonomic relevance, *F. varia* is significant because it exhibits monandry and completely sterile workers (Boleli et al., 1999; J. M. Peters et al., 1999), in contrast to all other social insects studied for recombination rates so far. The independently assembled genome of F. varia (de Paula Freitas et al., 2020) allowed us to assess genome coverage of our linkage map to further refine the recombination estimate. However, both available assemblies were highly fragmented (Our assembly: Scaffolds = 102,310 and N50 = 4687; Fvar_v1.2 assembly: Scaffolds = 2173 and N50 = 470,005) and therefore deemed insufficient for meaningful analyses of genomic correlates of local recombination rates, as in species with higher-quality genomic resources (J. C. Jones et al., 2019; C. F. Kent et al., 2012; H. Liu et al., 2015).

The 19 linkage groups of our linkage map did not match the haploid chromosome number of 15 (Kerr & da Silveira, 1972). This difference could result from a lack of high-quality markers in certain genomic regions in our study, leading to incomplete genome coverage. Alternatively, the cytological determination of the number of chromosomes could be incomplete because small chromosomes can be easily missed in species with numerous chromosomes. A recent discovery of haploid number of 17 in another Frieseomelitta species supports this notion (Nascimento et al., 2020). However, six of our linkage groups are smaller than the theoretical lower size limit of 100 cM (corresponding to one obligate crossover), which suggests that our linkage map is truly unsaturated. Given that over six-thousand markers were included in our analysis, this conclusion is surprising, but a systematic lack of sequencing results in AT-rich regions (The Honeybee Genome Sequencing Consortium, 2006) could be responsible. The unsaturated map

underestimates the actual genetic length by at least 120 cM (considering 30 cM depicts non-linkage between two groups, and we have potentially 4 excess groups). A corresponding adjustment increases the total genetic length of our linkage map to 2678 cM, resulting in a recombination estimate of 9.73 cM/Mbp.

The interpretation that our map is unsaturated is further supported by the comparison with the published genome "F_var1.2" (de Paula Freitas et al., 2020). However, each genomic scaffold that is not covered by our linkage map could be located in-between markers or represent true coverage gaps. Our markers cover about 25% of the scaffolds and 74% of the genome sequence. The missing scaffolds were generally shorter than the ones covered by our markers, indicating that these smaller scaffolds could indeed be located in the intervals between markers mapping to adjacent larger scaffolds. However, about 15% of missing scaffolds were larger than 100 kbp, and these are less likely to be located within the existing linkage groups. As an upper estimate, we thus used the missing 25% coverage of the sequenced genome to correct our total linkage map length and consequently genome-wide recombination estimate to 12.5 cM/Mbp.

Most of the mapped scaffolds correspond to unique linkage groups. However, 112 scaffolds were not unambiguously mapped to one linkage group due to conflicting nBLAST matches for their markers. This discrepancy between our linkage map and Fvar_v1.2 genome assembly may be due to inaccurate linkage mapping, nBLAST ambiguity due to sequence similarities of different genome locations, or problems in the genome assembly. Further discrepancies between the linkage map and the physical marker location were identified with respect to local marker order in a few scaffolds. Local marker ordering for linkage map construction can be error-prone when missing genotypes are incorporated. Our very stringent data exclusion standards have minimized the problem due to missing data but diminished our

sample size and thus statistical power to infer the correct local marker order. This interpretation is supported by our finding that 222 markers belonging to different genome scaffolds were not separated by any recombination event in our data. With increasing sample size, the physical distance would eventually translate into a certain, although potentially small, recombination fraction. For our genome-wide recombination estimate, this sampling problem represents a conservative error, and the estimate might have to be further corrected upwards.

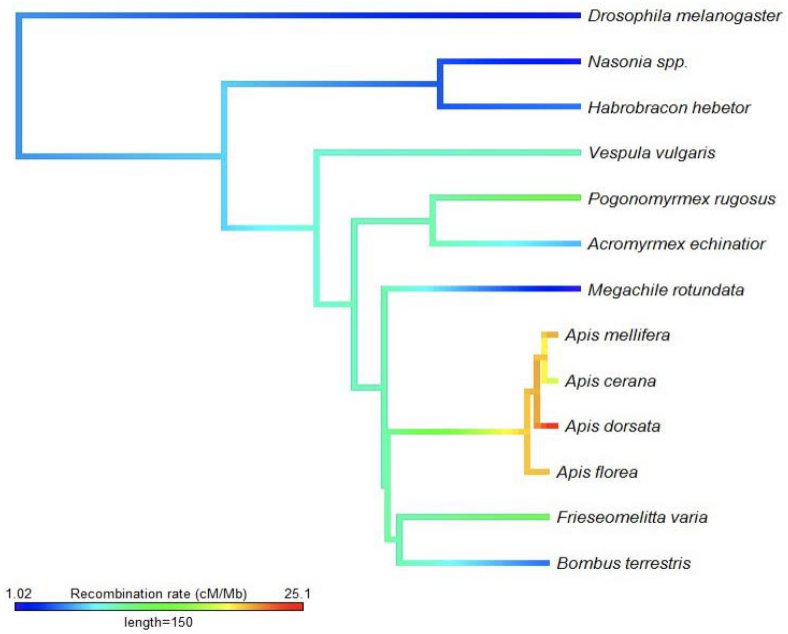
The number of chromosomes can itself impact genome-wide recombination rate, and the association between chromosome number and sociality has been tested with mixed results (L. Ross et al., 2015; Sherman, 1979). With at least 15 chromosomes, F. varia has a high number of chromosomes, and this contributes to a high genome-wide recombination rate if we assume at least one recombination event per chromosome. However, most linkage groups exceeded the corresponding value of 100cM, and the smaller groups likely have to be combined. The recombination rate estimates of our linkage groups were decreasing with the physical length of the corresponding genome sequence. However, this negative trend was not significant. Thus, the theoretically predicted relation may not exist in F. varia, particularly considering that some of the smaller linkage groups may, in fact represent fractions of large chromosomes. The absence of a negative relation between chromosome size and recombination rate has also been observed in Apis mellifera (Beye et al., 2006; H. Liu et al., 2015) and maybe another indication for selection of recombination in excess of the structurally required minimum.

Although the evolutionary conservation of extremely high recombination rates in the honey bee genus was established previously (Rueppell et al., 2016), based on our results, we cannot exclude the possibility that significantly elevated recombination rates may have originated before the evolution of honey bees and been evolutionarily conserved since the

divergence of stingless bees, bumble bees and honey bees (Figure II-3) about 80 million years ago (Cardinal et al., 2010). The recombination rates of orchid bees (Euglossini), the solitary sister taxon of honey bees (Woodard et al., 2011), is unknown. A high recombination rates of orchid bees would strengthen an ancestral origin of high recombination. In contrast, low recombination rates in the Euglossini, as predicted based on the solitary lifestyle, could indicate an evolutionary reduction of recombination rates in this taxon or multiple independent origins of elevated recombination rates in honey bees, bumble bees and stingless bees in accordance with eusociality (Woodard et al., 2011).

Figure II-3: Recombination rate evolution in Hymenoptera. Recombination rates in the solitary outgroup (Drosophila melanogaster (1.6 cM/Mb), as well as solitary Hymenoptera Nasonia spp (1.5 cM/Mb), Habrobracon hebetor (4.8 cM/Mb), and Megachile rotundata (1.0 cM/Mb) are generally low, while advanced eusocial species always exhibit higher estimates, including the newly studied stingless bee Frieseomellita varia (12.5 cM/Mb). However, estimates in honey bees remain particularly high (Apis florea: 20.8 cM/Mb, A. mellifera: 21.6 cM/Mb, A. cerana: 17.4 cM/Mb, and Apis dorsata: 25.1 cM/Mb), even when compared to other eusocial Hymenoptera, including ants (Acromyrmex echinatior: 6.4 cM/Mb and Pogonomyrmex rugosus: 14.0 cM/Mb), Bumble bees (Bombus terrestris: 8.9 cM/Mb), and wasps (Vespula vulgaris: 9.7 cM/Mb). The horizontal axis depicts approximate time, illustrating divergence between species. Recombination rate data sources: (J. C. Jones et al., 2019; Kawakami et al., 2019; H. Liu et al., 2017; Rueppell et al., 2016; Shi et al., 2013; Sirvio et al., 2006; Sirviö, Johnston, et al., 2011; Sirviö, Pamilo, et al., 2011; Wallberg et al., 2015; Wilfert et al., 2007). The tips of the tree are colored according

to recombination rate estimates. ML ancestral states at each node are estimated by fastAnc() function of Phytools and colored on the same gradient (Revell, 2012).



Compared to honey bees, our recombination rate estimates for *F. varia* are lower, regardless of species and methodology (Beye et al., 2006; H. Liu et al., 2015; Rueppell et al., 2016; Shi et al., 2013; Wallberg et al., 2015). This finding contrasts with the prediction of a higher rate in *F. varia*, based on either its monandry or its social complexity. Our results do not support the view that high recombination compensates for monandry, which reduces genetic diversity compared to polyandry. Thus, our results do not support genetic diversity arguments for the evolution of high recombination in social insects. Similarly, the stronger caste divergence of *F. varia* compared to honey bees (Boleli et al., 1999) and a specialized soldier caste (Grüter et al., 2017) do not coincide with a higher recombination rate, as predicted by our second hypothesis. In contrast, the high recombination rates of *Apis* and the less elevated rates of *F. varia* and other social Hymenoptera may provide some support for the "reduced genetic conflict" hypothesis: Selection for homogenizing genetic relatedness (Templeton, 1979) and against

selfish genetic elements (Haig & Grafen, 1991) is stronger in polyandrous than monandrous species (Galbraith et al., 2016), and honey bees exhibit not only exceptional recombination rates, but also an exceptional degree of polyandry (Tarpy & Nielsen, 2002). The absence of ovaries in workers of *F. varia* is an additional factor that might reduce intra-colonial conflict compared to honey bees (Boleli et al., 1999).

Conclusion

Our genome-wide recombination rate estimate of 9.3 – 12.5 cM/Mb for the stingless bee *Frieseomelitta varia* adds an important case study to the growing list of social insect species that exhibit more frequent meiotic recombination than their non-social counterparts. F. varia represents an independent taxon and indicates that elevated recombination rates in social insects are consistent, even though this species differs from previously studied social insects in regards to important life-history variables. Our study thus corroborates the association between high recombination rates and sociality in the Hymenoptera, although more comprehensive tests across many social taxa need to be performed, and our understanding of the proximate and ultimate causation of this association remains incomplete.

This study presented the the genomic recombination rate of a representative species of the important, highly social taxon Meliponini. With an estimate between 9.3 to 12.5 cM/Mb, we corroborate the association between high recombination rates and sociality in the Hymenoptera. This result strengthens the argument that advanced social evolution in social hymenopterans selects for high genomic recombination rates. Contrasting our new estimate to the consistently higher values of honey bees highlights the need for more empirical and theoretical work on the evolution of recombination in social insects.

Methods

Sampling, DNA extraction and Sequencing

Frieseomellita varia (Lepeletier) haploid males from a single mother were obtained from one colony from the southeast region of Brazil (Departamento de Genética Faculdade de Medicina de Ribeirão Preto, geographical coordinates: 21°10'12.2"S 47°51'34.2"W) between November 2018 and January 2019. The specimens were collected within the colony, kept in a glass vial on ice for about five minutes. Sex determination was based on presence of sexually dimorphic characters and gonads with the aid of a stereo microscope. To ensure that all offspring came from a single mother, the queen of the colony was color marked on the thorax (Posca Posta Pens, Japan) at the beginning of the experiment. During the collection period, no replacement of the queen was observed. Total genomic DNA was extracted from the whole body of 180 collected male offspring using the Wizard Genomic DNA Purification protocol (Promega, Dübendorf, Switzerland). The purity and concentration of extracted DNA were measured using a NanoDrop™ 1000 Spectrophotometer (Thermo Fisher Scientific, Wilmington, DE). Furthermore, DNA integrity was assessed by visually inspecting samples after gel electrophoresis (1.5% agarose, 1X SB Buffer).

From each sample, 200 ng of DNA was sent to the SNPsaurus™ sequencing facility (Eugene, Oregon) for SNP genotyping by whole-genome resequencing. In short, genomic DNA was converted to Illumina sequencing libraries with a partial Nextera DNA Flex™ reaction (SNPsaurus, Eugene, OR) and sequenced on a NovaSeq 6000 S4™ (Illumina Inc, San Diego, CA) lane with paired-end 150 bp reads. Sequence reads were quality filtered, and adaptors trimmed with bbduk (BBtools, Bushnell B. – sourceforge.net/projects/bbmap) using trim parameters: ktrim=r k=17 hdist=1 mink=8 minlen=100 qtrim=rtrimq=10pigz=t unpigz=t

ordered=t. The trimmed reads from two samples, FV116 and FV89, were combined to create a draft genome assembly with abyss-pe (Jackman et al., 2017) with default parameters. Reads from each sample were aligned to this draft assembly using bbmap (BBtools) using alignment parameters: minid=0.95 ambig=toss k=13 idtag maxindel=30 | samtools view -bSu - | samtools sort -@64 –o sort_file. The aligned reads were converted to a VCF format genotype using callvariants (BBtools) using callvariant parameters: ploidy=2 multisample=t nopassdot=f minavgmapq=15 minreadmapq=15 strandedcov=t. Variants that were identified and their surrounding 150 bp sequence were used as our SNP markers for linkage mapping as described below.

SNP filtering and linkage mapping

The VCF file containing high-quality SNPs and Indels was filtered before linkage map construction based on the following criteria using VCFTools (Danecek et al., 2011): all SNPs with >50% missing data were removed (--max-missing 0.5); SNPs with a quality score <30 were filtered out (--minQ 30); SNPs with a minor allele count of 3 or less were removed (--mac 3); and SNPs with a read depth of <6 were excluded (--minDP 6). All VCFTools filtering command lines can be found in **Appendix B**. Subsequently, the 76 individuals with the least missing data (<2%) were chosen to generate a linkage map. Initial grouping at LOD 8 resulted in 32 linkage groups. 106 markers that were unlinked or linked to only one other marker were discarded. A total of 9404 SNPs was left after this filtering step. The markers with more than one missing data point in this refined dataset were excluded in a final filtering step, leaving 3556 SNP markers for final linkage map construction.

The 3556 SNP markers were duplicated, and the doubled set was assigned the opposite phase for mapping ‘Phase unknown’ (Sirvio et al., 2006). SNPs were imported into RStudio

v1.2.1335 (RStudio Team, 2020) and analyzed with the RQTL package using Haldane mapping function (Broman et al., 2003). Linkage groups were formed using *formLinkageGroups()* based on a minimum LOD of 5 and a maximum recombination fraction of 0.3. Since markers were present in both phases, two symmetrical sets of linkage groups were generated as expected. After discarding one set, duplicate markers (=identical genotype information) were identified using the RQTL function - *findDupMarkers()* and eliminated when relating to the same SNP, leaving 1023 markers. The marker order in each linkage group was determined using the *orderMarkers()* command. Subsequently, all linkage groups were manually searched for gaps >20 cM, and to fill in those gaps, the *tryallpositions()* function was applied using 3975 previously excluded markers. After initial linkage map construction, 394 additional markers were manually added that had earlier been filtered out as duplicates. These markers were identical in genotype to markers already in the linkage map but physically mapped to a different genomic scaffold in the Fvar_1.2 genome (de Paula Freitas et al., 2020) and thus extended physical coverage. Thus, we had a total of 1417 markers in our final linkage map.

Comparison to F. varia genome

A nucleotide BLAST (nBLAST) search (Altschul et al., 1990) was performed for the sequence associated with each SNP marker in the *F. varia* genome assembly Fvar_v1.2 (GenBank assembly accession: GCA_011392965.1). An E-value threshold of 1e-50 was used, which returned at least one match for 1404 (of 1417 total) markers. The other markers were considered to be located in sequences that are missing from Fvar_v1.2. The best match of each sequence to a scaffold was considered for assigning scaffolds to linkage groups. When markers from different linkage groups matched the same scaffold, we assigned the scaffold to only one linkage group based on the following rules. First, scaffolds were assigned to a linkage group

based on a simple majority rule when the number of matching markers differed between linkage groups. In cases with an equal number of matching markers, the synteny of linkage groups and scaffolds was considered. Still unresolved cases were decided based on the E-value of individual nBLAST matches.

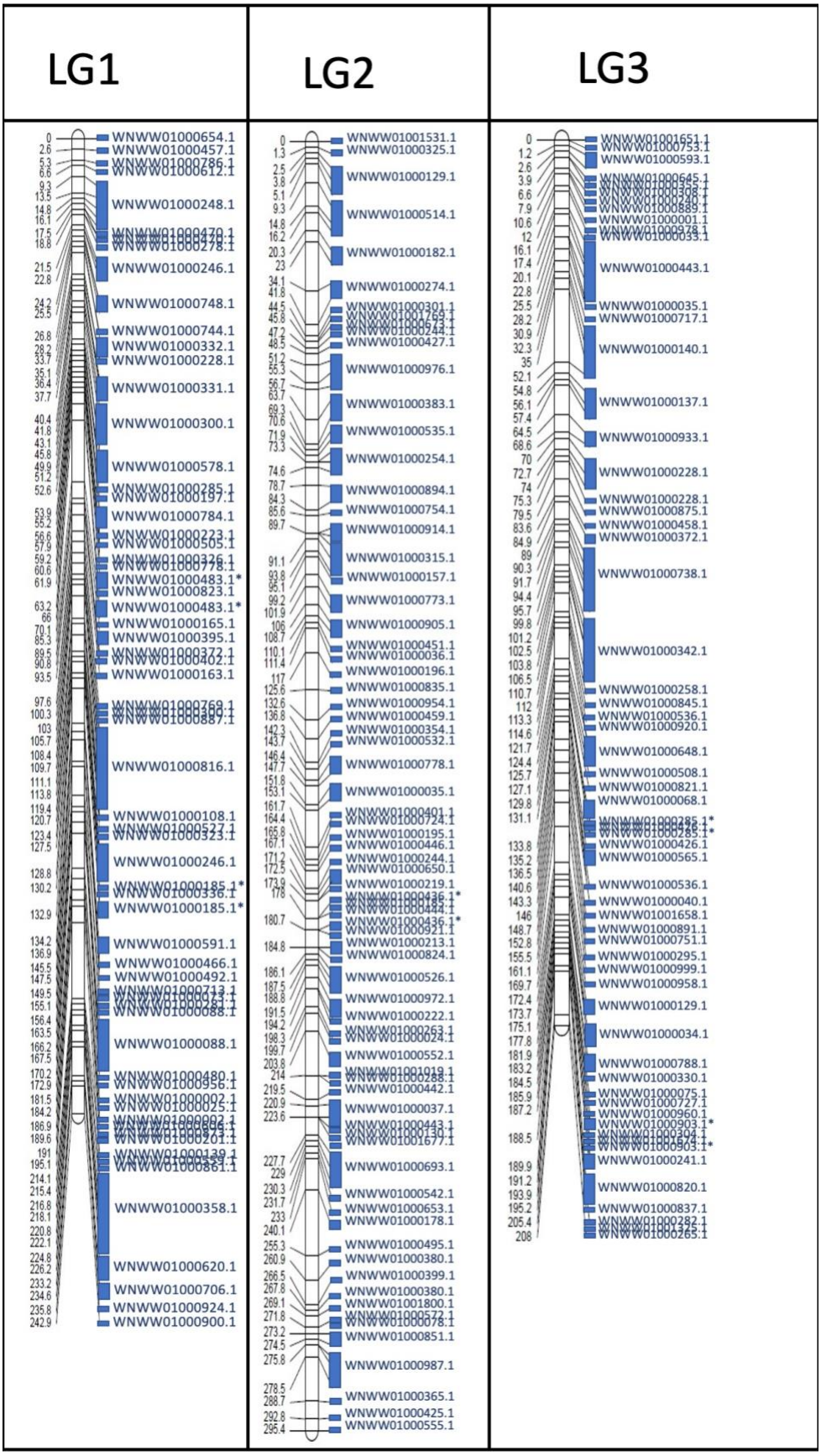
Comparative visualization of recombination rates

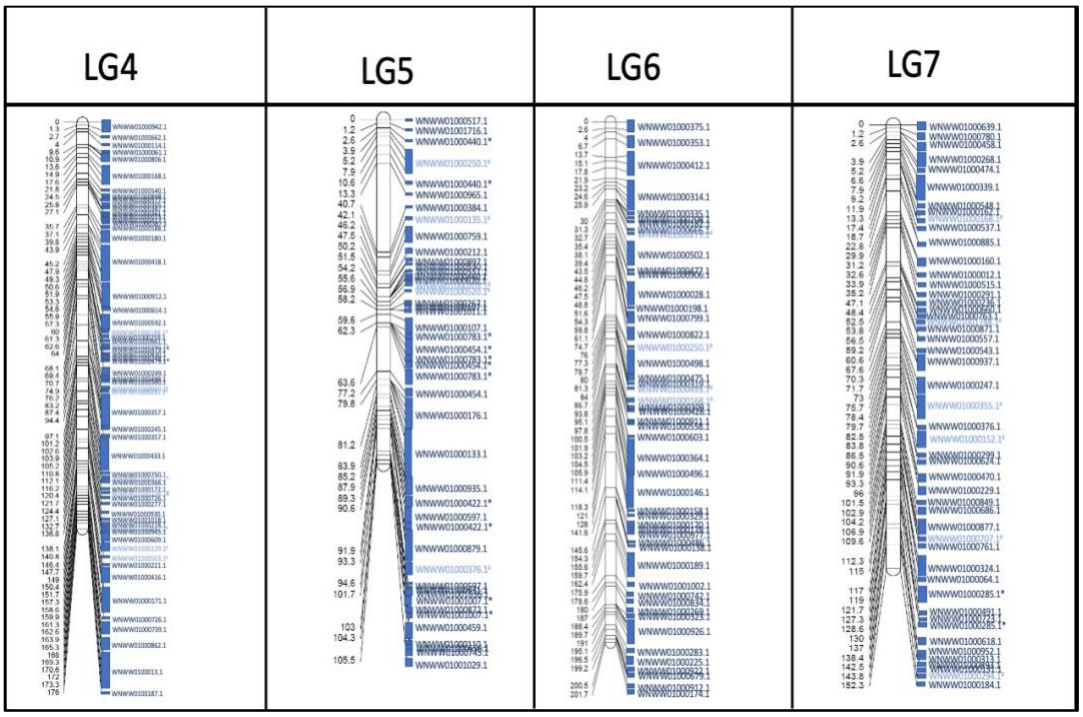
The R package *phytools* (Revell, 2012) was used to create a visual representation of the evolution of recombination rates in the order Hymenoptera by estimating ancestral states using fastAnc() function, based on their phylogeny (Brady et al., 2006; Cardinal & Danforth, 2011; Engel, 1998; Fath-Goodin & Webb, 2008; Garnery et al., 1991; Hasselmann et al., 2008; Litman et al., 2011; Misof et al., 2014; Park et al., 2011; R. S. Peters et al., 2017; Wenseleers & van Zweden, 2017; Woodard et al., 2011) and focusing on species with available genome-wide recombination rate estimates (J. C. Jones et al., 2019; Kawakami et al., 2019; H. Liu et al., 2017; Rueppell et al., 2016; Shi et al., 2013; Sirvio et al., 2006; Sirviö, Johnston, et al., 2011; Sirviö, Pamilo, et al., 2011; Wallberg et al., 2015; Wilfert et al., 2007).

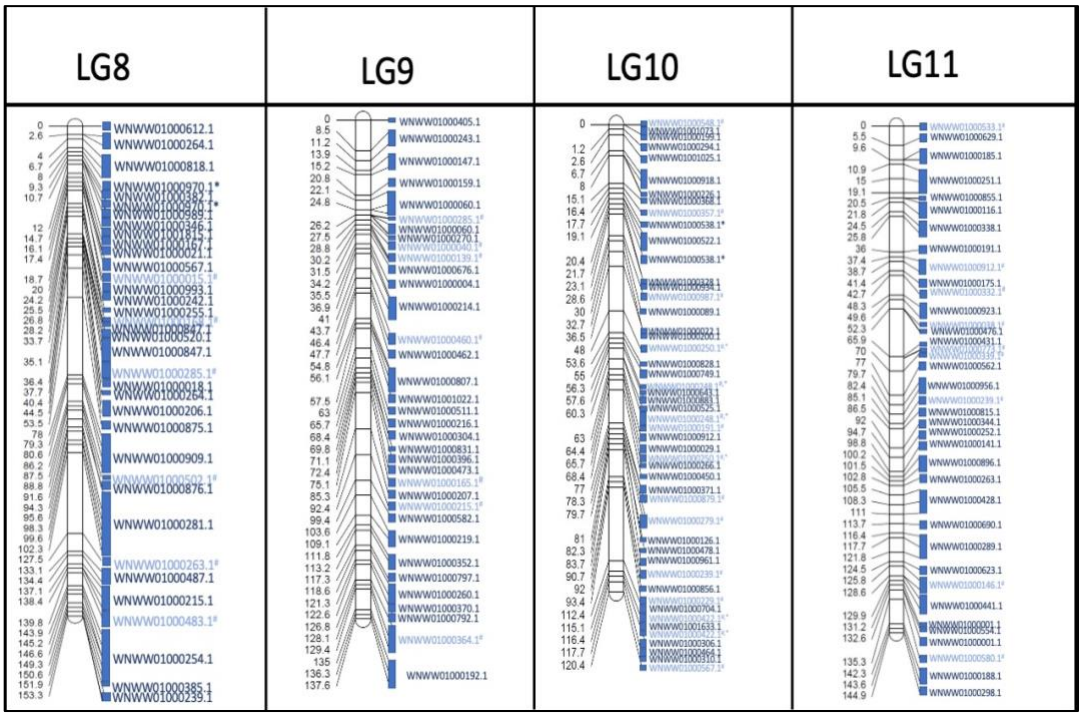
Supplementary Materials

The supplementary materials (high-resolution figures/tables and associated data files) for this chapter can also be accessed online at https://doi.org/10.1186/s12864-021-07987-3. Supplementary figures cited in the chapters are provided below in standard/reduced quality. Supplementary tables and files are not included here and are only available to view/download online.

Figure II-S1: Alignment of all linkage groups markers to F. varia genome assembly (F_var1.2). BLAST results show synteny between linkage groups to genome scaffolds. Some markers placed at the same position in the linkage map but returned hit to different scaffolds have denoted as an extra line. A marker without a BLAST hit points towards white space. Local ordering of some scaffolds shows hits more than once at some locations, denoted by an asterisk(*). Some scaffolds matched to more than one linkage group, and they have been highlighted with light blue text color and a hashtag superscript (#) for better visualization. Blue boxes are drawn to represent the matching genome scaffolds, but their size is only an approximate indicator of scaffold size.


LG1
LG2
LG3


LG4
LG5
LG6
LG7


LG8
LG9
LG10
LG11

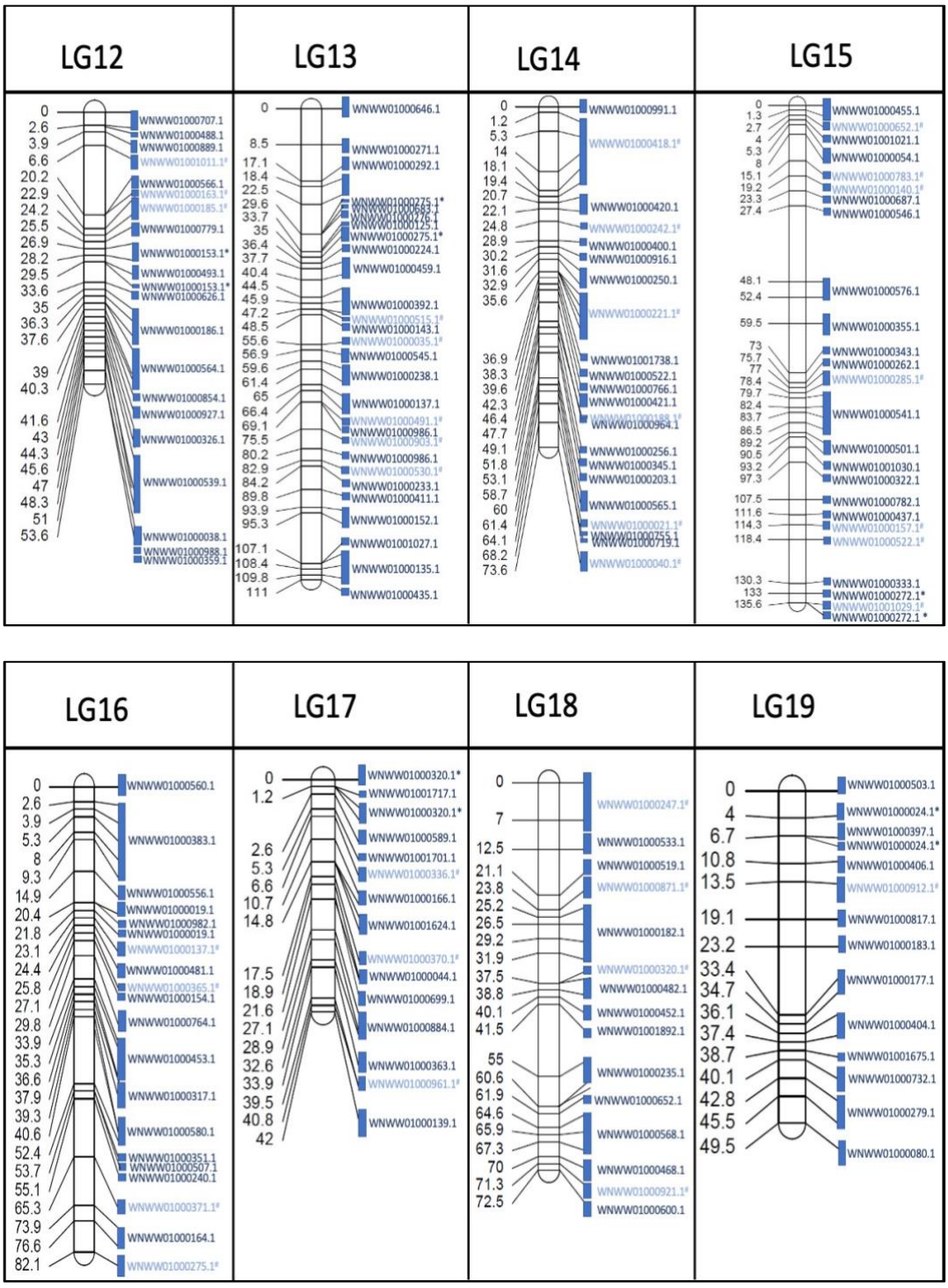

LG12
LG13
LG14
LG15
LG16
LG17
LG18
LG19

Figure II-S2: Relation between physical size and recombination rates of linkage groups. Spearman's correlation shows a negative trend between physical size to the recombination rate of linkage groups, although not statistically significant (R = -0.38, p= 0.11). This trend was expected since longer linkage groups will have less crossover per Mb and vice versa if we assume one obligate crossover per chromosome arm. The dark line shows a linear relationship with the shaded area represents a 95% confidence interval.

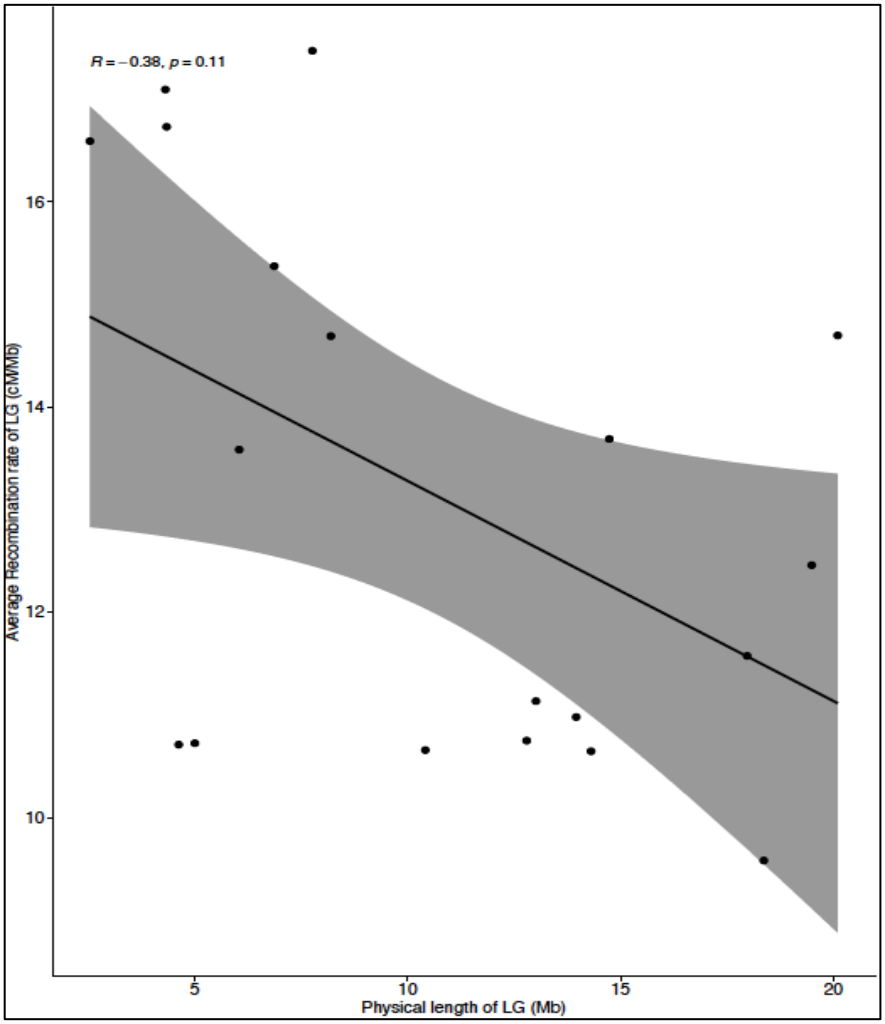


Table II-S1: Summary statistics of sequenced reads. The text file shows high-quality read counts for each male bee sample, % alignment to the reference, and proportion of the genotypes. Available to download at https://doi.org/10.5281/zenodo.4638539

Table II-S2: Sequence alignment output of markers to the genome assembly. BLAST output of mapped SNPs (with linkage group placement info) against *F. varia* genome assembly (F_var1.2). Available to download at https://doi.org/10.5281/zenodo.4638539

Table II-S3 (File S1): SNP markers variant and related statistics. Variant calling format (VCF) file that describes single nucleotide variation as well as genotype information of extracted 9514 markers. Available to download at https://doi.org/10.5281/zenodo.4638539

Associated contents

Abbreviations

cM: centimorgan; SNP: Single nucleotide polymorphism; VCF: Variant calling format; nBLAST: Nucleotide basic local alignment search tool; LG: Linkage group

Supplementary information

The online version contains supplementary material available at https://doi.org/10.1186/s12864-021-07987-3.

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Authors' contributions

OR and ZLPS conceived and supervised the project, DLL collected the samples and identified the sex of the specimen. FCPA and DLL extracted the DNA for sequencing. PW performed the linkage analyses and made figures and tables. OR advised and interpreted the results. FF contributed with access to F. varia genome first draft. PW and OR wrote the draft and revisions of this manuscript. All authors read, contributed to and approved the final version of the manuscript.

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Availability of data and materials

The raw sequencing data and draft genome assembly reported in this paper have been deposited in the NCBI BioProject accession number PRJNA668370(https://www.ncbi.nlm.nih.gov/bioproject/?term=PRJNA668370). In-text cited supplementary data (Figure S1, Figure S2, File S1, File S2, Table S1, and Table S2), R codes/macros (File S2), and data to generate phylogeny (File S3 and File S4) can be accessed as online supplementary materials and are also available to download at Zenodo database (https://doi.org/10.5281/zenodo.4638539).

Declarations

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Competing interests

The authors declare that they have no competing interests.

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CHAPTER III: ESTIMATION OF RECOMBINATION RATES IN SUBTERRANEAN TERMITES

Introduction

Termites are predominantly tropical eusocial insects classified at the taxonomic rank of infraorder Isoptera within the order Blattodea they share with cockroaches (Eggleton, 2010; Inward et al., 2007). There are approximately 3000 described species of termites in almost 300 genera (Krishna et al., 2013a) representing the second-largest group of insects (after ants) in terms of animal biomass (Charbonneau et al., 2013). Termites live together in complex societies and are characterized by the reproductive division of labor. There are typically three main adult castes: reproductives (queens, kings, and alates), workers, and soldiers (Eggleton, 2010), in addition to nymphs (resemble to small adults) that go through hemimetabolous development. The queen is generally the only egg-laying individual while the king is her consort, and his task is to mate with the queen regularly (Korb, 2008). Alates are winged male and female reproductives preparing to leave the nest to start new colonies. Workers perform several roles in a colony, including foraging, nursing, and housekeeping while soldiers defend the colonies. Some exceptions of these caste structures exist in some species that have no soldiers or species with no workers (Donovan et al., 2000). The breadth of polyphenism, a type of phenotypic plasticity in which more phenotypes are produced by the same genotypes, in termites is highest compared to all other eukaryotes (including other eusocial insects) (Simpson et al., 2011). Termite colonies can have several adult phenotypes simultaneously in a colony, depending on the species (Revely et al., 2021). Termites are one of the four major groups of eusocial insects (the other three being bees, wasps, and ants in the order Hymenoptera) that exhibit the highest

form of social behavior among all organisms. The factors and conditions that would have caused a convergent evolution of eusociality in hemimetabolous termites and holometabolous eusocial hymenopterans are unclear.

Eusociality in termites

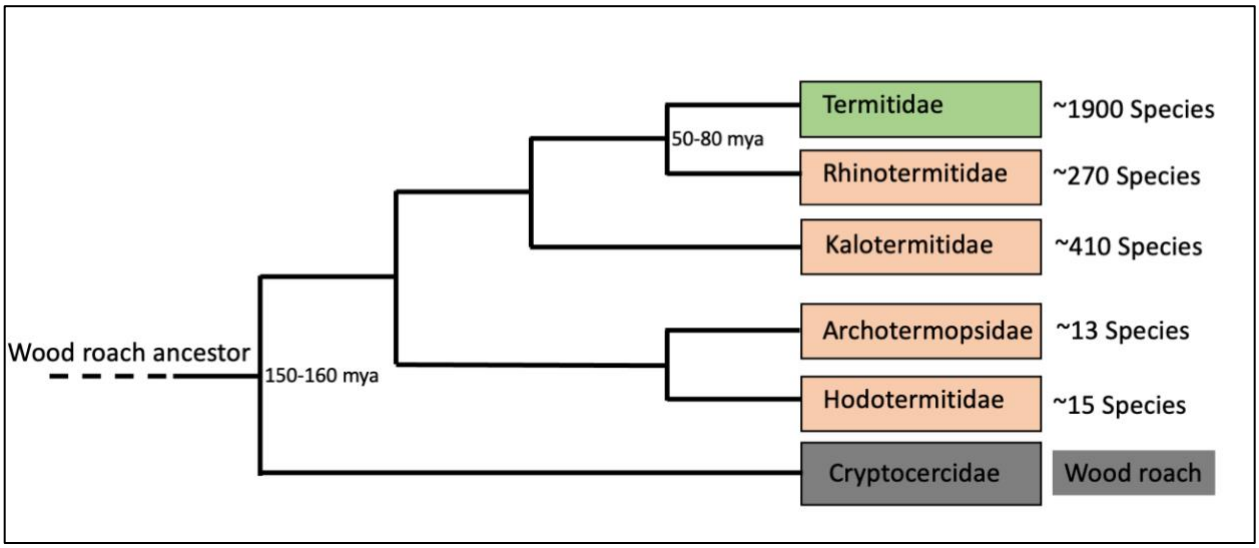
All termites are eusocial and have evolved from solitary cockroaches around 150 million years ago (mya) (Beccaloni & Eggleton, 2013; Inward et al., 2007). Kin selection is considered as a prominent evolutionary explanation in social insects to have evolved eusociality (Strassmann et al., 2011). Kin selection focuses on increasing the inclusive fitness of the group (Hamilton, 1964a, 1964b) by individuals who gain indirect fitness by raising relatives. In eusocial Hymenoptera, females develop from fertilized eggs while males develop from unfertilized eggs (haplodiploidy). The male offspring share 100% genes with their mother, while female offspring share 50% of genes with their mother. However, female offspring share 75% of their genes with sisters and thus indirectly pass on more genes by raising sisters than their own offspring (Hughes, Oldroyd, et al., 2008). The evidence for kin selection does not apply to diplodiploid termites based on the explanation of haplodiploid relatedness asymmetry. However, several other factors such as inbreeding and parthenogenesis have been suggested to affect relatedness among individuals and thus provide support for kin selection, although empirical evidence is weak (Korb & Thorne, 2017). Termites undergo regular inbreeding, creating asymmetry in gene transmission and higher relatedness but reducing fecundity and disease resistance (Calleri et al., 2006; Fei & Henderson, 2003). Parthenogenesis in termites has been observed in the form of a breeding system called Asexual queen succession (AQS) (Matsuura, 2010). In AQS, workers, soldiers, and alates (dispersing reproductives) are produced sexually while neotenic queens (non-dispersing queens) are produced parthenogenetically, which allows

the queen to maintain the full genetic contribution to the next generation while avoiding any loss in genetic diversity from inbreeding (Matsuura et al., 2009; Vargo et al., 2012). Sex allocation is female-biased in AQS species compared to non-AQS species, providing support to kin selection (Matsuura, 2017). While high genetic relatedness is essential for kin selection to operate and lead to the evolution of eusociality, genetic diversity seems to be important for social insect colonies to function (Oldroyd & Fewell, 2007) and resist disease (Sherman et al., 1988; Tarpy & Seeley, 2006). This problem may have selected for high recombination rates in social insects (see Chapter I). Recombination may increase the genotypic diversity while reducing variance in relatedness (thus reducing kin conflicts) in societies where kin selection is operating similar to what has been hypothesized for chromosome numbers (Sherman, 1979; Templeton, 1979). However, no data exist in termites to contribute to these arguments.

Termites feed primarily on wood and have evolved an obligatory mutualistic symbiotic relationship with gut microbes (along with the extant sister group to termites, the wood roach *Cyptocerus*) to digest cellulose (Nalepa, 2020). The termites' dependence on the symbionts requires extended parental (and older offspring) care for the young, overlapping of generation and group living which may have predispose termites to eusociality (Thorne, 1997). Acquisition of the symbionts ensures vertical transmission of these gut symbionts to offspring and drives their co-evolution with the host (Bignell, 2016; Nalepa et al., 2001). The symbioses between termites and microorganisms differ among taxa. While all 'lower' termites (all families except Termitidae) rely on cellulolytic protists to digest wood, phylogenetically derived termites such as Rhinotermitidae are associated with a handful of protists (even just a single species in Termitogen) (Kitade & Matsumoto, 1998; Radek et al., 2018). The 'higher' termites (family Termitidae) have evolved to complete loss of cellulolytic protists (but retained bacterial

symbionts) which was compensated by bacterial and fungal mutualists and changes in diets. However, the distinction of being 'higher' termites also reflects several derived traits such as true workers, distinctive caste differentiation, and complex nest architecture. (Bignell, 2016). The species diversity is highest in higher termites (about 70% of all species) which exhibit higher social complexity, while Kalotermitidae has the highest species diversity among lower termites (**Figure III-1**).

Figure III-1: Schematic cladogram of major termite families. Eusociality evolved around 150-160 mya while higher termites evolved around 50-80 mya. Family's names are represented in different colored boxes: Green - higher termites, Orange - lower termites, and Gray - non-termite family. Data Sources: (Chouvenc et al., 2021; Inward et al., 2007; Korb & Thorne, 2017).



Higher termites have a fixed number of chromosomes (2n=42) in comparison to the varied number of chromosomes in lower termites (2n = 28 to 56) (Bergamaschi et al., 2007). Genomes of five termite species have been genomes have been assembled, all of which has confirmed the basis of eusociality either by strengthening symbiosis with microbes or comparing

genetic and molecular profile against other eusocial insects such as bees (Harrison et al., 2018; Poulsen et al., 2014; Shigenobu et al., 2022; Terrapon et al., 2014). Genome size has also been linked to eusociality in termites since the genome size of socially complex *Macrotermes natalensi* is twice that of socially less complex *Zootermopsis nevadensis*, with an increased abundance of transposable elements in termites (Korb et al., 2015). Some of these transposable elements may play a causal role in gene family expansion that is associated with the transition to eusociality (Harrison et al., 2018). Association of eusociality to larger genomes and increased transposable elements have also been observed in eusocial snapping shrimp (Chak et al., 2021). Subterranean termites (Rhinotermitidae) exhibit intermediate social complexity between higher (Termitidae) and lower (rest of termite families) termites (Bourguignon et al., 2015). The first genome from Rhinotermitidae is of *Reticulitermes speratus* species which was made available publicly by two independent groups (Shigenobu et al., 2022) (Vargo et al., Unpublished). Analysis of the *R. speratus* genome revealed that gene duplication could facilitate social evolution through caste-biased expressions (Shigenobu et al., 2022). A similar observation was noted in honey bees which reported duplicated genes present higher levels of caste biased expressions than singleton genes (Chau & Goodisman, 2017) which may provide support of convergent evolution of eusociality in Blattodea and Hymenoptera. Despite termites being the second largest group that exhibit eusociality (Ruxton et al., 2014), genome sequencing efforts to understand genomic signatures of eusociality have not been extensive as for other eusocial insects such as bees (i5K Consortium, 2013).

Meiotic recombination rates in eusocial insects

All social Hymenoptera studied exhibit exceptionally high rates of meiotic recombination (Figure 1), which have been associated with eusociality (J. C. Jones et al., 2019; C. F. Kent & Zayed, 2013). Current arguments supporting high recombination in eusocial insects can be principally divided into three sets of hypotheses: the genotypic diversity hypothesis, the social innovation hypothesis, and the reduction of genetic conflict hypothesis (see Chapter I for details). While each of these hypotheses has gained a fair amount of support and criticism, more empirical data is needed to evaluate these theoretical arguments. All the data suggesting high recombination in eusocial insects are derived from studies on social Hymenoptera, and these hypotheses were never tested in any termite species. Recombination rate estimates from termites can be valuable in deciding which hypothesis holds in all eusocial insects irrespective of their differences in biological and ecological traits. For example, some species of termites are facultatively asexual while others are not (Matsuura, 2017) which can be used to test the genotypic diversity hypothesis. The social innovation hypothesis posits that high recombination rates evolved in eusocial Hymenoptera as a response to balance suboptimal conditions to increase linkage disequilibrium induced by lower effective population size. Termites show extremely low effective population size compared to other eusocial insects (Romiguier et al., 2014) which should select for high recombination rates; hence this hypothesis can also be tested. The prediction of the third hypothesis, the reduction in genomic conflict, is selection for lower recombination rates than eusocial Hymenoptera since the haplodiploid system generates a higher asymmetry in relatedness than diplodiploid termites (Husseneder et al., 1999). Within Hymenoptera, highly eusocial *Apis mellifera* show exceptionally high rates of recombination of 20-37 cM/Mb (H. Liu et al., 2015; Rueppell et al., 2016) while primitively eusocial *Bombus terrestris* show a relatively low

recombination rate of 8.9 cM/Mb. This, however, is still a very high rate compared to non-social insects, (Kawakami et al., 2019; Stolle et al., 2011) suggesting that among eusocial Hymenoptera the degree of sociality may be correlated to high recombination rates. Based on the genotypic diversity and social innovation hypotheses, I predict that highly eusocial termite species will exhibit recombination rates towards the higher end of the spectrum for social insects.

To test these predictions, I constructed genetic maps using SNP markers generated from nextRAD genotyping data for two species of economically and ecologically important termites of the genus Reticulitermes (Govorushko, 2019): *Reticulitermes speratus* and *Reticulitermes flavipes*. While they are closely related, *R. speratus* exhibits AQS, and *R. flavipes* does not. The objective of this study was to estimate genome-wide recombination rates and compare these estimates to eusocial Hymenoptera. As described above, all recombination studies in eusocial Hymenoptera have suggested a causal association of high recombination rates and eusociality, but the observed association may be due to the peculiarities of haplodiploidy, and thus my study is invaluable for understanding the relationship between recombination rate and sociality. Furthermore, these studies in termites allowed me to compare differences in recombination rates of males and females, which could not be performed in a haplodiploid eusocial species. Cytological evidence indicates chromosomal irregularities during male termite meiosis, and it was of interest to determine if these might influence/be correlated with recombination rates (Bergamaschi et al., 2007; Luykx, 1990; Syren & Luykx, 1977).

Methods

Sampling, DNA extraction and Sequencing

Two species of subterranean termites (*Reticulitermes flavipes* and *Reticulitermes speratus*) were used in this study. A total of 97 offspring of *R. flavipes* were field-collected from

a mature colony with a primary king and queen in Raleigh, NC, USA, in 2014, while 77 offspring of *R. speratus* were lab-reared in Kyoto, Japan, in 2014. Samples of *R. flavipes* included 49 male and 48 female offspring, while the sex of the *R. speratus* offspring samples could not be determined due to their small size. Genomic DNA was extracted from parents and all available offspring and sent to SNPsaurus LLC (Eugene, OR) for nextRAD genotyping. In brief, nextRAD involves the construction of Illumina Nextera libraries (Illumina, San Diego) and selective amplification using modified multiplex Nextera primers that extend over insert regions with a restrictive 9 bp sequence in their 3' ends for a systematically reduced representation of the genome in the resulting libraries. Pooled libraries were sequenced on an Illumina HiSeq4000 platform with a 1x150 bp configuration. Each offspring was genotyped once, while each parent was genotyped four times. Demultiplexing of reads, quality trimming, and variant calling (in a VCF format) were performed by SNPsaurus using their in-house, proprietary protocols.

SNP markers extraction and filtering

The VCF file containing SNPs and Indels was filtered using VCFTools (Danecek et al., 2011) with the following criteria: SNP calls with quality score <30 were removed (--minQ 30); SNP calls with a read depth of <6 were excluded (--minDP 6); SNPs with >50% missing data were removed (--max-missing 0.5); and SNPs with minor allele count of 3 or less were removed (--mac 3). Bash shell scripting was used to extract SNP markers and their genotypes in text format. The extraction resulted in 15709 raw SNP markers (loci) for *R. flavipes* and 9568 SNP markers for *R. speratus*. Sequences associated with these markers were also extracted to align the markers to the genome sequence. All the bash scripts used can be found in **Appendix B**.

These markers were quality filtered using Macro VBA programming and in-built functions of Microsoft Excel before they were used in linkage map construction. The first

filtering step was to categorize markers into “male-informative” and “female-informative” based on which parent was heterozygous at a particular locus. The markers that were heterozygous for both parents were excluded due to their lower information content (heterozygous offspring are uninformative). The second filtering step involved a check of genotype consistency using the replicate parental genotypes for each SNP: SNPs that showed less than three consistent genotypes (out of four) were excluded. The third step was to filter out segregation distortion. A relaxed segregation ratio of 90%:10% was used to ensure the removal of highly distorted markers for segregation. After these filtering steps, we obtained 3642 SNPs for *R. flavipes* male or king (RFK), 5082 for *R. flavipes* female or queen (RFQ), 2650 for *R. speratus* male (RSK), and 1972 for *R. speratus* female (RSQ).

Physical mapping of *R. speratus* SNPs to *R. speratus* genome

The alignment of RSK and RSQ markers to the high quality, super-scaffolded *R. speratus* genome assembly, TAMU-RSper-2021 (GenBank assembly accession: GCA_021186555.1) was performed using a combination of Bash shell scripting and Macro VBA codes in Microsoft Excel, which can be found in **Appendix B**. In brief, the sequences associated with SNP markers were cleaned from adaptor sequences to use as a query sequence file. Sequence alignment was performed using the nBLAST tool with default settings (Altschul et al., 1990). Most of the markers mapped to the 21 major scaffolds (corresponding to the 21 chromosomes) of the genome, but a few markers either did not map to any scaffolds, mapped to more than one scaffold, or mapped to a small scaffold (scaffolds beyond the 21 chromosomes). Markers that did not map to a major scaffold were discarded. For markers with multiple hits, the physical location that corresponded best to linkage information was selected if the ratio of e-values was within 1:10000 among hits. BLAST returned significant matches for 2514 (out of 2650) and 1870 (out

of 1972) SNP sequences for RSK and RSQ. The estimated genome coverage was calculated by summing each chromosome's physical length covered by SNPs based on these BLAST results.

The mapped markers were duplicated to include each marker in both possible phases for mapping 'Phase unknown' (Sirvio et al., 2006). To verify whether the mapped markers were genetically linked within each scaffold, all markers were grouped at LOD ≥ 3 and recombination fractions of ≤ 0.4 using the *formLinkageGroup()* command of the RQTL package (Broman et al., 2003) in RStudio v1.2.5033 (RStudio Team, 2022). Since markers were present in both phases, two symmetrical sets of linkage groups were generated as expected, and one set was discarded. The resulting 21 linkage groups contained 2194 and 1736 markers for RSK and RSQ, respectively. The genotypes of these remaining markers were corrected for potential sequencing errors indicated by double-crossovers around a single locus. Such genotypes were replaced with missing in Microsoft Excel using Macro codes (**Appendix B**) and manual checks.

The resulting genotype matrix of each chromosome (loci x individuals) was used to determine the recombination events by counting phase change events in Microsoft Excel (Manual count method or MCM). Because it is impossible to distinguish gene conversion from recombination events without a-priori information on track length, the range of numbers of recombination events was estimated under the following five different assumptions:

(1) Each phase change represents a true recombination event

(2) Phase changes with a minimum tract length of 10 kb represent true recombination events

(3) Phase changes with a minimum tract length of 50 kb represent true recombination events

(4) Phase changes with a minimum tract length of 100 kb represent true recombination events

(5) Phase changes represent true recombination events when supported by at least three consecutive genotypes

These estimates of recombination events were multiplied by100 to obtain estimates of the length of the genetic linkage map in centimorgans (cM) since each crossover event between two loci represent a distance of 1 Morgan (or 100 cM). Subsequently, the recombination rate in cM/Mb was calculated for each chromosome by dividing its genetic map length by the corresponding physical size.

Linkage analysis of *R. flavipes* SNPs and its physical mapping to *R. speratus* genome

Linkage analysis was performed for RFK and RFQ markers before their alignment to the *R. speratus* genome because the genome assembly is not available for *R. flavipes,* and genome rearrangements can occur even between closely related species (Rhie et al., 2021). First, the dataset was doubled for 'Phase unknown' mapping (as described in the previous section). Grouping of the 3642 (RFK) and 5082 (RFQ) markers was performed using RQTL (Broman et al., 2003) at LOD ≥ 8 and recombination fractions of ≤ 0.25 to retain only high-quality markers that show linkage. Markers in small groups (≤ 3 markers) were discarded while groups (51 groups for RFK and 21 for RFQ) with ≥ 4 markers were retained. This step resulted in 2580 markers for RFK and 3298 markers for RFQ. These markers were then aligned to the *R. speratus* genome using BLAST (as described in the previous section), which returned 2295 (out of 2580) and 2934 (out of 3298) hits for RFK and RFQ, respectively. Based on the mapping results, the markers were grouped into 21 chromosomes, duplicate markers (markers at the same genomic position and derived from identical sequences) were removed, and genotypes of these remaining

markers were corrected for potential sequencing errors based on flanking information to account for true recombination events in Microsoft Excel using Macro codes (**Appendix B**) and manual check. This step resulted in 1974 markers for RFK and 2518 markers for the RFQ dataset. Finally, recombination events were counted, and recombination rates were estimated for each of the five assumptions described for *R. speratus* in the previous section.

Plotting pairwise recombination fractions against physical distance

Pairwise recombination fractions matrices (loci x loci) were calculated for marker pairs in each group by using *pull.rf()* function of RQTL package (Broman et al., 2003). These n x n matrices were transformed into a one-dimensional array using custom Macro VBA code to plot against physical distances of corresponding marker pairs in Microsoft Excel. All R and Macro codes can be found in **Appendix B**.

Estimation of genetic lengths and plotting maps using RQTL

Mapped markers in the order of physical assembly for all four datasets (RSK, RSQ, RFK, and RFQ) were imported to RQTL, and genetic maps were estimated using the *est.map()* function of the RQTL package (Broman et al., 2003) (Automated method or AM) using an average error probability of 0.028 which was observed in parental genotype across four datasets. Since the marker order was unchanged, the genetic lengths (and corresponding recombination rates) for each dataset using this method were expected to be the same as estimated by the Manual count method. Markers that were poorly behaved were identified using *droponemarker()* function of the RQTL package (Broman et al., 2003) and removed from the dataset to minimize large gaps (50+ cM). This resulted in 2106 markers for RSK, 1691 markers for the RSQ dataset, 1954 markers for RFK, and 2513 markers for the RFQ dataset, which were plotted for genetic maps using *lmv.linkage.plot()* function of LinkageMapView package (Ouellette et al., 2018).

Correlation analyses

Correlation analysis was performed for chromosome lengths against recombination rate estimates using *ggplot()* function of R package ggplot2 in conjunction with *pivot_longer()* function of R-package tidyverse (Wickham, n.d.; Wickham et al., 2019). The R codes can be found in **Appendix B**. Correlation of recombination rate estimates using MCM, and AM was performed by CORREL function of Microsoft Excel.

Results

SNP markers from both species (*Reticulitermes flavipes* and *Reticulitermes speratus*) were mapped against *R. speratus* genome assembly generated by SMRT Sequencing (Pacific Biosciences of California, Inc.), TAMU-RSper-2021, when it became available (GenBank assembly accession: GCA_021186555.1). The total genome length for 21 chromosomes in the physical assembly was 873 Mb. Most of the markers mapped to the 21 chromosomes of the genome with high coverage (**Table III-S1 and Table III-S2**), for which the summary is provided in **Table III-1**.

Table III-1: Summary of BLAST mapping against *R. speratus* genome

Dataset	Total input markers	Markers with at least one BLAST hit	% Mapped markers	% of mapped markers mapped to 21 chromosomes	% Estimated genome coverage
RSK	2650	2514	94.87	98.80	97.70
RSQ	1972	1870	94.83	99.09	96.38
RFK	2580	2295	88.95	95.07	93.86
RFQ	3298	2934	88.96	98.16	97.84

The final number of markers used were 2194 for RSK, 1736 for RSQ, 1974 for RFK, and 2518 for RFQ (see **Table III-S1** for marker numbers for each group) for my Manual Count Method or MCM (see Methods for details). The genome-wide recombination rate estimates for both sexes in both species based on the different tract length assumptions range between 2.03 to 12.08 cM/Mb (**Table III-2**).

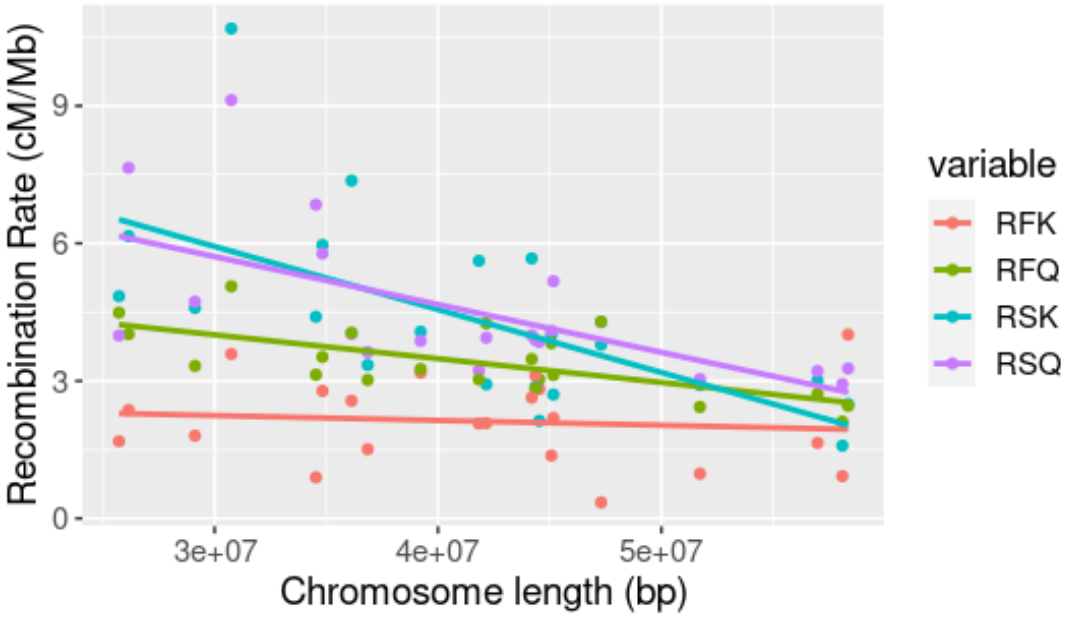
Table III-2: Average recombination rate estimates for all datasets using MCM and AM

Criteria	Recombination rates (cM/Mb)			
Each phase change represents a true recombination event (MCM)	RSK	RSQ	RFK	RFQ
Phase changes with a minimum tract length of <10 kb represent true recombination events (MCM)	12.08	8.80	3.55	4.65
Phase changes with a minimum tract length of < 50 kb represent true recombination events (MCM)	6.65	5.91	3.48	4.54
Phase changes with a minimum tract length of < 100 kb represent true recombination events (MCM)	6.49	5.68	3.33	4.41
Phase changes represent true recombination events when supported by at least three consecutive genotypes (MCM)	6.31	5.51	3.11	4.26
Automated method using RQTL (AM)	4.34	4.50	2.03	3.40

Even when using the most conservative criterion to count recombination events, the recombination rate was variable among chromosomes. It ranged from 1.59 to 10.69 cM/Mb in RSK, 2.93 to 9.12 cM/Mb in RSQ, 0.35 to 3.59 cM/Mb in RFK, and 2.11 to 5.06 cM/Mb in RFQ (see **Table III-S3-S6** for details). The recombination rates of chromosomes negatively correlated with their physical sizes (**Figure III-2**) for RSK (Pearson correlation coefficient R = -0.64, p =

0.001), RSQ (R = -0.63, p=0.002), and RFQ (R=-0.67, p=0.0008). However, this correlation was not significant for RFK (R= -0.11, p=0.64).

Figure III-2: Recombination rate as a function of a chromosome length. Most conservative estimates of recombination rates obtained using manual count method (MCM) for each chromosome are plotted against the chromosome lengths (in bp). RSK, RSQ, and RFQ show a significant negative correlation (Pearson correlation coefficients. RSK: R = -0.64, p = 0.001; RSQ: R = -0.63, p = 0.002; RFQ: R = -0.67, p = 0.0008;), while the correlation for RFK was not significant (Pearson correlation coefficients, R = -0.11, p = 0.64).



A second estimate for recombination rates was obtained using the RQTL package (AM – see Methods) for markers ordered according to physical mapping. Some markers were removed based on map expansion; therefore, the final number of markers used for AM were 2106 for RFK, 1691 for RFQ, 1954 for RSK, and 2513 for RFQ (see **Table III-S1** for marker numbers for each group). The genetic maps of RSK and RSQ were 7816.4 cM (average marker density of 1 marker every 3.7 cM) and 6933 cM (average marker density of 1 marker every 4.1 cM) long,

respectively (**Figures III-3 and III-4; Table III-S7**). These genetic lengths correspond to genome-wide recombination rates of 8.95 cM/Mb and 7.94 cM/Mb for RSK and RSQ, respectively (**Table III-2**) using the *R. speratus* genome length of 873.11 Mb. Based on the Haldane map function of d = -1/2* ln(1-2r), where d = distance between two marker pairs while r is recombination fractions ("Haldane's Mapping Function," 2008), a gap of 84.9 cM is expected for recombination fraction of 0.40 that we chose for *R.speratus* maps. All groups except one linkage group each in RSK (RSK-X) and RSQ (RSQ-XI) had gaps bigger than the expected value of 84.9 cM (**Figures III-S1 and III-S2**).

Figure III-3: Genetic map of R. speratus male (RSK). The final length of the map was 7816 cM, which consisted of 21 linkage groups ranging from 168.9 cM to 600.8 cM. The linkage groups are sorted according to the descending size of chromosomes in the physical genome assembly. Group 16 had the most markers (n=228), while group 20 had the least number of markers (n=59). Each horizontal black line indicates an SNP marker, and their vertical position indicates recombination distances among markers in cM. Please note that the y-axis scale (cM) is different than *R. speratus* plots since the lengths in *R. speratus* are shorter than *R. flavipes*. The color depicts approximate marker density within linkage groups – red being most dense and blue being least dense. For a complete plot with marker labels and positions, please refer to Figure III-S1.

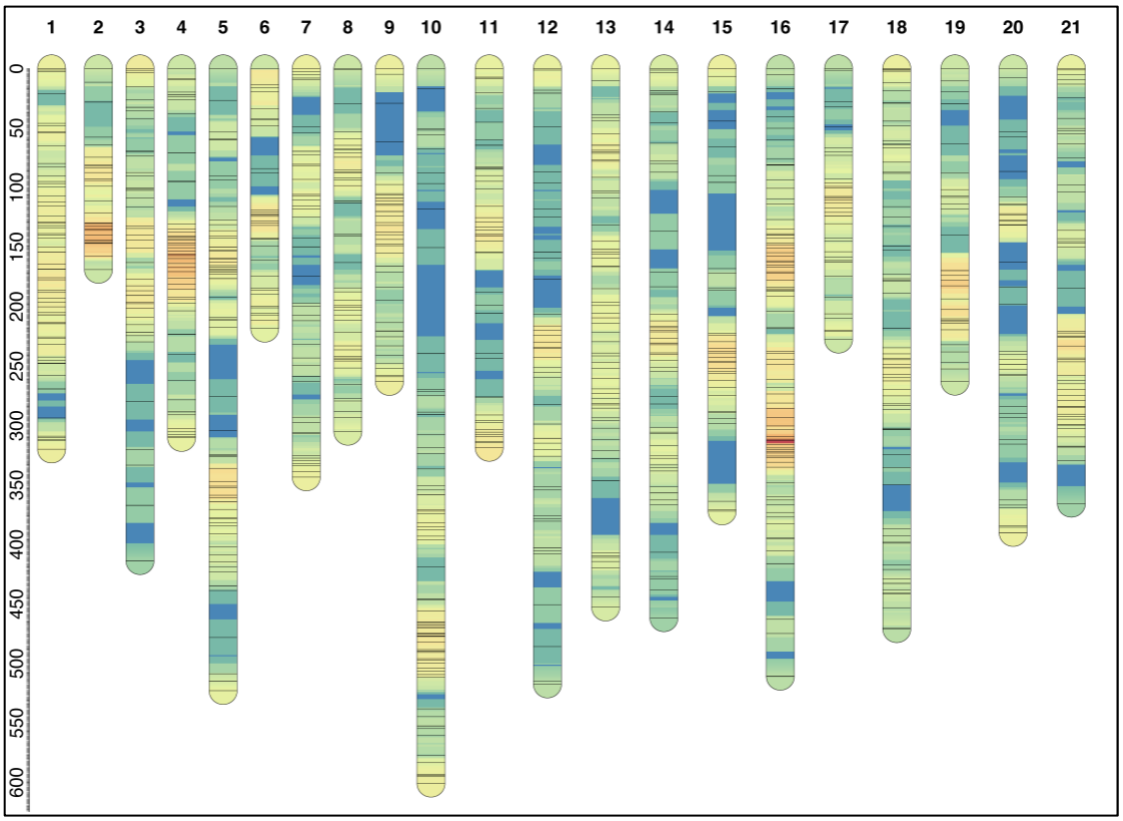
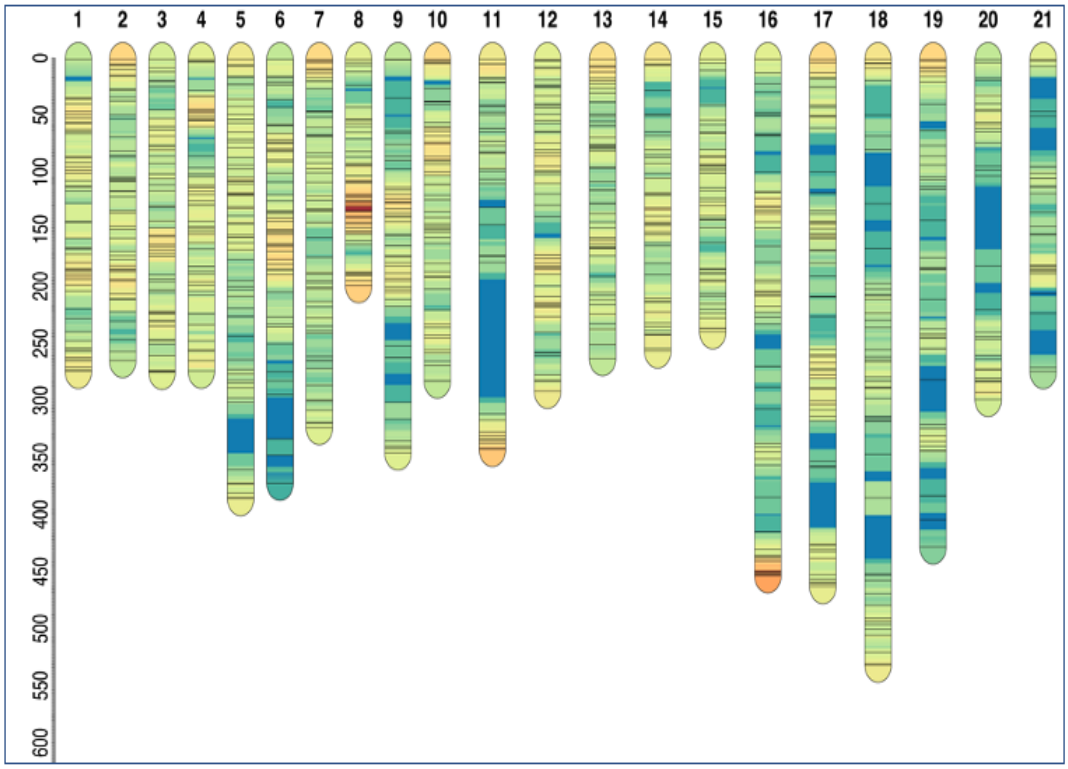


Figure III-4: Genetic map of R. speratus female (RSQ). The final length of the map was 6933 cM, which consisted of 21 linkage groups ranging from 201.4 cM to 539.7 cM. The linkage groups are sorted according to the descending size of the chromosome in the physical genome assembly. Group 17 had the most markers (n=104), while group 21 had the least number of markers (n=41). Each horizontal black line indicates an SNP marker, and their vertical position indicates recombination distances among markers in cM. Please note that the y-axis scale (cM) is different than *R. speratus* plots since the lengths in *R. speratus* are shorter than *R. flavipes*. The color depicts approximate marker density within linkage groups – red being most dense and blue being least dense parts. For a complete plot with marker labels and positions, please refer to Figure III-S2.



RFK and RFQ had a total map length of 2225.8 cM (average marker density of 1 marker every 1.14 cM) and 3438.5 cM (average marker density of 1 marker every 1.37 cM), respectively

(**Figures III-5 and III-6; Table III-S7**). These genetic lengths translate to 2.55 cM/Mb and 3.94 cM/Mb for RFK and RFQ, respectively (**Table 4**) using the *R. speratus* genome length of 873.11 Mb. Initial groupings for RFK and RFQ were performed at a recombination fraction of 0.25. According to the map function, this would translate to about 35 cM gap; however, 6 groups of RFK and 3 groups of RFQ had gaps larger than expected (**Figure III-S3 and III-S4**).

Figure III-5: Genetic map of R. flavipes male (RFK). The final length of the map was 2226 cM, which consisted of 21 linkage groups ranging from 9 cM to 306.5 cM. The linkage groups are sorted according to the descending size of chromosomes in the physical genome assembly. Group 1 had the most markers (n=150,) while group 17 had the least number of markers (n=26). Each horizontal black line indicates an SNP marker, and their vertical position indicates recombination distances among markers in cM. Please note that the y-axis scale (cM) is different than *R. flavipes* plots since the lengths in *R. speratus* are shorter than *R. flavipes*. The color depicts approximate marker density within linkage groups – red being most dense and blue being least dense parts. For a complete plot with marker labels and positions, please refer to Figure III-S3.

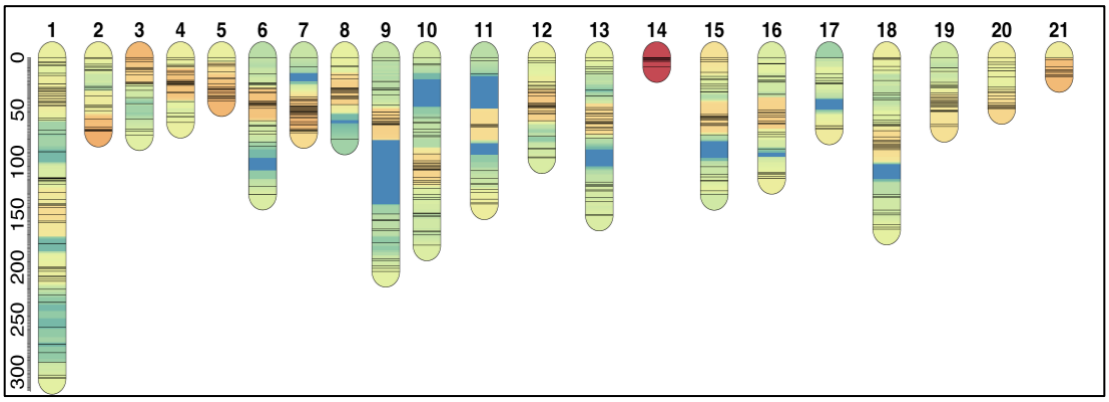
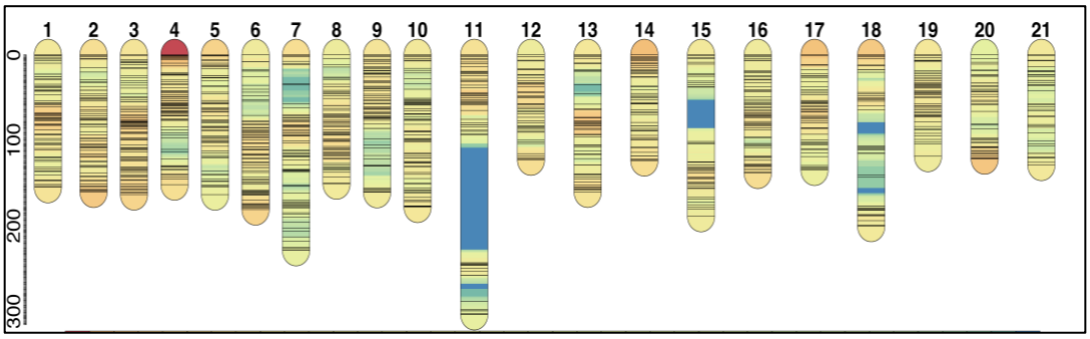


Figure III-6: Genetic map of R. flavipes female (RFQ). The final length of the map was 3439 cM, which consisted of 21 linkage groups ranging from 118.7 cM to 303.9 cM. The linkage groups are sorted according to the descending size of chromosomes in genome assembly. Group 3 had the most markers (n=177,) while group 21 had the least markers (n=67). Each horizontal black line indicates an SNP marker, and their vertical position indicates recombination distances among markers in cM. Please note that the y-axis scale (cM) is different than *R. flavipes* plots since the lengths in *R. speratus* are shorter than *R. flavipes*. The color depicts approximate marker density within linkage groups – red being most dense and blue being least dense parts. For a complete plot with marker labels and positions, please refer to Figure III-S4.



The estimates of AM were lower than the most relaxed criterion of MCM (**Table III-S8**); however, these two estimates correlated positively for all datasets (p-values for Pearson's correlations: RSK =0.0001, RSQ<0.0001, RFK<0.0001, and RFQ <0.0001).

SNP markers for each group from all four datasets were plotted for pairwise recombination fractions against pairwise physical distances. Plots for all groups of both females (RSQ and RFQ) showed the expected monotonous increase of recombination distance with physical distance until approximating the asymptote of 50% (example shown in **Figure III-7**; all

chromosomes are plotted in **Figures III-S5 and S6**). However, male chromosomes in both species did not follow this pattern. Instead, most exhibited no or a negligible correlation between physical and genetic distance (example shown in **Figure III-8**; all chromosomes are plotted in **Figures III-S7 and S8**).

Figure III-7: Pairwise recombination fraction plotted against corresponding physical distances in a R. flavipes female group (RFQ-XX). Each data point depicts a marker pair of the chromosome plotted. Pairwise recombination fractions for the marker pairs are plotted on the y-axis while the physical distance between marker pair (in bp) is shown on the x-axis.

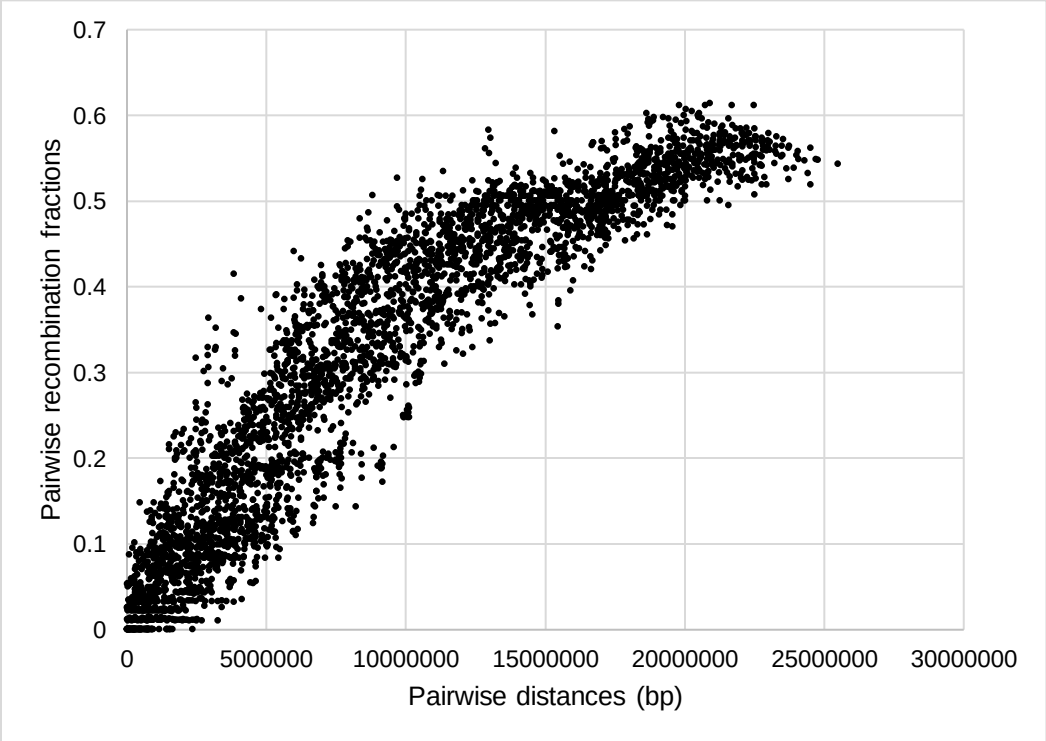
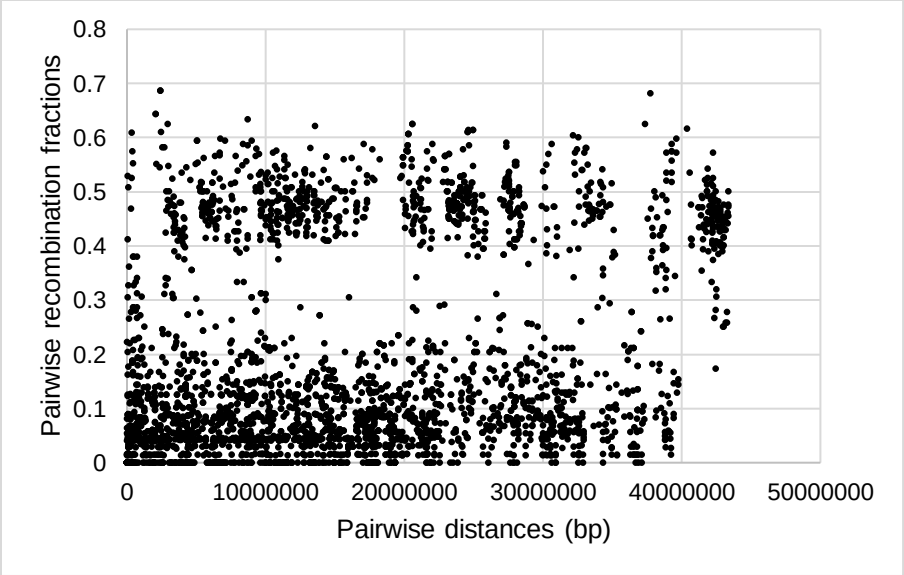


Figure III-8: Pairwise recombination fraction plotted against corresponding physical distances in a R. speratus male group (RSK-IX). Each data point depicts a marker pair of the chromosome plotted. Pairwise recombination fractions for the marker pairs are plotted on the y-axis while the physical distance between marker pair (in bp) is shown on the x-axis.



Discussion

Eusocial Hymenoptera exhibits exceptionally high rates of recombination, which led to the notion that eusociality is correlated with selection for increased meiotic recombination. Hypotheses related to high recombination in eusocial insects have been generated solely based on empirical evidence from haplodiploid Hymenoptera species. In contrast, no recombination data has been available for any species of termites despite being the most important diplodiploid eusocial insect group. Here, I constructed genome-wide recombination maps of two subterranean termite species – *Reticulitermes flavipes* and *Reticulitermes speratus*, representing intermediate eusocial complexity within termites (not to be confused with the degree of sociality – all termites are highly eusocial) (Vargo & Husseneder, 2009). The recombination rates presented here are the

first estimates for any termite species (and Blattodea in general) and thus make an important contribution towards understanding the relationship between recombination and eusociality. Since termites were the first group that evolved eusociality (about 80 million years before eusociality evolved in Hymenoptera) (Cardinal & Danforth, 2011), the estimates of these two species of termites presents a significant expansion in the breadth of recombination rate data in eusocial insects.

We employed a manual count (MCM) and an automated linkage mapping program, RQTL (AM), to estimate the recombination rates. The MCM resulted in a range of recombination rates, while a single estimate for each dataset was obtained using AM (**Table III-2**). Although MCM provides recombination rate estimates based on different track lengths, I will use estimates obtained from AM in further discussion due to its widespread use in linkage mapping. The genome-wide rates of recombination were 8.95 cM/Mb for *R. speratus* male, 7.94 cM/Mb for *R. speratus* female, 2.55 cM/Mb for *R. flavipes* male, and 3.94 cM/Mb for *R. flavipes* female. Thus, no strong sex differences were observed based on these overall estimates, while the two species differed 2-3 fold.

These rates were calculated using a genome size of 873.11 Mb from a recently released PacBio SMRT sequencing generated *R. speratus* genome assembly (GenBank assembly accession- GCA_021186555.1). The genome size estimate was very close to the estimation of 881 Mb in another recently published genome assembly of *R. speratus* generated by Illumina sequencing technology (Shigenobu et al., 2022) which was estimated earlier to be 1046 Mb long based on Feulgen image analysis densitometry (Koshikawa et al., 2008). In the absence of a sequence-based genome size estimate for *R. flavipes*, the genome size of *R. speratus* was used instead since these species are closely related. Although an estimate of 1044 Mb genome size for

R. flavipes is available based on flow cytometry analysis (Hanrahan & Johnston, 2011), sequence-based genome size estimates are considered better (Pflug et al., 2020), and therefore I employed the *R. speratus* physical genome size. This substation is supported by the result that almost all *R. flavipes* markers mapped to the *R. speratus* genome sequence. The recombination rate estimates obtained in this study, particularly for *R. flavipe*s, fall on the lower end of the spectrum of recombination rates observed for other eusocial insects (see **Figure II-4** in Chapter II). Since recombination fractions between markers are a function of physical distance and should converge at the upper limit of 0.5 in a recombining population (Allen-Brady & Camp, 2011; Xu, 2013), the relation between physical distance and recombination fraction in both termite female suggests a normal, though an elevated pattern of recombination (**Figure III-7; Figures III-S5 and S6**). However, male chromosomes in both species did not follow this pattern (**Figure III-8; Figures III-S7 and S8**), suggesting meiotic recombination is unconventional. Therefore, the values of recombination rates for males do not represent the true estimates, and I will continue the discussion on female recombination rates and discuss male linkage patterns separately below.

The female recombination rates of termites fit in the notion that eusocial insects have higher recombination rates. While *R. speratus* showed an intermediate recombination rate, *R. flavipes* rates were the lowest compared to all the eusocial species studied so far. The recombination rates are even lower than primitive eusocial bumblebees (Kawakami et al., 2019; Stolle et al., 2011), which suggests recombination rate may not be related to the degree of sociality. This result argues against the predictions of 'genotypic diversity' and 'social innovation' hypotheses. The presence of facultative parthenogenesis may drive the evolution of high recombination and thus support the view of 'reduction of genetic conflict' hypothesis, but it

may not be the only explanation in all termites (see next paragraph). Based on our estimates of recombination rates of both Reticulitermes species, I speculate that colony size may have an impact on recombination rates. Colony sizes of *Reticulitermes* termites (Bourke, 1999; R. W. Howard et al., 1982; Su et al., 1993) and *Acromyrmex* ants (H. Li et al., 2020) are several folds higher than other eusocial insects (Figure X in Chapter IV), but they both exhibit comparatively lower recombination rates than eusocial species with relatively small colony size such as honey bees (H. Liu et al., 2015; Rueppell et al., 2016; Shi et al., 2013).

Both *R. speratus* and *R. flavipes* are biologically very similar species except for the presence of facultative parthenogenesis (called asexual queen succession or AQS) in *R. speratus* (Matsuura et al., 2009). The higher recombination rate in *R. speratus* compared to *R. flavipes* in this study supports the hypothesis that species with facultative parthenogenesis might compensate to promote heterozygosity in parthenogens by increasing meiotic recombination. The faster accumulation of deleterious mutations is considered a significant disadvantage of asexual reproduction (Kondrashov, 1994; Muller, 1964). The deleterious alleles are rapidly purged from the population by being directly exposed in the homozygous state (without the masking effect of dominance) in haplodiploid species (L. Ross et al., 2019). In the AQS, parthenogens are homozygous for a single maternal allele at most loci due to terminal fusion (except where crossing over has occurred). The parthenogens carrying homozygous recessive deleterious alleles do not survive, thus mimicking purging in *R. speratus* similar to haploid males in haplodiploid organisms (Matsuura, 2017). This purging of deleterious alleles results into the loss of individuals but could preserve co-adapted gene complexes in surviving individuals. The purging selection seems to benefit AQS species and can thus select for high recombination rates. However, additional factors related to eusociality must be acting in termites since many termites

do not exhibit AQS (Matsuura, 2010). High recombination in response to AQS in termites provides a support to the reduction of genetic conflict, which predicts high recombination can reduce the variance of relatedness (and thus kin-conflict) in social insect colonies.

Meiotic recombination facilitates proper chromosome segregation in most species (Sansam & Pezza, 2015), but in some cases, it is not required, and other processes are used to stabilize homolog conjunction during meiosis (Da Ines et al., 2014; Lenormand et al., 2016). The pairwise linkage patterns of genetic markers in *R. speratus* and *R. flavipes* males indicate extensive genetic exchange between homologous chromosomes but are incompatible with the traditional patterns of recombination. According to the Haldane-Huxley rule, the heterogametic sex does not recombine in the species in which only one sex recombines (Lenormand & Dutheil, 2005; Nei, 1969), which is what I observed. However, the expected value for recombination rates in a completely non-recombining genome would be close to 0 cM/Mb. In contrast, I obtained estimates of 8.95 cM/Mb for *R. speratus male* and 2.55 cM/Mb for *R. flavipes* male. Interestingly these two values were close to the estimates of respective female rates. I did not find any study that reported recombination rates for the achiasmate sex of any species, suggesting the possibility that genetic exchange, as observed in my study, could occur more generally in the absence of conventional recombination. The lack of such studies may be because researchers do not make linkage maps due to the labor and cost involved when expecting trivial results. Recent methodological progress has made physical maps more common due to increased affordability in sequencing technologies. With expanding long-range sequencing technologies, more detailed studies of genetic exchanges between homologous chromosomes during meiosis may resolve the conundrum of male termite meiosis.

Four chromosomes of the *R. flavipes* male map had genetic map lengths of less than 50 cM (Supplementary Table 8), which suggests the absence of the postulated one obligate crossover per chromosome and meiosis (Haag et al., 2017). However, the genetic length less than 50 cM does not rule out the presence of a terminal crossover. Species that lack meiotic recombination in males such as *Drosophila melanogaster* employ alternative molecular and genetic pathways for homolog conjucntion and chromosomal segregation (Arya et al., 2006; Thomas et al., 2005). Based on the unusual pattern of linkage, it is difficult to conclude whether termite males have no recombination and rely on the presence of an unconventional meiosis process that is yet to be discovered.

Many termites show the formation of chains or rings of several chromosomes during male meiosis, which has been thought to be a consequence of inbreeding to maintain genetic heterozygosity through neo-sex chromosomes (Charlesworth & Wall, 1999). It has been observed that the Y chromosome and some autosomes segregate together as a single linkage group during meiosis in several lower termites, including *R. speratus* (Luykx, 1990; Matsuura, 2002, 2010; Syren & Luykx, 1977). The impact of these translocation complexes on meiotic recombination is unknown. However, suppression of recombination has been observed in the neo-Y chromosome (Y chromosome fused with autosomes) (Satomura et al., 2019) which suggests that translocation complexes might behave similarly. If meiotic recombination is suppressed on Y chromosome-associated translocation complexes, then mutations linked with these complexes cannot be unlinked by crossing over (Charlesworth & Charlesworth, 2000; Hill & Robertson, 1966). Furthermore, these translocation complexes generate sex-dependent asymmetric relatedness in colonies, hypothesized as an analog to asymmetry in eusocial Hymenoptera and support the kin selection theory of eusocial evolution (Matsuura, 2002). *R.*

flavipes has not been studied for translocation complexes, but its presence can be speculated based on the similar linkage patterns to *R. speratus* in this dissertation. Although, the pairwise linkage correlation to physical distances seems to fit in expectations of a map function towards the end (marker pairs aggregate around recombination fraction of 0.5) in most of these chromosomes (Supplementary Figures 1 and 3). This could represent localized meiotic recombination in the telomeric region. Similar observations have been made in some organisms such as fission yeast *Schizosaccharomyces pombe* (Chikashige et al., 1994; Scherthan et al., 1996). Such telomeric clustering has been associated with chromosome pairing, meiotic recombination, and spindle formation (Moiseeva et al., 2017; Yoshida et al., 2013). My results indicate termite males might be exhibiting either somewhat similar or a different non-canonical meiosis (Zickler & Kleckner, 2016) however, further molecular and genetic studies are needed to reveal the mechanistic pathway of meiosis in termites.

The evolutionary conservation of high recombination rates in eusocial Hymenoptera but not in closely related non-eusocial Hymenoptera suggest the evolution of eusociality in insects likely entailed selection of increased recombination rates (J. C. Jones et al., 2019) however, such studies in close non-social relatives of termites (such as wood roaches) are warranted to establish the validity of the claim. The emergence of genome assemblies from termite species (and other eusocial insects) provides an opportunity to study the factors that control the distribution of recombination at a finer scale. Although it is worth noting that fine-scale studies on genomes usually focus on the number of crossovers (CO) while non-crossover (NCO) gene conversion events are ignored despite the assumption that 90% of recombination events are NCOs (Cole et al., 2012). I did not calculate NCO rates in this study due to a lack of data and conflicting views on distinguishing CO and NCO in non-model organisms such as termites. The criterion of track

length criteria to define what should be described as an NCO event varies substantially among different taxa (Baudat et al., 2010; R. Li et al., 2019; P. Lu et al., 2012; Mancera et al., 2008). It is possible that NCO and resulting gene conversion is a powerful way of exchanging genetic material and creating genetic diversity in eusocial insects, although available reports are conflicting (Bessoltane et al., 2012; H. Liu et al., 2015). I did use different track length criteria to estimate recombination rates using MCM (see Methods for details) which resulted in a range of recombination rate estimates (**Table III-2**). The final estimates (AM) that I used for discussion fall in the middle of this range for all four datasets.

In conclusion, this study presents genome-wide recombination rates from two representative species of eusocial Blattodea. The female estimates are in the range of 3.94-7.94 cM/Mb and corroborate the association between high recombination rates and sociality in insects. However, this association is more pronounced in eusocial Hymenoptera. Thus, the selection related to eusociality operates more strongly in ants, bees, and wasps than in termites. Regardless of these differences, my study significantly widens the taxonomic perspective to strengthen the argument that advanced eusociality selects for high recombination rates. This study also describes a conundrum in the meiosis of male termites due to their unusual linkage pattern that may indicate the presence of a non-traditional process of genetic exchange during meiosis that needs to be explored further.

Supplementary Materials

Table III-S1: Chromosomes of genome and number of markers used in both MCM and AM for each group across all four datasets

Group number	Chromosome Name (TAMU-RSper-2021)	Chromosome Length (bp)	Final number of markers in maps							
			RSK-MCM	**RSK-AM**	**RSQ-MCM**	**RSQ-AM**	**RFK-MCM**	**RFK-AM**	**RFQ-MCM**	**RFQ-AM**

I	SceRxO1_3;HRSCAF=11	58358007	132	130	96	96	154	150	140	140
II	SceRxO1_1;HRSCAF=1	58102824	94	94	81	81	112	112	151	151
III	SceRxO1_5;HRSCAF=67	56990857	99	95	86	86	85	81	177	177
IV	SceRxO1_42;HRSCAF=223	51725093	126	126	93	91	118	118	146	146
V	SceRxO1_6;HRSCAF=83	47301639	137	133	95	95	111	111	119	118
VI	SceRxO1_9;HRSCAF=112	45165337	77	75	101	94	123	123	145	145
VII	SceRAO1_13;HRSCAF=145	45075441	71	69	83	79	128	128	119	119
VIII	SceRxO1_39;HRSCAF=220	44536134	87	84	89	86	91	91	129	129
IX	SceRxO1_14;HRSCAF=146	44362055	83	79	76	74	101	101	102	102
X	SceRxO1_237;HRSCAF=454	44196343	121	118	92	90	96	96	116	116
XI	SceRxO1_2;HRSCAF=3	42164237	80	80	61	59	76	76	136	134
XII	SceRxO1_4;HRSCAF=20	41829876	96	92	94	94	109	109	116	114
XIII	SceRxO1_11;HRSCAF=133	39222847	120	120	74	74	90	90	128	128
XIV	SceRxO1_7;HRSCAF=87	36853656	90	90	77	77	65	60	114	114
XV	SceRxO1_330;HRSCAF=578	36130529	93	81	64	64	109	109	100	100
XVI	SceRxO1_31;HRSCAF=209	34828934	236	228	101	101	108	108	108	108
XVII	SceRxO1_8;HRSCAF=99	34534844	80	68	104	104	26	26	125	125
XVIII	SceRxO1_12;HRSCAF=138	30746150	111	96	94	85	94	94	100	100
XIX	SceRxO1_428;HRSCAF=696	29120842	98	90	73	68	49	49	93	93
XX	SceRxO1_10;HRSCAF=124	26148132	59	59	61	52	58	54	87	87
XXI	SceRxO1_26;HRSCAF=198	25718616	104	99	41	41	71	68	67	67
Total	**All chromosomes**	**873112393**[a]	**2194**	**2106**	**1736**	**1691**	**1974**	**1954**	**2518**	**2513**

[a] Sum

Table III-S2: Coverage of each group for all four datasets

Group number	Scaffold length (bp)	RSK		RSQ		RFK		RFQ	
		Covered length (bp)	%Coverage	Covered length (bp)	%Coverage	Covered length (bp)	%Coverage	Covered length (bp)	%Coverage
I	58358007	57151092	97.93	54798326	93.90	56791167	97.32	57523859	98.57
II	58102824	54299669	93.45	55265488	95.12	47018967	80.92	57978133	99.79
III	56990857	56911865	99.86	53178772	93.31	56171324	98.56	55899849	98.09
IV	51725093	51388070	99.35	51208212	99.00	49202718	95.12	51286501	99.15
V	47301639	46895378	99.14	46838532	99.02	44771164	94.65	46613127	98.54
VI	45165337	43879901	97.15	44732676	99.04	44063885	97.56	44070504	97.58

VII	45075441	44181388	98.02	43668828	96.88	44148851	97.94	44117657	97.88
VIII	44536134	42460171	95.34	43886768	98.54	43597721	97.89	43690619	98.10
IX	44362055	43396830	97.82	43708961	98.53	44073285	99.35	43729795	98.57
X	44196343	43938220	99.42	43296883	97.96	43643158	98.75	43329311	98.04
XI	42164237	41552168	98.55	37153869	88.12	40960386	97.14	41295968	97.94
XII	41829876	41067204	98.18	40458367	96.72	40107275	95.88	40905250	97.79
XIII	39222847	38697847	98.66	38553705	98.29	38680279	98.62	38874769	99.11
XIV	36853656	35195393	95.50	36678387	99.52	29198457	79.23	35700927	96.87
XV	36130529	35202651	97.43	34630918	95.85	35560136	98.42	35616681	98.58
XVI	34828934	34204093	98.21	34521563	99.12	34333412	98.58	34109385	97.93
XVII	34534844	34438573	99.72	33868078	98.07	29199199	84.55	33792513	97.85
XVIII	30746150	29905287	97.27	29288506	95.26	28773885	93.59	28787017	93.63
XIX	29120842	28721145	98.63	28917225	99.30	26788125	91.99	28850737	99.07
XX	26148132	24715496	94.52	22568219	86.31	17813057	68.12	25485140	97.46
XXI	25718616	24832408	96.55	24307617	94.51	24621162	95.73	22610826	87.92
All	**873112393**	**853034849**	**97.70**[a]	**841529900**	**96.38**[a]	**819517613**	**93.86**[a]	**854268568**	**97.84**[a]

[a] Average

Table III-S3: Average recombination events and rates for all groups of R. speratus male (RSK) using MCM

Group	Total changes		10 Kb		50 kb		100 kb		Changes supported by at least 3 genotypes	
	Rec. events	Rec. rate	Rec. events	Rec. rate	Rec. events	Rec. rate	Rec. events	Rec. rate	Rec. events	Rec. rate
RSK-I	4.42	7.57	2.03	3.47	1.95	3.34	1.92	3.29	1.45	2.49
RSK-II	1.92	3.31	1.27	2.19	1.19	2.06	1.17	2.01	0.92	1.59
RSK-III	5.74	10.07	2.26	3.97	2.23	3.92	2.21	3.87	1.71	3.01
RSK-IV	3.23	6.25	2.04	3.94	1.96	3.79	1.96	3.79	1.51	2.91
RSK-V	6.31	13.34	2.88	6.10	2.83	5.99	2.75	5.82	1.79	3.79

RSK-VI	3.09	6.84	1.75	3.88	1.75	3.88	1.75	3.88	1.22	2.70
RSK-VII	3.31	7.35	2.30	5.10	2.30	5.10	2.27	5.04	1.81	4.00
RSK-VIII	3.26	7.32	1.78	4.00	1.57	3.53	1.36	3.06	0.95	2.13
RSK-IX	3.66	8.26	2.94	6.62	2.90	6.56	2.49	5.62	1.27	2.87
RSK-X	6.12	13.84	3.79	8.58	3.66	8.29	3.47	7.85	2.51	5.67
RSK-XI	2.88	6.84	2.26	5.36	2.23	5.30	2.18	5.17	1.23	2.93
RSK-XII	6.09	14.56	2.81	6.71	2.78	6.64	2.68	6.40	2.35	5.62
RSK-XIII	4.32	11.03	2.09	5.33	2.06	5.26	2.04	5.20	1.60	4.07
RSK-XIV	3.97	10.78	2.04	5.53	1.96	5.32	1.96	5.32	1.23	3.35
RSK-XV	4.92	13.62	3.29	9.09	3.26	9.02	3.26	9.02	2.66	7.37
RSK-XVI	7.44	21.37	2.97	8.54	2.97	8.54	2.87	8.24	2.08	5.97
RSK-XVII	5.84	16.92	2.48	7.18	2.48	7.18	2.48	7.18	1.52	4.40
RSK-XVIII	8.68	28.22	5.47	17.78	5.31	17.28	5.18	16.85	3.29	10.69
RSK-XIX	5.34	18.33	2.35	8.07	2.12	7.27	2.06	7.09	1.34	4.59
RSK-XX	3.17	12.12	2.91	11.13	2.86	10.93	2.83	10.83	1.61	6.16

RSK-XXI	4.05	15.75	1.84	7.17	1.83	7.12	1.81	7.02	1.25	4.85
Average	**4.66**	**11.20[a]**	**2.55**	**6.13[a]**	**2.49**	**5.98[a]**	**2.41**	**5.81[a]**	**1.68**	**4.04[a]**

[a] Weighted average

Table III-S4: Average recombination events and rates for all groups of R. speratus female (RSQ) using MCM

Group	Total changes		10 Kb		50 kb		100 kb		Changes supported by at least 3 genotypes	
	Rec. events	Rec. rate	Rec. events	Rec. rate	Rec. events	Rec. rate	Rec. events	Rec. rate	Rec. events	Rec. rate
RSQ-I	2.74	4.70	2.71	4.65	2.69	4.61	2.64	4.52	1.91	3.27
RSQ-II	2.62	4.52	2.62	4.52	2.62	4.52	2.62	4.52	1.70	2.93
RSQ-III	2.64	4.63	2.58	4.53	2.58	4.53	2.47	4.33	1.83	3.21
RSQ-IV	3.49	6.75	3.49	6.75	3.42	6.60	3.36	6.50	1.57	3.04
RSQ-V	3.89	8.24	3.79	8.02	3.56	7.52	3.24	6.86	2.03	4.28
RSQ-VI	4.81	10.64	4.10	9.09	3.87	8.57	3.48	7.71	2.34	5.18
RSQ-VII	3.69	8.18	2.60	5.76	2.39	5.30	2.05	4.55	1.84	4.09
RSQ-VIII	2.23	5.02	2.13	4.78	2.13	4.78	2.12	4.75	1.71	3.85
RSQ-IX	3.51	7.90	1.95	4.39	1.90	4.27	1.87	4.22	1.73	3.89
RSQ-X	3.51	7.93	2.01	4.55	1.88	4.26	1.88	4.26	1.76	4.00
RSQ-XI	2.79	6.62	1.99	4.71	1.96	4.65	1.96	4.65	1.66	3.94
RSQ-XII	2.92	6.99	1.83	4.38	1.78	4.25	1.70	4.07	1.35	3.23
RSQ-XIII	2.66	6.79	1.97	5.03	1.95	4.97	1.87	4.77	1.52	3.87

RSQ-XIV	2.68	7.26	1.66	4.51	1.58	4.30	1.56	4.23	1.34	3.63
RSQ-XV	2.34	6.47	1.51	4.17	1.51	4.17	1.51	4.17	1.45	4.03
RSQ-XVI	4.19	12.04	2.35	6.75	2.27	6.53	2.19	6.30	2.01	5.78
RSQ-XVII	4.31	12.48	2.55	7.37	2.52	7.30	2.49	7.22	2.36	6.84
RSQ-XVIII	5.77	18.75	2.96	9.63	2.96	9.63	2.94	9.55	2.81	9.12
RSQ-XIX	4.60	15.79	1.58	5.44	1.58	5.44	1.56	5.35	1.38	4.73
RSQ-XX	3.88	14.85	2.18	8.34	2.18	8.34	2.18	8.34	2.00	7.65
RSQ-XXI	2.14	8.33	1.73	6.72	1.26	4.90	1.26	4.90	1.03	3.99
Average	**3.40**	**8.18[a]**	**2.40**	**5.76[a]**	**2.31**	**5.57[a]**	**2.24**	**5.38[a]**	**1.78**	**4.28[a]**

[a] Weighted average

Table III-S5: Average recombination events and rates for all groups of R. flavipes male (RFK) using MCM

Groups	Total changes		10 Kb		50 kb		100 kb		Changes supported by at least 3 genotypes	
	Rec. events	Rec. rate	Rec. events	Rec. rate	Rec. events	Rec. rate	Rec. events	Rec. rate	Rec. events	Rec. rate
RFK-I	4.26	7.30	4.25	7.28	4.16	7.13	3.33	5.71	1.21	2.07
RFK-II	1.04	1.79	1.04	1.79	1.02	1.76	0.99	1.70	0.54	0.92
RFK-III	1.27	2.22	1.23	2.15	1.19	2.08	1.18	2.08	0.94	1.65
RFK-IV	0.98	1.89	0.91	1.75	0.91	1.75	0.85	1.63	0.51	0.98
RFK-V	1.11	2.35	1.11	2.35	0.97	2.05	0.82	1.74	0.16	0.35
RFK-VI	1.57	3.47	1.57	3.47	1.48	3.29	1.36	3.01	0.99	2.19
RFK-VII	1.70	3.77	1.56	3.45	1.49	3.32	1.43	3.18	0.62	1.37
RFK-VIII	1.94	4.35	1.94	4.35	1.94	4.35	1.89	4.24	1.26	2.82
RFK-IX	1.91	4.30	1.89	4.25	1.84	4.14	1.81	4.09	1.38	3.11

RFK-X	1.82	4.13	1.82	4.13	1.68	3.80	1.64	3.71	1.16	2.64
RFK-XI	1.30	3.08	1.25	2.96	1.21	2.86	1.19	2.81	0.88	2.08
RFK-XII	1.38	3.30	1.34	3.20	1.26	3.00	1.24	2.96	0.87	2.07
RFK-XIII	1.61	4.10	1.61	4.10	1.56	3.97	1.52	3.86	1.25	3.18
RFK-XIV	1.01	2.74	1.01	2.74	0.93	2.52	0.91	2.46	0.56	1.51
RFK-XV	1.78	4.94	1.78	4.94	1.68	4.65	1.60	4.42	0.93	2.57
RFK-XVI	1.31	3.76	1.27	3.64	1.24	3.55	1.22	3.49	0.97	2.78
RFK-XVII	0.61	1.76	0.59	1.70	0.53	1.52	0.51	1.46	0.31	0.90
RFK-XVIII	1.74	5.67	1.68	5.47	1.62	5.26	1.37	4.46	1.10	3.58
RFK-XIX	0.71	2.44	0.71	2.44	0.69	2.37	0.65	2.23	0.53	1.81
RFK-XX	1.05	4.02	1.01	3.86	0.93	3.54	0.80	3.08	0.62	2.37
RFK-XXI	0.78	3.05	0.78	3.05	0.78	3.05	0.74	2.89	0.43	1.68
Average	**1.47**	**3.54[a]**	**1.44**	**3.48[a]**	**1.39**	**3.33[a]**	**1.29**	**3.11[a]**	**0.82**	**1.97[a]**

[a] Weighted average

Table III-S6: Average recombination events and rates for all groups of R. flavipes female (RFQ) using MCM

Groups	Total changes		10 Kb		50 kb		100 kb		Changes supported by at least 3 genotypes	
	Rec. events	Rec. rate	Rec. events	Rec. rate	Rec. events	Rec. rate	Rec. events	Rec. rate	Rec. events	Rec. rate
RFQ-I	1.77	3.04	1.77	3.04	1.77	3.04	1.77	3.04	1.43	2.46
RFQ-II	1.91	3.28	1.70	2.93	1.62	2.79	1.56	2.68	1.23	2.11
RFQ-III	2.14	3.76	2.10	3.69	2.08	3.65	2.06	3.62	1.55	2.71
RFQ-IV	1.92	3.71	1.77	3.43	1.73	3.35	1.63	3.15	1.26	2.43
RFQ-V	2.54	5.36	2.47	5.23	2.45	5.19	2.43	5.14	2.03	4.29

RFQ-VI	2.14	4.75	2.02	4.47	2.02	4.47	1.84	4.06	1.41	3.12
RFQ-VII	2.64	5.86	2.64	5.86	2.64	5.86	2.62	5.81	1.72	3.82
RFQ-VIII	1.72	3.87	1.68	3.77	1.64	3.68	1.54	3.45	1.36	3.03
RFQ-IX	1.78	4.02	1.78	4.02	1.70	3.83	1.58	3.56	1.26	2.84
RFQ-X	1.99	4.50	1.85	4.18	1.80	4.08	1.76	3.99	1.54	3.48
RFQ-XI	2.41	5.72	2.41	5.72	2.31	5.48	2.27	5.38	1.79	4.25
RFQ-XII	1.84	4.39	1.79	4.29	1.74	4.17	1.74	4.17	1.27	3.03
RFQ-XIII	1.96	4.99	1.90	4.84	1.90	4.84	1.69	4.31	1.28	3.26
RFQ-XIV	1.49	4.06	1.47	4.00	1.45	3.94	1.38	3.75	1.11	3.02
RFQ-XV	1.73	4.79	1.73	4.79	1.73	4.79	1.71	4.74	1.46	4.05
RFQ-XVI	1.75	5.03	1.71	4.91	1.55	4.44	1.47	4.23	1.23	3.52
RFQ-XVII	1.85	5.34	1.82	5.28	1.78	5.16	1.64	4.75	1.08	3.13
RFQ-XVIII	2.02	6.57	2.02	6.57	1.90	6.17	1.86	6.04	1.56	5.06
RFQ-XIX	1.30	4.46	1.28	4.39	1.15	3.96	1.15	3.96	0.97	3.32
RFQ-XX	1.29	4.93	1.25	4.77	1.21	4.61	1.21	4.61	1.05	4.02
RFQ-XXI	1.34	5.21	1.32	5.13	1.32	5.13	1.32	5.13	1.15	4.49
Average	**1.88**	**4.53**[a]	**1.83**	**4.41**[a]	**1.79**	**4.30**[a]	**1.73**	**4.15**[a]	**1.37**	**3.29**[a]

[a] Weighted average

Table III-S7: Genetic map length (in cM) obtained by AM for all four datasets

	RSK		RSQ		RFK		RFQ	
Chromosome	Genetic length (cM)	Avg. Marker spacing	Genetic length (cM)	Avg. Marker spacing	Genetic length (cM)	Avg. Marker spacing	Genetic length (cM)	Avg. Marker spacing
I	319.9	2.50	277.8	2.9	306.5	2.1	155.1	1.1
II	168.9	1.80	268.1	3.4	70.6	0.6	160.6	1.1
III	413.8	4.40	278.6	3.3	74	0.9	163.6	0.9

IV	310.2	2.50	277.6	3.1	62.1	0.5	152	1
V	522.9	4.00	391.2	4.2	41.5	0.4	163.7	1.4
VI	218.3	2.90	377.6	4.1	130.6	1.1	181.2	1.3
VII	343.3	5.00	327.9	4.2	71.9	0.6	228.9	1.9
VIII	305	3.70	201.4	2.4	78.1	0.9	150.9	1.2
IX	263.1	3.40	350.6	4.8	204.2	2	161	1.6
X	600.8	5.10	286.4	3.2	179.1	1.9	178.2	1.5
XI	318.5	4.00	347.4	6	139.8	1.9	303.9	2.3
XII	517.4	5.70	295.5	3.2	95.8	0.9	122.9	1.1
XIII	452.7	3.80	266.4	3.6	150.6	1.7	160.5	1.3
XIV	461.7	5.20	259.6	3.4	9	0.2	123.8	1.1
XV	372	4.70	242.3	3.8	130.8	1.2	189	1.9
XVI	510.9	2.30	460	4.6	115.5	1.1	138.4	1.3
XVII	227.5	3.40	469.7	4.6	68.5	2.7	134.8	1.1
XVIII	470.9	5.00	539.7	6.4	163.9	1.8	200.6	2
XIX	262.9	3.00	434.4	6.5	66	1.4	118.7	1.3
XX	390.1	6.70	302.8	5.9	48.9	0.9	121.6	1.4
XXI	365.5	3.70	278	6.9	18.4	0.3	129.1	2
Total	**7816.4**	**3.71[a]**	**6933**	**4.1[a]**	**2225.8**	**1.14[a]**	**3438.5**	**1.37[a]**

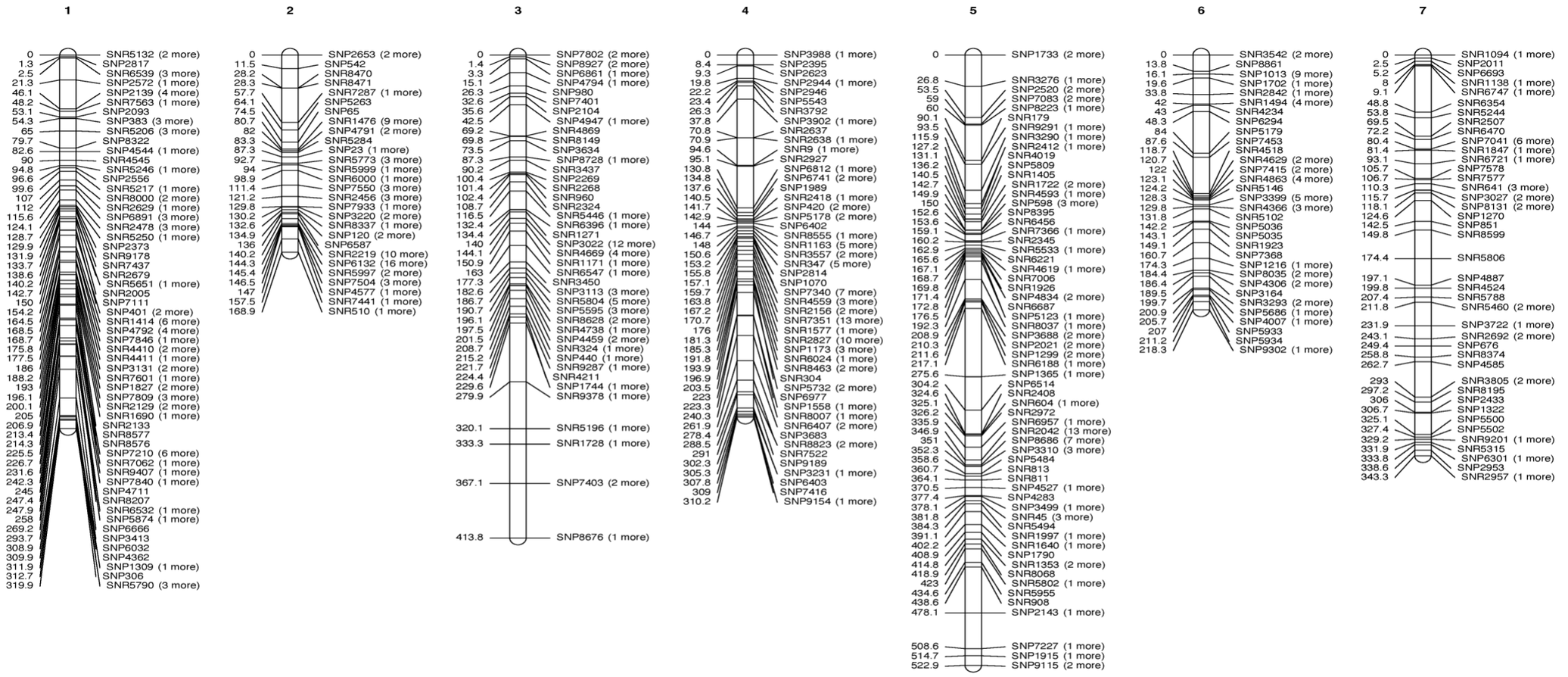
[a] Weighted average

Table III-S8: Recombination rate estimates comparison between MCM and AM for all four datasets

	RSK	**RSQ**	**RFK**	**RFQ**

Chromosome	MCM	AM	MCM	AM	MCM	AM	MCM	AM
I	7.57	5.48	4.70	4.76	7.30	5.25	3.04	2.66
II	3.31	2.91	4.52	4.61	1.79	1.22	3.28	2.76
III	10.07	7.26	4.63	4.89	2.22	1.30	3.76	2.87
IV	6.25	6.00	6.75	5.37	1.89	1.20	3.71	2.94
V	13.34	11.05	8.24	8.27	2.35	0.88	5.36	3.46
VI	6.84	4.83	10.64	8.36	3.47	2.89	4.75	4.01
VII	7.35	7.62	8.18	7.27	3.77	1.60	5.86	5.08
VIII	7.32	6.85	5.02	4.52	4.35	1.75	3.87	3.39
IX	8.26	5.93	7.90	7.90	4.30	4.60	4.02	3.63
X	13.84	13.59	7.93	6.48	4.13	4.05	4.50	4.03
XI	6.84	7.55	6.62	8.24	3.08	3.32	5.72	7.21
XII	14.56	12.37	6.99	7.06	3.30	2.29	4.39	2.94
XIII	11.03	11.54	6.79	6.79	4.10	3.84	4.99	4.09
XIV	10.78	12.53	7.26	7.04	2.74	0.24	4.06	3.36
XV	13.62	10.30	6.47	6.71	4.94	3.62	4.79	5.23
XVI	21.37	14.67	12.04	13.21	3.76	3.32	5.03	3.97
XVII	16.92	6.59	12.49	13.60	1.76	1.98	5.34	3.90
XVIII	28.22	15.32	18.75	17.55	5.67	5.33	6.57	6.52
XIX	18.33	9.03	15.79	14.92	2.44	2.27	4.46	4.08
XX	12.12	14.92	14.85	11.58	4.02	1.87	4.93	4.65
XXI	15.75	14.21	8.33	10.81	3.05	0.72	5.21	5.02
Weighted Average	**11.20**	**8.95**	**8.18**	**7.94**	**3.54**	**2.55**	**4.53**	**3.94**

Figure III-S1: All linkage groups of *R. speratus* male (RSK) along with genetic distances and marker names. Each linkage group is named according to the chromosome number of genome assembly. Distances among markers are indicated in cM to the left of the linkage groups and SNP marker names are shown on the right. If there are more than one marker at the same position, then only one marker name is shown and number of rest of the markers are mentioned in the bracket after the marker name.


1
0 SNR5132 (2 more)
1.3 SNP2817
2.5 SNR6539 (3 more)
21.3 SNP2572 (1 more)
46.1 SNP2139 (4 more)
48.2 SNR7563 (1 more)
53.1 SNP2093
54.3 SNP383 (3 more)
65 SNR5206 (3 more)
79.7 SNP8322
82.6 SNP4544 (1 more)
90 SNR4545
94.8 SNR5246 (1 more)
96.6 SNP2556
99.6 SNR5217 (1 more)
107 SNR8000 (2 more)
112 SNR2629 (1 more)
115.6 SNP6891 (3 more)
124.1 SNR2478 (3 more)
128.7 SNR5250 (1 more)
129.9 SNP2373
131.9 SNR9178
133.7 SNR7437
138.6 SNR2679
140.2 SNR5651 (1 more)
142.7 SNR2005
150 SNP7111
154.2 SNP401 (2 more)
164.5 SNR1414 (6 more)
168.5 SNP4792 (4 more)
168.7 SNP7846 (1 more)
175.8 SNR4410 (2 more)
177.5 SNR4411 (1 more)
186 SNP3131 (2 more)
188.2 SNR7601 (1 more)
193 SNP1827 (2 more)
196.1 SNP7809 (3 more)
200.1 SNR2129 (2 more)
205 SNR1690 (1 more)
206.9 SNR2133
213.4 SNR8577
214.3 SNR8576
225.5 SNP7210 (6 more)
226.7 SNR7062 (1 more)
231.6 SNR9407 (1 more)
242.3 SNP7840 (1 more)
245 SNP4711
247.4 SNR8207
247.9 SNR6532 (1 more)
258 SNP5874 (1 more)
269.2 SNP6666
293.7 SNP3413
308.9 SNP6032
309.9 SNP4362
311.9 SNP1309 (1 more)
312.7 SNP306
319.9 SNR5790 (3 more)
2
0 SNP2653 (2 more)
11.5 SNP542
28.2 SNR8470
28.3 SNR8471
57.7 SNR7287 (1 more)
64.1 SNP5263
74.5 SNP65
80.7 SNR1476 (9 more)
82 SNP4791 (2 more)
83.3 SNR5284
87.3 SNP23 (1 more)
92.7 SNR5773 (3 more)
94 SNR5999 (1 more)
98.9 SNR6000 (1 more)
111.4 SNP7550 (3 more)
121.2 SNR2456 (3 more)
129.8 SNP7933 (1 more)
130.2 SNP3220 (2 more)
132.6 SNR8337 (1 more)
134.9 SNP120 (2 more)
136 SNP6587
140.2 SNR2219 (10 more)
144.3 SNP6132 (16 more)
145.4 SNR5997 (2 more)
146.5 SNP7504 (3 more)
147 SNP4577 (1 more)
157.5 SNR7441 (1 more)
168.9 SNR510 (1 more)
3
0 SNP7802 (2 more)
1.4 SNP8927 (2 more)
3.3 SNP6861 (1 more)
15.1 SNP4794 (1 more)
26.3 SNP980
32.6 SNP7401
35.6 SNP2104
42.5 SNP4947 (1 more)
69.2 SNR4869
69.8 SNR8149
73.5 SNP3634
87.3 SNP8728 (1 more)
90.2 SNR3437
100.4 SNP2269
101.4 SNR2268
102.4 SNR960
108.7 SNR2324
116.5 SNR5446 (1 more)
132.4 SNR6396 (1 more)
134.4 SNR1271
140 SNP3022 (12 more)
144.1 SNR4669 (4 more)
150.9 SNR1171 (1 more)
163 SNR6547 (1 more)
177.3 SNR3450
182.6 SNP3113 (3 more)
186.7 SNR5804 (5 more)
190.7 SNP5595 (3 more)
196.1 SNR8628 (2 more)
197.5 SNR4738 (1 more)
201.5 SNP4459 (2 more)
208.7 SNR324 (1 more)
215.2 SNP440 (1 more)
221.7 SNR9287 (1 more)
224.4 SNR4211
229.6 SNP1744 (1 more)
279.9 SNR9378 (1 more)
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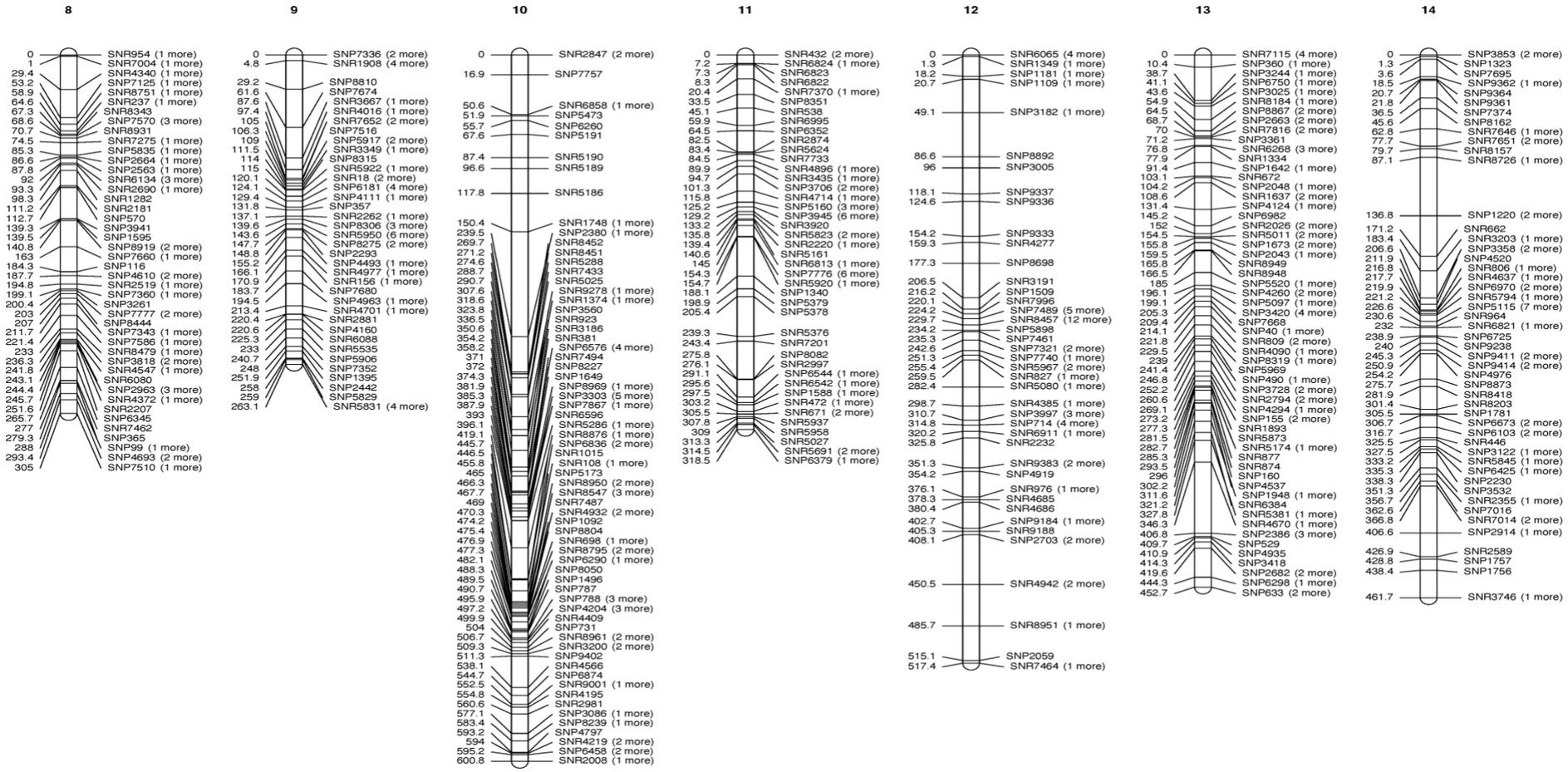
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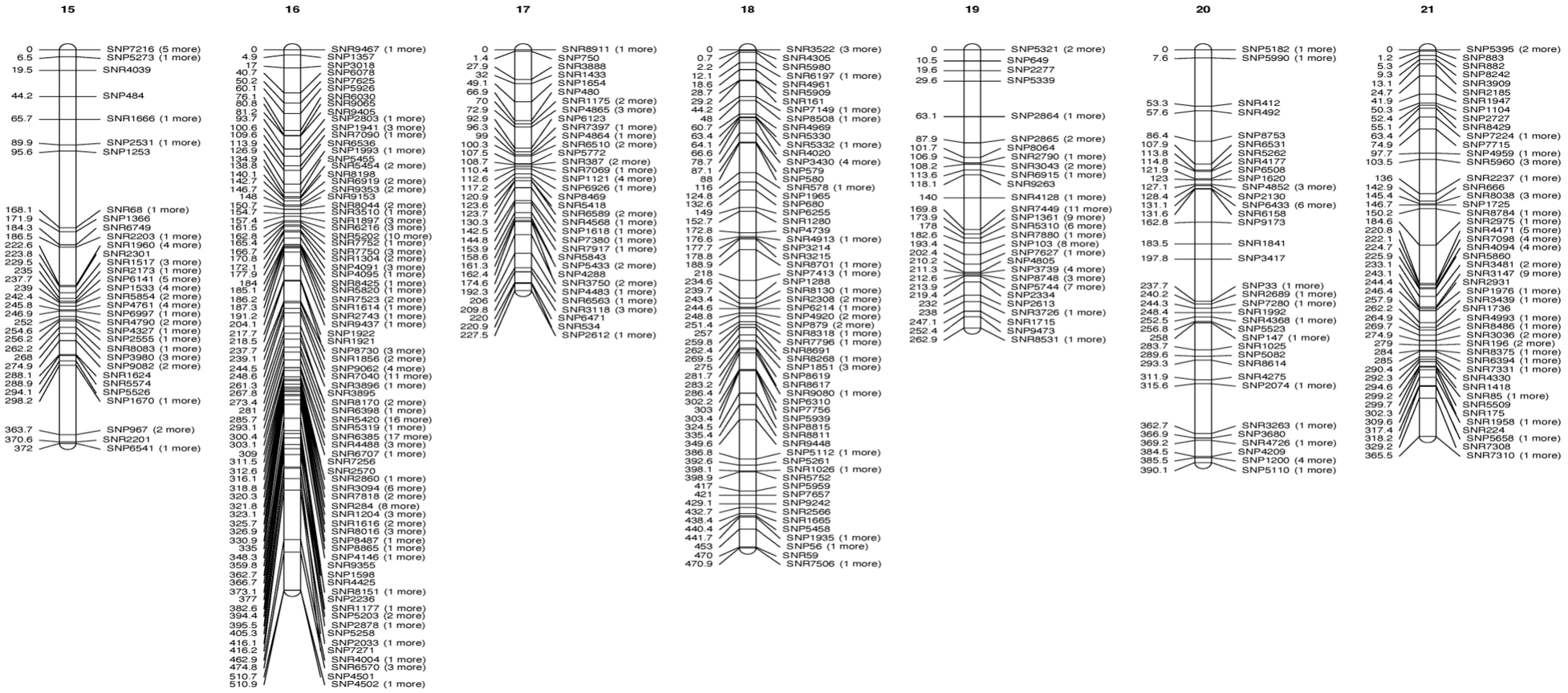
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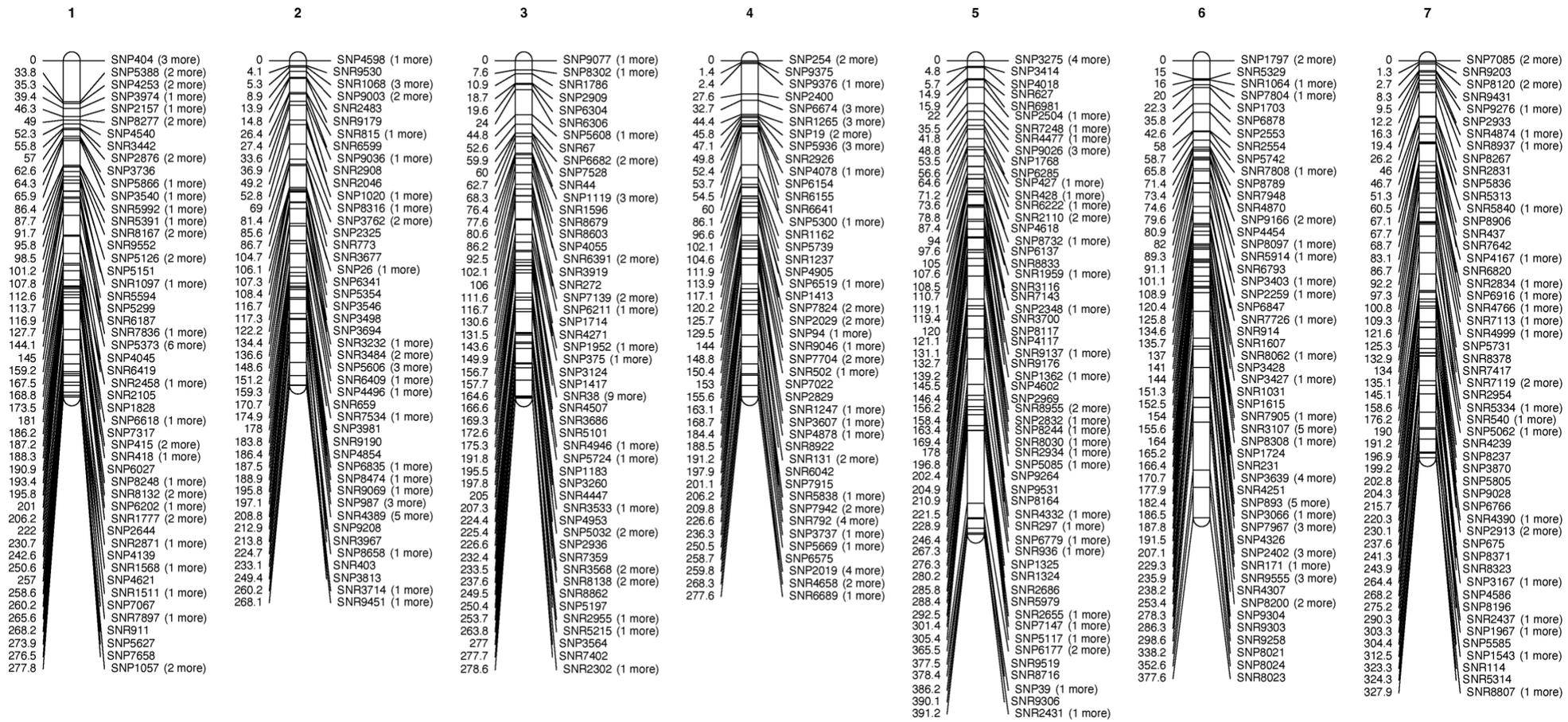
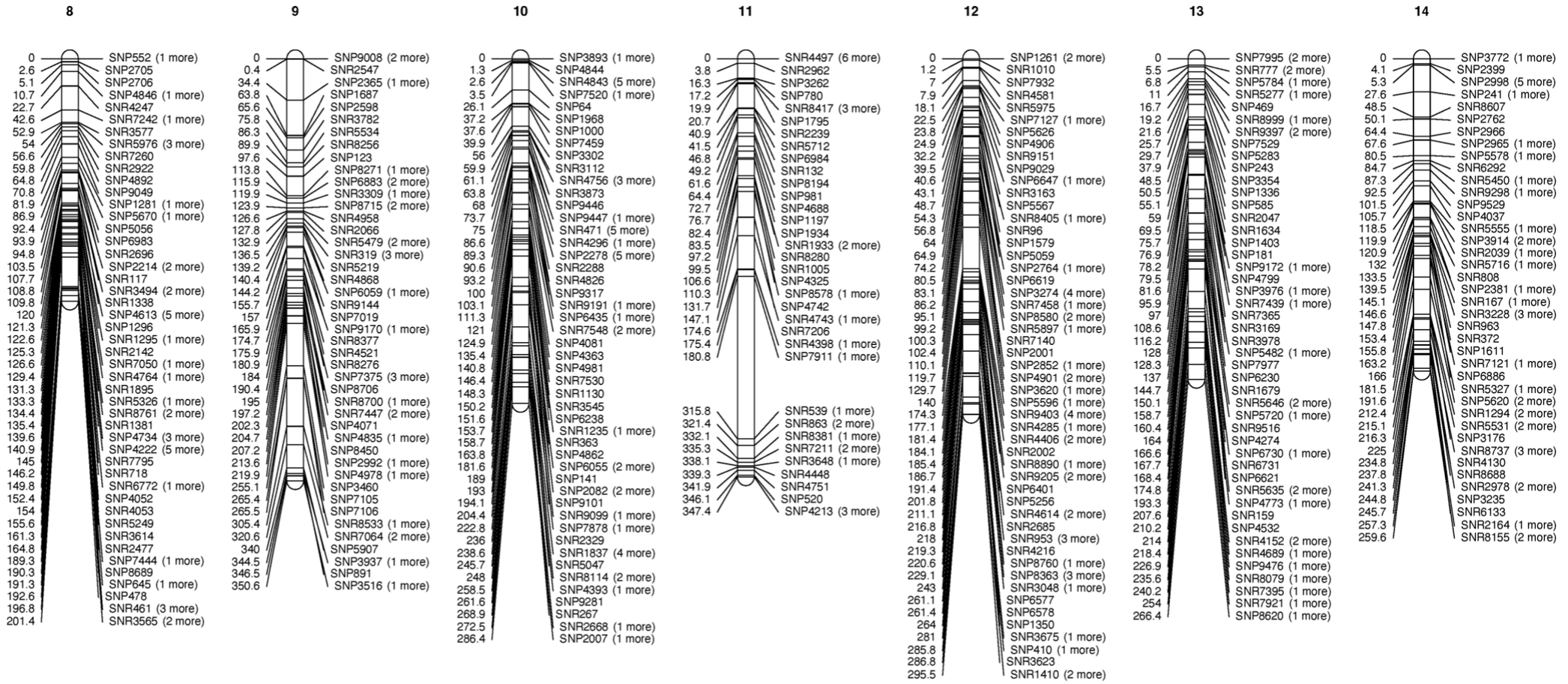
21
0 SNP5395 (2 more)
1.2 SNP883
5.3 SNR882
9.3 SNP8242
13.1 SNR3909
24.7 SNR2185
41.9 SNR1947
50.3 SNP1104
52.4 SNP2727
55.1 SNR8429
63.4 SNP7224 (1 more)
74.9 SNP7715
97.7 SNP4959 (1 more)
103.5 SNR5960 (3 more)
136 SNR2237 (1 more)
142.9 SNR666
145.4 SNR8038 (3 more)
146.7 SNP1725
150.2 SNR8784 (1 more)
184.6 SNR2975 (1 more)
220.8 SNR4471 (5 more)
222.1 SNR7098 (4 more)
224.7 SNR4094 (4 more)
225.9 SNR5860
233.1 SNR3481 (2 more)
243.1 SNR3147 (9 more)
244.4 SNR2931
246.4 SNP1976 (1 more)
257.9 SNR3439 (1 more)
262.2 SNR1736
264.9 SNR4993 (1 more)
269.7 SNR8486 (1 more)
274.9 SNR3036 (2 more)
279 SNR196 (2 more)
284 SNR8375 (1 more)
285 SNR6394 (1 more)
290.4 SNR7331 (1 more)
292.3 SNR4330
294.6 SNR1418
299.2 SNR85 (1 more)
299.7 SNR5509
302.3 SNR175
309.6 SNR1958 (1 more)
317.4 SNR224
318.2 SNP5658 (1 more)
329.2 SNR7308
365.5 SNR7310 (1 more)

Figure III-S2: All linkage groups of *R. speratus* female (RSQ) along with genetic distances and marker names. Each linkage group is named according to the chromosome number of genome assembly. Distances among markers are indicated in cM to the left of the linkage groups and SNP marker names are shown on the right. If there are more than one marker at the same position, then only one marker name is shown and number of rest of the markers are mentioned in the bracket after the marker name.

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5.1 SNP2706
10.7 SNP4846 (1 more)
22.7 SNR4247
42.6 SNR7242 (1 more)
52.9 SNR3577
54 SNR5976 (3 more)
56.6 SNR7260
59.8 SNR2922
64.8 SNP4892
70.8 SNP9049
81.9 SNP1281 (1 more)
86.9 SNP5670 (1 more)
92.4 SNP5056
93.9 SNP6983
94.8 SNR2696
103.5 SNP2214 (2 more)
107.7 SNR117
108.8 SNR3494 (2 more)
109.8 SNR1338
120 SNP4613 (5 more)
121.3 SNP1296
122.6 SNR1295 (1 more)
125.3 SNR2142
126.6 SNR7050 (1 more)
129.4 SNR4764 (1 more)
131.3 SNR1895
133.3 SNR5326 (1 more)
134.4 SNR8761 (2 more)
135.4 SNR1381
139.6 SNP4734 (3 more)
140.9 SNP4222 (5 more)
145 SNR7795
146.2 SNR718
149.8 SNR6772 (1 more)
152.4 SNP4052
154 SNR4053
155.6 SNR5249
161.3 SNR3614
164.8 SNR2477
189.3 SNP7444 (1 more)
190.3 SNP8689
191.3 SNP645 (1 more)
192.6 SNP478
196.8 SNR461 (3 more)
201.4 SNR3565 (2 more)
9
0 SNP9008 (2 more)
0.4 SNR2547
34.4 SNP2365 (1 more)
63.8 SNP1687
65.6 SNP2598
75.8 SNR3782
86.3 SNR5534
89.9 SNR8256
97.6 SNP123
113.8 SNP8271 (1 more)
115.9 SNP6883 (2 more)
119.9 SNR3309 (1 more)
123.9 SNP8715 (2 more)
126.6 SNR4958
127.8 SNR2066
132.9 SNR5479 (2 more)
136.5 SNR319 (3 more)
139.2 SNR5219
140.4 SNR4868
144.2 SNP6059 (1 more)
155.7 SNR9144
157 SNP7019
165.9 SNP9170 (1 more)
174.7 SNR8377
175.9 SNR4521
180.9 SNR8276
184 SNP7375 (3 more)
190.4 SNP8706
195 SNR8700 (1 more)
197.2 SNR7447 (2 more)
202.3 SNP4071
204.7 SNP4835 (1 more)
207.2 SNP8450
213.6 SNP2992 (1 more)
219.9 SNP4978 (1 more)
255.1 SNP3460
265.4 SNP7105
265.5 SNP7106
305.4 SNR8533 (1 more)
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344.5 SNP3937 (1 more)
346.5 SNP891
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3.5 SNP7520 (1 more)
26.1 SNP64
37.2 SNP1968
37.6 SNP1000
39.9 SNP7459
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59.9 SNR3112
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63.8 SNR3873
68 SNP9446
73.7 SNP9447 (1 more)
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86.6 SNR4296 (1 more)
89.3 SNP2278 (5 more)
90.6 SNR2288
93.2 SNR4826
100 SNP9317
103.1 SNR9191 (1 more)
111.3 SNP6435 (1 more)
121 SNR7548 (2 more)
124.9 SNP4081
135.4 SNP4363
140.8 SNP4981
146.4 SNR7530
148.3 SNR1130
150.2 SNR3545
151.6 SNP6238
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158.7 SNR363
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181.6 SNP6055 (2 more)
189 SNP141
193 SNP2082 (2 more)
194.1 SNP9101
204.4 SNR9099 (1 more)
222.8 SNP7878 (1 more)
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238.6 SNR1837 (4 more)
245.7 SNR5047
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258.5 SNP4393 (1 more)
261.6 SNP9281
268.9 SNR267
272.5 SNR2668 (1 more)
286.4 SNP2007 (1 more)
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40.9 SNR2239
41.5 SNR5712
46.8 SNP6984
49.2 SNR132
61.6 SNP8194
64.4 SNP981
72.7 SNP4688
76.7 SNP1197
82.4 SNP1934
83.5 SNR1933 (2 more)
97.2 SNR8280
99.5 SNR1005
106.6 SNP4325
110.3 SNP8578 (1 more)
131.7 SNP4742
147.1 SNR4743 (1 more)
174.6 SNR7206
175.4 SNR4398 (1 more)
180.8 SNP7911 (1 more)
315.8 SNR539 (1 more)
321.4 SNR863 (2 more)
332.1 SNR8381 (1 more)
335.3 SNR7211 (2 more)
338.1 SNR3648 (1 more)
339.3 SNR4448
341.9 SNR4751
346.1 SNP520
347.4 SNP4213 (3 more)
12
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1.2 SNR1010
7 SNP7932
7.9 SNR4581
18.1 SNR5975
22.5 SNP7127 (1 more)
23.8 SNP5626
24.9 SNP4906
32.2 SNR9151
39.5 SNP9029
40.6 SNP6647 (1 more)
43.1 SNR3163
48.7 SNP5567
54.3 SNR8405 (1 more)
56.8 SNR96
64 SNP1579
64.9 SNP5059
74.2 SNP2764 (1 more)
80.5 SNP6619
83.1 SNP3274 (4 more)
86.2 SNR7458 (1 more)
95.1 SNP8580 (2 more)
99.2 SNR5897 (1 more)
100.3 SNR7140
102.4 SNP2001
110.1 SNP2852 (1 more)
119.7 SNP4901 (2 more)
129.7 SNP3620 (1 more)
140 SNP5596 (1 more)
174.3 SNR9403 (4 more)
177.1 SNR4285 (1 more)
181.4 SNR4406 (2 more)
184.1 SNR2002
185.4 SNP8890 (1 more)
186.7 SNR9205 (2 more)
191.4 SNP6401
201.8 SNP5256
211.1 SNR4614 (2 more)
216.8 SNR2685
218 SNR953 (3 more)
219.3 SNR4216
220.6 SNP8760 (1 more)
229.1 SNP8363 (3 more)
243 SNR3048 (1 more)
261.1 SNP6577
261.4 SNP6578
264 SNP1350
281 SNR3675 (1 more)
285.8 SNP410 (1 more)
286.8 SNR3623
295.5 SNR1410 (2 more)
13
0 SNP7995 (2 more)
5.5 SNR777 (2 more)
6.8 SNP5784 (1 more)
11 SNR5277 (1 more)
16.7 SNP469
19.2 SNR8999 (1 more)
21.6 SNR9397 (2 more)
25.7 SNP7529
29.7 SNP5283
37.9 SNP243
48.5 SNP3354
50.5 SNP1336
55.1 SNP585
59 SNR2047
69.5 SNR1634
75.7 SNP1403
76.9 SNP181
78.2 SNP9172 (1 more)
79.5 SNP4799
81.6 SNP3976 (1 more)
95.9 SNR7439 (1 more)
97 SNR7365
108.6 SNR3169
116.2 SNR3978
128 SNP5482 (1 more)
128.3 SNP7977
137 SNP6230
144.7 SNR1679
150.1 SNR5646 (2 more)
158.7 SNP5720 (1 more)
160.4 SNR9516
164 SNP4274
166.6 SNP6730 (1 more)
167.7 SNR6731
168.4 SNP6621
174.8 SNR5635 (2 more)
193.3 SNP4773 (1 more)
207.6 SNR159
210.2 SNP4532
214 SNR4152 (2 more)
218.4 SNR4689 (1 more)
226.9 SNP9476 (1 more)
235.6 SNR8079 (1 more)
240.2 SNR7395 (1 more)
254 SNR7921 (1 more)
266.4 SNP8620 (1 more)
14
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4.1 SNP2399
5.3 SNP2998 (5 more)
27.6 SNP241 (1 more)
48.5 SNR8607
50.1 SNP2762
64.4 SNP2966
67.6 SNP2965 (1 more)
80.5 SNP5578 (1 more)
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87.3 SNR5450 (1 more)
92.5 SNR9298 (1 more)
101.5 SNP9529
105.7 SNP4037
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119.9 SNP3914 (2 more)
120.9 SNR2039 (1 more)
132 SNR5716 (1 more)
133.5 SNR808
139.5 SNP2381 (1 more)
145.1 SNR167 (1 more)
146.6 SNR3228 (3 more)
147.8 SNR963
153.4 SNR372
155.8 SNP1611
163.2 SNR7121 (1 more)
166 SNP6886
181.5 SNR5327 (1 more)
191.6 SNP5620 (2 more)
212.4 SNR1294 (2 more)
215.1 SNR5531 (2 more)
216.3 SNP3176
225 SNR8737 (3 more)
234.8 SNR4130
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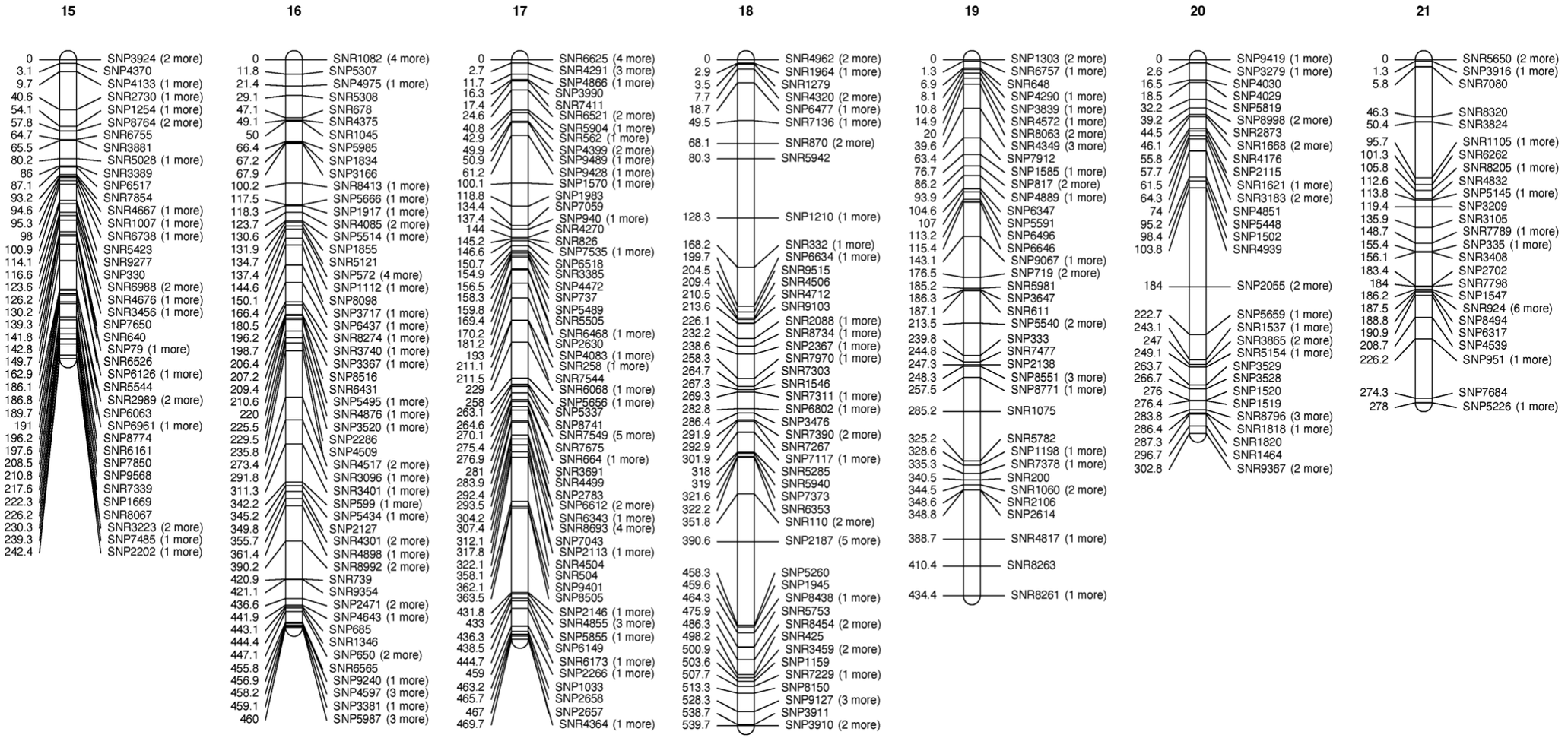
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64.7 SNR6755
65.5 SNR3881
80.2 SNR5028 (1 more)
86 SNR3389
87.1 SNP6517
93.2 SNR7854
94.6 SNR4667 (1 more)
95.3 SNR1007 (1 more)
98 SNR6738 (1 more)
100.9 SNR5423
114.1 SNR9277
116.6 SNP330
123.6 SNR6988 (2 more)
126.2 SNR4676 (1 more)
130.2 SNR3456 (1 more)
139.3 SNP7650
141.8 SNR640
142.8 SNP79 (1 more)
149.7 SNR6526
162.9 SNP6126 (1 more)
186.1 SNR5544
186.8 SNR2989 (2 more)
189.7 SNP6063
191 SNP6961 (1 more)
196.2 SNP8774
197.6 SNR6161
208.5 SNP7850
210.8 SNP9568
217.6 SNR7339
222.3 SNP1669
226.2 SNR8067
230.3 SNR3223 (2 more)
239.3 SNP7485 (1 more)
242.4 SNP2202 (1 more)
16
0 SNR1082 (4 more)
11.8 SNP5307
21.4 SNP4975 (1 more)
29.1 SNR5308
47.1 SNR678
49.1 SNR4375
50 SNR1045
66.4 SNP5985
67.2 SNP1834
67.9 SNP3166
100.2 SNR8413 (1 more)
117.5 SNP5666 (1 more)
118.3 SNP1917 (1 more)
123.7 SNR4085 (2 more)
130.6 SNP5514 (1 more)
131.9 SNP1855
134.7 SNR5121
137.4 SNP572 (4 more)
144.6 SNP1112 (1 more)
150.1 SNP8098
166.4 SNP3717 (1 more)
180.5 SNP6437 (1 more)
196.2 SNR8274 (1 more)
198.7 SNR3740 (1 more)
206.4 SNP3367 (1 more)
207.2 SNP8516
209.4 SNR6431
210.6 SNP5495 (1 more)
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225.5 SNP3520 (1 more)
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361.4 SNR4898 (1 more)
390.2 SNR8992 (2 more)
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421.1 SNR9354
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443.1 SNP685
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118.8 SNP1983
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146.6 SNP7535 (1 more)
150.7 SNP6518
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156.5 SNP4472
158.3 SNP737
159.8 SNP5489
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211.5 SNR7544
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363.5 SNP8505
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436.3 SNP5855 (1 more)
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463.2 SNP1033
465.7 SNP2658
467 SNP2657
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2.9 SNR1964 (1 more)
3.5 SNR1279
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49.5 SNR7136 (1 more)
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199.7 SNP6634 (1 more)
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209.4 SNR4506
210.5 SNR4712
213.6 SNR9103
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232.2 SNR8734 (1 more)
238.6 SNP2367 (1 more)
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264.7 SNR7303
267.3 SNR1546
269.3 SNR7311 (1 more)
282.8 SNP6802 (1 more)
286.4 SNP3476
291.9 SNR7390 (2 more)
292.9 SNR7267
301.9 SNP7117 (1 more)
318 SNR5285
319 SNR5940
321.6 SNP7373
322.2 SNR6353
351.8 SNR110 (2 more)
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503.6 SNP1159
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513.3 SNP8150
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538.7 SNP3911
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14.9 SNR4572 (1 more)
20 SNR8063 (2 more)
39.6 SNR4349 (3 more)
63.4 SNP7912
76.7 SNP1585 (1 more)
86.2 SNP817 (2 more)
93.9 SNP4889 (1 more)
104.6 SNP6347
107 SNP5591
113.2 SNP6496
115.4 SNP6646
143.1 SNP9067 (1 more)
176.5 SNP719 (2 more)
185.2 SNR5981
186.3 SNP3647
187.1 SNR611
213.5 SNP5540 (2 more)
239.8 SNP333
244.8 SNR7477
247.3 SNP2138
248.3 SNP8551 (3 more)
257.5 SNP8771 (1 more)
285.2 SNR1075
325.2 SNR5782
328.6 SNP1198 (1 more)
335.3 SNR7378 (1 more)
340.5 SNR200
344.5 SNR1060 (2 more)
348.6 SNR2106
348.8 SNP2614
388.7 SNR4817 (1 more)
410.4 SNR8263
434.4 SNR8261 (1 more)
20
0 SNP9419 (1 more)
2.6 SNP3279 (1 more)
16.5 SNP4030
18.5 SNP4029
32.2 SNP5819
39.2 SNP8998 (2 more)
44.5 SNR2873
46.1 SNR1668 (2 more)
55.8 SNP4176
57.7 SNP2115
61.5 SNR1621 (1 more)
64.3 SNR3183 (2 more)
74 SNP4851
95.2 SNP5448
98.4 SNP1502
103.8 SNR4939
184 SNP2055 (2 more)
222.7 SNP5659 (1 more)
243.1 SNR1537 (1 more)
247 SNR3865 (2 more)
249.1 SNR5154 (1 more)
263.7 SNP3529
266.7 SNP3528
276 SNP1520
276.4 SNP1519
283.8 SNR8796 (3 more)
286.4 SNR1818 (1 more)
287.3 SNP1820
296.7 SNR1464
302.8 SNR9367 (2 more)
21
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1.3 SNP3916 (1 more)
5.8 SNR7080
46.3 SNR8320
50.4 SNR3824
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112.6 SNR4832
113.8 SNP5145 (1 more)
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148.7 SNR7789 (1 more)
155.4 SNP335 (1 more)
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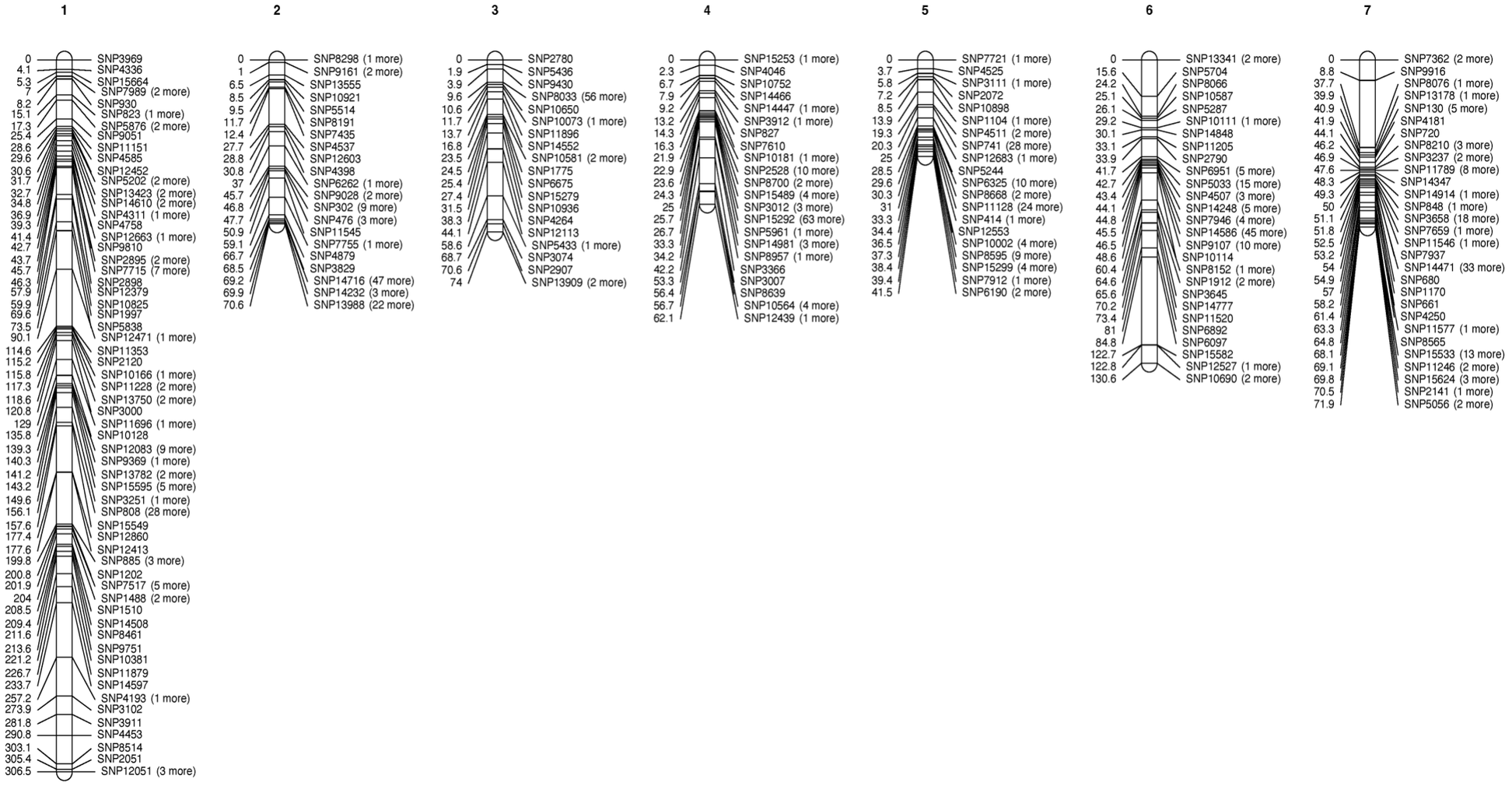
183.4 SNP2702
184 SNR7798
186.2 SNP1547
187.5 SNR924 (6 more)
188.8 SNP8494
190.9 SNP6317
208.7 SNP4539
226.2 SNP951 (1 more)
274.3 SNP7684
278 SNP5226 (1 more)

Figure III-S3: All linkage groups of *R. flavipes* male (RFK) along with genetic distances and marker names. Each linkage group is named according to the chromosome number of genome assembly. Distances among markers are indicated in cM to the left of the linkage groups and SNP marker names are shown on the right. If there are more than one marker at the same position, then only one marker name is shown and number of rest of the markers are mentioned in the bracket after the marker name.



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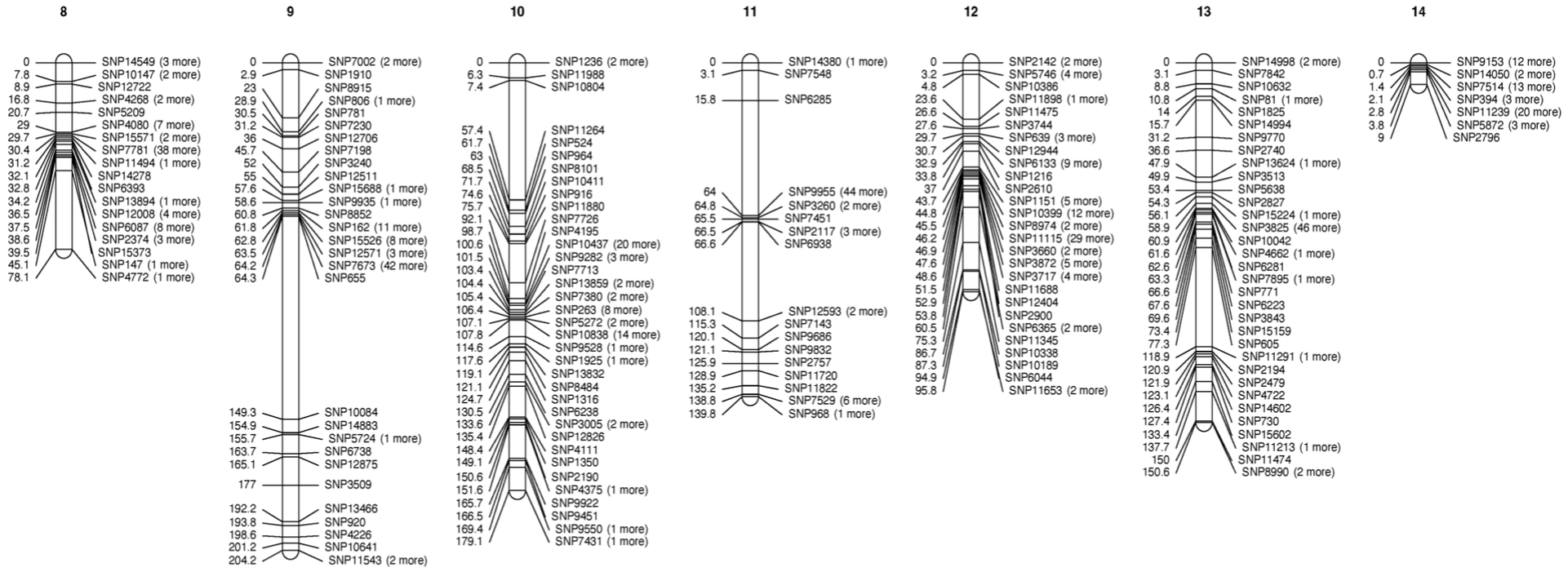
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29.7 SNP15571 (2 more)
30.4 SNP7781 (38 more)
31.2 SNP11494 (1 more)
32.1 SNP14278
32.8 SNP6393
34.2 SNP13894 (1 more)
36.5 SNP12008 (4 more)
37.5 SNP6087 (8 more)
38.6 SNP2374 (3 more)
39.5 SNP15373
45.1 SNP147 (1 more)
78.1 SNP4772 (1 more)
9
0 SNP7002 (2 more)
2.9 SNP1910
23 SNP8915
28.9 SNP806 (1 more)
30.5 SNP781
31.2 SNP7230
36 SNP12706
45.7 SNP7198
52 SNP3240
55 SNP12511
57.6 SNP15688 (1 more)
58.6 SNP9935 (1 more)
60.8 SNP8852
61.8 SNP162 (11 more)
62.8 SNP15526 (8 more)
63.5 SNP12571 (3 more)
64.2 SNP7673 (42 more)
64.3 SNP655
149.3 SNP10084
154.9 SNP14883
155.7 SNP5724 (1 more)
163.7 SNP6738
165.1 SNP12875
177 SNP3509
192.2 SNP13466
193.8 SNP920
198.6 SNP4226
201.2 SNP10641
204.2 SNP11543 (2 more)
10
0 SNP1236 (2 more)
6.3 SNP11988
7.4 SNP10804
57.4 SNP11264
61.7 SNP524
63 SNP964
68.5 SNP8101
71.7 SNP10411
74.6 SNP916
75.7 SNP11880
92.1 SNP7726
98.7 SNP4195
100.6 SNP10437 (20 more)
101.5 SNP9282 (3 more)
103.4 SNP7713
104.4 SNP13859 (2 more)
105.4 SNP7380 (2 more)
106.4 SNP263 (8 more)
107.1 SNP5272 (2 more)
107.8 SNP10838 (14 more)
114.6 SNP9528 (1 more)
117.6 SNP1925 (1 more)
119.1 SNP13832
121.1 SNP8484
124.7 SNP1316
130.5 SNP6238
133.6 SNP3005 (2 more)
135.4 SNP12826
148.4 SNP4111
149.1 SNP1350
150.6 SNP2190
151.6 SNP4375 (1 more)
165.7 SNP9922
166.5 SNP9451
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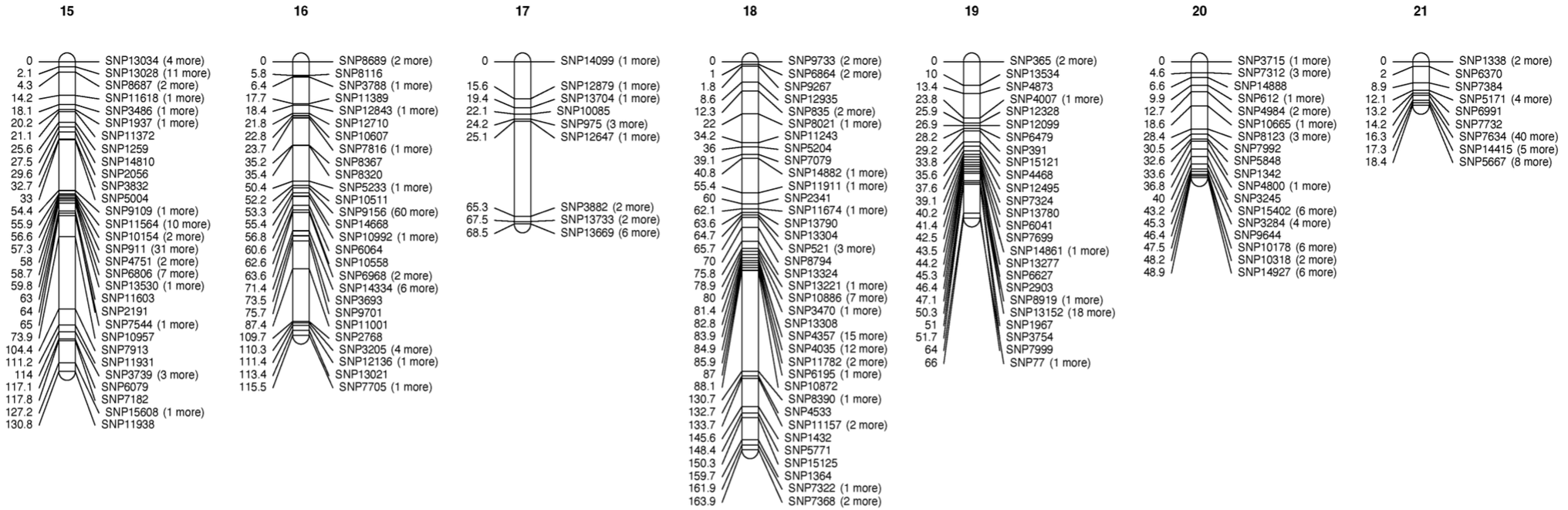
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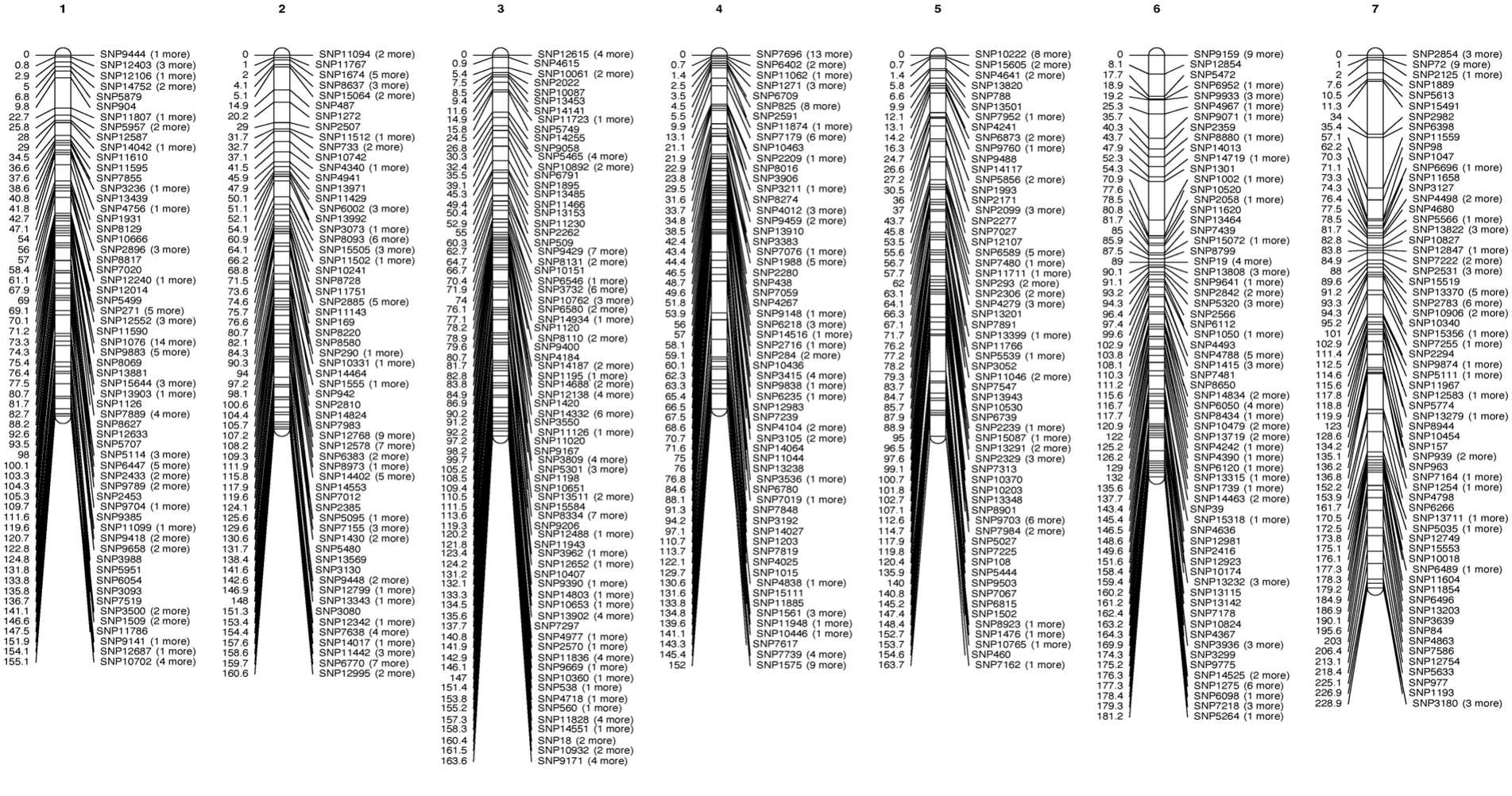
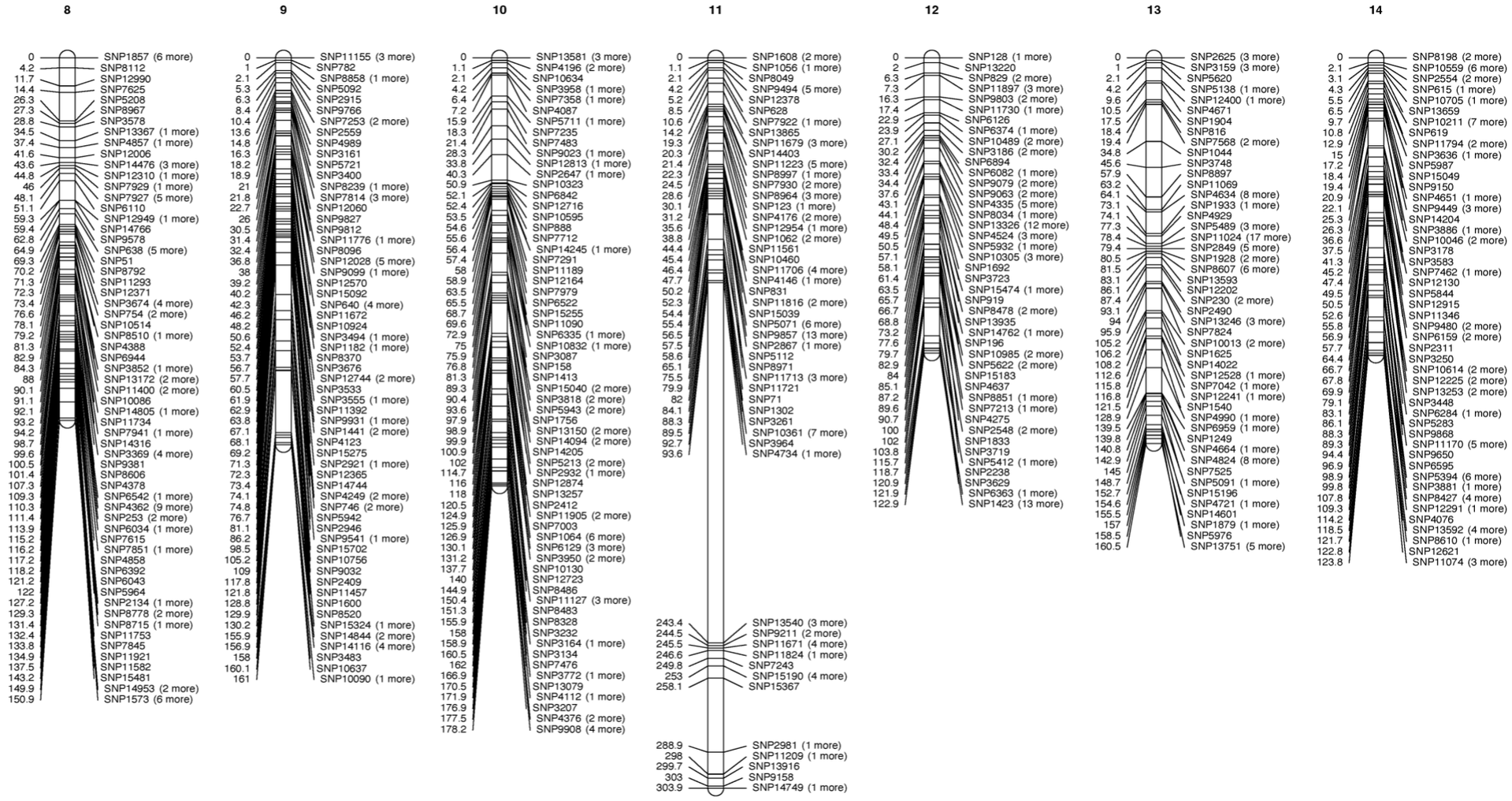
18.4 SNP5667 (8 more)

Figure III-S4: All linkage groups of *R. flavipes* female (RFQ) along with genetic distances and marker names. Each linkage group is named according to the chromosome number of genome assembly. Distances among markers are indicated in cM to the left of the linkage groups and SNP marker names are shown on the right. If there are more than one marker at the same position, then only one marker name is shown and number of rest of the markers are mentioned in the bracket after the marker name.

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82.9 SNP6944
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132.4 SNP11753
133.8 SNP7845
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137.5 SNP11582
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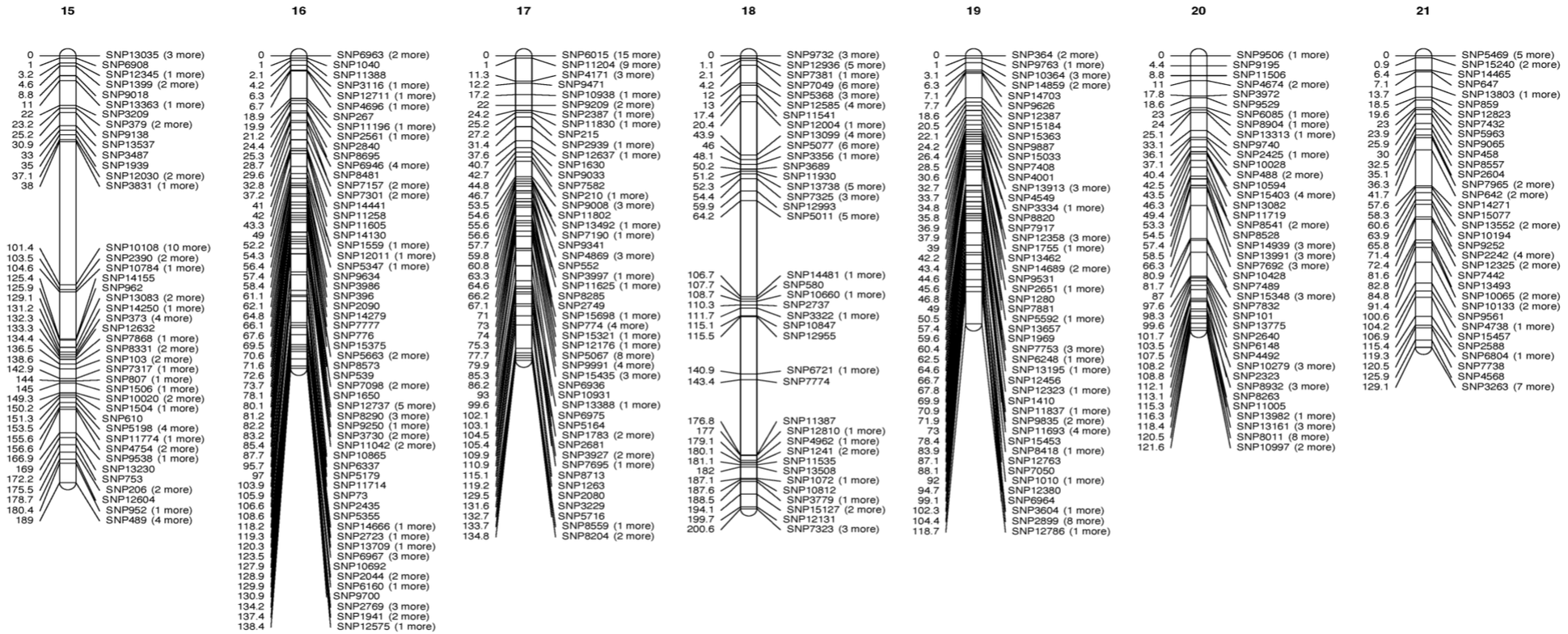
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107.7 SNP580
108.7 SNP10660 (1 more)
110.3 SNP2737
111.7 SNP3322 (1 more)
115.1 SNP10847
115.5 SNP12955
140.9 SNP6721 (1 more)
143.4 SNP7774
176.8 SNP11387
177 SNP12810 (1 more)
179.1 SNP4962 (1 more)
180.1 SNP1241 (2 more)
181.1 SNP11535
182 SNP13508
187.1 SNP1072 (1 more)
187.6 SNP10812
188.5 SNP3779 (1 more)
194.1 SNP15127 (2 more)
199.7 SNP12131
200.6 SNP7323 (3 more)
19
0 SNP364 (2 more)
1 SNP9763 (1 more)
3.1 SNP10364 (3 more)
6.3 SNP14859 (2 more)
7.1 SNP14703
7.7 SNP9626
18.6 SNP12387
20.5 SNP15184
22.1 SNP15363
24.2 SNP9887
26.4 SNP15033
28.5 SNP7408
30.6 SNP4001
32.7 SNP13913 (3 more)
33.7 SNP4549
34.8 SNP3334 (1 more)
35.8 SNP8820
36.9 SNP7917
37.9 SNP12358 (3 more)
39 SNP1755 (1 more)
42.2 SNP13462
43.4 SNP14689 (2 more)
44.6 SNP9531
45.6 SNP2651 (1 more)
46.8 SNP1280
49 SNP7881
50.5 SNP5592 (1 more)
57.4 SNP13657
59.6 SNP1969
60.4 SNP7753 (3 more)
62.5 SNP6248 (1 more)
64.6 SNP13195 (1 more)
66.7 SNP12456
67.8 SNP12323 (1 more)
69.9 SNP1410
70.9 SNP11837 (1 more)
71.9 SNP9835 (2 more)
73 SNP11693 (4 more)
78.4 SNP15453
83.9 SNP8418 (1 more)
87.1 SNP12763
88.1 SNP7050
92 SNP1010 (1 more)
94.7 SNP12380
99.1 SNP6964
102.3 SNP3604 (1 more)
104.4 SNP2899 (8 more)
118.7 SNP12786 (1 more)
20
0 SNP9506 (1 more)
4.4 SNP9195
8.8 SNP11506
11 SNP4674 (2 more)
17.8 SNP3972
18.6 SNP9529
23 SNP6085 (1 more)
24 SNP8904 (1 more)
25.1 SNP13313 (1 more)
33.1 SNP9740
36.1 SNP2425 (1 more)
37.1 SNP10028
40.4 SNP488 (2 more)
42.5 SNP10594
43.5 SNP15403 (4 more)
46.3 SNP13082
49.4 SNP11719
53.3 SNP8541 (2 more)
54.5 SNP8528
57.4 SNP14939 (3 more)
58.5 SNP13991 (3 more)
66.3 SNP7692 (3 more)
80.9 SNP10428
81.7 SNP7489
87 SNP15348 (3 more)
97.6 SNP7832
98.3 SNP101
99.6 SNP13775
101.7 SNP2640
103.5 SNP6148
107.5 SNP4492
108.2 SNP10279 (3 more)
108.8 SNP2323
112.1 SNP8932 (3 more)
113.1 SNP8263
115.3 SNP11005
116.3 SNP13982 (1 more)
118.4 SNP13161 (3 more)
120.5 SNP8011 (8 more)
121.6 SNP10997 (2 more)
21
0 SNP5469 (5 more)
0.9 SNP15240 (2 more)
6.4 SNP14465
7.1 SNP647
13.7 SNP13803 (1 more)
18.5 SNP859
19.6 SNP12823
23 SNP7432
23.9 SNP5963
25.9 SNP9065
30 SNP458
32.5 SNP8557
35.1 SNP2604
36.3 SNP7965 (2 more)
41.7 SNP642 (2 more)
57.6 SNP14271
58.3 SNP15077
60.6 SNP13552 (2 more)
63.9 SNP10194
65.8 SNP9252
71.4 SNP2242 (4 more)
72.4 SNP12325 (2 more)
81.6 SNP7442
82.8 SNP13493
84.8 SNP10065 (2 more)
91.4 SNP10133 (2 more)
100.6 SNP9561
104.2 SNP4738 (1 more)
106.9 SNP15457
115.4 SNP2588
119.3 SNP6804 (1 more)
120.5 SNP7738
125.9 SNP4568
129.1 SNP3263 (7 more)

Figure III-S5: Plots of pairwise recombination fraction and pairwise physical distances for *R.speratus* female. Each data point depicts a marker pair of the chromosome plotted. Pairwise recombination fractions for the marker pairs are plotted on the y-axis while the physical distance between marker pair (in bp) is shown on the x-axis.

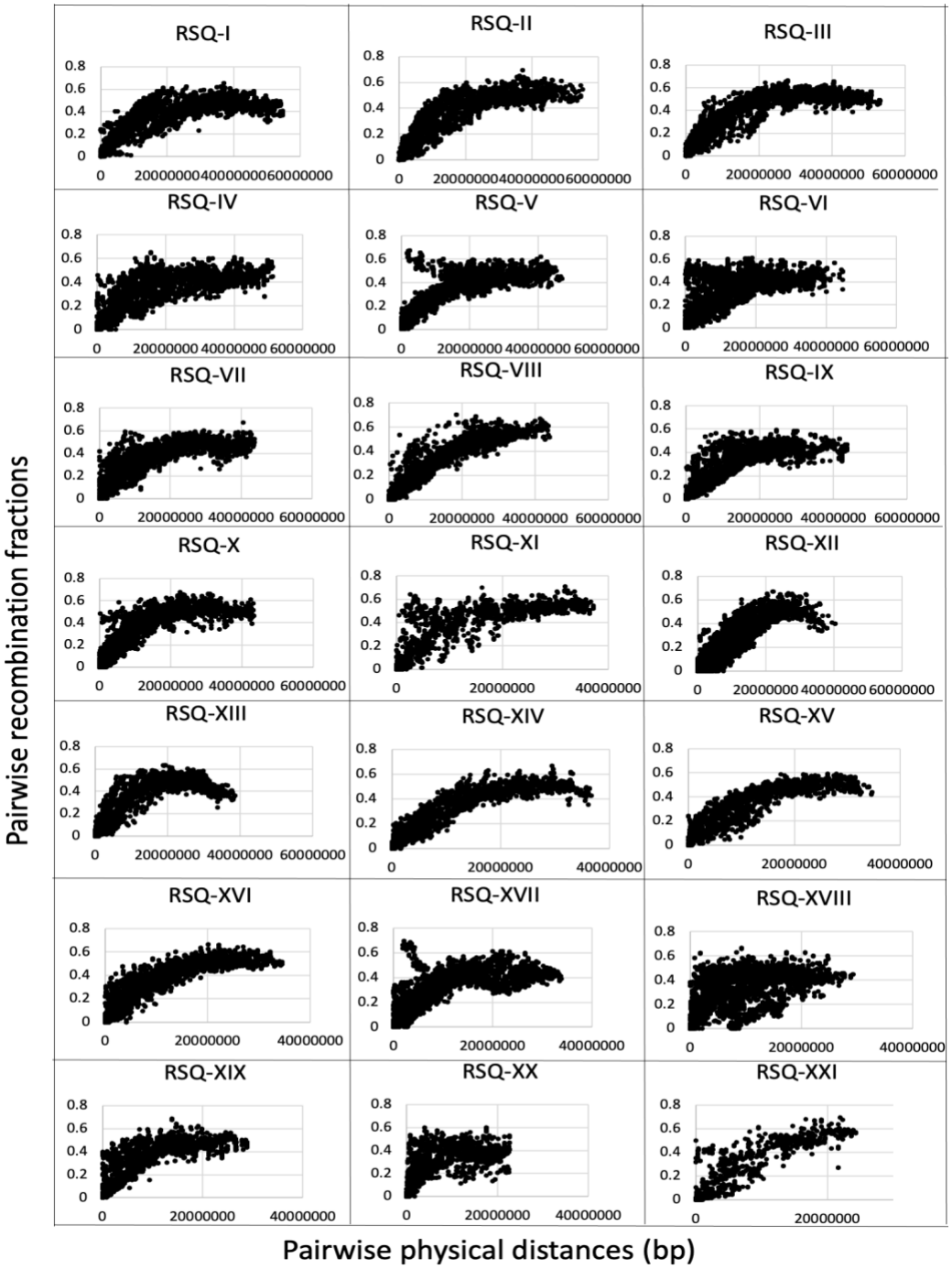


Figure III-S6: Plots of pairwise recombination fraction and pairwise physical distances for *R.flavipes* female. Each data point depicts a marker pair of the chromosome plotted. Pairwise recombination fractions for the marker pairs are plotted on the y-axis while the physical distance between marker pair (in bp) is shown on the x-axis.

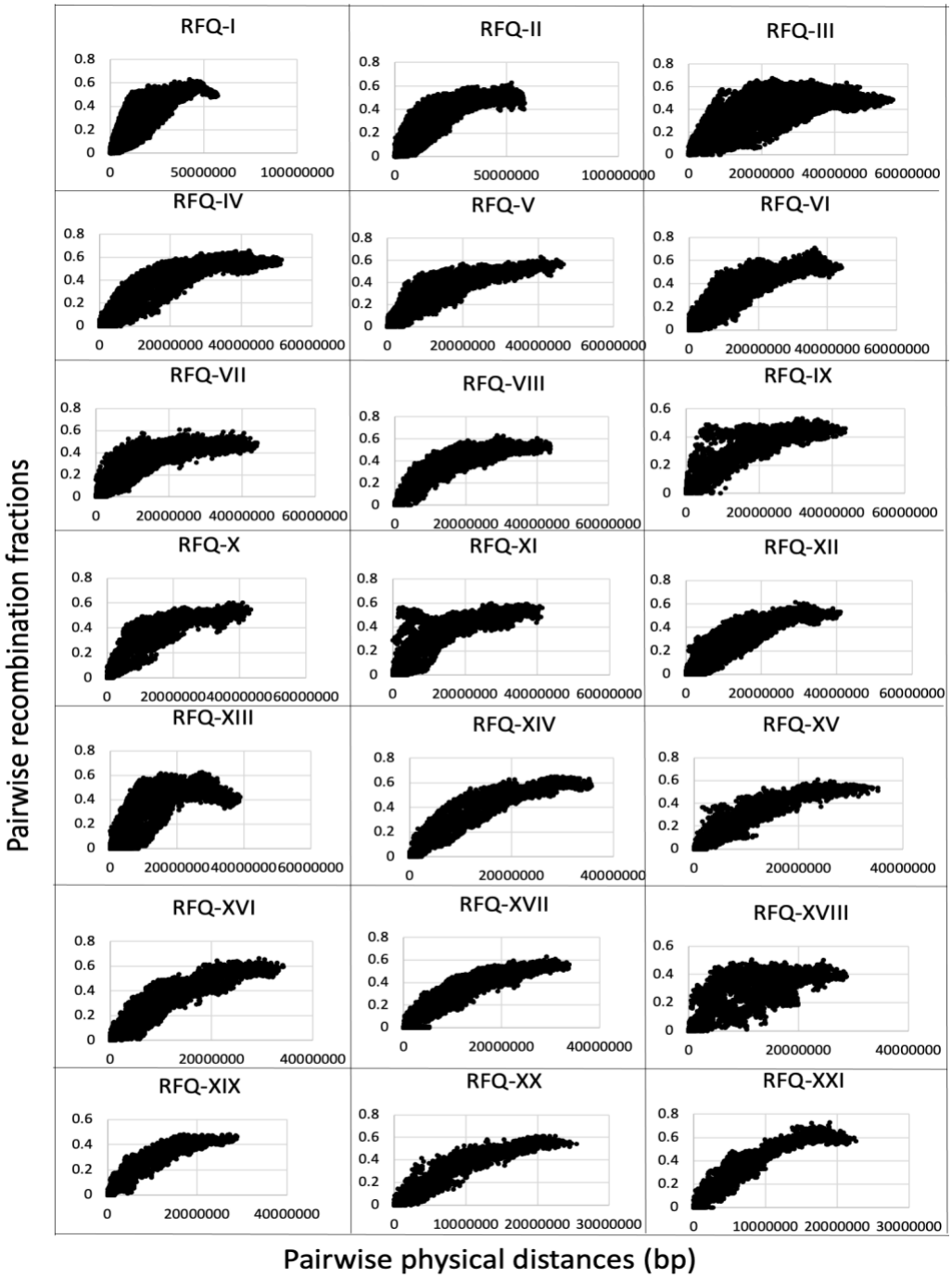


Figure III-S7: Plots of pairwise recombination fraction and pairwise physical distances for *R.speratus* male. Each data point depicts a marker pair of the chromosome plotted. Pairwise recombination fractions for the marker pairs are plotted on the y-axis while the physical distance between marker pair (in bp) is shown on the x-axis.

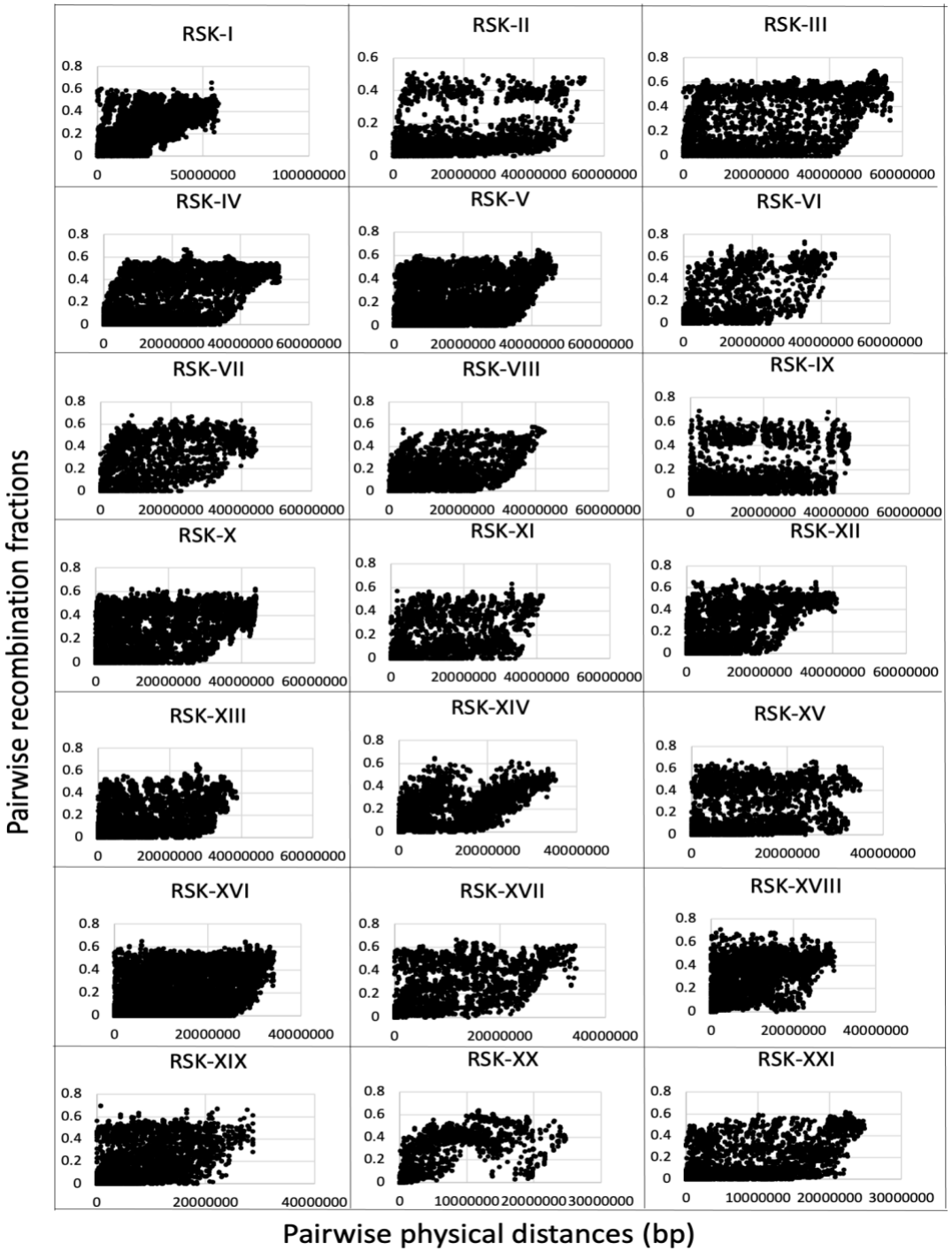
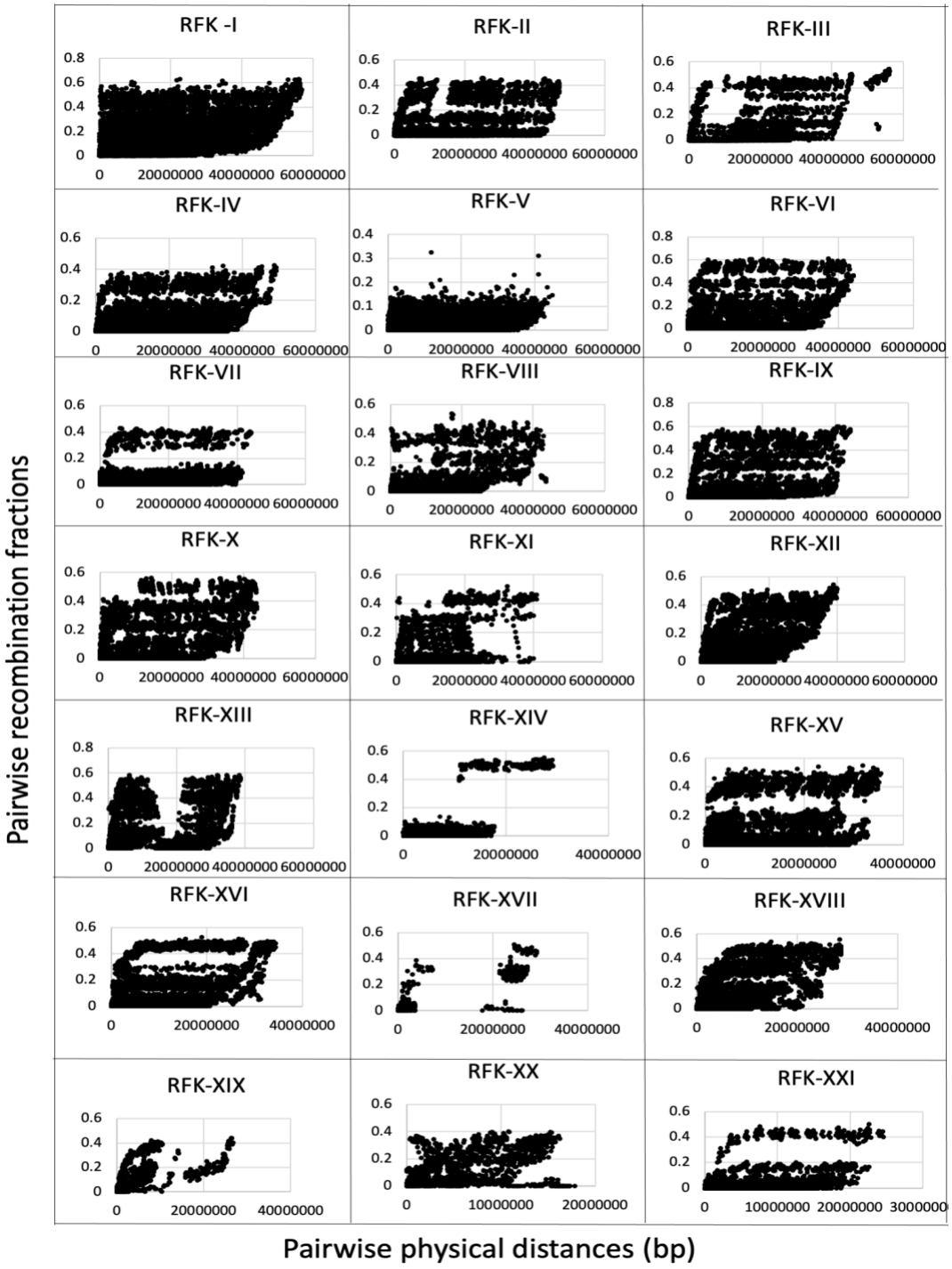


Figure III-S8: Plots of pairwise recombination fraction and pairwise physical distances for *R.flavipes* male. Each data point depicts a marker pair of the chromosome plotted. Pairwise recombination fractions for the marker pairs are plotted on the y-axis while the physical distance between marker pair (in bp) is shown on the x-axis.



CHAPTER IV: GENERAL DISCUSSION

The reasons and conditions behind the evolution of eusociality – the highest level of social organization – remain a mystery since it is contrary to the basic premise of Darwin's natural selection (Darwin, 1859). The consequence of social evolution, particularly at the genomic level, are only beginning to be explored. The motivation behind this dissertation was to explore one of the many open questions related to eusociality – the pervasiveness of high recombination rates in eusocial insect societies (Wilfert et al., 2007). Current explanations to describe the correlation between eusociality and high recombination rates can be divided into three hypotheses: the genotypic diversity hypothesis, the social innovation hypothesis, and the reduction of genetic conflict hypothesis (Chapter I). This dissertation examined meiotic recombination rates in three different eusocial insects – *Frieseomelitta varia* (Hymenoptera, Apidae), *Reticulitermes speratus* (Blattodea, Rhinotermitidae), and *Reticulitermes flavipes* (Blattodea, Rhinotermitidae). These estimates are the first recombination rate values for any species of stingless bees and termites and contribute to the breadth of available recombination rate data. The obtained recombination rates were not only used to evaluate the validity of the existing hypotheses but also discuss how these rates correlate to eusocial insects based on their biology and life-history traits (**Table IV-1**).

Chapter I describes the background and rationale behind the objective of this dissertation in more detail. The big question related to this objective is how eusociality repeatedly evolved in different taxa of animals -most notably in many insect species of order Hymenoptera (wasps, bees, and ants) and Blattodea (termites). The hypothesis of high recombination rates in eusocial insects arose after the first linkage map described in the western honey bee (*Apis mellifera*) in 1995 showed an exceptional meiotic recombination rate (Hunt & Page, 1995). Meiotic

recombination occurs in almost all sexual organisms because it is required for proper segregation of chromosomes during gamete formation and to create a novel allelic combination in offspring, but the recombination rates vary between genomes, individuals, populations, and species (Stapley et al., 2017). The notion of high recombination rate in eusocial insects got strengthening support after it was discovered that seven more eusocial hymenopterans – three honey bees (Hymenoptera, Apidae), two ants (Hymenoptera, Formicidae), one wasp (Hymenoptera, Vespidae), and one bumblebee (Hymenoptera, Apidae) also exhibit high recombination rates (Rueppell et al., 2016; Shi et al., 2013; Sirvio et al., 2006; Sirviö, Johnston, et al., 2011; Sirviö, Pamilo, et al., 2011; Stolle et al., 2011; Wilfert et al., 2006) while closely related solitary hymenopterans do not (J. C. Jones et al., 2019; Wilfert et al., 2007). The arguments presented in these studies indicate eusociality is associated with these high recombination rates. However, more data is needed from unexplored taxa of eusocial insects since factors and conditions differ between diverse groups of eusocial insects (Brian, 1983; Starr, 2020). Some of these factors include the presence of parthenogenesis, the extent of queen-worker caste divergence, and degree of sociality.

Parthenogenesis accumulates deleterious mutations in response to the reduction in heterozygosity which reduces the efficacy of natural selection (Keightley & Otto, 2006; Matsuura et al., 2004). Species with parthenogenesis might compensate to promote heterozygosity in parthenogens by increasing meiotic recombination. Arrhenotokous parthenogenesis (unfertilized eggs develop into males) is common in eusocial Hymenoptera due to their haplodiploidy, while thelytokous parthenogenesis (unfertilized eggs develop into females) is not as common in eusocial insects (Matsuura, 2017; Rabeling & Kronauer, 2013). Chapter III in this dissertation examined two closely related termite species - *Reticulitermes*

speratus (exhibits facultative parthenogenesis) and *Reticulitermes flavipes* (no parthenogenesis) for recombination rates. As predicted, the meiotic recombination rate in *R. speratus* was higher than *R. flavipes*. Relatedness asymmetry created in three Reticulitermes species (*R. speratus*, *R. virginicus*, and *R lucifugus*) due to parthenogenesis has been proposed as an analogous system to asymmetry created in eusocial Hymenoptera due to haplodiploidy (Kobayashi et al., 2013). High recombination can reduce the variance of relatedness between individuals of kin-based societies. Thus the results of high recombination in the species I tested can provide some support to 'the reduction of genetic conflict' hypothesis in termites. Although, many termites do not show parthenogenesis (Matsuura, 2010) which suggests that the reduction of genetic conflict hypothesis may not apply to all termites or additional factors are driving the evolution of high recombination in termites.

Social insect colonies in which workers develop ovaries are correlated with the reduction in task performance and promotion of worker selfishness (Mattila et al., 2012), suggesting higher queen-worker caste divergence should favor selflessness and stability in the colony. Stronger queen-worker divergence should facilitate more innovation (as predicted by the social innovation hypothesis) and thus should exhibit higher recombination rates. Chapter II deals with *Frieseomelitta varia*, a Brazilian stingless bee that shows strong queen-worker caste divergence, and therefore it is expected to exhibit a higher recombination rate than other eusocial insects. Contrary to this prediction, *F. varia* showed a lower recombination rate than other eusocial insects with relatively weak queen-worker divergence, such as honey bees. The results in termites supported the correlation of worker-reproductive caste divergence to recombination rates (Chapter III). The hemimetabolous development in termites suggests early independence in workers to perform colony tasks better (Alexander et al., 1991). Furthermore, developmental

plasticity in termites is more common than eusocial Hymenoptera, which provides greater flexibility in responses to change in the environment (Higashi et al., 2000). This plasticity indicates a reduced worker-reproductive caste divergence and may select for lower recombination rates than honey bees. The contradictory results in *F. varia* and termites indicate strong caste divergence may not be the primary factor in the adaptation of increased recombination rates in eusocial insects.

The prediction of both 'genotypic diversity' and 'social innovation' hypotheses suggest the degree of sociality and level of social complexity may be related to the extent of recombination rates in eusocial insects based on comparative rates of eusocial and closely related nonsocial insects (J. C. Jones et al., 2019; C. F. Kent & Zayed, 2013; Rehan & Toth, 2015; Wilfert et al., 2007). *F. varia* is more socially complex and advanced than its sister group of primitively eusocial bumblebees (Hedtke et al., 2013; Rasmussen & Cameron, 2010). Higher recombination rates in this advanced eusocial bee species than bumblebees (Stolle et al., 2011) suggest a link of social complexity to recombination rates. However, termite results show either similar or lower recombination rates than bumblebee provides contradictory results. Compared to recombination rates of polyandrous honey bees, monandrous species *B. terrestris*, *F. varia, R. speratus,* and *R. flavipes* show lower recombination rates. In fact, monogamy was the ancestral state in all the eusocial lineages (Boomsma, 2009). Polyandrous species enhances the intracolonial genetic diversity and reduces relatedness through multiple mating, which may cause within-colony conflicts (Heinze, 2010) and hence should select for higher recombination rates. My results show a lower recombination rate in eusocial monandrous species than eusocial polyandrous species, providing support for the 'reduction of genetic conflict' hypothesis.

At a taxonomic level, the recombination rate estimate for *F. varia* in this dissertation completes the comparison of Apis, Bombus, and Meliponini. It suggests the possibility of a high recombination rate being an ancestral condition in corbiculate bees, which can be tested by estimating the recombination rate for the last group of corbiculate bees, Euglossini. The condition of high recombination in the common ancestor of corbiculate bees can help resolve the conflicting view of whether eusociality evolved once or twice in this group (Cardinal & Danforth, 2011). The recombination rates of *R. speratus* and *R. flavipes* present first estimates for any termite species that can help researchers include the data when testing hypotheses related to recombination rates in eusocial insects to reduce the skew of eusocial Hymenoptera in published studies.

The intermediate placement of termites on the recombination rate spectrum compared to other eusocial insects suggest high recombination rates may be a necessary variable in eusocial evolution but this correlation seems more pronounced in Eusocial Hymenoptera. The reasons may be associated with the contrasting biological, ecological, and life-history traits. For example, colony size could be a potential factor in the selection of high recombination rates in eusocial insects. The effect of large colony size on recombination is not known, but eusocial insects with larger colonies, such as both termite species and leaf-cutting ant, show a comparatively lower recombination rate (**Table IV-1**); however, more empirical data is needed to test this correlation.

In this dissertation, I also observed an unusual linkage pattern in males of both species of termites (Chapter III). This pattern could be linked to translocation complexes (Y chromosome and some autosomes segregate together as a single linkage group) which is observed in many species of lower termites, including *R. speratus* (Luykx, 1990; Matsuura, 2002, 2010; Syren & Luykx, 1977). The presence of such translocation complexes in termites are hypothesized as a

consequence of inbreeding to maintain heterozygosity through neo-sex chromosomes. Furthermore, suppression of recombination has been observed in neo-Y chromosomes (Satomura et al., 2019) which suggest a similar suppression might be working in termite males. An indication of the presence of telomeric clustering, such as observed in asynaptic fission yeast, is also observed in these two termite species. Chiasmata at the end of chromosomes do not appear to promote efficient segregation in drosophila (Koehler et al., 1996) and are associated with a significant fraction of chromosome 21 trisomies (Down Syndrome) in humans (Lamb et al., 1997). My results indicate the possibility of an unconventional process of meiosis in termite males or significant suppression of meiotic recombination.

In summary, this dissertation provides estimates of the meiotic recombination rate in three eusocial insects. It contributes to the breadth of available recombination rate data and supports the view that high recombination rates are associated with eusociality. It is yet to be determined which mechanisms might have caused the increase in recombination rates in these species, but insights can be gained by comparing some contrasting traits between the species for which we have data available (**Table IV-1**). The efforts of social insect scientists to understand this peculiar convergent and repeated evolution of eusociality is growing the understanding in this subject field, but more empirical research is needed to get a clear picture of this fascinating world. The knowledge gained from this dissertation is a major step towards completing some piece of this gigantic puzzle.

Table IV-1: Recombination rates along with biological and life-history traits for eusocial insects

Common name	Species	Order	Social structure	Colony size (Approx)	Parthenogenesis	Polyandry/Polygyny	Presence of complete sterile workers[e]	Recombination rate (cM/Mb)[f]	Recombination rate reference
Giant honeybee	*Apis dorsata*	Hymenoptera	Advanced eusocial	10,000-70,000	Arrhenotokous[a]	Polyandry	Yes	25.1	(Rueppell et al., 2016)
Western honeybee	*Apis mellifera*	Hymenoptera	Advanced eusocial	10,000-80,000	Arrhenotokous[a]	Polyandry	No	21.6	(Wallberg et al., 2019)
Dwarf honeybee	*Apis florea*	Hymenoptera	Advanced eusocial	3,000-10,000	Arrhenotokous[a]	Polyandry	No	20.8	(Rueppell et al., 2016)
Eastern honeybee	*Apis cerana*	Hymenoptera	Advanced eusocial	3,000-10,000	Arrhenotokous[a]	Polyandry	No	17.4	(Shi et al., 2013)
Desert harvester ant	*Pogonomyrmex rugosus*	Hymenoptera	Advanced eusocial	1,000-15,000	Arrhenotokous[a]	Polyandry	No	14.0	(Sirviö et al., 2011a)
Brazilian stingless bee	*Frieseomellita varia*	Hymenoptera	Advanced eusocial	800-1,600	Arrhenotokous[a]	No	Yes	12.5	This dissertation
Common wasp	*Vespula vulgaris*	Hymenoptera	Advanced eusocial	500-5,000	Arrhenotokous[a]	Polyandry and Polygyny[c]	No	9.70	(Sirviö, et al., 2011b)

Buff-tailed bumblebee	*Bombus terrestris*	Hymenoptera	Primitively eusocial	10-150	Arrhenotokous[a]	No	No	8.90	(Stolle et al., 2011)
Asian subterranean termite	*Reticulitermes speratus*	Blattodea	Advanced eusocial	100,000-500,000	Thelytokous[b]	Polygyny[d]	Yes	7.94	This dissertation
Leaf-cutting ant	*Acromyrmex echinatior*	Hymenoptera	Advanced eusocial	50,000-150,000	Arrhenotokous[a]	Polyandry and Polygyny[c]	No	6.40	(Sirvio et al., 2006)
Eastern subterranean termite	*Reticulitermes flavipes*	Blattodea	Advanced eusocial	200,000-5,000,000	No	Polygyny[d]	Yes	3.94	This dissertation

[a] Haplodipoidy sex determination system

[b] Facultative parthenogenesis

[c] Facultative polygyny

[d] Secondary polygyny by neotenics recruitments

[e] Non-reproductive caste with immature ovary/inactivated ovaries/degenerated ovaries

[f] Female recombination rates

Data sources: (Boleli et al., 1999; Boomsma et al., 2014; Bourke, 1999; da Silva, 2021; del Castillo & Fairbairn, 2012; Grube & Forschler, 2004; Haverty et al., 2000; Hughes, Ratnieks, et al., 2008; H. Li et al., 2020; Noirot, 1990; Reed & Landolt, 2019; Rodriguez-Serrano et al., 2012; Schmid-Hempel & Schmid-Hempel, 2000; Seeley et al., 1982; Su et al., 1993; The Tree of Sex Consortium, 2014; Toth et al., 2004; Tsunoda et al., 1999; Wattanachaiyingcharoen et al., 2002; Whitford & Ettershank, 1975).

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APPENDIX A: RECOMBINATION RATES FOR DIFFERENT ANIMAL GROUPS AND DATA USED IN FIGURE I-1

Species	**Common name**	**Group (Figure I-1)**	**Class**	**Order**	**Genome size (Mb)**	**Map Length (cM)**	**Rec Rate (cM/Mb)**	**Data Reference**
Acyrthosiphon pisum	Pea aphids	Insects	Insecta	Hemiptera	165.00	394.00	2.39	(Hawthorne & Via, 2001)
Aedes aegypti	Mosquito	Insects	Insecta	Diptera	942.14	235.00	0.25	(Juneja et al., 2014)
Aedes albopictus	Asian tiger mosquito	Insects	Insecta	Diptera	1090.47	212.60	0.19	(Sutherland et al., 2011)
Anopheles funestus	Sub saharan mosquito	Insects	Insecta	Diptera	225.22	145.00	0.64	(Wondji et al., 2007)
Bactrocera cucurbitae	Melon fly	Insects	Insecta	Diptera	373.00	646.00	1.73	(Sim & Geib, 2017)
Biston betularia	Peppered moth	Insects	Insecta	Lepidoptera	500.00	1638.00	3.28	(Van't Hof et al., 2013)
Bombyx mori	Silk moth	Insects	Insecta	Lepidoptera	513.45	3320.00	6.47	(Zhan et al., 2009)
Clunio marinus	Midge fly	Insects	Insecta	Diptera	95.00	179.65	1.89	(Kaiser & Heckel, 2012)

Culex pipiens	Common housemosquito	Insects	Insecta	Diptera	684.60	189.90	0.28	(Hickner et al., 2013)
Drosophila serrata	Fruit fly	Insects	Insecta	Diptera	205.38	245.30	1.19	(Stocker et al., 2012)
Drosophila melanogaster	Fruit fly	Insects	Insecta	Diptera	130.00	287.30	2.21	(Comeron et al., 2012)
Drosophila pseudoobscura	Fruit fly	Insects	Insecta	Diptera	125.00	525.10	4.20	(Ortiz-Barrientos et al., 2006)
Heliconius melpomene	Postman butterfly	Insects	Insecta	Lepidoptera	293.40	1364.23	4.65	(Davey et al., 2016)
Leptinotarsa decemlineata	Colorado potato beetle	Insects	Insecta	Coleoptera	449.88	1032.00	2.29	(Hawthorne, 2001)
Mycalesis anynana	Squinting bushbrown	Insects	Insecta	Lepidoptera	479.22	1642.20	3.43	(Beldade et al., 2009)
Nilaparvata lugens	Brown planthopper	Insects	Insecta	Hemiptera	1140.79	1093.30	0.96	(Jairin et al., 2013)
Papilio glaucus	Eastern tigerswallowtail	Insects	Insecta	Lepidoptera	430.32	1167.00	2.71	(Winter & Porter, 2010)
Rhyzopertha dominica	Lesser grain borer	Insects	Insecta	Coleoptera	476.00	390.10	0.82	(Schlipalius et al., 2002)

Tribolium castaneum	Red flour beetle	Insects	Insecta	Coleoptera	202.94	571.00	2.81	(Lorenzen et al., 2005)
Tribolium echinatum	Flour beetle	Insects	Insecta	Coleoptera	245.00	968.00	3.95	(Yezerski et al., 2003)
Artemia franciscana	Brine shrimp	Other Invertebrates	Branchiopoda	Anostraca	948.66	1177.00	1.24	(De Vos et al., 2013)
Daphnia magna	Water flea	Other Invertebrates	Branchiopoda	Anomopoda	129.54	1614.50	12.46	(Dukić et al., 2016)
Daphnia pulex	Water flea	Other Invertebrates	Branchiopoda	Anomopoda	197.21	1206.00	6.12	(Cristescu et al., 2006)
Eriocheir sinensis	Chinese mitten crab	Other Invertebrates	Malacostraca	Decapoda	1680.00	5125.53	3.05	(Cui et al., 2015)
Portunus trituberculatus	Gazami crab	Other Invertebrates	Malacostraca	Decapoda	2259.18	3519.45	1.56	(L. Liu et al., 2012)
Scylla paramamosain	Mud crab	Other Invertebrates	Malacostraca	Decapoda	1603.92	2746.40	1.71	(Ma et al., 2016)
Penaeus japonicus	Caridean shrimp	Other Invertebrates	Malacostraca	Decapoda	2767.74	3610.90	1.30	(X. Lu et al., 2016)
Penaeus monodon	Giant tiger prawn	Other Invertebrates	Malacostraca	Decapoda	2170.00	3488.50	1.61	(Baranski et al., 2014)
Penaeus vannamei	Whiteleg shrimp	Other Invertebrates	Malacostraca	Decapoda	2640.00	4271.43	1.62	(Y. Yu et al., 2015)

Argopecten irradians	Atlantic bay scallop	Other Invertebrates	Bivalvia	Pectinida	865.53	1917.30	2.22	(Zhu et al., 2014)
Crassostrea gigas	Pacific oyster	Other Invertebrates	Bivalvia	Ostreida	557.74	588.00	1.05	(Hedgecock et al., 2015)
Crassostrea virginica	Atlantic oyster	Other Invertebrates	Bivalvia	Ostreida	675.00	905.00	1.34	(Z. Yu & Guo, 2003)
Hyriopsis cumingii	Freshwater mussel	Other Invertebrates	Bivalvia	?	3000.00	2713.00	0.90	(Bai et al., 2016)
Mizuhopecten yessoensis	Scallop	Other Invertebrates	Bivalvia	Pectinida	1437.66	1918.65	1.33	(S. Wang et al., 2017)
Notochlamys hexactes	Notochlamys	Other Invertebrates	Bivalvia	Ostreoida	1244.02	1561.80	1.26	(A. Zhan et al., 2009)
Ostrea edulis	European flat oyster	Other Invertebrates	Bivalvia	Ostreida	1144.26	536.40	0.47	(Harrang et al., 2015)
Ruditapes philippinarum	Manila clam	Other Invertebrates	Bivalvia	Venerida	1967.00	1926.98	0.98	(Nie et al., 2017)
Bracon Near hebetor	Parasitoid wasp	Parasitic Hymenoptera	Insecta	Hymenoptera	165.00	800.00	4.85	(Wilfert et al., 2007)
Bracon brevicornis	Parasitoid wasp	Parasitic Hymenoptera	Insecta	Hymenoptera	165.00	536.10	3.25	(Holloway et al., 2000)

*Nasonia girault*i	Pteromalid wasp	Parasitic Hymenoptera	Insecta	Hymenoptera	283.61	620.00	2.19	(Diao et al., 2016)
Trichogramma brassicae	Parasitoid wasp	Parasitic Hymenoptera	Insecta	Hymenoptera	246.00	1330.00	5.41	(Laurent et al., 1998)
Acromyrmex echinatior	Leaf cutter ant	Social Hymenoptera	Insecta	Hymenoptera	335.00	2033.80	6.07	(Sirvio et al., 2006)
Apis cerana	Asian honey bee	Social Hymenoptera	Insecta	Hymenoptera	226.00	3942.70	17.45	(Shi et al., 2013)
Apis mellifera	Western honey bee	Social Hymenoptera	Insecta	Hymenoptera	229.83	4964.00	21.60	(Wallberg et al., 2015)
Bombus terrestris	Bumble bee	Social Hymenoptera	Insecta	Hymenoptera	274.00	2047.00	8.90	(Stolle et al., 2011)
Pogonomyrmex rugosus	Desert harvester ant	Social Hymenoptera	Insecta	Hymenoptera	255.00	2823.00	11.07	(Sirviö, Pamilo, et al., 2011)
Vespula vulgaris	Common wasp	Social Hymenoptera	Insecta	Hymenoptera	219.80	2129.00	9.69	(Sirviö, Johnston, et al., 2011)

Ambystoma tigrinum	Tiger salamandor	Vertebrates	Amphibia	Urodela	30875.46	5251.30	0.17	(Smith et al., 2005)
Hyla arborea	European tree frog	Vertebrates	Amphibia	Anura	4649.69	1770.72	0.38	(Brelsford et al., 2016)
Rana temporaria	Common frog	Vertebrates	Amphibia	Anura	4169.21	1698.80	0.41	(Cano et al., 2011)
Xenopus tropicalis	Western clawedfrog	Vertebrates	Amphibia	Anura	1440.40	1668.00	1.16	(Wells et al., 2011)
Anas platyrhynchos	Wild duck	Vertebrates	Aves	Anseriformes	1375.72	1766.00	1.28	(Huang et al., 2009)
Coturnix japonica	Japanese quail	Vertebrates	Aves	Galliformes	1320.30	2816.00	2.13	(Kikuchi et al., 2005)
Cyanistes caeruleus	Eurasian blue tit	Vertebrates	Aves	Passeriformes	1437.66	935.00	0.65	(Hansson et al., 2010)
Ficedula albicollis	Collared flycatcher	Vertebrates	Aves	Passeriformes	1118.34	1787.00	1.60	(Backström et al., 2008)
Gallus gallus	Red junglefowl	Vertebrates	Aves	Galliformes	1230.26	2762.20	2.25	(Pengelly et al., 2016)
Meleagris gallopavo	Wild turkey	Vertebrates	Aves	Galliformes	1431.14	2324.00	1.62	(Aslam et al., 2010)
Melospiza melodia	Song sparrow	Vertebrates	Aves	Passeriformes	1398.54	1731.00	1.24	(Nietlisbach et al., 2015)

Parus major	Great tit	Vertebrates	Aves	Passeriformes	1476.78	1916.82	1.30	(van Oers et al., 2014)
Taeniopygia guttata	Zebra finch	Vertebrates	Aves	Passeriformes	1222.50	1479.00	1.21	(Backström et al., 2010)
Anguilla japonica	Japanese eel	Vertebrates	Actinopterygii	Anguilliformes	1151.14	1436.50	1.25	(Kai et al., 2014)
Anoplopoma fimbria	Sable fish	Vertebrates	Actinopterygii	Scorpaeniformes	757.95	1332.80	1.76	(Rondeau et al., 2013)
Astatotilapia	Small freshwaterfish	Vertebrates	Actinopterygii	Cichliformes	948.66	1249.30	1.32	(Sanetra et al., 2009)
Astyanax mexicanus	Mexican tetra fish	Vertebrates	Actinopterygii	Characiformes	1191.24	2110.70	1.77	(Carlson et al., 2015)
Carassius auratus	Goldfish	Vertebrates	Actinopterygii	Cypriniformes	1643.04	5252.00	3.20	(Kuang et al., 2016)
Coregonus clupeaformis	Freshwater whitefish	Vertebrates	Actinopterygii	Salmoniformes	2386.32	3061.00	1.28	(Gagnaire et al., 2013)
Ctenopharyngodon idella	Grass carp	Vertebrates	Actinopterygii	Cypriniformes	1004.55	1176.10	1.17	(Xia et al., 2010)
Cynoglossus semilaevis	Tongue sole	Vertebrates	Actinopterygii	Pleuronectiformes	606.36	1624.00	2.68	(Song, Li, et al., 2012)

Cyprinus carpio	Common carp	Vertebrates	Actinopterygii	Cypriniformes	1741.92	3565.90	2.05	(Zhao et al., 2013)
Danio rerio	Zebrafish	Vertebrates	Actinopterygii	Cypriniformes	1817.12	2177.36	1.20	(Bradley et al., 2011)
Dicentrarchus labrax	European bass	Vertebrates	Actinopterygii	Perciformes	762.84	1373.10	1.80	(Chistiakov et al., 2008)
Epinephelus aeneus	White grouper	Vertebrates	Actinopterygii	Perciformes	1075.80	969.50	0.90	(Dor et al., 2014)
Esox lucius	Northern pike	Vertebrates	Actinopterygii	Esociformes	1095.36	1289.30	1.18	(Rondeau et al., 2014)
Gadus morhua	Atlantic cod	Vertebrates	Actinopterygii	Gadiformes	909.54	1421.92	1.56	(Hubert et al., 2010)
Gasterosteus aculeatus	Three-spinedstickleback	Vertebrates	Actinopterygii	Gasterosteiformes	625.92	1980.74	3.16	(Rastas et al., 2016)
Haplochromis chilotes	Cichlid	Vertebrates	Actinopterygii	Cichliformes	1075.80	1225.68	1.14	(Henning et al., 2017)
Haplochromis sauvagei	Cichlid	Vertebrates	Actinopterygii	Cichliformes	1075.80	1130.63	1.05	(Henning et al., 2014)
Hippoglossus hippoglossus	Atlantic halibut	Vertebrates	Actinopterygii	Pleuronectiformes	713.94	1514.00	2.12	(Palaiokostas et al., 2013)
Hypophthalmichthys molitrix	Silver carp	Vertebrates	Actinopterygii	Cypriniformes	978.00	1561.10	1.60	(Guo et al., 2013)

Ictalurus punctatus	Channel catfish	Vertebrates	Actinopterygii	Siluriformes	993.65	3240.00	3.26	(S. Liu et al., 2016)
Kryptolebias marmoratus	Mangrove killifish	Vertebrates	Actinopterygii	Cyprinodontiformes	680.37	1248.00	1.83	(Kanamori et al., 2016)
Labeo rohita	Rohu	Vertebrates	Actinopterygii	Cypriniformes	1950.00	1373.80	0.70	(Robinson et al., 2014)
Larimichthys crocea	Large yellow croaker	Vertebrates	Actinopterygii	Acanthuriformes	678.94	5451.30	8.03	(Ao et al., 2015)
Lates calcarifer	Barramundi	Vertebrates	Actinopterygii	Perciformes	684.60	1412.90	2.06	(L. Wang et al., 2017)
Lepomis macrochirus	Bluegill	Vertebrates	Actinopterygii	Perciformes	987.78	1576.75	1.60	(W.-J. Wang et al., 2010)
Lucania goodei	Bluefin killifish	Vertebrates	Actinopterygii	Cyprinodontiformes	1319.32	392.00	0.30	(Berdan et al., 2014)
Lucania parva	Rainwater killifish	Vertebrates	Actinopterygii	Cyprinodontiformes	1391.69	605.00	0.43	(Berdan et al., 2014)
Maylandia zebra	Zebra mbuna	Vertebrates	Actinopterygii	Cichliformes	848.78	1933.00	2.28	(O'Quin et al., 2013)

Misgurnus anguillicaudatus	Pond loach	Vertebrates	Actinopterygii	Cypriniformes	1594.14	723.35	0.45	(Morishima et al., 2008)
Nothobranchius furzeri	Turquoise killifish	Vertebrates	Actinopterygii	Cyprinodontiformes	1242.52	1965.00	1.58	(Kirschner et al., 2012)
Oncorhynchus kisutch	Coho salmon	Vertebrates	Actinopterygii	Salmoniformes	2767.74	358.55	0.13	(McClelland & Naish, 2008)
Oncorhynchus mykiss	Rainbow trout	Vertebrates	Actinopterygii	Salmoniformes	2592.68	3600.00	1.39	(Guyomard et al., 2012)
Oncorhynchus nerka	Red salmon	Vertebrates	Actinopterygii	Salmoniformes	2858.69	3186.50	1.11	(Larson et al., 2016)
Oncorhynchus tshawytscha	Chinook salmon	Vertebrates	Actinopterygii	Salmoniformes	2709.06	3119.70	1.15	(McKinney et al., 2016)
Oreochromis mossambicus	Mozambique tilapia	Vertebrates	Actinopterygii	Cichliformes	978.00	1067.60	1.09	(F. Liu et al., 2013)
Oreochromis niloticus	Nile tilapia	Vertebrates	Actinopterygii	Cichliformes	1058.20	704.00	0.67	(Kocher et al., 1998)
Paralichthys olivaceus	Olive flounder	Vertebrates	Actinopterygii	Pleuronectiformes	694.38	1695.15	2.44	(Song, Pang, et al., 2012)

Phalloceros caudimaculatus	Dusky millions fish	Vertebrates	Actinopterygii	Cyprinodontiformes	700.00	1477.00	2.11	(Gutiérrez & García, 2011)
Poecilia reticulata	Guppy	Vertebrates	Actinopterygii	Cyprinodontiformes	865.53	899.00	1.04	(Tripathi et al., 2009)
Salmo salar	Atlantic salmon	Vertebrates	Actinopterygii	Salmoniformes	3048.43	5961.00	1.96	(Tsai et al., 2016)
Salmo trutta	Brown trout	Vertebrates	Actinopterygii	Salmoniformes	2875.32	1403.00	0.49	(Leitwein et al., 2017)
Sciaenops ocellatus	Red drum	Vertebrates	Actinopterygii	Acanthuriformes	381.42	1815.30	4.76	(Hollenbeck et al., 2015)
Scleropages formosus	Asian arowana	Vertebrates	Actinopterygii	Osteoglossiformes	777.36	2218.30	2.85	(Shen et al., 2014)
Scophthalmus maximus	Turbot	Vertebrates	Actinopterygii	Pleuronectiformes	841.08	2622.09	3.12	(W. Wang et al., 2015)
Seriola quinqueradiata	Yellowtail	Vertebrates	Actinopterygii	Carangiformes	811.74	1128.60	1.39	(Aoki et al., 2015)
Sparus aurata	Gilt-head bream	Vertebrates	Actinopterygii	Perciformes	929.10	3899.00	4.20	(Palaiokostas et al., 2016)

Takifugu rubripes	Japanese puffer	Vertebrates	Actinopterygii	Tetraodontiformes	391.20	1696.30	4.34	(Kai et al., 2011)
Thunnus orientalis	Pacific bluefin tuna	Vertebrates	Actinopterygii	Scombriformes	800.00	1162.60	1.45	(Uchino et al., 2016)
Xiphophorus maculatus	Southern platyfish,	Vertebrates	Actinopterygii	Cyprinodontiformes	885.09	1328.30	1.50	(Amores et al., 2014)
Bison bison	American bison	Vertebrates	Mammalia	Artiodactyla	4792.20	2647.00	0.55	(Schnabel et al., 2003)
Bos taurus	Cattle	Vertebrates	Mammalia	Artiodactyla	3520.80	3159.10	0.90	(Ihara et al., 2004)
Canis lupus	Gray wolf	Vertebrates	Mammalia	Carnivora	2748.18	2085.10	0.76	(Wong et al., 2010)
Capra hircus	Goat	Vertebrates	Mammalia	Artiodactyla	3168.72	2737.00	0.86	(Schibler et al., 1998)
Equus caballus	Horse	Vertebrates	Mammalia	Perissodactyla	3149.16	2772.00	0.88	(Swinburne et al., 2006)
Felis silvestris	Wild cat	Vertebrates	Mammalia	Carnivora	2894.88	4464.00	1.54	(G. Li et al., 2016)
Macaca mulatta	Rhesus monkey	Vertebrates	Mammalia	Primates	3290.97	2048.00	0.62	(Rogers et al., 2006)
Macropus eugenii	Tammar wallaby	Vertebrates	Mammalia	Diprotodontia	1153.00	1402.40	1.22	(C. Wang et al., 2011)

Microtus ochrogaster	Prairie vole	Vertebrates	Mammalia	Rodentia	2287.34	1707.00	0.75	(McGraw et al., 2011)
Monodelphis domestica	Gray short-tailed opossum	Vertebrates	Mammalia	Didelphimorphia	3598.44	715.00	0.20	(Samollow et al., 2007)
Oryctolagus cuniculus	European rabbit	Vertebrates	Mammalia	Lagomorpha	3107.25	1419.00	0.46	(Sternstein et al., 2015)
Ovis aries	Domestic sheep	Vertebrates	Mammalia	Artiodactyla	2941.82	3304.00	1.12	(Johnston et al., 2016)
Ovis canadensis	Bighorn sheep	Vertebrates	Mammalia	Artiodactyla	2590.55	3051.00	1.18	(Poissant et al., 2010)
Papio hamadryas	Hamadryas baboon	Vertebrates	Mammalia	Primates	3457.23	2354.00	0.68	(Cox et al., 2013)
Peromyscus maniculatus	Deer mouse	Vertebrates	Mammalia	Rodentia	4264.08	1499.00	0.35	(Steen et al., 1999)
Rattus norvegicus	Brown rat	Vertebrates	Mammalia	Rodentia	3286.08	1503.00	0.46	(Tortereau et al., 2012)
Sus scrofa	Wild boar	Vertebrates	Mammalia	Artiodactyla	2922.26	2012.00	0.69	(Tortereau et al., 2012)

APPENDIX B: CODES AND COMMAND LINES USED

(A) R-Codes, macros, and terminal command lines used in Chapter II.

Annotated text file that describes all the codes used at different analyses performed in this genetic map study.

Waiker et al (2021). Frieseomelitta varia linkage mapping

‘#' or " ' " at the beginning of the sentence represent a comment

---

(1) Ubuntu terminal command line

VCF file filtering

#SNPs filtered for at least 50% missing data, minimum quality score of 30 and Minor allele frequency of 3

vcftools --vcf fv.vcf --max-missing 0.5 --minQ 30 --minDP 6 --mac 3 --recode --recode-INFO-all --out fv_filter1

#Extracting SNP genotype information from filtered VCF file

vcftools --vcf fv_filtered.recode.vcf --extract -FORMAT -info GT

---

(2) Example codes for data filtering using Macro VBA

#highlight the rows that have same data in four columns

```
Sub samedata()                                          'name of macro code
LastRow = Cells(Rows.Count, "A").End(xlUp).Row     'define last row containing data in col A
```

```
LastCol = Cells(1, Columns.Count).End(xlToLeft).Column  ' define last colcontaining data for row 1
For yrow = 2 To LastRow                    'for loop that runs from row 2 to last row
    If Cells(yrow, "B") = Cells(yrow, "C") And Cells(yrow, "C") = Cells(yrow, "D") And Cells(yrow, "D") = Cells(yrow, "E") And Cells(yrow, "B") = Cells(yrow, "E") Then   ' If-then statement to compare values between different cells
        If Cells(yrow, "F") = Cells(yrow, "G") And Cells(yrow, "G") = Cells(yrow, "H") And Cells(yrow, "H") = Cells(yrow, "I") And Cells(yrow, "I") = Cells(yrow, "F") Then
            Cells(yrow, 1).EntireRow.Interior.ColorIndex = 3                    'Highlight entire row with a specific color if above criteria meets
        End If
    End If                  ' logical statement to instruct the program to stop if statement
    Next yrow                          'for loop goes to next row
    End Sub                                'end macro
```

#Copy entire rows if a cell has a specific color and paste it to new excel sheet

```
Sub Sortbycolor()                      'macro name
Dim Sourcews As Worksheet              ' defining worksheets as variable 'Worksheet'
    Dim Destws As Worksheet
    LastRow = Cells(Rows.Count, "A").End(xlUp).Row
    Set Sourcews = ActiveSheet             'Setting current worksheet as active
    Set Destws = Worksheets.Add            'create a new sheet to paste the values
```

```
    zrow = 2
    For yrow = 1 To LastRow
        If Sourcews.Cells(yrow, 1).Interior.Color = vbRed Then  'If then statement to check if a
cell has a specific background color
        Sourcews.Cells(yrow, 1).EntireRow.Copy Destws.Cells(zrow, 1) ' If criteria meets then
paste the row to destinamtion worksheet
        zrow = zrow + 1                                         'increasing the value of
destination row number to paste next value in empty row
        End If
    Next yrow
End Sub
```

#Compare the markers from a list and highlight the row

```
Sub compareandhighlightmarkers()
x = 1
Do While Cells(x, 1) <> ""      'List of markers that need to be tested
        Sheets(1).Select              'Sheet containing marker number --Markers to delete
        temp = Cells(x, 1)            ' temporary variable to hold marker information
        Sheets(2).Select
        Lastrow = Cells(Rows.Count, 1).End(xlUp).Row
        For zrow = 2 To Lastrow
          If Cells(zrow, 1) = temp Then     'compares if value matches
```

```
                Cells(zrow, 1).EntireRow.Interior.ColorIndex = 3  'highlight the row if condition
meets
            End If
        Next zrow
    x = x + 1
Loop
End Sub
```

#compare a list of SNPs name to a bigger list with map distance and if match then put map distance next to the SNP

```
Sub Addmapdistance()
x = 2
Do While Cells(x, 1) <> ""    'first column has the SNP list with ID
        temp = Cells(x, 1)
        Lastrow = Cells(Rows.Count, 5).End(xlUp).Row    'row with all markers in col 5
        For zrow = 2 To Lastrow
            If Cells(zrow, 5) = temp Then
                Cells(zrow, 7) = Cells(x, 2)
            End If
        Next zrow
x = x + 1
Loop
```

```
End Sub
```

#check file and highlight if the value of a column is lesser than a threshold value

```
Sub Highlight_rowbycondition() 'Highlight rows if cell has certain condition (Conditional
formatting)
Lastrow = Cells(Rows.Count, 5).End(xlUp).Row    'row with all markers in col 5 - the other list
which does not have an ID
        For zrow = 1 To Lastrow
          If Cells(zrow, 6) < 150 Then
            Cells(zrow, 6).EntireRow.Interior.ColorIndex = 3
          End If
        Next zrow
End Sub
```

---

(3) R codes

#Installing RQTL package

```
install.packages("qtl")
```

#Loading library in R

```
library(qtl)
```

#Setting Working directory

```
setwd("C:/fakepath")
```

#Setting parameters to print maximum lines in R output window

```
options(max.print=1000000)
```

Loading the CSV genotype file in R where genotypes are either coded as 'A' or 'H' for homozygous and heterozygous

fv<- read.cross("csvr", "C:/fakepath", "FV_inputfile.csv")

Plotting missing data to inspect any severe missingness

plotMissing(fv, main="Missing data for FV markers")

#Find duplicate markers in vector dupmar

dupmar <- findDupMarkers(fv, exact.only = F)

#drop duplicate markers

fv <- drop.markers(fv, unlist(dupmar))

#writenew file with no duplicate marker

write.cross(fv, format='csvr',filestem = "nodupLG1")

#check new numbers of markers (optional confirmatory step)

totmar(fv)

#estimating recombination fraction between each marker pait and calculate LOD score for a test of rf=0.5

fv<- est.rf(fv)

#Inspecting list markers for potentially switched allels

checkAlleles(fv, threshold=5)

Plotting marker pairs for potentially switched alleles

rf <- pull.rf(fv)

lod <- pull.rf(fv, what="lod")

plot(as.numeric(rf), as.numeric(lod), xlab="Recombination fraction", ylab="LOD score")

Inferring linkage groups

lg <- formLinkageGroups(fv, max.rf=0.25, min.lod= 5)

table(lg[,2])

reorganizing inferred linkage groups

lg<- formLinkageGroups(fv, max.rf=0.25, min.lod=5, reorgMarkers = T)

#Pull Recombination fraction matrix to inspect potential connections between markers of linkage groups

RFmatrix_endmarkers <- pull.rf(fv, what="lod")

write.table(RFmatrix_endmarkers, 'LODmatrix_endmarkers.csv', sep='\t')

#Ordering markers within linkage groups and saving as a csv file on local computer (repeat code for each linkage group)

fv1<- orderMarkers(lg, chr = 1, error.prob = 0.001)

sink(file = "FV_LG1.csv")

pull.map(fv1,chr = 1)

sink()

#Drop one suspected bad marker at a time to inspect if gaps are being created by that marker

dropone <- droponemarker(lg, error.prob=0.001)

par(mfrow=c(2,1))

plot(dropone, lod=1, ylim=c(-100,0))

plot(dropone, lod=2, ylab="Change in chromosome length")

par(mfrow=c(1,1))

#Tryallpositions() to try an additional marker if it fits in already created linakge map

tryallpositions(lg,"SNPxx", chr = 1, error.prob = 0.001)

#Loop code to try multiple markers for tryallpositions using a list of test markers

markers<- scan(file ="listofextramarkers.csv", character(), quote = "", skip = 1)

output <- vector("list", length(markers))

names(output) <- markers

for(i in seq_along(markers)) {

output[[i]] <- tryallpositions(lg, markers[i], error.prob = 0.001) #specify an LG using argument chr=x to avoid intensive never ending computation

}

sink(file="Trymarker_allLG.csv")

output

sink()

#Plotting linkage groups using library LinkageMapView

library(LinkageMapView)

outfile = file.path("C:/fakepath", "fv1.pdf")

lmv.linkage.plot(fv1, outfile) #repeat for each linkage group

Plotting all linkage groups in a single plot along with marker density

maxpos <- 310 # draw tickmarks at each cM from 0 to largest position of linkage groups to be drawn

at.axis <- seq(0, maxpos)

axlab <- vector()

for (lab in 0:maxpos) {

if (!lab %% 50) {

```
    axlab <- c(axlab, lab)
  }
  else {
    axlab <- c(axlab, NA)
  }
}
outfile = file.path("C:/fakepath", "linkagemapwithdensity.pdf")
lmv.linkage.plot(fv, outfile, denmap = TRUE, cex.axis = 2,cex.lgtitle = 4 ,at.axis =
at.axis,labels.axis = axlab, pdf.height = 16)
#Phylogenetic tree - comparison of different species' recmbination rates
library(phytools)   #package to create phylogeny figure
library(ggplot2)
tree2<-read.tree("FileS3.tre")
x2<-read.csv("FileS4.csv",header=TRUE,row.names=1)
x2<-setNames(x2[,1],rownames(x2))
obj<-contMap(tree2,x2,plot=FALSE, method= "fastAnc")
obj<-setMap(obj,invert=TRUE)
plot(obj,fsize=c(1,0.8),outline=FALSE,lwd=c(6,7),leg.txt="Recombination rate (cM/Mb)")
#Correlation analysis Physical length and genetic length for each LG
#q-q plot for normality assumption
ggqqplot(my_data$Contigs_length_Mb, ylab = "Physical length")
ggqqplot(my_data$Avg.RR, ylab = "Rec. rates")
```

#Normality check statistical test

shapiro.test(my_data$Contigs_length_Mb)

shapiro.test(my_data$Avg.RR)

#plotting correlation graph

library("ggpubr")

my_data <- read.csv("Map_summary.csv")

ggscatter(my_data, x = "Contigs_length_Mb", y = "Avg.RR",

add = "reg.line", conf.int = TRUE,

cor.coef = TRUE, cor.method = "spearman",

xlab = "Physical length of LG (Mb)", ylab = "Average Recombination rate of LG (cM/Mb)")

#Rho statistic for spearman correlation test

rho<-cor.test(my_data$Contigs_length_Mb, my_data$Avg.RR, method = "spearman")

rho

(B) **R-Codes, macros, and terminal command lines used in Chapter III.**

I. VCF file filtering:

(1) [Bash script] SNPs filtered for at least 50% missing data, minimum quality score of 30, read depth of 6 and minor allele frequency of 3

vcftools --vcf raw_vcf_file.vcf --max-missing 0.5 --minQ 30 --minDP 6 --mac 3 --recode --recode-INFO-all --out vcf_filter1

(2) [Bash script] Extraction of genotype information from filtered VCF files

vcftools --vcf vcf_filtered.recode.vcf --extract -FORMAT -info GT

(3) [Bash script] Example code to extract SNP markers and genotype from a VCF file

bcftools view -v snps 2015_termiteRF.vcf | bcftools query -f '%ID\t%REF\t%ALT\t[%GT\t]\n' > SNP_sequences_and_genotype.txt

II. BLAST Alignment

(1) [Macro VBA] Example code to retrieve sequences of SNP markers for a subset of SNP markers

```
Sub Macro1()
' Column A contains subset of SNP name for which sequence retrival
'needs to be done
' Column D contains SNP name that needs to be compared (all
'extracted SNPs) while column E has corresponding sequences
' If col A matches column D then column E value goes to column B
x = 1
Do While Cells(x, 1) <> ""    'first column has the SNP name
   temp = Cells(x, 1)
   Lastrow = Cells(Rows.Count, 4).End(xlUp).Row    'row with
allmarkers in col D
```

```
    For zrow = 1 To Lastrow
      If Cells(zrow, 4) = temp Then
        Cells(x, 2) = Cells(zrow, 5)
      End If
    Next zrow
  x = x + 1
  Loop
  End Sub
```

(2) [Bash script] Converting extracted sequences to FASTA format

```
awk '{print ">" $1 "\n"$2}' RSQ_query_seqs.csv >
RSQ_query_seqs.fa
tr , '\n' < RSQ_query_seqs.fa > RSQ_query_seqs_fasta.fa
```

(3) [Bash script] Making database using genome assembly

```
makeblastdb -in jasmine-tex2319-mb-hirise-ohpe7__03-05-2021__hic_output.fasta -out
jasmine-tex2319-mb-hirise-ohpe7__03-05-2021__hic_output -parse_seqids -dbtype nucl
```

(4) [Bash script] Example code to get BLAST output with all hits in the output file

```
blastn -db jasmine-tex2319-mb-hirise-ohpe7__03-05-2021__hic_output -query
RSQ_query_seqs_fasta.fa -outfmt 7 -out RSQ_mapping.txt
```

(5) [Bash script] Example code to get BLAST output with single best hits in the output file

blastn -db jasmine-tex2319-mb-hirise-ohpe7__03-05-2021__hic_output -query RSQ_query_seqs_fasta.fa -outfmt 6| sort -u -k1,1 --merge > RSQ_best_single_hits.blastn

III. Plotting Pairwise recombination fractions against physical distance

(1) [R-code] Example codes to get recombination fractions matrix using genotype file as input

```
library(qtl)
rsk<- read.cross("csvr", "~/RSK_Groups", "RSK-I.csv")
RSK_Pullmap <- pull.rf(rsk, what=c("rf", "lod"))
write.table(RSK_Pullmap, 'RSK-I_RFmatrix.csv', sep='\t')
```

(2) [Macro VBA] Example code to linearize pairwise matrices

```
Sub Linearize_pairwise_matrix()
Lastrow = Cells(Rows.Count, 6).End(xlUp).Row
Lastcol = Cells(1, Columns.Count).End(xlToLeft).Column
zrow = 2
For yrow = 2 To Lastrow
   For ycol = yrow + 6 To Lastcol
      Cells(zrow, 2) = Cells(yrow, 6)
      Cells(zrow, 3) = Cells(1, ycol)
      Cells(zrow, 4) = Cells(yrow, ycol)
```

```
        zrow = zrow + 1
    Next ycol
Next yrow
End Sub
```

(3) [Macro VBA] Example code to retrieve corresponding physical distances

```
Sub Physical_distance_for_markerpairs()
Lastrow = Cells(Rows.Count, 1).End(xlUp).Row
Lastm1 = Cells(Rows.Count, 6).End(xlUp).Row
Lastm2 = Cells(Rows.Count, 7).End(xlUp).Row
For yrow = 2 To Lastrow
   For m1 = 2 To Lastm1
   If Cells(m1, 6) = Cells(yrow, 1) Then
   Cells(m1, 9) = Cells(yrow, 2)
   End If
   Next m1
   For m2 = 2 To Lastm2
   If Cells(m2, 7) = Cells(yrow, 1) Then
   Cells(m2, 10) = Cells(yrow, 2)
   End If
   Next m2
Next yrow
```

End Sub

IV. Codes to make Correlation plot

##Correlation using Tidyverse

```
library(ggplot2)
library(dplyr)
library(tidyverse)
#setwd("~/Library/CloudStorage/OneDrive-UNCG/Lab Work/Linkage maps RS and RF_June 2017/JoinMap/Mapping_to_genome/ManuscriptFiles_Oct2021/Combined_Results")
my_data <- read.csv("Physical_size_vs_RR.csv")
head(my_data)
my_data.long <- my_data %>%   #changing data frame to long format as ggplot2 prefers
  select("Length","RSK", "RSQ", "RFK","RFQ") %>%
  pivot_longer(-Length,names_to="variable", values_to="value")
head(my_data.long)
my_formula <- y~x
p<- ggplot(my_data.long, aes(Length, value, colour=variable))+geom_point()+
geom_smooth(method=lm, se=FALSE, formula = my_formula,
fullrange=TRUE)+theme(text = element_text(size = 14))
p+xlab("Chromosome length (bp)")+ ylab("Recombination Rate (cM/Mb)"
```

APPENDIX C: COPYRIGHT INFORMATION

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Prashant Waiker <p_waiker@uncg.edu>

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Best wishes,

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