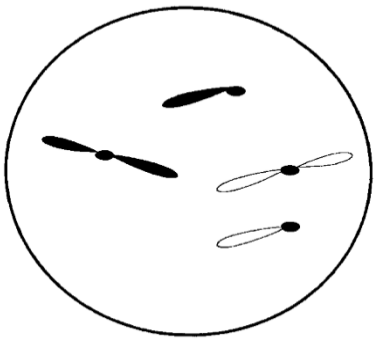
Stages of mitosis

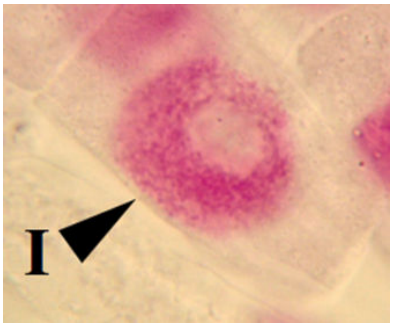
Photo credits: http://botit.botany.wisc.edu/images/130/Mitosis/Allium_Root_Prep._Slides unless otherwise indicated

For a cell that is 2n = 2x = 4

Interphase

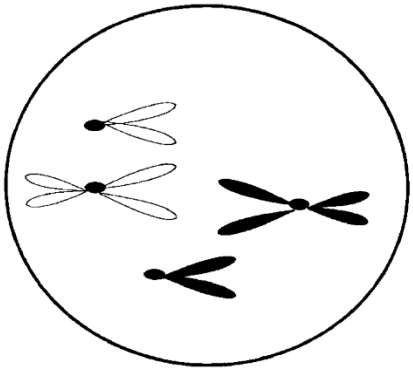


Would be decondensed, shown condensed in the diagram to show individual chromosomes

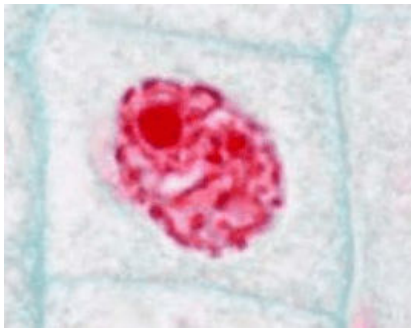


Paperwhite (Narcissus papyraceus) courtesy of course alumna Chandler Maddox

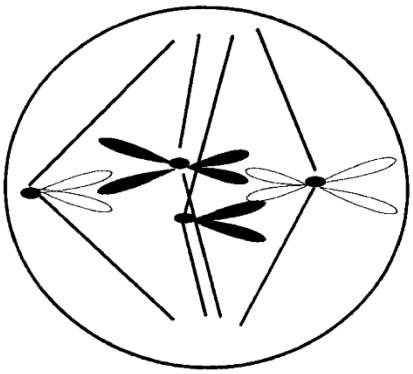
Prophase



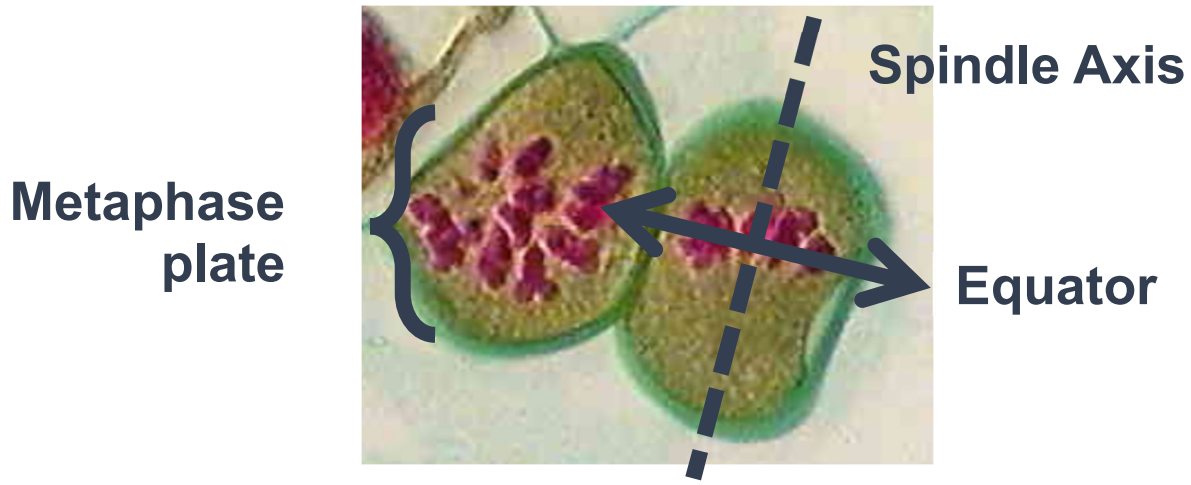
Prophase: chromosomes are duplicated, but not paired



Metaphase

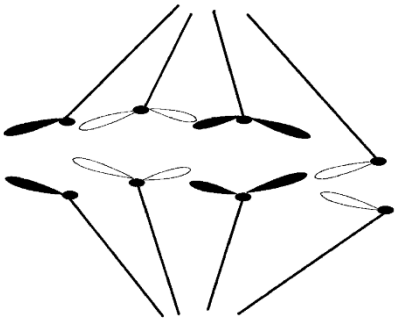


Orientation Terminology

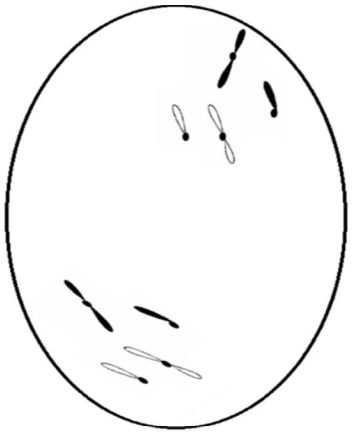


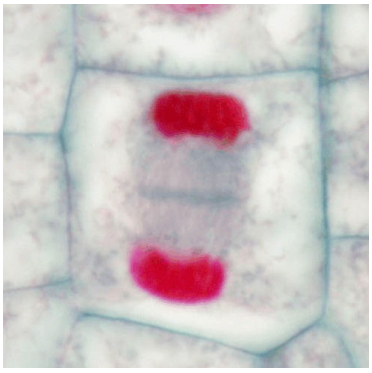
https://www.iasprr.org/old/iasprr-pix/lily/meta-i.jpg

Anaphase

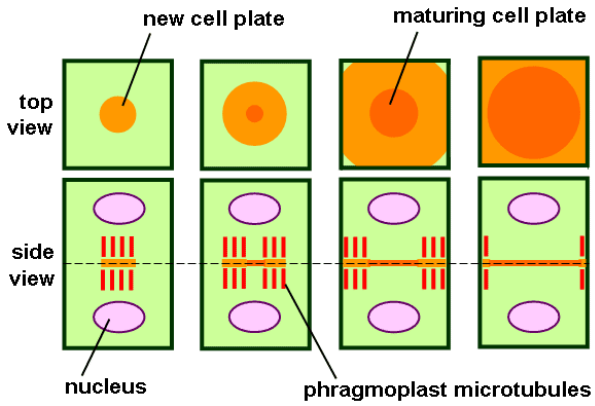


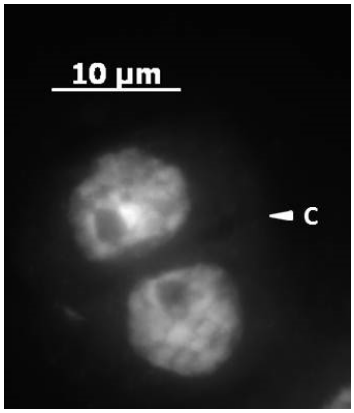
Telophase





Cytokinesis





Cotton, courtesy of course alumnus Nino Brown

Chromosome Number Convention

Swift, 1950. Physiol. Zool. 23:169-191

_n = _x = _c = ___

c = 'constant value'

c = the number of DNA copies present per genome

= the number of copies present of each chromosome

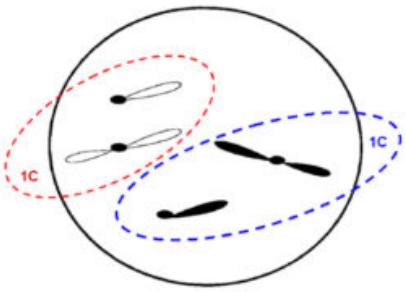
= the number of chromosomes/chromatids

× = one chromosome set (= genome = haploid chromosome set)

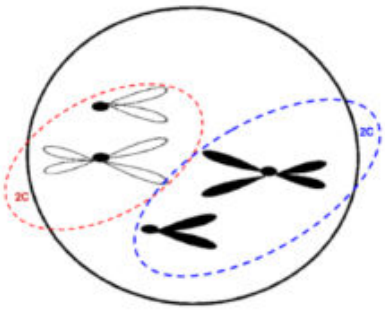
= the number of centromeres per genome (= haploid chromosome set) = monoploid

n = the gametic chromosome number; 2n = the sporophytic chromosome number

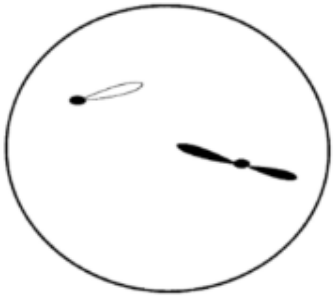
A. A cell with 2n = 2x = 2C = 4



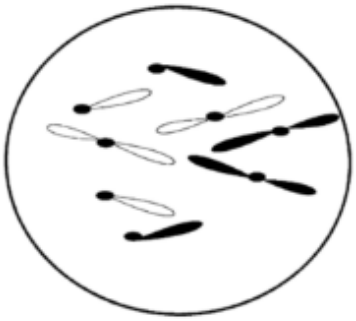
B. When the previous cell is ready for meiosis, it becomes 2n = 2x = 4C = 4



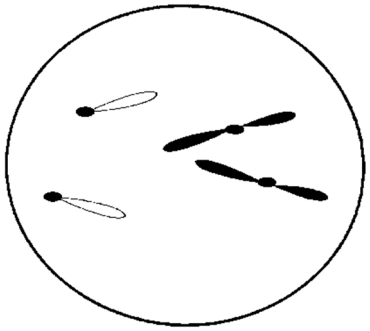
C. Following meiosis, each resulting gamete would be n = x = C = 2



D. If the chromosome number of the original cell is doubled with colchicine, it becomes 2n = 4x = 4C = 8



E. When the tetraploid cell undergoes meiosis, the resulting cell would be n = 2x = 2C = 4



Note: for Stage E, some authors sometimes call the DNA content 1C

- To avoid confusion between haploids with one genome vs haploids with more than one genome, new terminology was introduced

C_x Terminology

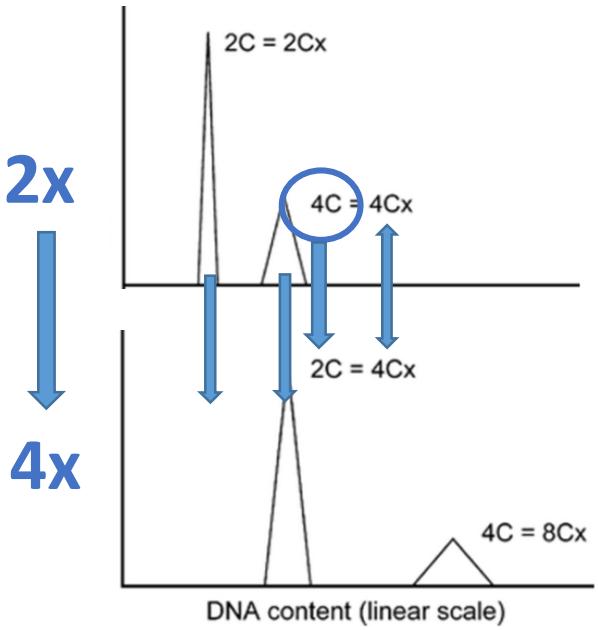
Greilhuber et al., 2005

Cx = x = the size of the **monoploid** genome

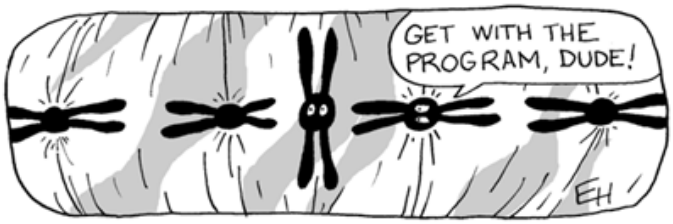
- Diagram C above becomes Cx = 2

C = n = the size of the **holoploid** genome

- Diagram C above becomes C = Cx = 2
- Diagram E above becomes C = 2Cx = 4
- Diagram D above becomes 2C = 4Cx
  - But, an octoploid cell in that individual becomes 4C = 8Cx
- Diagram A above becomes 2C = 2Cx
  - But, a tetraploid cell in that individual would be 4C = 4Cx



Modifications to Mitosis



Normal cell division entails:

A. DNA replication
B. Sister chromatid separation
C. Chromosome separation (nuclear division)
D. Cytokinesis

Interruptions to mitosis

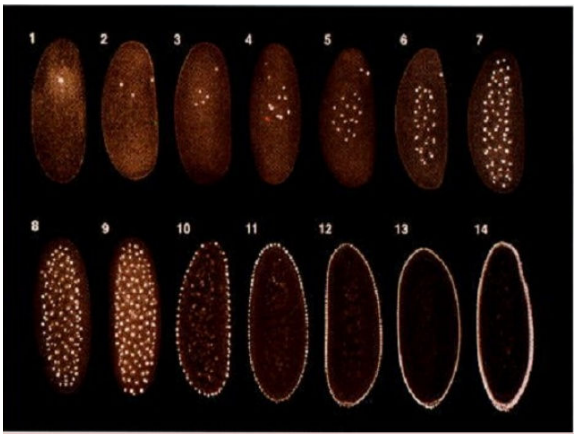
1. A → B → C ~~→~~ D — multinucleate condition, syncytium
2. A → B ~~→~~ C ~~→~~ D — **endomitosis,** which leads to **polysomaty**
3. A ~~→~~ B ~~→~~ C ~~→~~ D — **endoreduplication,** which leads to **polyteny**
4. → B → C → D — **reduction**, as in Meiosis I; **somatic reduction**
5. A → B → C → D (abnormal) — **aneusomaty**, e.g. sports in plants

Interruption before cytokinesis

A → B → C ~~→~~ D

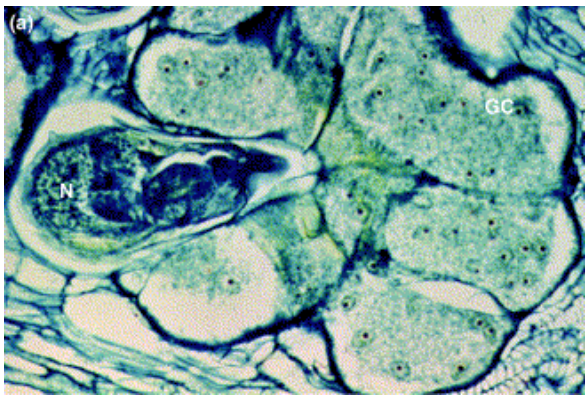
Multinucleate conditions

Found in tapetal cells, endosperm cells, and nematode feeding sites in plant root cells



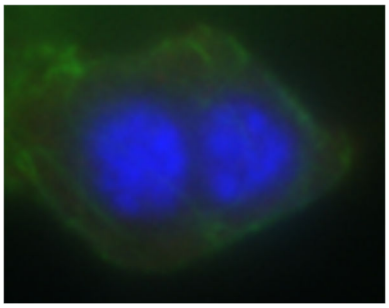
Drosophila multinucleate condition during embryogenesis

- "a series of nuclear divisions without cell division creates a **syncytium**"
  - Molecular Biology of the Cell, 4th edition
- "A **syncytium** is a multinucleate cell which can result from multiple cell fusions of uninuclear cells, in contrast to a coenocyte, which can result from multiple nuclear divisions without accompanying cytokinesis."
  - Daubenmire, R. F. (1936). "The Use of the Terms Coenocyte and Syncytium in Biology". Science. 84 (2189): 533–534.
- The second definition is the one used by nematologists

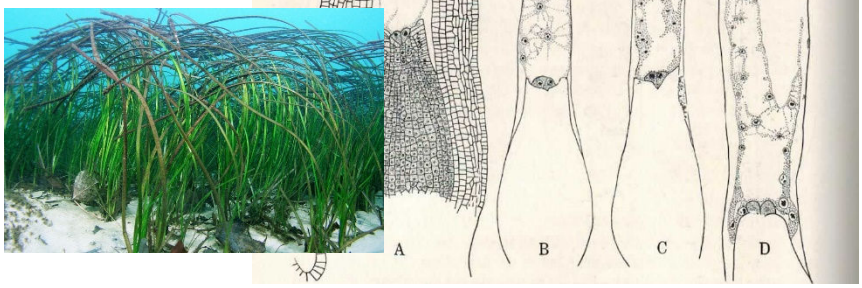


A (N) nematode at the 9 o'clock position and multinucleate (GC) giant cells upon which it feeds. Photo by RS Hussey.

Multinucleate cells



Maize tapetum cells
Course alumnus, Kyle Swentowsky



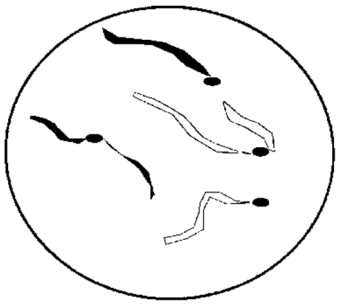
Endosperm formation in eelgrass, Zostera marina (Dahlgren, 1939)

Eelgrass photo: https://aggietranscript.ucdavis.edu/the-relationship-between-genetic-diversity-and-disturbance-in-the-eelgrass-species-zostera-marina/

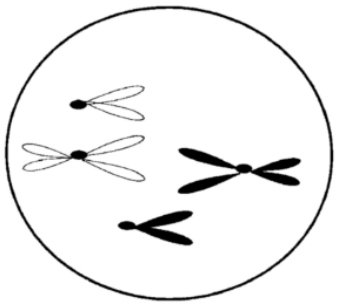
Endomitosis and Polysomaty

A → B ~~→~~ C ~~→~~ D

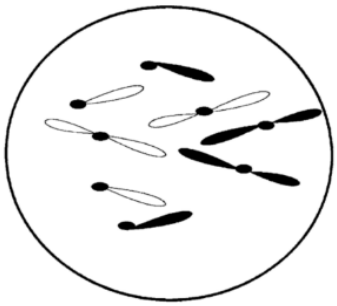
- Chromosomes are replicated but there is no cell division
- One nucleus re-forms around a doubled chromosome set



Endoprophase



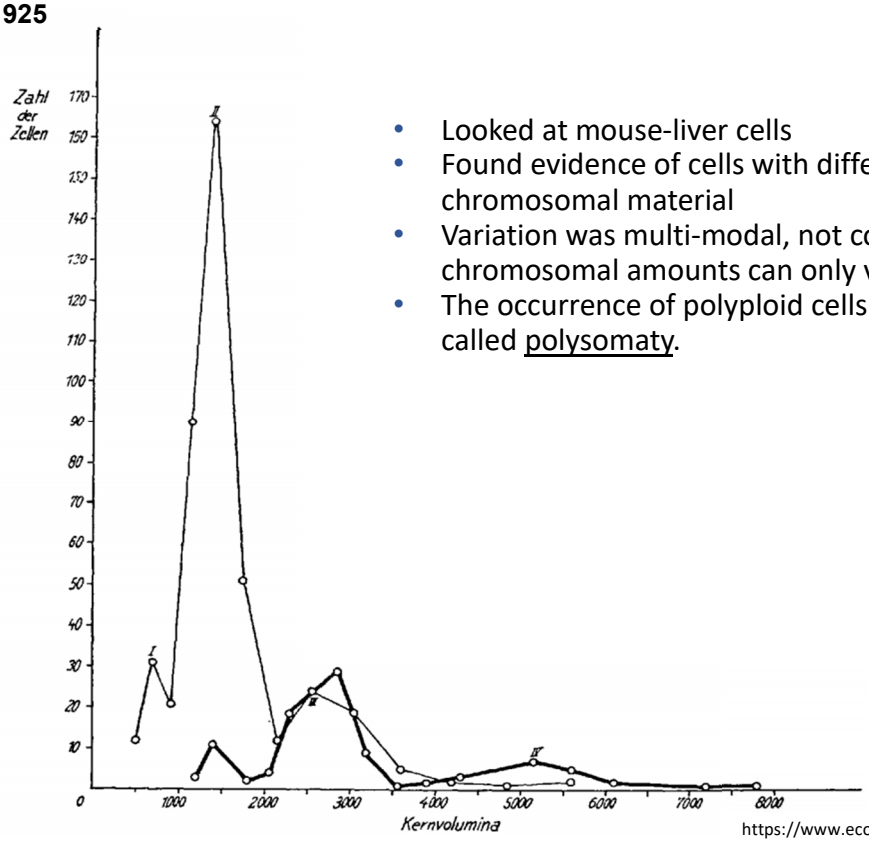
Endometaphase



Endoanaphase

2n = 2x = 2C = 4

Jacobj, 1925



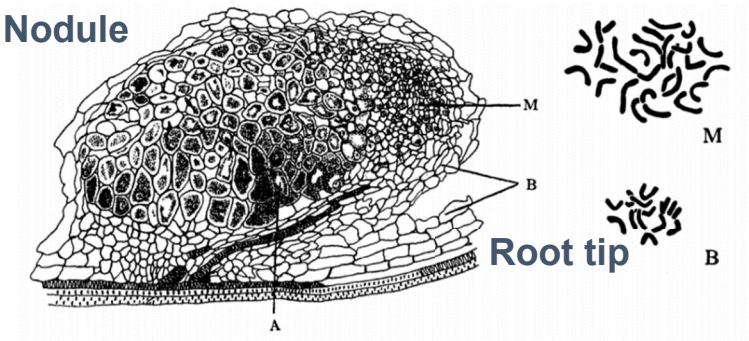
- Looked at mouse-liver cells
- Found evidence of cells with differing amounts of chromosomal material
- Variation was multi-modal, not continuous, suggesting that chromosomal amounts can only vary by discrete factors
- The occurrence of polyploid cells in otherwise diploid tissues is called <u>polysomaty</u>.

https://www.economyexterminators.com/pest/house-mice/

Wipf & Cooper, 1938; Wipf, 1939

Verified previous suggestions that root nodule cells of legumes have twice the chromosome number

Common vetch, red clover and pea



Common vetch
Vicia angustifolia
2n = 12

Red clover
Trifolium pratense
2n = 14

Pea
Pisum sativum
2n = 14

https://pladias.cz/en/taxon/overview/Vicia%20angustifolia
https://www.seed-bank.ca/product/red-clover-seeds/
https://www.mediastorehouse.com/auscape/photographer-galleries/nature-production-collection/pea-pisum-sativum-18980773.html

Wipf, 1939

- 4x versions have 8x chromosomes in nodules.

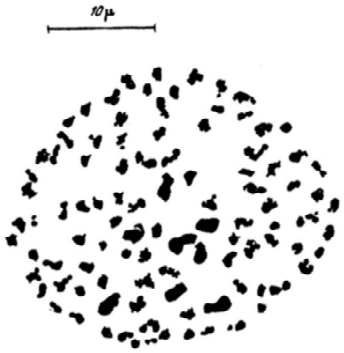
Anaphase in a nodule of 8x alfalfa, with 128 chromosomes going to each pole

http://www.glbinvest.com/abouttheproject/alfalfa

Alfalfa
Medicago sativa
2n = 2x = 16
2n = 4x = 32
2n = 8x = 64 → 2n = 16x = 128

Geitler, 1939

- Has XO sex determination system, and male is the XO
- X chromosome is heteropigmatic, i.e., stains deeply in interphase cells
- Makes it possible to count the number of X chromosomes in a given cell
- Found cells that were up to 512x, 1024x, or 2048x.
- Means that 8, 9, or 10 rounds of mitosis without cytokinesis had taken place
- Termed this endomitosis, where chromatids fall apart without cytokinesis

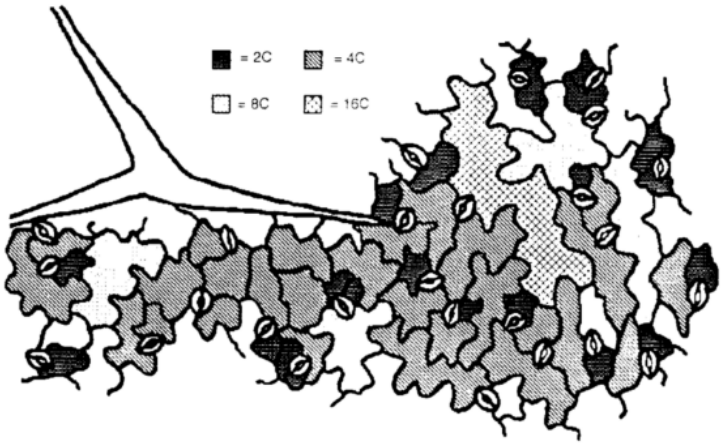


A cell with 8 heteropigmatic X chromosomes in ♀ water strider, indicating the cell is 16x.

Gerris lateralis.
Water strider

Wikimedia commons

- **Pattern of endopolyploidy can be highly variable**



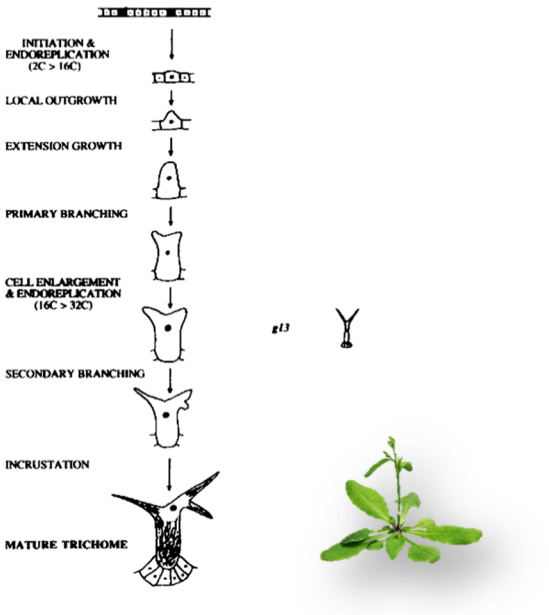
*From **Melaragno et al., 1993**. Endopolyploidy in the polysomatal epidermis of arabidopsis*

$$V = {}^{4}/_{3}\pi r^{3}$$

- Note relationship between endopolyploidy and cell size:
  - Doubling the DNA amount doubles the cell volume.
  - Volume of sphere = $^{4}/_{3}\pi\ r^{3}$
  - Diameter of doubled sphere is 1.26x

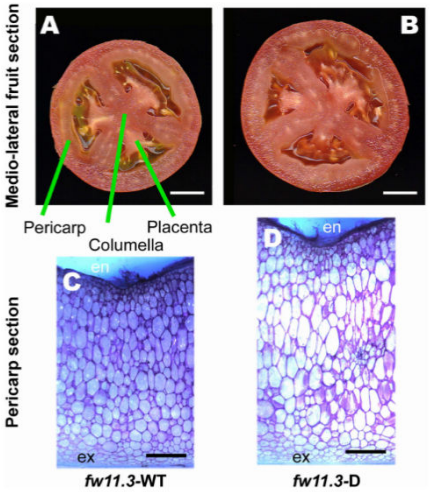
Hülskamp et al., 1994

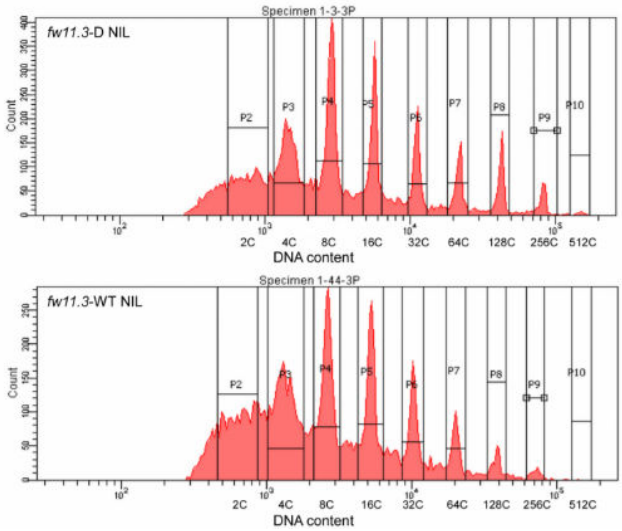
- Note also that endomitosis can play a role in development, and
  - it can be under genetic control
  - In this case, the GL3 gene controls endomitosis during trichome development in arabidopsis



Mu et al., 2017 (van der Knaap lab) - Endopolyploidy & fruit size

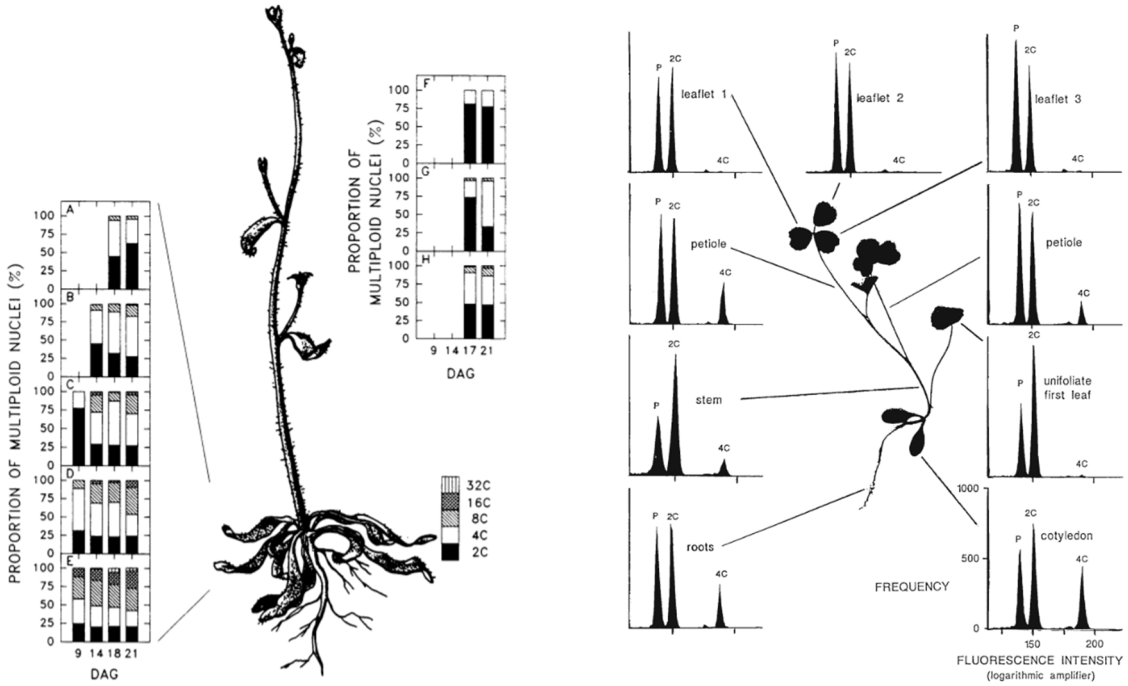
- Fruit weight allele increases fruit size by increasing cell size by increasing ploidy level





- **Endopolyploidy in different tissues**

Galbraith et al., 1991 **Blondon et al., 1991**



- Alfalfa (right) - endopolyploidy in tissues with high metabolic requirements?
- Arabidopsis (left) - more endopolyploidy in older tissues

- **Levels of endopolyploidy**

Nagl, 1976; 1978

Family	Species	Cells/tissues	Endopoly-ploidy x=genome
Araceae	Arum maculatum	endosperm austoria	24,576x
Cucurbitaceae	Cucumis sativus	nucellus	16x
Fabaceae	Lupinus regalis	tapetum	8x
	Phaseolus coccineus	suspensor	4,096x
	P. vulgaris	endosperm	96x
	Vicia faba	stem epidermis	61x
Geraniaceae	Geranium phaeum	integument	512x
Rosaceae	Prunus sp.	fruit	32x
Crassulaceae	Crassula arborescens	mesophyll	16x

- **DNA content vs ploidy level**

Nagl, 1976

Nuclear DNA contents and maximum endopolyploidy levels in various plants and animals

Species	DNA (pg/2C)	Max. C level
Capsella bursa-pastoris	1.7	1,024
Cucurbita pepo	2.6	384
Phaseolus coccineus	2.7	8,192
Tropaeolum majus	2.7	2,048
Helianthus annuus	6.1-9.9	16
Hordeum vulgare	13.4	256
Lathyrus spp.	9-20	64
Vicia faba	23.9 - 28.7	16
Allium cepa	35.5	8
Drosophila melanogaster	0.36	2,048
Chironomus tentans	0.5	32,768
Bombyx mori	1.0	524,288
Aplysia californica	2.0	200,000
Rattus rattus	6.1	4,096

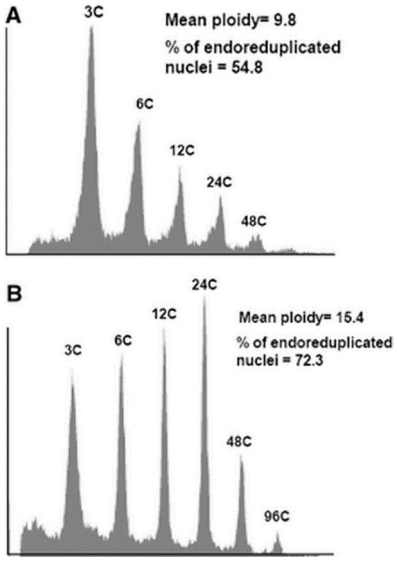
- In general, there is an inverse correlation between the DNA content of a given species and the incidence of endomitosis, at least in plants

- Multiple nuclei and endopolyploidy thought to be a way to increase gene copy number when lots of gene product is needed

- Polyteny accomplishes the same goals

- **Genetic control**

Coelho et al., 2007



Endoreduplication in maize inbreds Mo17 (top) and Sg18 (bottom)

Endoreduplication in maize endosperm takes place right before seed fill starts

- Endoreduplication is under genetic control, as evidenced by differences between maize inbreds.
  - 3 QTLs affect average ploidy
  - 2 QTLs affect % endoreduplication

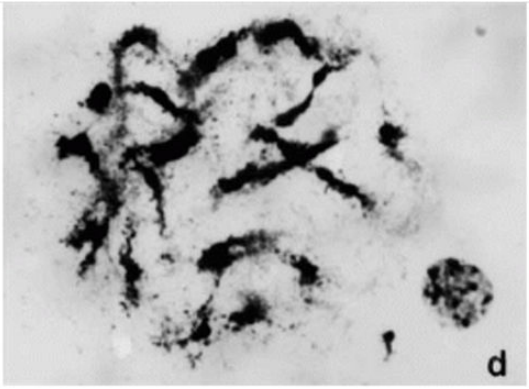
Polyteny

A → ~~B~~ → ~~C~~ → D

- Differs from endomitosis in that the chromatids remain attached to each other
- In plants, found in very specialized cells, such as endosperm, ovules, young seeds, and embryo suspensors.
- Also found in tapetum of anther walls and in the antipodal cells of the embryo sacs

Mosquito polytene chromosomes

Cowpea polytene chromosomes

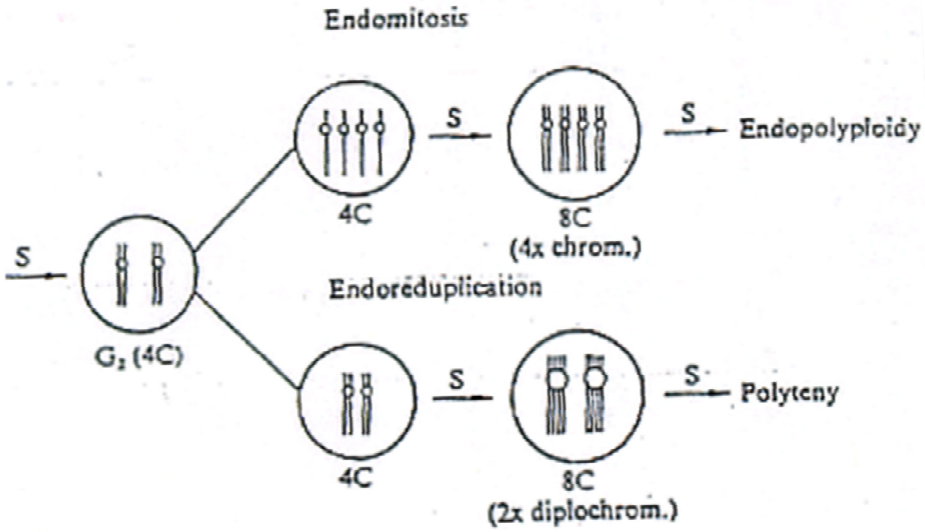


Cowpea tapetal cell. Note a nucleus containing non-polytene chromosomes right over the "d"

Mosquito: http://www.impact-malaria.com/FR/EPS/Formations_et_cours_internationaux/Formation_de_la_Liverpool_School_LSTMH/cours_liverpool/Unit_2/2_8.html
Cowpea: Carvalheira GMG. 2000. Plant polytene chromosomes. Genet. Mol. Biol. 23:1043-1050.

- **Endomitosis vs Endoreduplication**

Nagl, 1976



Somatic reduction

→ B → C → D

Schrader, 1921; Schrader and Hughes-Schrader, 1931

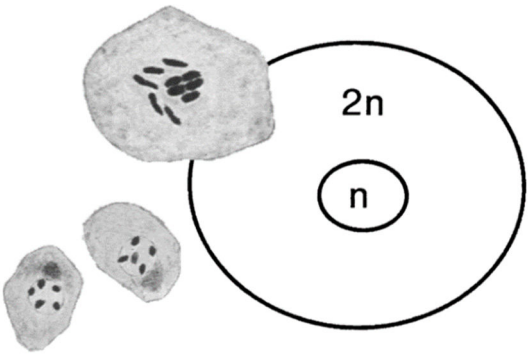
Coccids, which have extremely unusual cytology

- The outer part produces eggs through meiosis
- The inner part produces sperm through mitosis
  - ∴ somatic reduction had occurred in the cells that produce the sperm

Coconut mealybug, Nipaecoccus nipae. Photograph by Lyle J. Buss, University of Florida

Haplodiploid

- Paternal genome loss



Gonad of Icerya purchasi, the cottony-cushion scale

Sally Hughes-Schrader (1895–1984)
Franz Schrader (1891–1962)
From Richmond, 2020

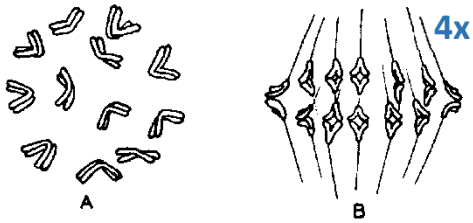
Haploidization also occurs in fungi and in the zygotes of some interspecific crosses of barley, and intergeneric crosses such as maize × wheat

Berger, 1938

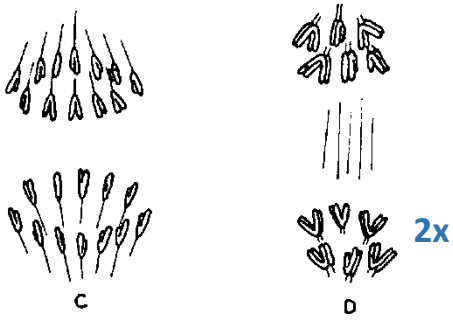
Somatic reduction in mosquito

Culex pipiens, 2n = 6

https://www.eurekalert.org/multimedia/pub/132452.php



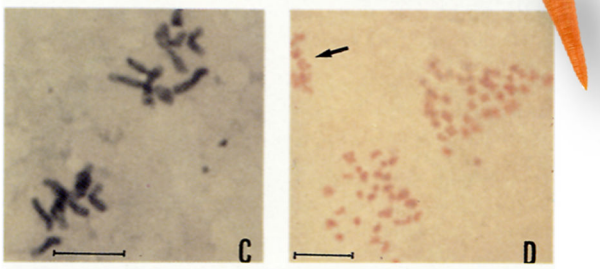
A. 24 chromosomes in 12 pairs at metaphase
B. Early anaphase
C. Middle anaphase
D. Late anaphase-- the 12 chromosomes form 6 pairs
- etc.



- **Reductional groupings**

Huskins, 1948

Nuti Ronchi et al., 1992



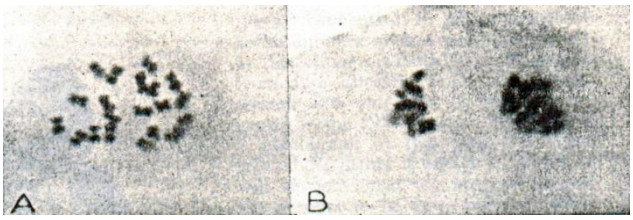
Bar = 5 µm

- **True-breeding mutants of sorghum**

1963-1976: Ross, Franzke, & Sanders

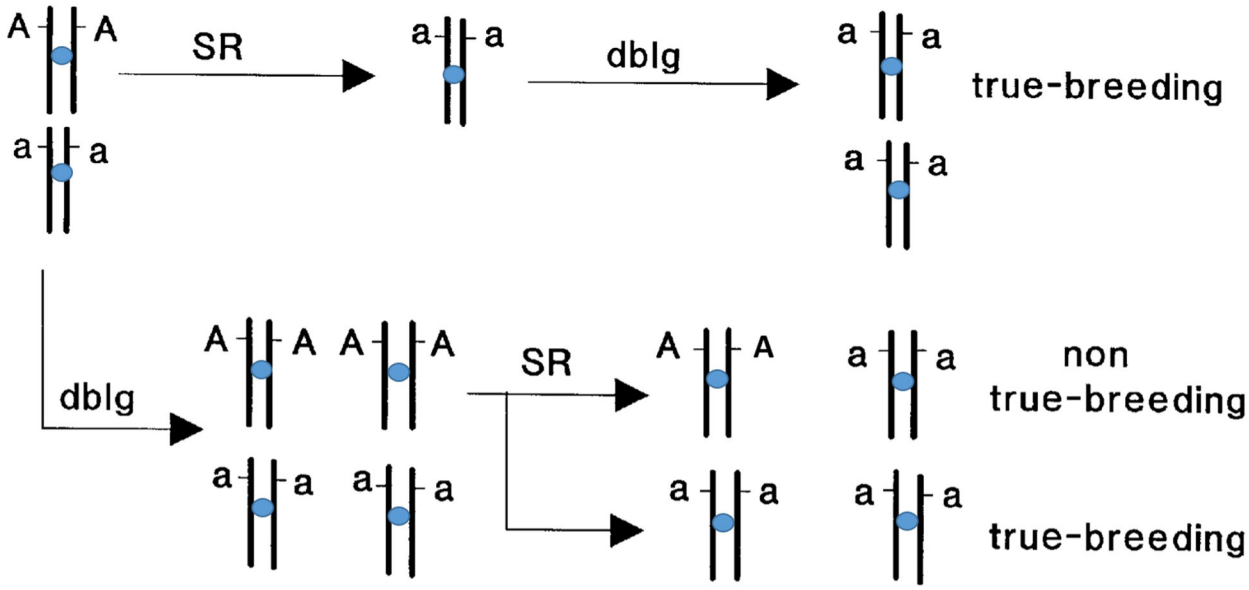
- True-breeding mutants of sorghum (2n = 20)
- Treated seedlings of 'Experimental 3' with colchicine
- Obtained true-breeding and nontrue-breeding mutants
- Mutations affected multiple characteristics

- The basis for haploidization via somatic reduction appears to be via the formation of Reductional groupings



Franzke & Ross, 1952

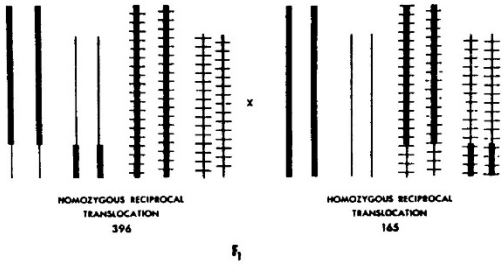
Hypothesis



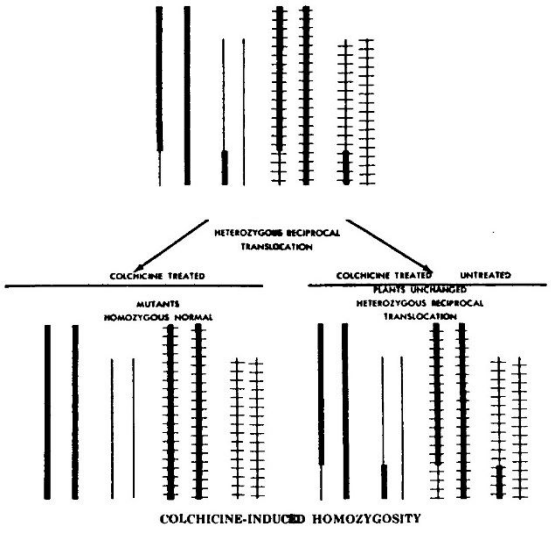
Simantel & Ross, 1963

Validated the hypothesis, using 4 pairs of homologous chromosomes involved in reciprocal translocations

- Crossing these gave them a heterozygote for 2 reciprocal translocations, which they exposed to colchicine:



Got 6 true-breeding mutants, all of which had the normal chromosomes.



- The only possible explanation is somatic reduction + doubling
- or by doubling followed by somatic reduction

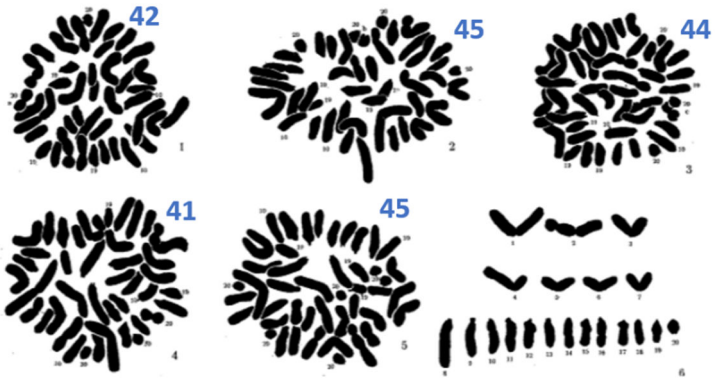
Aneusomaty

A → B → C → D

Paphiopedilum wardii, Wikimedia commons

Termed by Duncan 1945

- Was studying root tip cells of Burmese lady slipper orchids (2n = 40)
- Found tips with 2n = 27-31 in some plants, 41-45 in other plants and 38-40 in others



- Prevalent in plants
- Results from:
  - Chromosome non-congregation at metaphase
  - Chromosome lagging
  - Chromatid non-disjunction
  - Split spindles
  - Chromosome elimination in somatic hybrids
- Is under genetic control

Britton & Hull, 1957

- Root tips from the same blackberry plant
- Both parents were 2n = 49