**115. The following is from:**
Mneimneh S. 2012. Crossing over … Markov meets Mendel. PLOS Computational Biology. 8: e1002462.
The following diagram is from the field of computer science, and illustrates the attempt of a computer scientist to explain crossing over.

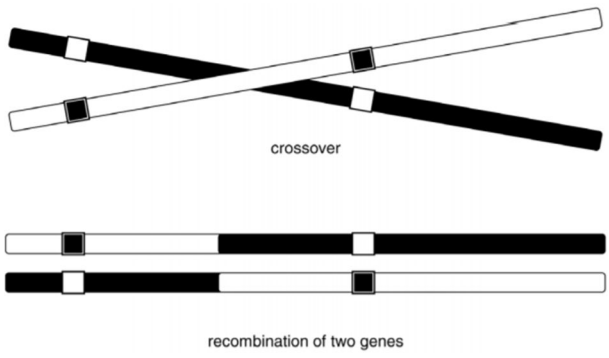



**Figure 2. One chromosomal crossover and a genetic recombination.**

A. Pretend that you are going back one century in time. You do not know anything about how chromosomes cross over, but you have lots of hypotheses and $F_2$ segregation data on hand. Would your $F_2$ genotype categories to be explainable by the crossing over model in the diagram? Explain why or why not in your answer.

B. The premise of the author is that current mapping algorithms have quirks in them that lead to wrong distances. With the current models:

"the probability of recombination depends on the chromosome length and, therefore, two chromosomes that are locally similar but have different lengths exhibit different local recombination behavior. *This is not biologically justifiable*." In other words, linkage should not depend on the chromosome length.

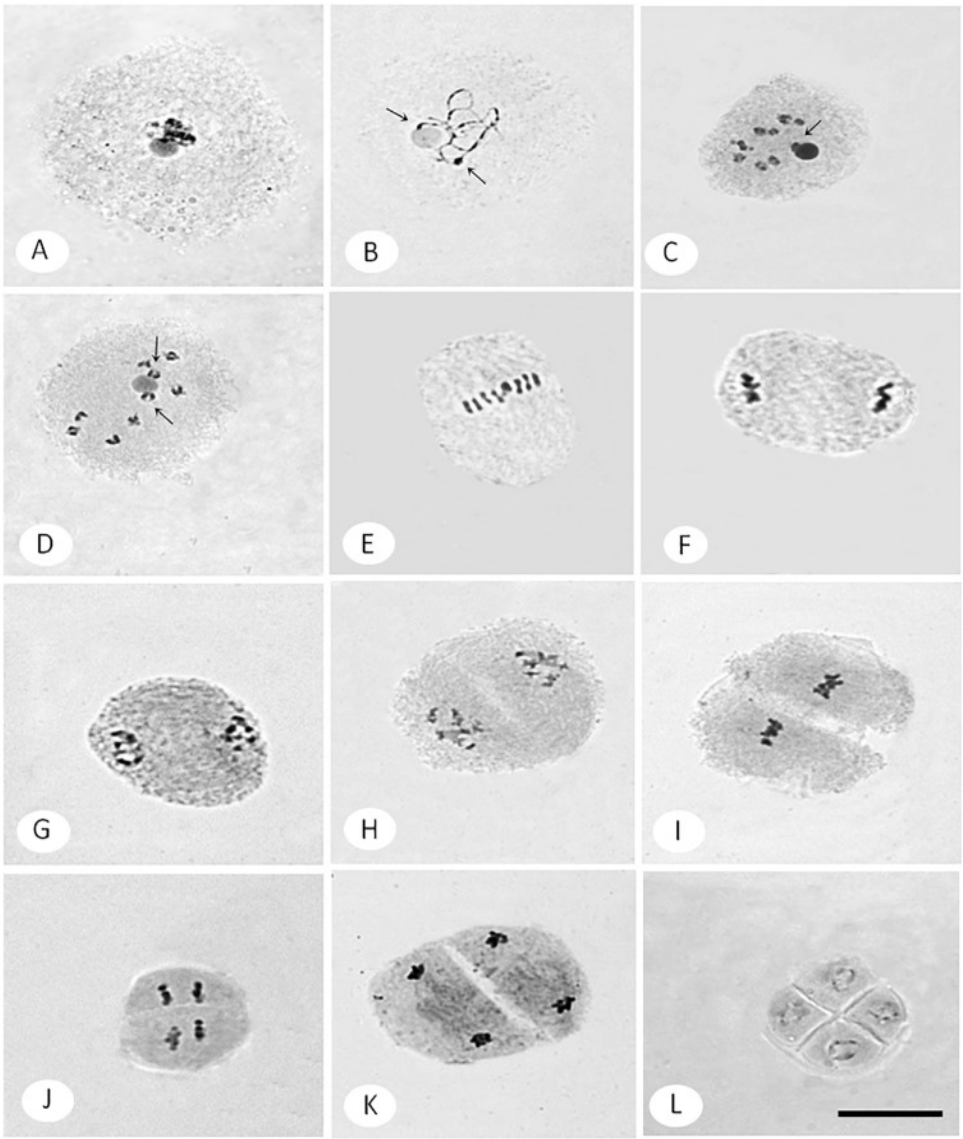
Evaluate the premise that linkage should not depend on chromosome length. Give specific reason or examples of crossing over biology to justify your answer.

C. "Independent assortment: This is impossible due to linkage where distance [ie length of chromosome] is a determining factor in the recombination." In other words, independent assortment would not be possible if chromosome length is truly what determines recombination.

Evaluate the premise that linkage & chromosome length affect independent assortment. Give specific reasons or example of meiosis biology to justify your answer.

**116. The following is from: (will be revealed after exam)**
Morais LC, F Souza Sobrinho and VH Techio. 2018. Comparative microsporogenesis between diploid and ….. South African Journal of Botany. 119:258-264.

**Answer the following questions based on the figure.**




A. What process is shown by this set of photos? Do not use 'meiosis' as an answer.

B. Name each of the stages show in A-L. Do not use 'prophase' as an answer.

| | | |
|---|---|---|
| A: | E: | I: |
| B: | F: | J: |
| C: | G: | K: |
| D: | H: | L: |

C. For this plant, _____n = _____ x = _____

Which figure(s) can contribute to this answer? _____

D. What is the C value in photos B through E? _____

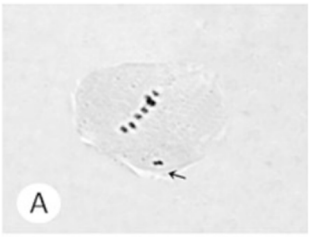
E. Without knowing anything else about this plant, is it most likely a monocot or dicot?

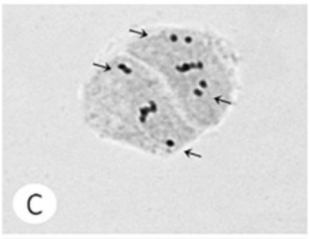
Which figure(s) allow you to make that conclusion? _____

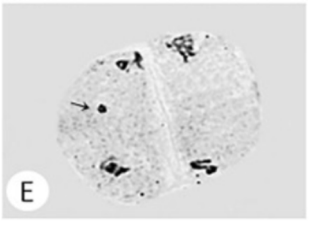
The diagnostic feature is:

_____

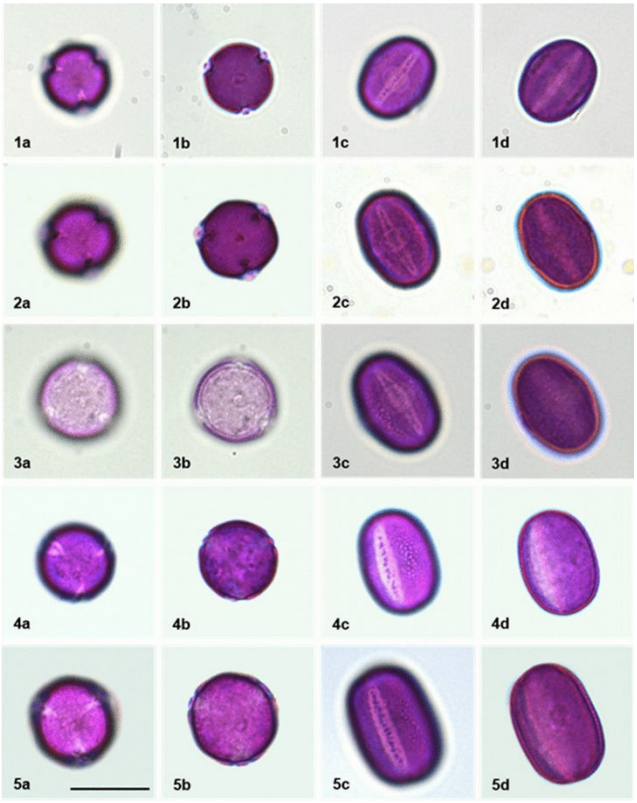
F. What phenomenon is shown in figures A, C & E, and what will the resulting sporad look like?



**117. The following is from:**
Benhizia H, Y Benhizia, R Djeghar, F Pustahija, S Siljak-Yakolev & N Khalfallah. 2020. Cytogenetic characterization, nuclear genome size, and pollen morphology of some *Hedysarum* L. taxa (Fabaceae) from Algeria, with emphasis on the origin of *H. perrauderianum* Coss. & Durieu. *Genetic Resources and Crop Evolution* **68**: 679–691.




In this paper, the authors looked at 4 diploid species of hedysarum (a fodder crop), and at a related 4x species .

A) Based on the pollen samples at right, which row is the 4x species?

B) What is the basis for your assertion?

**118. The following is from** Zhou Q, J Wu, Y Sang, Z Zhao, P Zhang and M Liu. 2020. Effects of colchicine on *Populus canescens* ectexine structure and 2n pollen production. Frontiers in Plant Science 11: 295

Sometimes, papers get published that challenge credibility, or at least, challenge conventions. In this paper, the authors were trying to obtain 2n pollen in poplars by injecting colchicine into anthers at various stages. The authors sampled male flowers to determine the stage of meiosis, and then proceeded to inject them with 10 μM colchicine a different number of times at 2-hour intervals.

The frequency of success is in the table at right. Eleven injections at pachytene gave the best results. Based on SSR analysis, the 2n pollen contained sister chromatids.

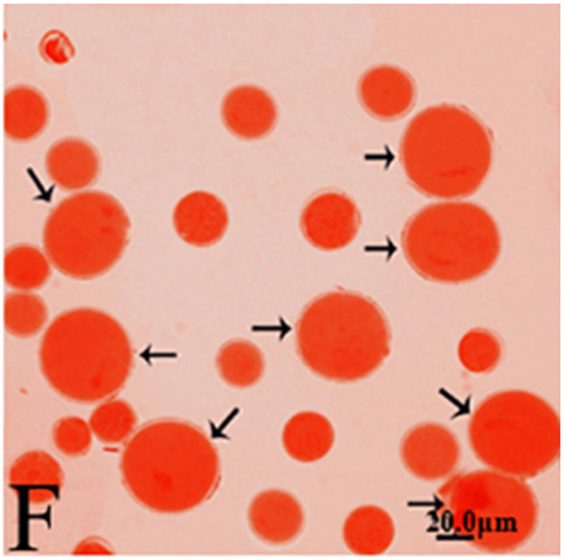
| Dominant meiotic stage of PMCs | No. of colchicine injections times | Frequency of colchicine-induced 2n pollen (%) |
|---|---|---|
| Leptotene | 3 | 4.79 ± 1.46 |
| | 5 | 6.42 ± 2.13 |
| | 7 | 9.40 ± 1.32 |
| | 9 | 8.19 ± 0.99 |
| | 11 | 10.44 ± 4.41 |
| Pachytene | 3 | 5.46 ± 0.90 |
| | 5 | 6.22 ± 0.89 |
| | 7 | 9.04 ± 2.62 |
| | 9 | 16.70 ± 3.95 |
| | 11 | 30.27 ± 8.69 |
| Diplotene | 3 | 4.18 ± 1.52 |
| | 5 | 5.79 ± 0.60 |
| | 7 | 8.76 ± 0.45 |
| | 9 | 9.48 ± 1.31 |
| | 11 | 9.68 ± 1.76 |
| Diakinesis | 3 | 6.99 ± 1.31 |
| | 5 | 7.81 ± 0.74 |
| | 7 | 8.17 ± 0.56 |
| | 9 | 10.53 ± 0.82 |
| | 11 | 20.36 ± 1.49 |
| Metaphase I | 3 | 2.75 ± 0.43 |
| | 5 | 3.91 ± 1.53 |
| | 7 | 4.34 ± 1.08 |
| | 9 | 11.03 ± 1.23 |
| | 11 | 15.11 ± 4.99 |
| Control | | 2.08 ± 0.40 |

A. Recap the mode of action of colchicine.

B. What are the chromosomes doing at pachytene?

C. When the mode of action of colchicine is considered in light of the cellular events taking place when the colchicine is applied, are the results as you would expect? Explain your answer as to why or why not. Try to give an alternative explanation as to how their system may work.

D. The following figure shows the resulting 2n pollen grains (shown by the arrows).




Fully discuss whether the size of these 2n pollen grains fits with the usual expectations.

E. To determine if their 2n pollen was functional, they crossed to a 2x female. They got 6741 seeds, of which 4955 germinated, and 5 were 3x. The frequency of 3x was far lower than expected from their frequency of 2n pollen. Their explanation is that 2n pollen tubes grow more slowly did n pollen grains.

Why should they have or have not expected a low frequency of 3x plants? Is there another explanation for the low frequency of 3x progeny? Would a different female parent have been better? Explain your answer.

**Extra credit**

If the smaller grains are haploid, calculate the volume of the 2n pollen in the photo.

**119. The following is from: (will be given after the exam)**
Xia Q-M, L-K Miao, K-D Xie, Z-P Yin, X-M Wu, C-L Chen, JW Grosser & W-W Guo. 2020. Localization and characterization of *Citrus* centromeres by combining half-tetrad analysis and CenH3-associated sequence profiling. Plant Cell Reports, 39:

There is a variety of tangerine that produces 2n eggs. In this work, the authors were trying to more precisely map the position of the centromere. They began by finding SNPs that are heterozygous in it. It was then pollinated by 4x males, and the progeny was genotyped for the maternal SNPs. Some of the data for chromosome 8 are below:

*univela-morocco.com/products/citrus/nadorcott-tangerine/*

**Table S2 Genotypes of 2n megagametophytes and rates of heterozygosity restitution (HR) for each locus**

| No. | Maternal | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 168 | GC | GC | GC | CC | GG | GC | GG | CC | GG | GC | GC | CC | CC | GG | CC | GG | GG | GC | GC | CC | GC | CC | CC | GC | GG | GG | GG | GC | GG | GG | CC | GG | CC | GG | GG | GG | GG |
| 169 | TA | TA | TA | AA | TT | TA | TT | AA | TT | AA | TA | AA | AA | TT | AA | TT | TT | TA | AA | AA | TA | AA | AA | TA | TT | TT | TT | TT | TT | TT | AA | TT | AA | TT | TT | TT | TT |
| 170 | AG | AG | AG | GG | AA | AA | AA | N | AA | GG | AA | GG | GG | AA | GG | AA | AA | AG | GG | GG | AG | GG | GG | AG | AA | AA | AA | AA | AA | AA | GG | AA | GG | AA | AA | AA | AA |
| 171 | TA | TA | TT | AA | TT | TT | TT | AA | TT | TA | TT | AA | AA | TT | AA | TT | TT | TT | AA | AA | TT | AA | AA | TA | TT | TT | TT | TT | TT | TT | AA | TT | AA | TT | TT | TT | TT |
| 172 | GT | GG | GG | GG | TT | TT | TT | GG | TT | GG | GG | GG | GG | GG | TT | GG | GG | GG | GG | GG | TT | GG | GG | TT | TT | TT | TT | TT | TT | TT | GG | TT | GG | TT | TT | TT | GG |
| 173 | TA | TT | AA | TT | AA | AA | AA | TT | AA | TT | AA | TT | TA | AA | AA | AA | AA | AA | TT | TT | AA | TT | TT | AA | AA | AA | AA | AA | AA | AA | TT | AA | TT | AA | AA | AA | AA |
| 174 | TG | GG | TT | GG | TT | TT | TT | GG | TT | GG | TT | GG | GG | TT | TT | GG | TT | TT | GG | GG | N | TT | GG | GG | TT | TT | TT | TT | TT | TT | GG | TT | GG | TT | TT | TT | TT |
| 175 | CT | TT | CC | TT | CC | CC | CC | TT | CC | CT | CC | TT | CT | CC | TT | CC | CC | CC | TT | TT | CC | TT | TT | CC | CC | CC | CC | CC | CC | CC | TT | CC | TT | CC | CC | CC | CC |
| 176 | GA | AA | GG | AA | GG | GG | GG | GA | GG | AA | GG | AA | AA | GG | AA | GG | GG | GG | AA | AA | GG | AA | AA | GG | GG | GG | GG | GG | GG | GG | AA | GG | AA | GG | GG | GG | GG |
| 177 | CT | TT | CC | TT | CC | CC | CC | TT | CC | TT | CC | TT | TT | CC | CC | TT | CC | CC | TT | TT | TT | CC | TT | TT | CC | CC | CC | CC | CC | CC | TT | CC | TT | CC | CC | CC | CC |
| 178 | GA | GG | AA | GG | AA | AA | GG | GG | AA | GG | AA | GG | GG | GA | AA | AA | AA | GG | GG | GG | AA | AA | GG | GG | AA | GG | GG | GG | GG | GG | AA | GG | GG | GG | AA | AA | GG |
| 179 | CT | TT | CC | TT | CC | CC | CC | TT | CC | TT | CC | TT | TT | CC | CC | TT | CC | CC | TT | TT | CC | TT | TT | CC | CC | CC | CC | CC | CC | CC | TT | CC | TT | CC | CC | CC | CC |
| 180 | TA | AA | TT | AA | TT | TT | TT | AA | TT | AA | TT | TA | AA | TT | TT | AA | TT | TT | AA | AA | TT | AA | AA | TT | TT | TT | TT | TT | TT | TT | AA | TT | N | TT | TT | TT | TT |
| 181 | AT | TT | TT | AT | AT | AT | AT | AT | AT | AA | AT | AT | AT | AA | TT | AA | AT | AT | AA | AT | AT | AT | AT | AA | TT | TT | TT | TT | TT | TT | TT | TT | TT | AA | AA | AT | AT |
| 182 | GC | CC | GG | CC | GG | GG | GG | CC | GG | CC | GG | CC | CC | GG | GG | CC | GG | GG | CC | CC | GG | CC | CC | GG | GG | GG | GG | GG | GG | GG | CC | GG | CC | GG | GG | GG | GG |
| 183 | GT | GT | GG | GT | GG | GG | GG | GT | GG | GT | GG | GT | GT | GG | GT | GG | GG | GG | GT | GT | GG | GT | GT | GG | GG | GG | GG | GG | GG | GG | GT | GG | GT | GG | GG | GG | GG |
| 184 | CT | CC | TT | CC | TT | TT | TT | CC | TT | CC | TT | CC | CT | CT | TT | TT | TT | TT | CC | CC | TT | CT | CC | TT | TT | TT | TT | TT | TT | TT | CC | TT | CC | TT | TT | CT | TT |
| 185 | CT | TT | CC | TT | CC | CC | CC | TT | CC | TT | CC | TT | TT | CC | TT | CC | CC | CC | TT | TT | CC | TT | TT | CC | CC | CC | CC | CC | CC | CC | TT | CC | TT | CC | CC | CC | CC |
| 186 | CG | GG | CG | GG | CC | CC | CC | CG | CC | GG | CC | GG | GG | CC | GG | CC | CC | CC | GG | GG | CC | GG | GG | CG | CC | CC | CC | CC | CG | CC | GG | CG | GG | CC | CG | CC | CC |
| 187 | CT | CT | CC | TT | TT | CC | CT | TT | TT | TT | CC | CC | CT | CC | CT | CT | TT | TT | CT | CT | CC | CC | CT | TT | CC | TT | CC | TT | CT | CT | TT | CT | CC | CT | CT | CC | CT |

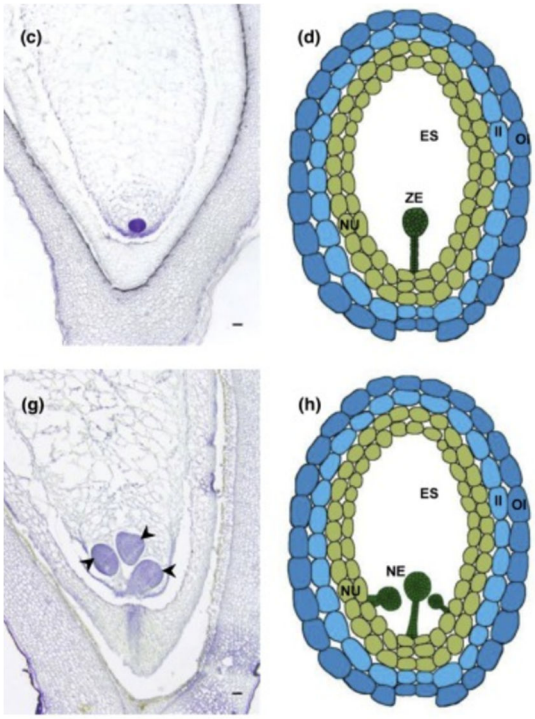
A. Which SNP markers are right on the centromere?

B. Which marker is the most distant? _____

C. Provide the marker-centromere distance for the 1st 4 markers.

| | |
|---|---|
| 168 | |
| 169 | |
| 170 | |
| 171 | |

**120. The following is from**: (will be revealed after the exam)
Xu Y, H J, X Wu, AMG Koltunow, X Deng, Q Xu. 2020. Regulation of nucellar embryony, a mode of sporophytic apomixis in *Citrus* resembling somatic embryogenesis. Current Opinion in Plant Biology 5959: 101984




The photos show 2 embryo sacs and interpretive drawings.

A. What phenomenon is shown in g & h?

B. How will the genotype of the resulting seedlings compare with that of the female parent?

C. Is there a chance the embryos could be coming from a cell other than the nucellus? Explain.

D. If so, what would be the genotype of the resulting plant?

121. **The following is from:**

FIAN International Secretariat. 2018. A Human Rights Analysis of Gene Drives. Self published. 9 pp.

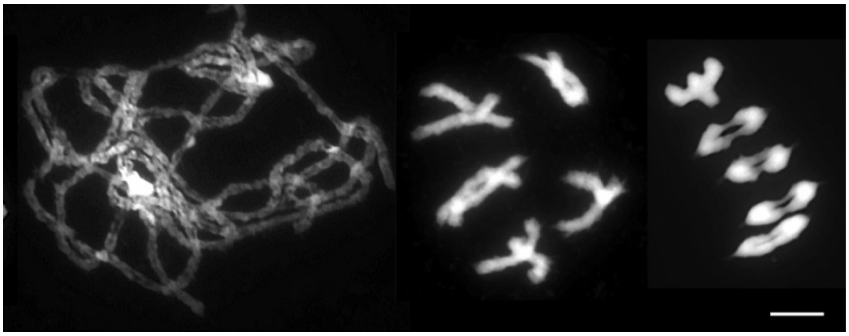
### 3. *Gene drives threaten biodiversity and ecosystems*

Ongoing research on gene drives explicitly aims to remove or eradicate species. Gene drives have the potential to forever change the genetic makeup of species, or even drive certain species to extinction. Indeed, they are designed to set off a chain reaction, which is potentially uncontrollable and unstoppable. "Removing a pest may seem attractive from the point of view of efficient monoculture food production, but even pests have their place in the food chain and may in other contexts (particularly outside of farmland) turn out to be essential or keystone species for maintaining biodiversity."[16] This means that the intended extinction of one species could lead to the unintended extinction of others because of the disruption of food chains and ecosystems. Another risk of gene drive technology is that it could produce new invasive species or organisms, the spread of which would be impossible to control.

At right is an excerpt from their arguments on why gene drives should never be deployed.
An international development agency is considering a project to eradicate insect pests via gene drives, but is having second thoughts after reading the FIAN report.
They have called you in as a science consultant to evaluate the 3rd reason, given here. What explanation and conclusions would you give them?

122. The following is from the reference below, which will be posted after the exam:

T Mandáková, M Kubová & MA Lysak. 2022. Genomes, repeatones and interphase chromosome organization in the meadowfoam family (Limnanthaceae, Brassicales). The Plant Genome, 110(5): 1462-1475.



a. Name the 3 stages depicted in the figure, and explain the distinguishing features used for your identification of the relevant stage

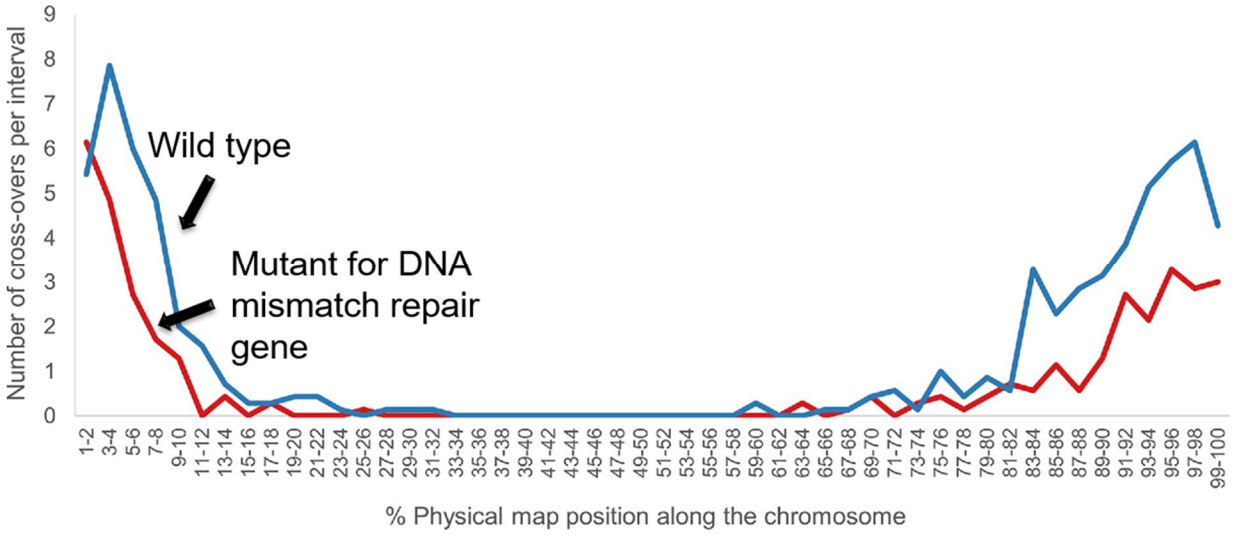
b. Based on the 3rd stage shown, this plant is 2n = _____X = _____ C = _____

c. Also based on the 3rd stage shown, how many crossovers are most chromosomes exhibiting?

d. Based on the total number of COs shown in the 3rd stage, what is the predicted genome length in centiMorgans?

123. The following is from the reference below, which will be posted after the exam:

Schreiber M, Y-Y Chen, L Ramsay & R Waugh. 2022. Measuring the frequency an distribution of meiotic crossovers in homozygous barley inbred lines. Frontiers in Plant Science 13: 965217




In this work, the authors were measuring crossover along the length of a chromosome of a crop plant, with n = 75.

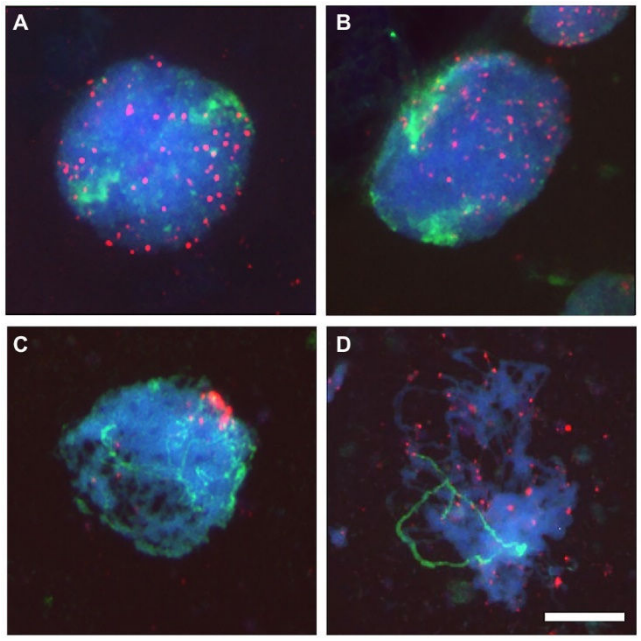
a) Classify this chromosome according to its centromeric position, and explain what observations led to your classification.

b) In this case, the mutant has decreased recombination. Discuss the impact of the reduced crossover frequency on i) the ability of this cultivar to serve as a parent for a new cultivar, and ii) adaptability of a plant in general to a given area over seed increase generations

124. The following is from the reference below, which will be posted after the exam:

Aguilar MA & P Prieto. 2021. Telomeres and subtelomeres dynamics in the context of early chromosome interactions during meiosis and their implications in plant breeding. Frontiers Plant Science 12: 672489

In these photos, telomeres have been stained red with FISH. Green represents a chromosome pair introgressed from another species that is stained using GISH.



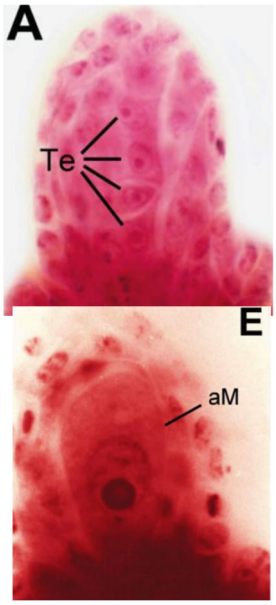

a) What is the phenomenon shown in c) and what is the stage of division shown in c)?

b) What is the purpose of the phenomenon shown in c? I.e., what is happening here.

c) The green chromosomes have the same telomere as the recurrent parent, but differ from the recurrent parent in their subtelomeric sequences, and hence do not pair with the blue chromosomes, and thus preventing gene introgression via homologous recombination. In the future, what might be done to solve this problem?

125. The following is from the reference below, which will be posted after the exam:

Palumbo F, E Pasquale, E Albertini & G Barcaccia. 2021. A review of unreduced gametes and neopolyploids in alfalfa: How to fill the gap between well-established meiotic mutants and next-generation genomic resources. Plants, 10(5): 999.




a) Figure A shows a linear tetrad of megaspores following meiosis. Explain what will happen to each of the 4 megaspores

b) Figure E shows a 2n megaspore formed by *omission of the first division*. The authors are working with a crop that is normally cross pollinated, heterozygous, and heterogenous. They are very interested in converting it to an apomict, but this crop lacks parthenogenesis. Describe what is needed to convert the mutants they have into an apomict, and justify the methodology you propose. Because they are starting with FDR eggs in a heterogenous crop, the process should be simpler than the example shown in class.

126 The following is from the reference below, which will be posted after the exam:

Anirban A, A Hayward, HT Hung T, AK Masouleh, RJ Henry & TJ O'Hare. 2023. Breaking the tight genetic linkage between the a1 and sh2 genes led to the development of anthocyanin-rich purple-pericarp super-sweetcorn. Scientific Reports, 13(1): 1050, 1-13. doi: 10.1038/s41598-023-28083-4

As background, a purple sweet corn could be commercially desirable.
There are a few genes that can give the sweet phenotype in corn: *sugary1*, *sugary enhancer1*, *brittle1*, and *shrunken2* (*sh2*). Of these, *sh2* gives the "super sweet" phenotype that is preferred due to a higher sugar content and ability to last longer in storage. Currently, there is purple sweet corn on the market based on the *su1* gene, but not on the *sh2* gene.
Purple pericarp (a maternal tissue) is conditioned by the *anthocyaninless1* gene (*A1*), the dominant allele of which is native to Peru. Commercial sweet corn hybrids are all colorless pericarp (*a1a1*). Hence, the desired genotype is *A1__ sh2 sh2*. The problem is that *A1* and *sh2* are linked in *trans* at just 140 kb (<0.1 cM) apart. So, a crossover is needed between *A1* and *sh2*. Currently, such a recombination happens <1 in 1000 F2 plants, making it difficult to get enough plants to evaluate and breed with.

a) You have been tasked with developing purple super-sweet corn. Describe 2 strategies (realistic, timely, and practical) that you could try the next growing season to obtain greater numbers of recombinants, and explain your rationale for choosing this strategy.

b) Given a longer time horizon (>3 years) describe a strategy you would use, and explain why you chose it. To avoid regulations and export restrictions, the use of gene editing, RNAi, and transgenics is off the table.

127. The following is from the reference below, which will be posted after the exam:

Emerson RA, GW Beadle & AC Fraser. 1935. A summary of linkage studies in maize. Cornell University Agricultural Experiment Station Memoir 180.

The data below comes from a 3-point test cross whereby

- gl1 = glossy seedling 1 = glossy cuticle wax on juvenile leaves that are normally glaucous
- v5 = virescent seedling 5 = yellow-green colored seedlings
- va1 = variable sterile 1, as opposed to full fertility

Parental cross: *V Gl Va / V Gl Va* x *v gl va / v gl va*
Green – glaucous – fertile x virescent – glossy – variable

Test cross: *V Gl Va / v gl va* x *v gl va / v gl va*
Green – glaucous – fertile x virescent – glossy – variable

Test cross progeny:

| Phenotype | Number observed |
|---|---|
| Virescent – glaucous - fertile | 60 |
| Virescent – glossy – fertile | 48 |
| Virescent – glaucous - variable | 4 |
| Virescent – glossy - variable | 270 |
| Green – glaucous - fertile | 235 |
| Green – glossy - fertile | 7 |
| Green – glaucous - variable | 40 |
| Green – glossy – variable | 62 |
| | 726 |

a) The V – Gl distance =

b) The Gl – Va distance =

c) The V – Va measured map distance =

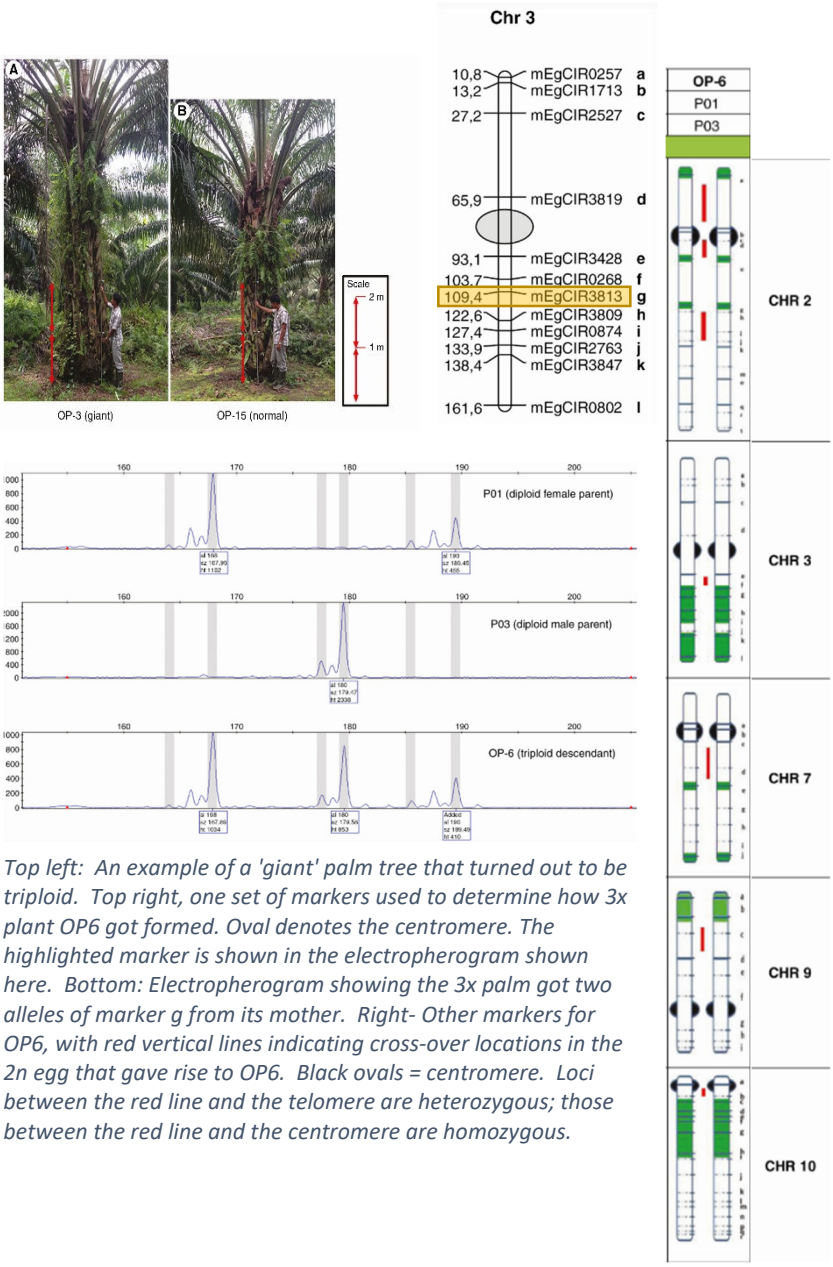
d) The V – Va best estimate of true map distance =

e) The interference observed for the DCOs =

128. The following is from the reference below, which will be posted after the exam:

Pomiès V, N Turnbull, S Le Squin, I Syahputra, E Suryana, T Durand-Gasselin, B Cochard & F Bakry. 2022. Occurrence of triploids in oil palm and their origin. Annals of

Occasionally, giant individuals are found in oil palm plantations. In this study, these palms were found to be triploid or tetraploid, derived via 2n gametes.
The authors were trying to determine if the 2n gametes involved were FDR or SDR based on molecular markers. Here, the electropherogram shows data for one of the markers used for one 3x individual named OP6.
Based on the data presented, was this individual derived from an FDR or SDR gamete? Explain the basis for your answer.

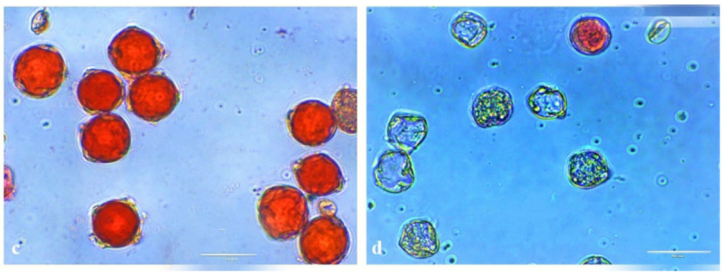



*Top left: An example of a 'giant' palm tree that turned out to be triploid. Top right, one set of markers used to determine how 3x plant OP6 got formed. Oval denotes the centromere. The highlighted marker is shown in the electropherogram shown here. Bottom: Electropherogram showing the 3x palm got two alleles of marker g from its mother. Right- Other markers for OP6, with red vertical lines indicating cross-over locations in the 2n egg that gave rise to OP6. Black ovals = centromere. Loci between the red line and the telomere are heterozygous; those between the red line and the centromere are homozygous.*

129. **Extra credit**

The following is from the reference below, which will be posted after the exam:

Kumar A, S Siddappa, V Bhardwaj, Dalamu, B Singh, N Sharma, B Dipta, V Kumar, U Goutam & S Sood. 2023. Generation of asynaptic mutants of potato by disrupting StDMC1 gene using RNA interference approach. Life, 13(1): 174



The use of true potato seed (TPS) remains an option, and efforts continue to reduce the amount of recombination/segregation that takes place when TPS is used. Knowing that FDR pollen will restore fertility to synaptic mutants, the authors engineered a potato variety (2n = 4x = 48) with RNAi to knock out a gene involved in chromosome pairing. The photo shows pollen obtained from the original parent (L) and from the pairing mutant (R), whereby most of the pollen aborted.

Assuming that the transgene is fully expressed, and that a diploid potato is used, what is the expected frequency of fertile n pollen grains?

**The following is from:** https://www.stop-genedrives.eu/en/


"This overrides the **natural rules of inheritance and evolution**. This mechanism is then repeated independently in each new generation, resulting in a risky and uncontrollable **genetic chain reaction**. Gene Drive Organisms are supposed to **replace or even exterminate** their conspecifics in nature. Their future release could have unforeseeable and irreversible consequences for ecosystems and food webs. In the worst case, this could lead to further species extinction and the **collapse of entire ecosystems**, as well as endangering human health and food security."

Write a paragraph evaluating to what extent gene drives can be dangerous. Use examples or refereed reference citations to back up your position.