

Nuts & Bolts in Ants, Bees & Wasps: Describing the Meiotic Gene Inventory in Hymenoptera

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Meiosis, the cellular process involving chromosomal recombination and formation of haploid gametes, is widely conserved among eukaryotes. Many meiotic genes studied in model organisms are required for proper gamete formation, yet meiotic gene losses have been observed in other systems that clearly engage in meiosis and sexual reproduction¹. A meiotic gene inventory (MGI) has been deployed to investigate the mechanistic capacity for meiosis, with an emphasis on examining organisms that deviate from canonical modes of sexual reproduction^{2,3,4}. Assessing presence/absence and relative evolutionary rates of MGI components may offer insight into how changes in reproduction may result in modification of genes with roles important for sexual function.

Hymenopterans are haplodiploid, making the insect order a unique group for identifying molecular evolution dynamics in meiosis genes (**Fig. 1**). Males develop from parthenogenetically produced haploid eggs, and sperm production in males is ameiotic. When unreduced gametes from males fertilize eggs, the resulting diploid eggs develop into females. There are also several reported occasions of asexual reproduction in Hymenoptera⁵. In this life cycle, parthenogenetically produced eggs are diploid and female, and males are absent. Asexual reproduction in hymenopterans can be purely clonal (apomictic) or involve alternative modes of meiotic recombination (automictic)⁵.

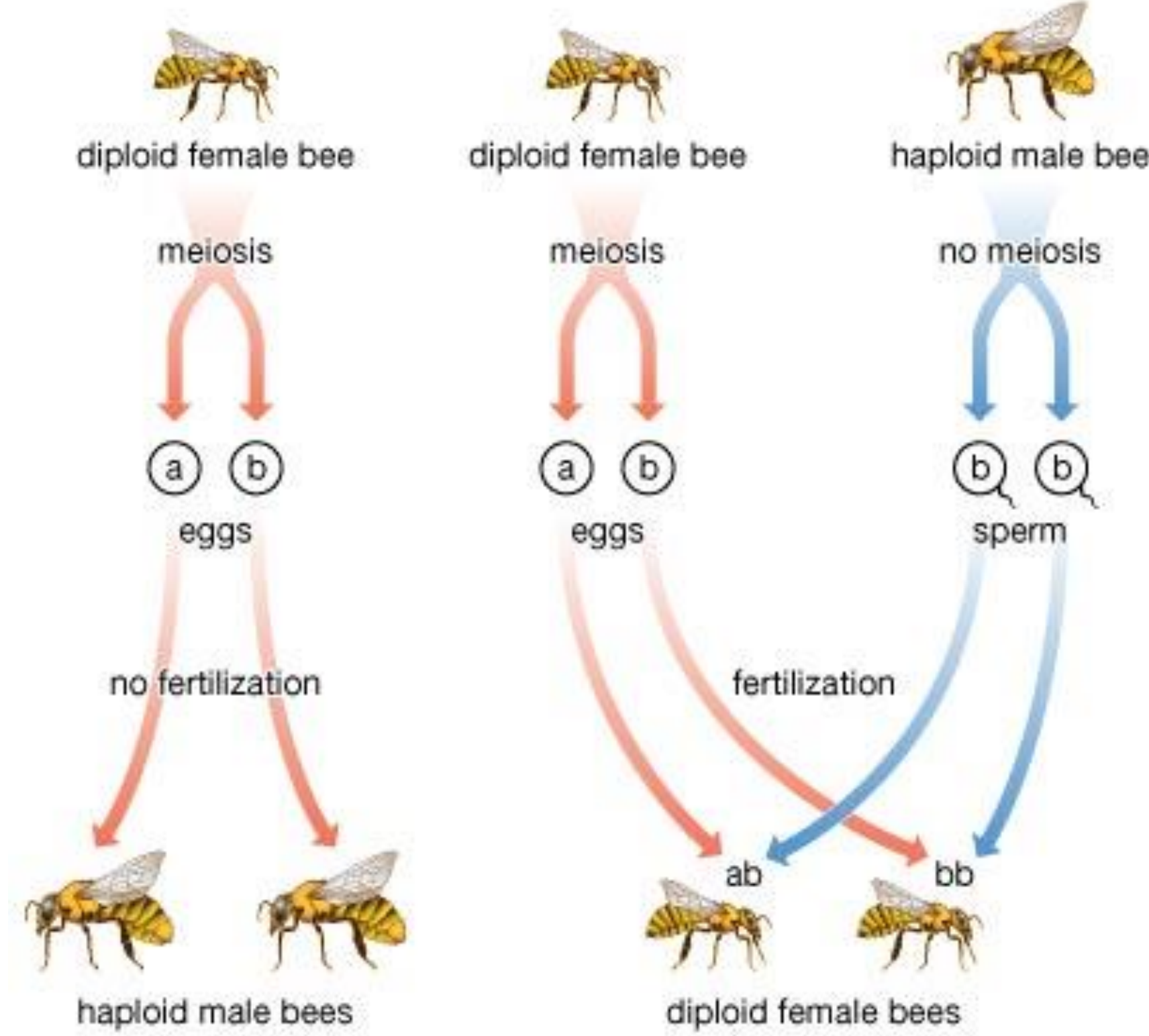


Fig. 1: Hymenopteran life cycle. (<http://www.britannica.com/animal/hymenopteran>)

Identifying meiosis genes across Hymenoptera

A MGI dataset was previously reported in two Hymenopteran and seven non-Hymenopteran insects⁶. We used meiotic gene homologs from four insects (*Nasonia vitripennis*, *Aedes aegypti*, *Drosophila melanogaster*, *Tribolium castaneum*) as a reference for recently assembled Hymenopteran genomes to assess **a)** overall patterns of MGI conservation among Hymenoptera, and **b)** if loss of sexual reproduction in the parasitoid wasp *Diachasma muliebre* results in subsequent loss of MGI genes relative to a closely related sexual lineage, *Diachasma alloeum*.

Methods

- Used annotated MGI genes in *Nasonia* and non-Hymenopteran outgroups as queries to conduct tBLASTn searches for homologs in 17 species representing the broad Hymenopteran phylogeny, reciprocal BLASTx to confirm gene identity
- Retrieved coding DNA and protein sequences for MGI genes with predicted models
- Manually inspected predicted models, annotated transcription start site, exon-intron boundaries, stop codons

Examining relative molecular evolution in *Diachasma*

The asexual wasp *Diachasma muliebre* is an emerging model for the study of the effects of sex loss. We evaluated whether loss of sexual reproduction is associated with changes in mutational patterns in the MGI. If *D. muliebre* reproduces we would expect to see signatures of relaxed s higher mutational loads in meiotic genes. Alterr mutational changes could underlie a global pat evolution that could facilitate asexual lineage p

Methods

- Assembled genomes for *D. muliebre* and closely related sexual lineages
- Perform phylogenetic analysis on aligned gene regions with meiosis-specific roles

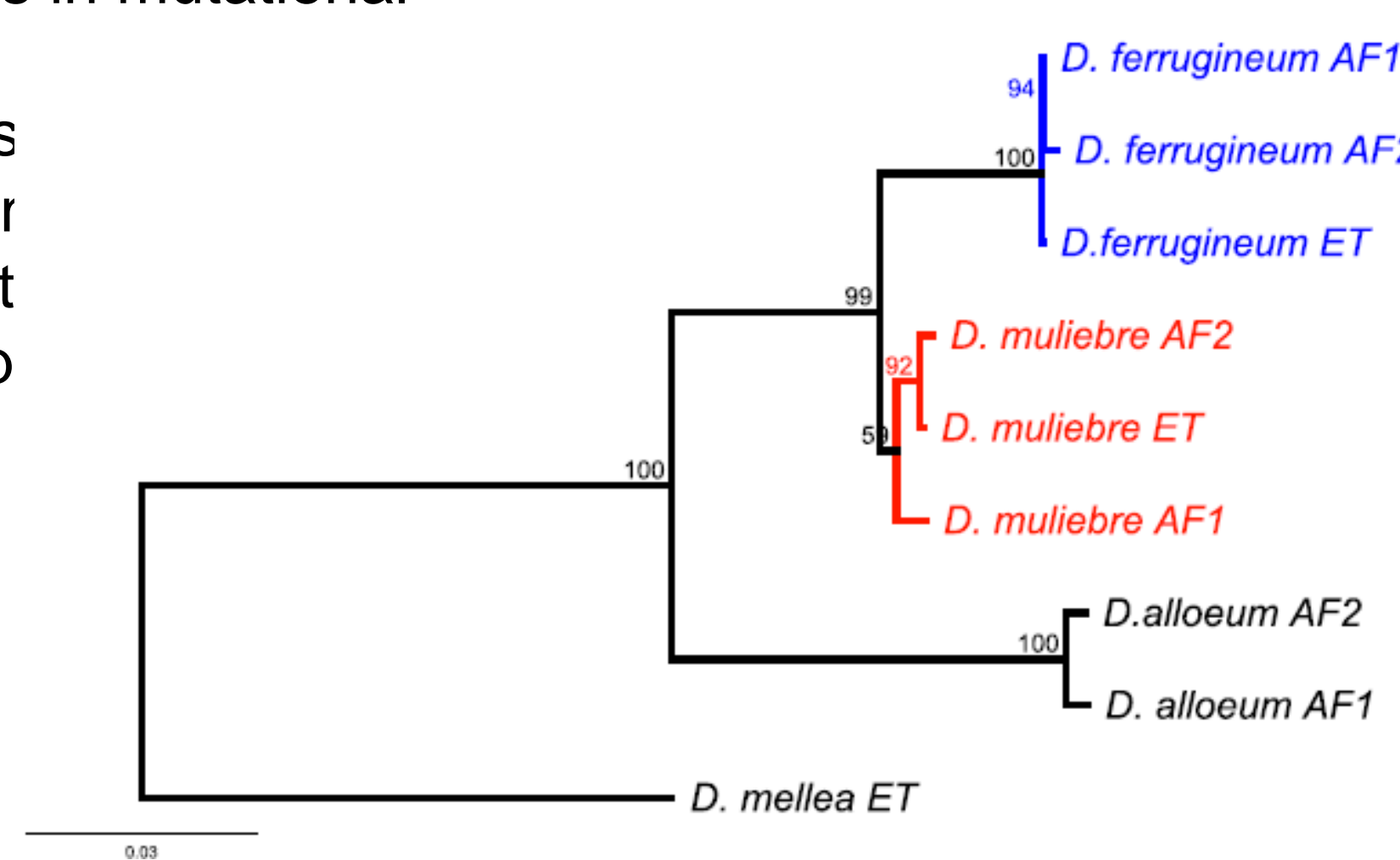


Fig. 2: COI tree. *D. ferrugineum* (blue) is the closest sexual lineage to the asexual wasp *D. muliebre* (red). AF: sequenced by traditional Sanger techniques; ET: sequences extracted from whole mitochondrial genomes

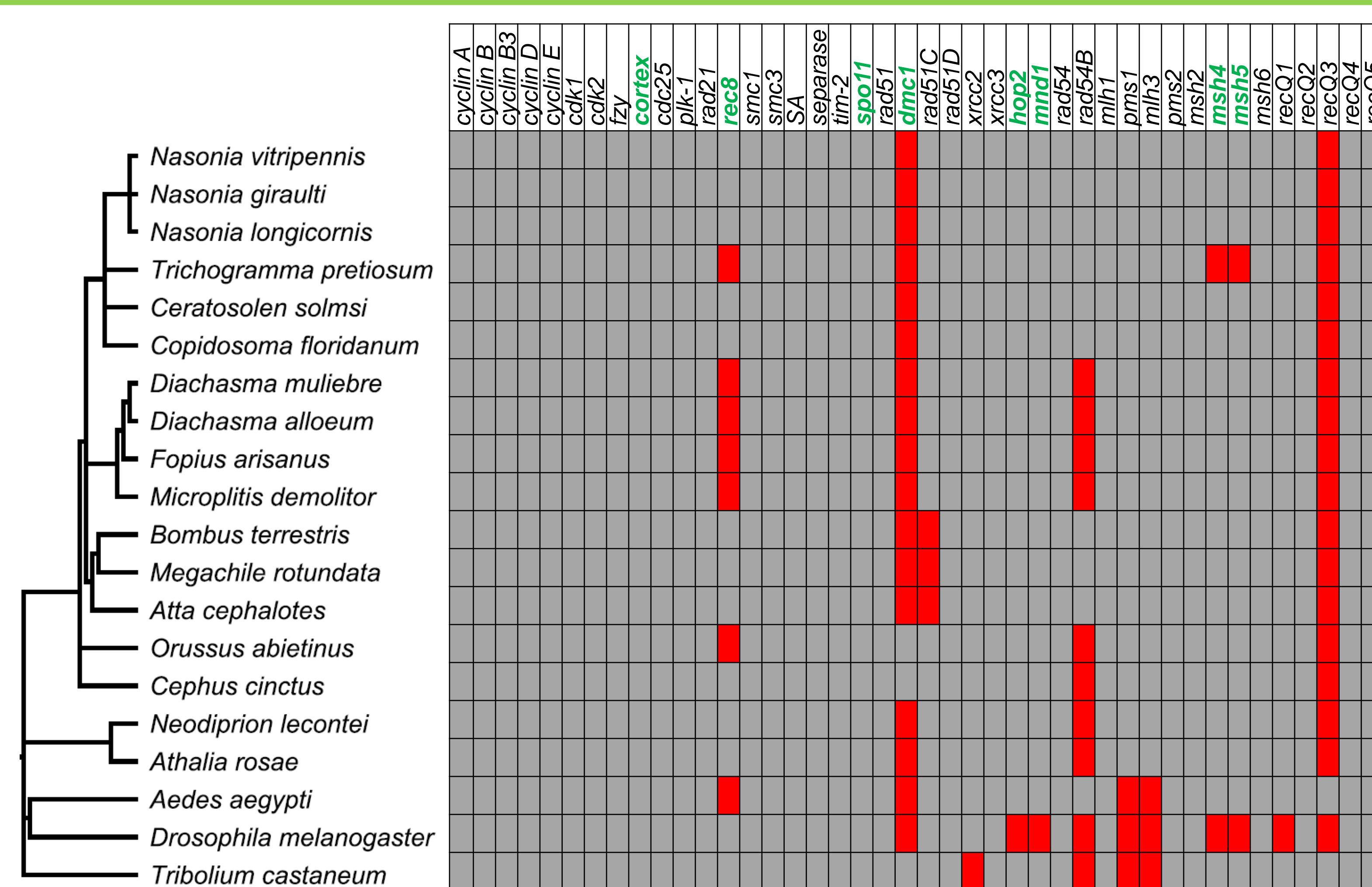
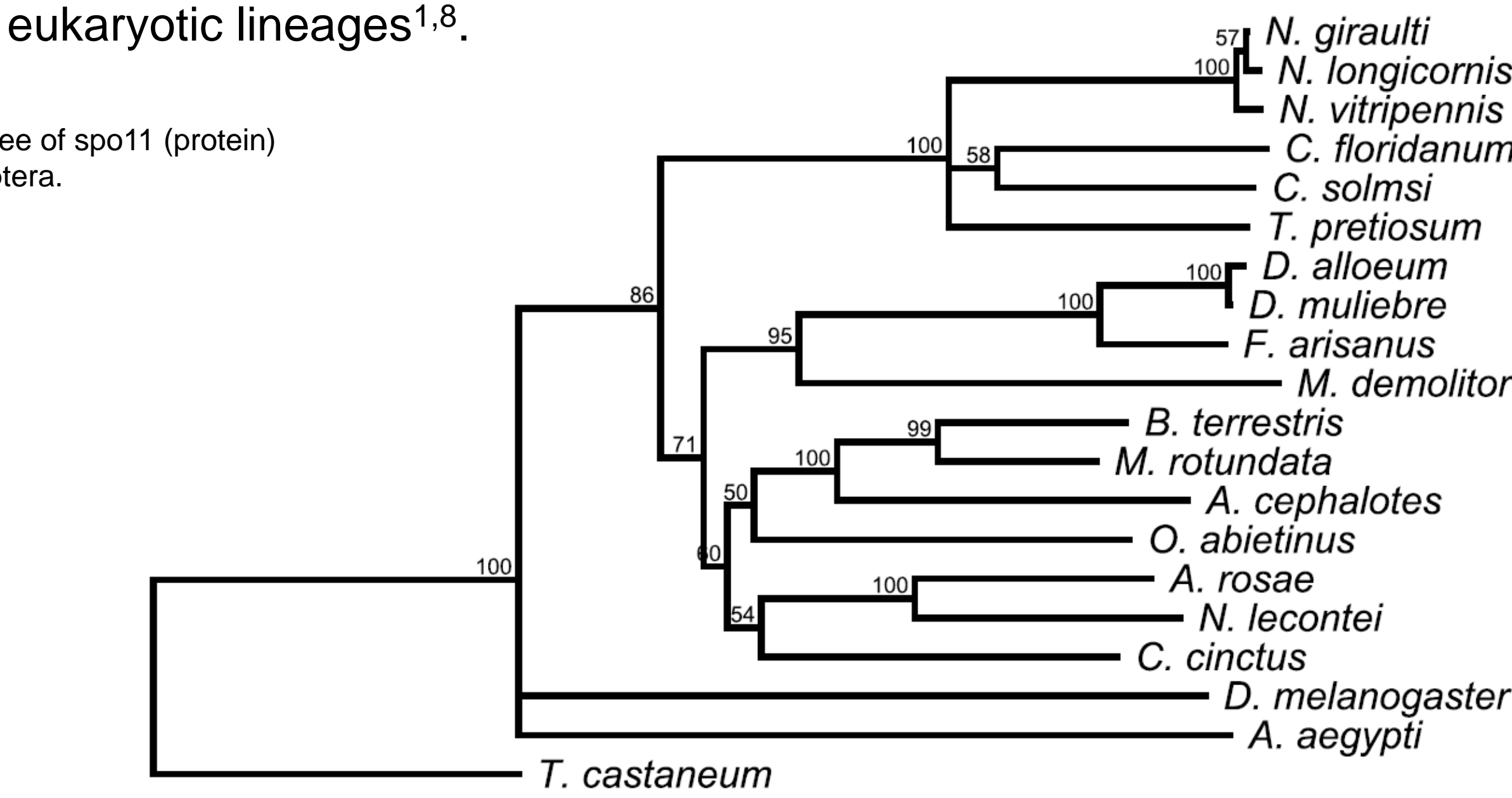


Fig. 3 LEFT: Cladogram of Hymenopteran phylogeny. RIGHT: Meiotic gene inventory in Hymenoptera. Grey boxes indicate gene is present. Red boxes indicate gene was not found in the analysis. Gene names highlighted in green are specific to meiosis, gene names in black have roles in mitosis/meiosis

Describing the MGI in Hymenoptera

- The majority of genes involved in meiosis are conserved in most Hymenopterans (**Fig. 3**), and meiosis-specific genes found in all Hymenopterans (e.g. *spo11*, **Fig. 4**) are likely mandatory for proper gamete formation
- Some genes are dispensable for meiosis in Hymenoptera, including meiosis-specific genes (e.g. *rec8*, *dmc1*) which are required for meiosis in some model systems
- Gene losses can be shared in smaller clades. The *rad51C* gene has been lost in bees and ants, while *rad54B* may have been lost independently in braconid wasps and basal Hymenopterans
- Genes with products that interact in meiotic processes may be under similar selective regimes. The *msh4/msh5* heteroduplex forms a sliding clamp on homologous chromosomes and is involved in resolution of Holliday junctions⁷. Homologs were not recovered for the moth parasitoid *Copidosoma floridanum*. The independent loss of *msh4/msh5* is documented for diverse eukaryotic lineages^{1,8}.

Fig. 4: NJ tree of *spo11* (protein) in Hymenoptera.



Literature Cited

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Evaluating rates of molecular evolution in *Diachasma*

In six meiosis genes that were analyzed for *Diachasma* wasps (**Fig. 5A**), various patterns of molecular evolution between sexual and asexual lineages after divergence from a common ancestor (**Fig. 5B**). Overall, the number of substitutions was greater in the sexual lineage ($Z_M/Z_F < 1$, **Fig. 5C**), however this is largely influenced by the pattern seen for the *MSH4* gene. Further investigation is required to determine whether this result is biologically informative or a result of technical error.

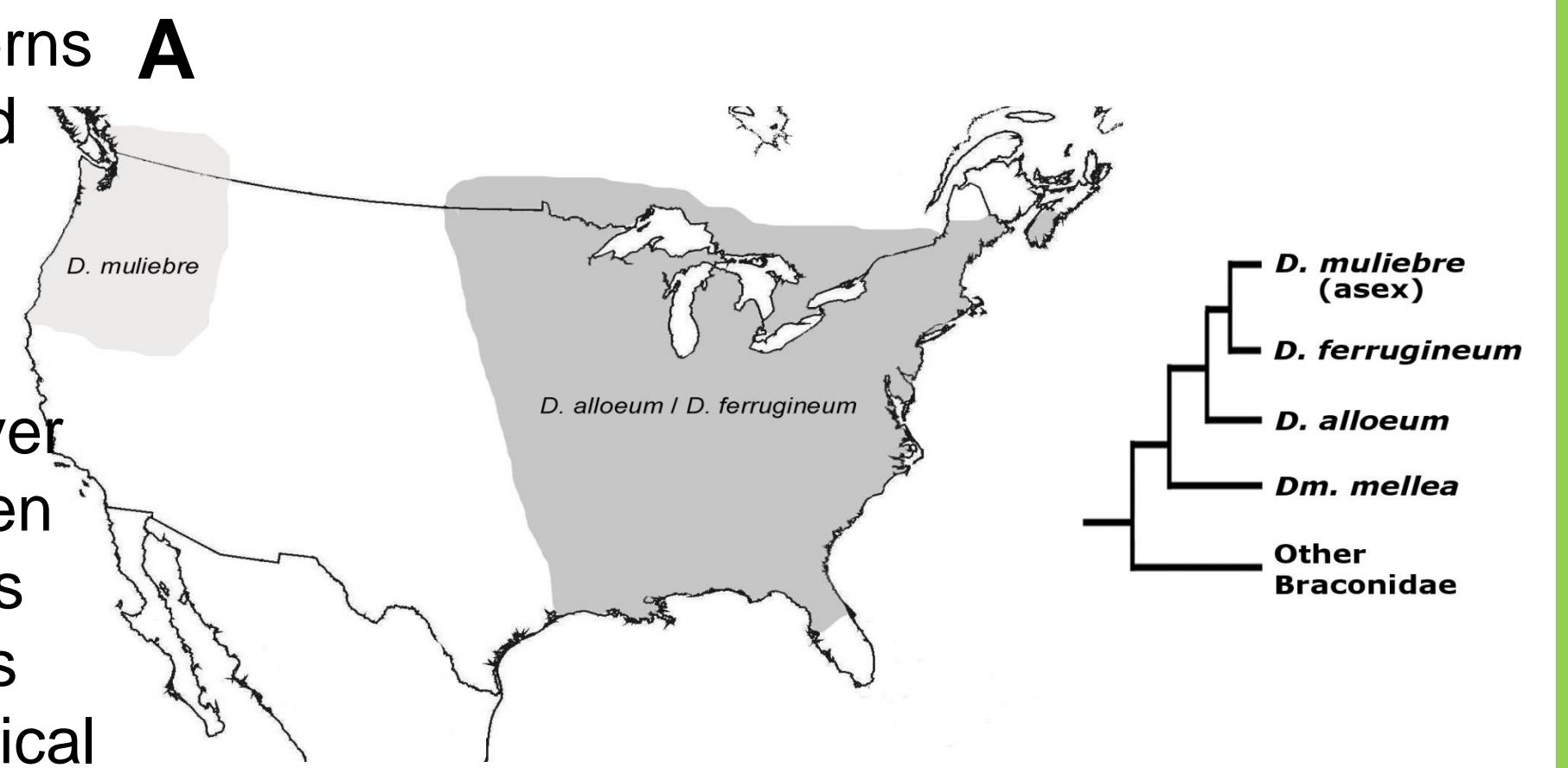
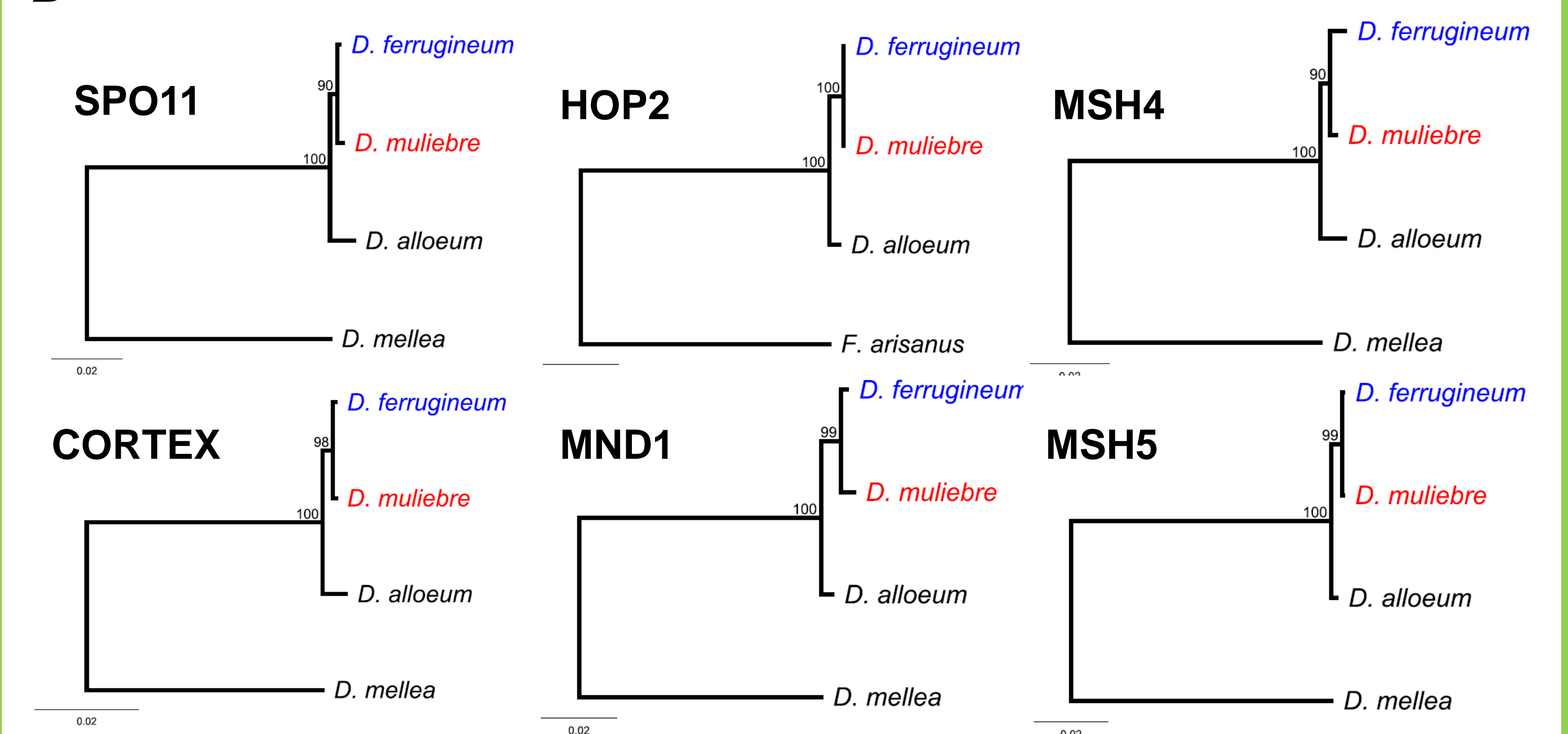
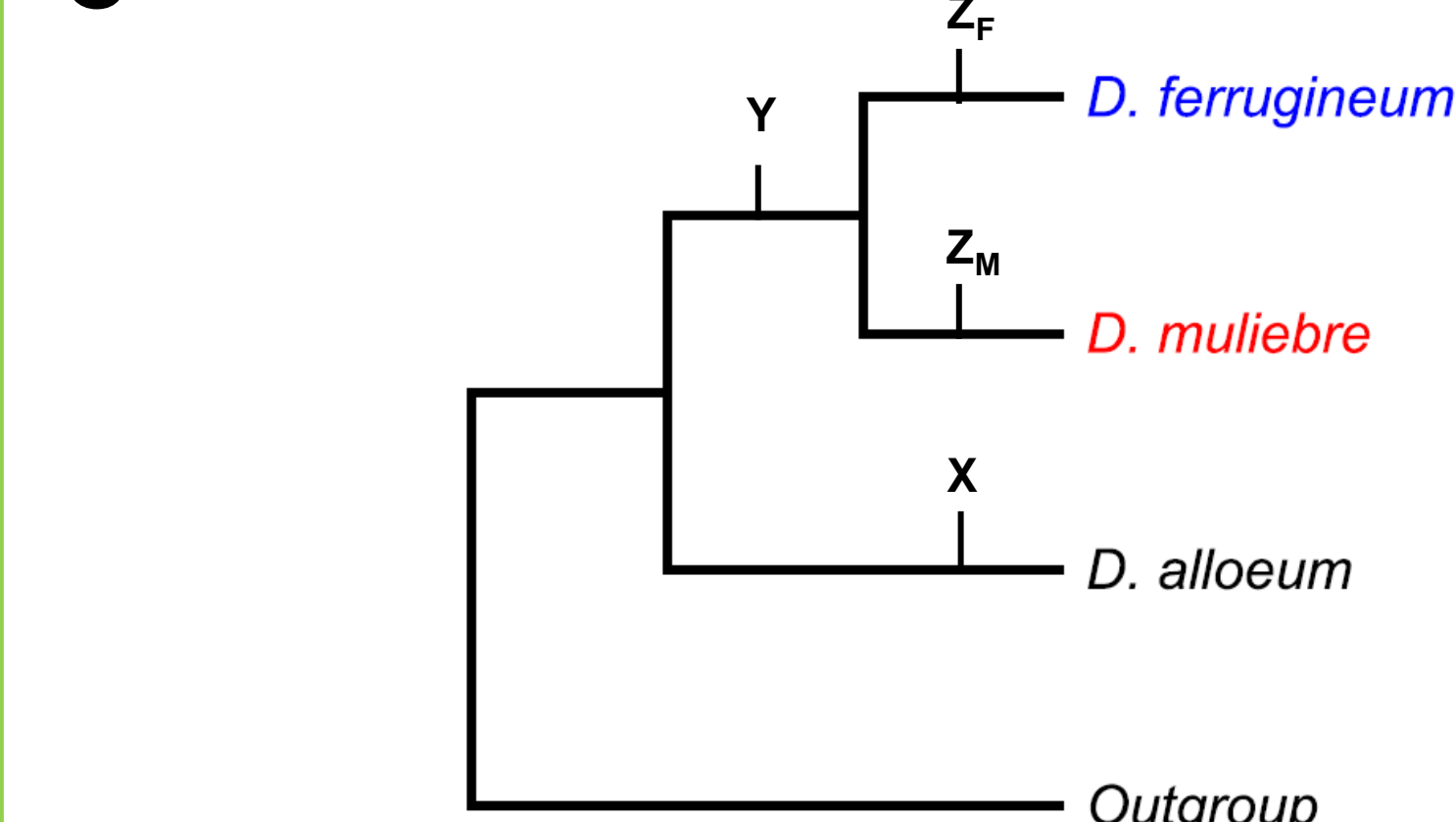


Fig. 5 A: Geographic distribution and phylogeny of *Diachasma* wasps. B: NJ trees of meiosis genes (DNA) comparing relative molecular evolution in sexual *D. ferrugineum* (blue) and asexual *D. muliebre* (red). C: Quantification of genetic distances using MP

B



C



		Genetic Distance				
Gene	Length	X	Y	Z _F	Z _M	Z _M /Z _F
SPO11	1197	8	3	1	2	2
CORTEX	1692	8	3	1	1	1
HOP2	618	4	5	0	0	0
MND1	609	2	3	1	2	2
MSH4	3196	16	9	12	6	0.5
MSH5	2346	3	7	0.5	0.5	1
Total				15.5	11.5	0.74
Total w/o MSH4				3.5	5.5	1.57

A suite of genes sufficient for meiosis was identified in *D. muliebre*, suggesting that this asexual lineage may still undergo meiotic processes despite apparent loss of sex. Heterozygosity/homozygosity ratios in natural populations of *D. muliebre* are consistent with automictic reproduction *via* central or terminal fusion⁹. Whole genome data can be analyzed to assess heterozygosity on a broader scale and distinguish between central and terminal fusion reproductive pathways (**Fig. 6**)¹⁰.

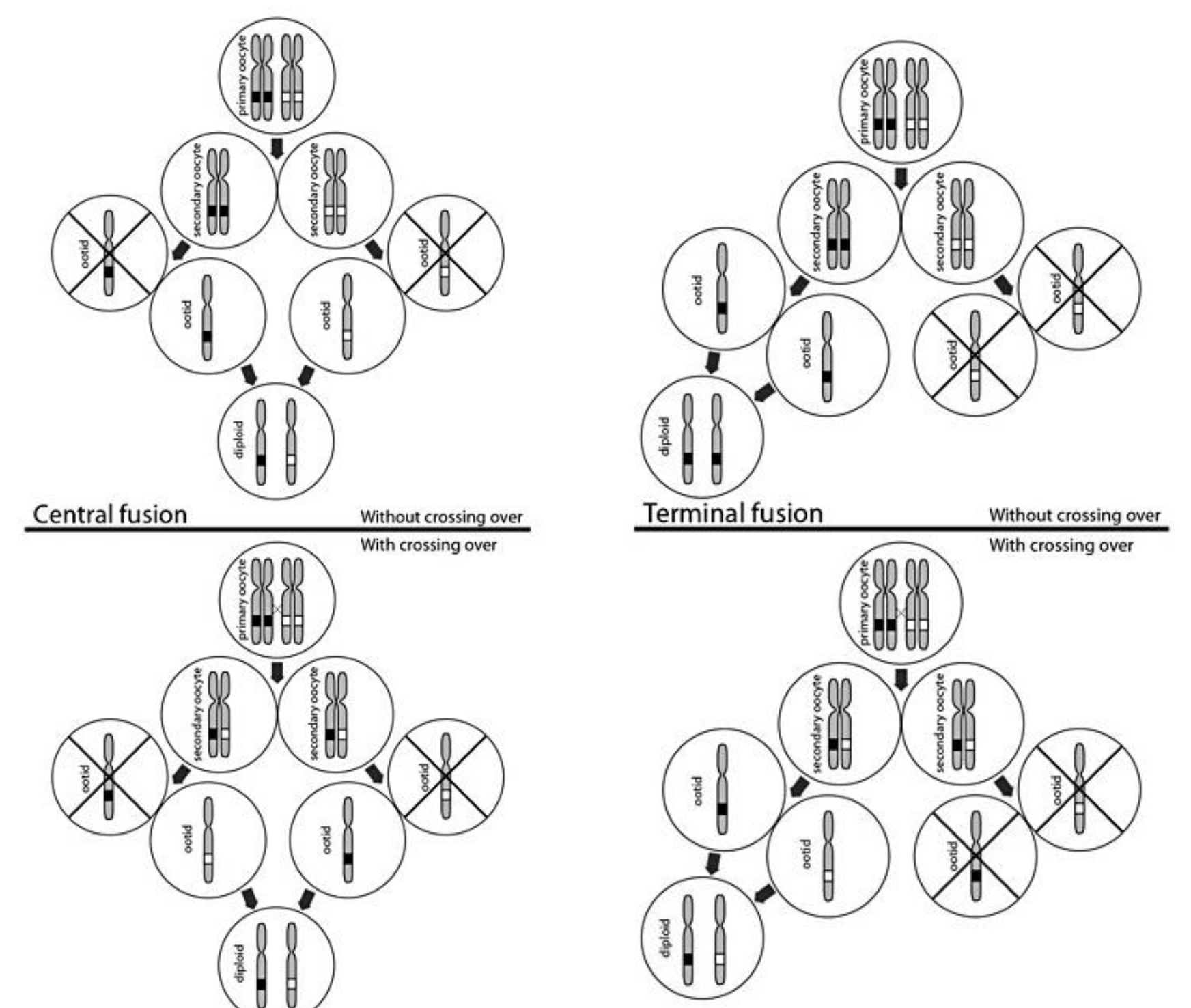


Fig. 6: Formation of gametes *via* central/terminal fusion (Stenburg and Saura 2013)