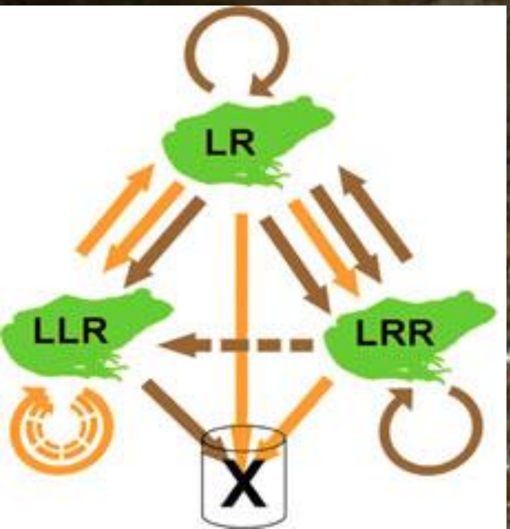
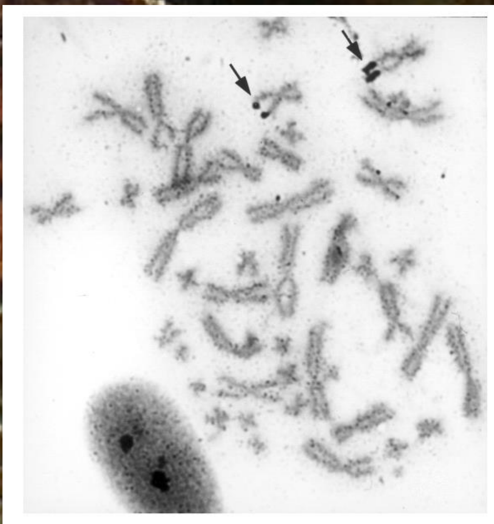
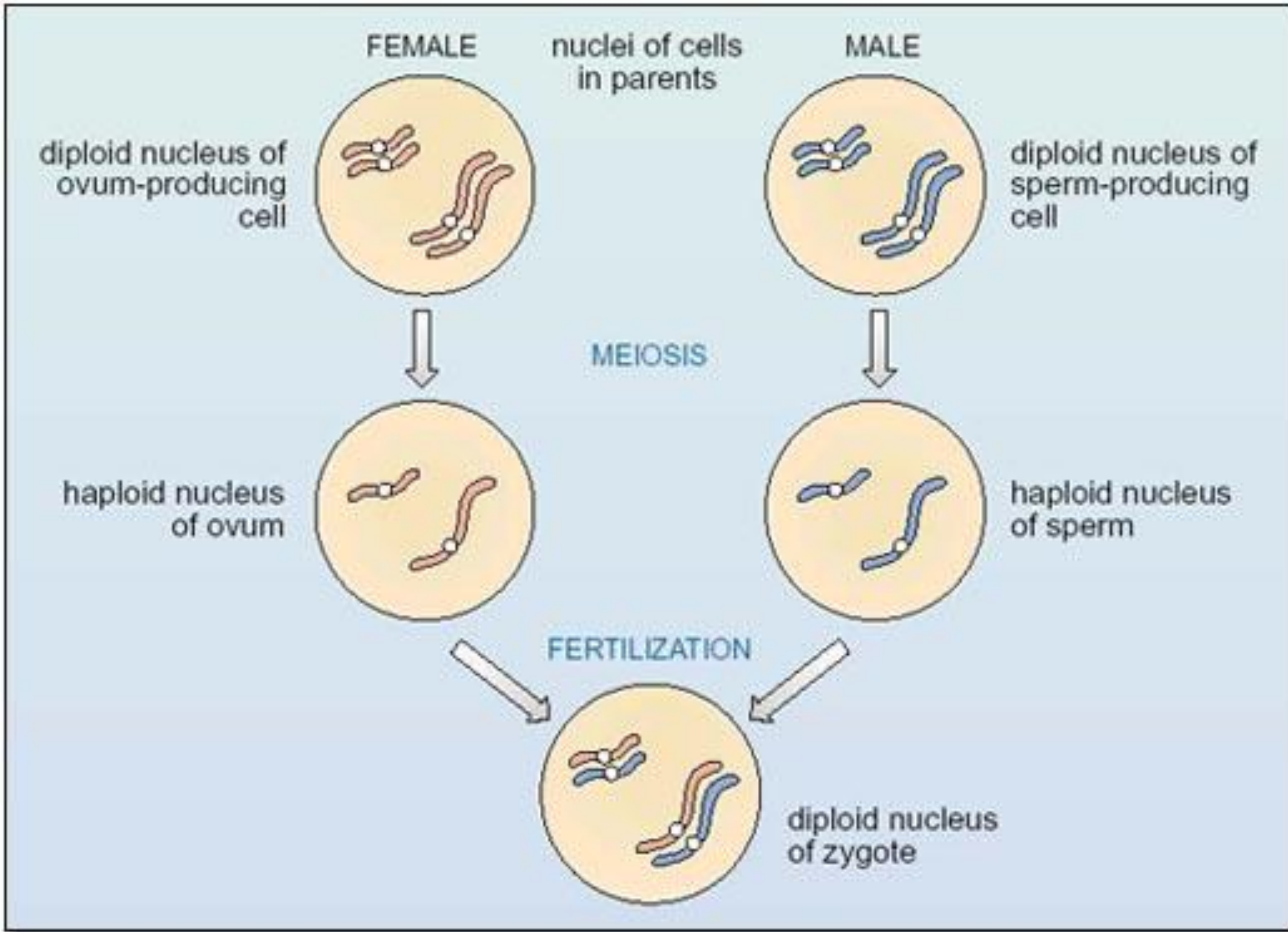
On the origin of unisexual species by the means of hybridization

or the preservation of clonal races in the struggle for life

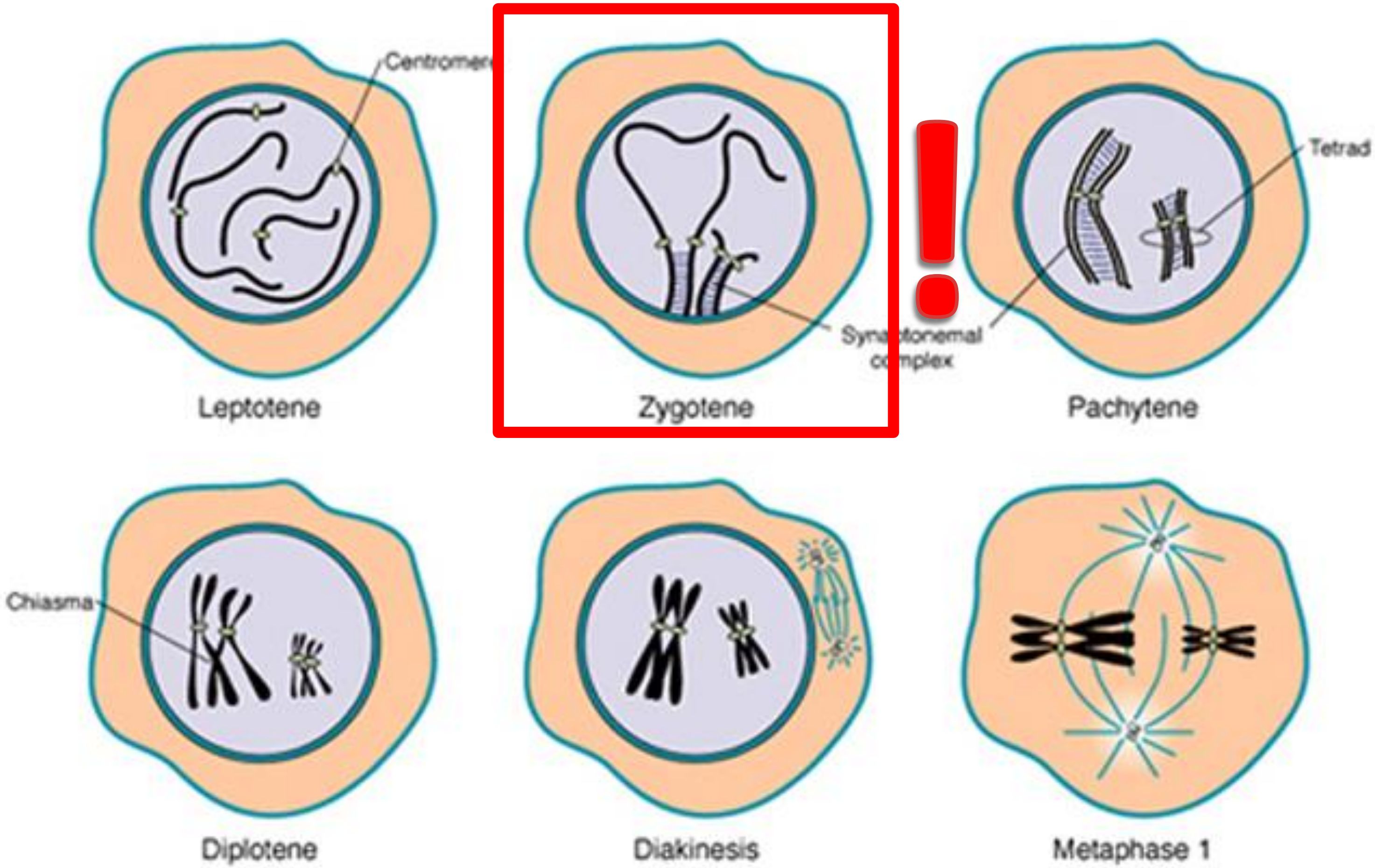




Normal sexual reproduction



Meiosis in hybrids meets pairing difficulties



Meiosis abnormalities

Partial or full hybrid sterility

Escaping hybrid sterility

- Some meiosis disturbances may lead to the formation of unreduced egg.
- If such egg develops as a normal zygote, the hybrid acquires a capacity to clonal reproduction.

Darevskia armeniaca

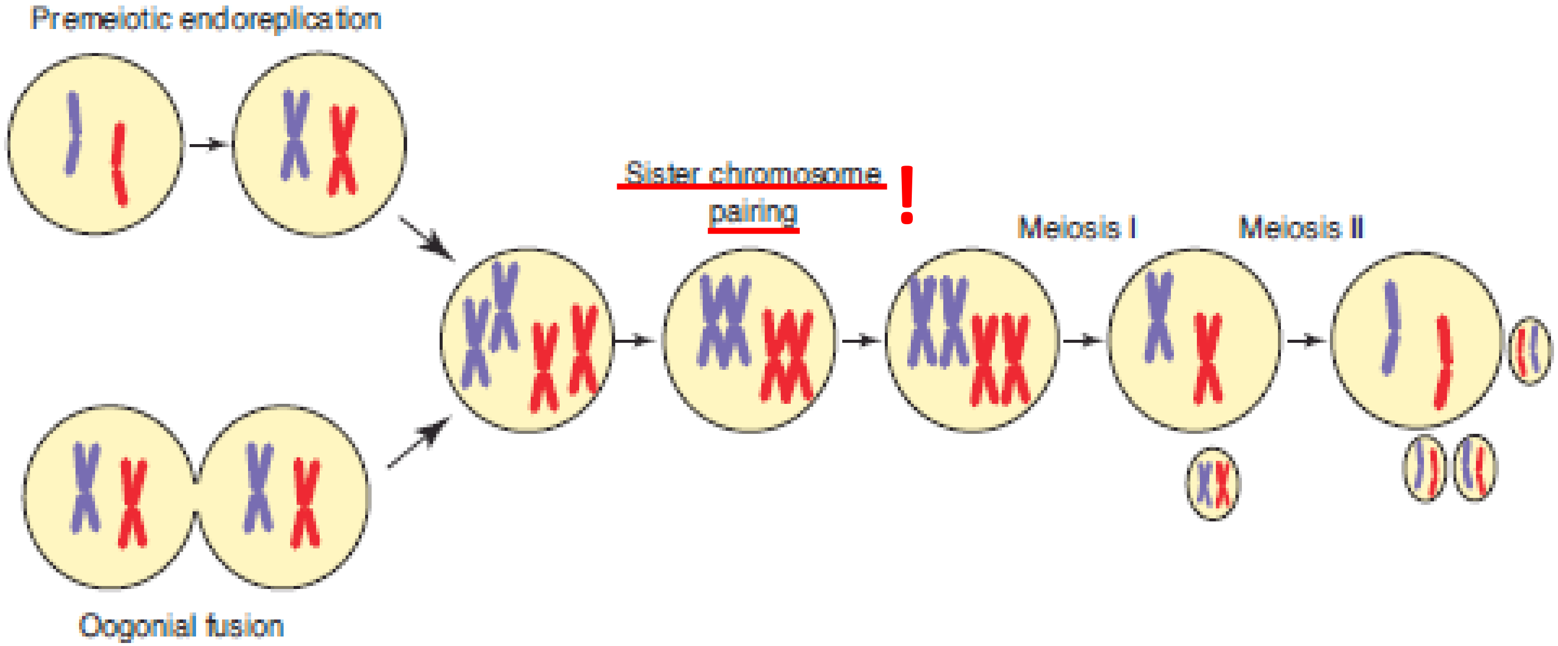
Mechanisms of unreduced egg formation

- Apomixis in *Poecilia formosa*:
  - 2n=46 univalents, no pairing and recombination
  - Leptotene, zygotene, pachytene, lampbrush stage present
  - Cleavage of sister chromatids as in mitosis

Poecilia formosa

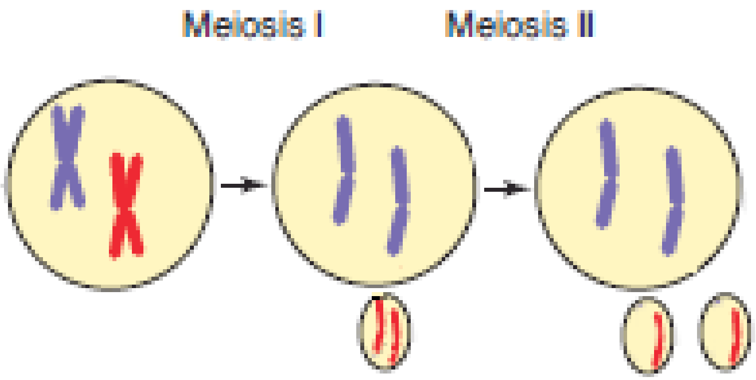
Mechanisms of unreduced egg formation

- Endoreplication or oogonial fusion followed by quasi-normal meiosis of tetraploid cell.
- Present in most natural systems.

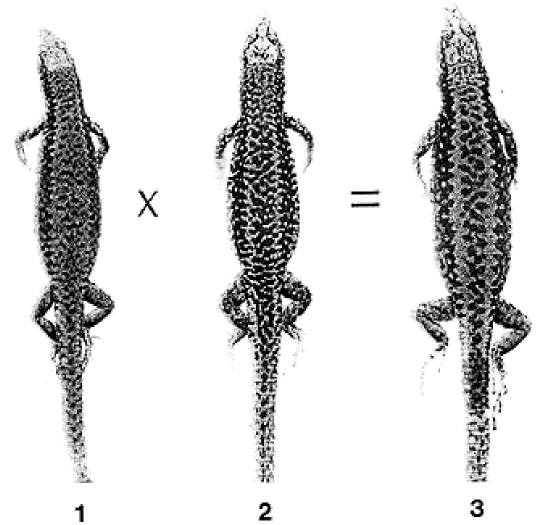


Mechanisms of unreduced egg formation

- Skipping the meiosis II, or fusion of an egg and second polar body.
- Present in some cases of spontaneous reptilian parthenogenesis.

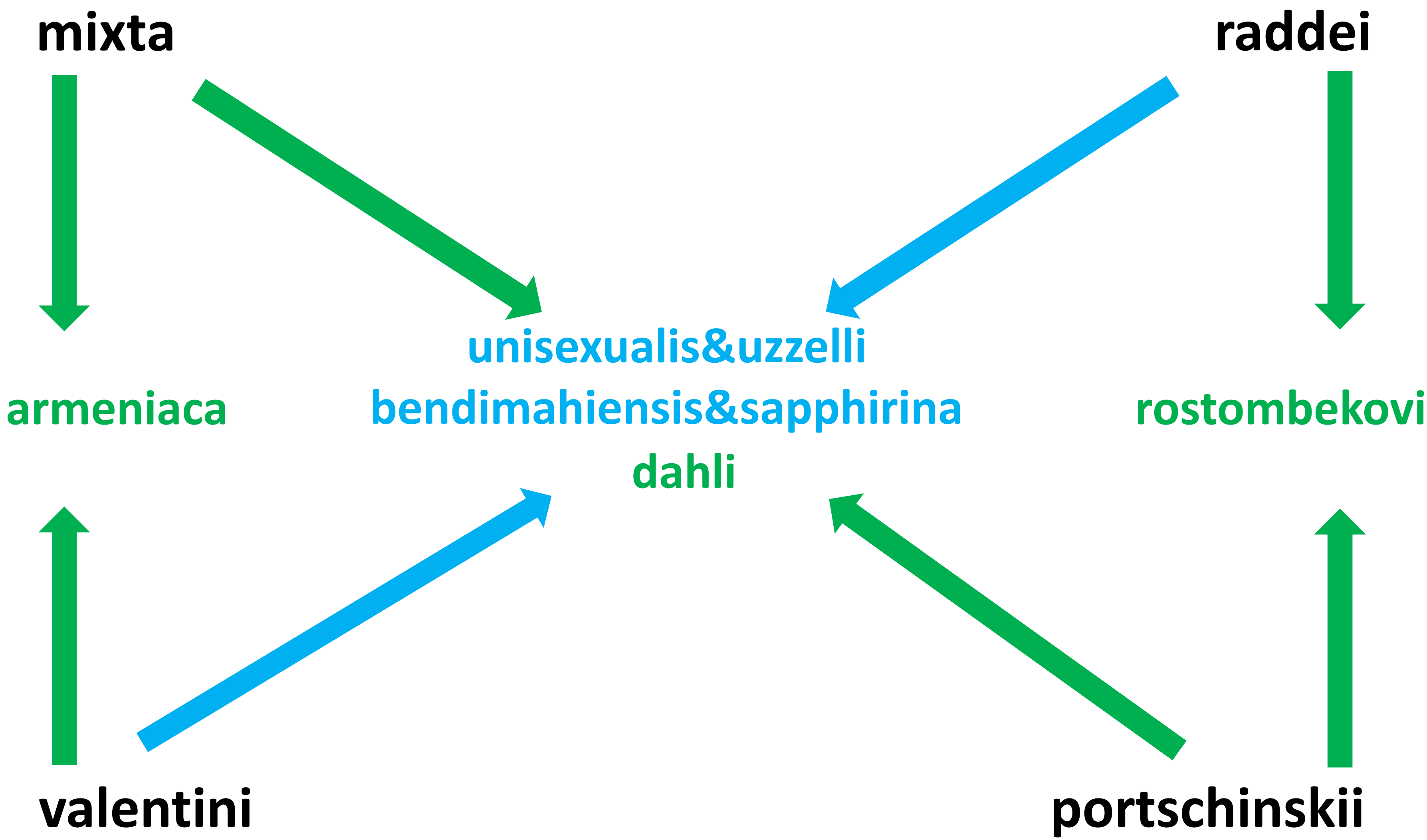


Parthenogenesis: a case of *Darevskia*



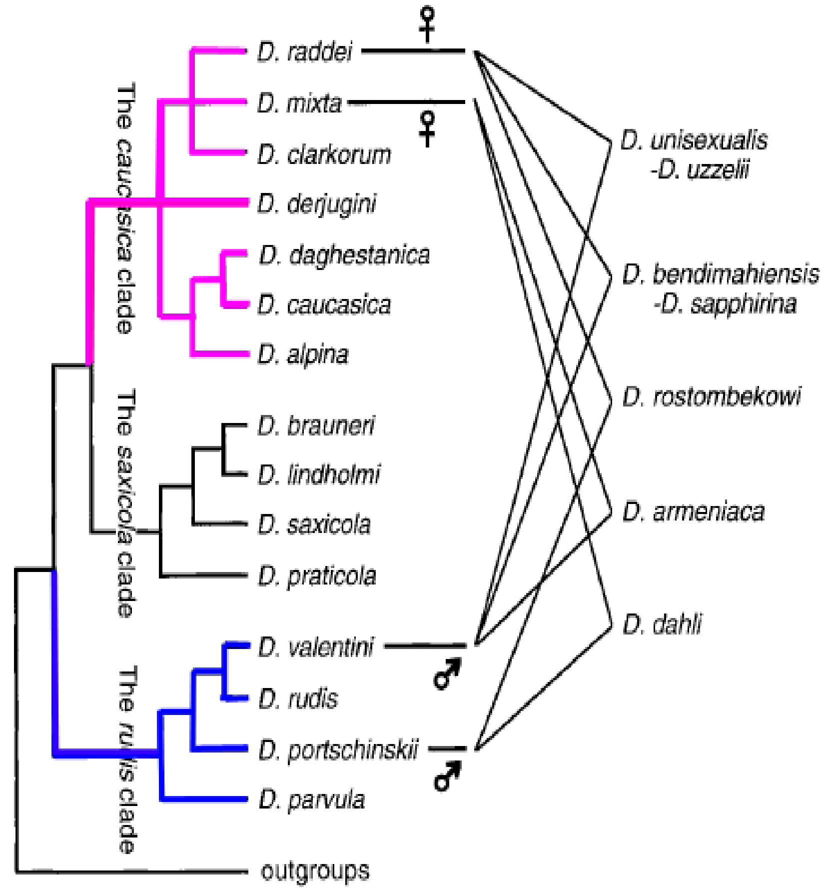
I. S. Darevski (1924-2009)

The phylogenetic origin of unisexual *Darevskia*

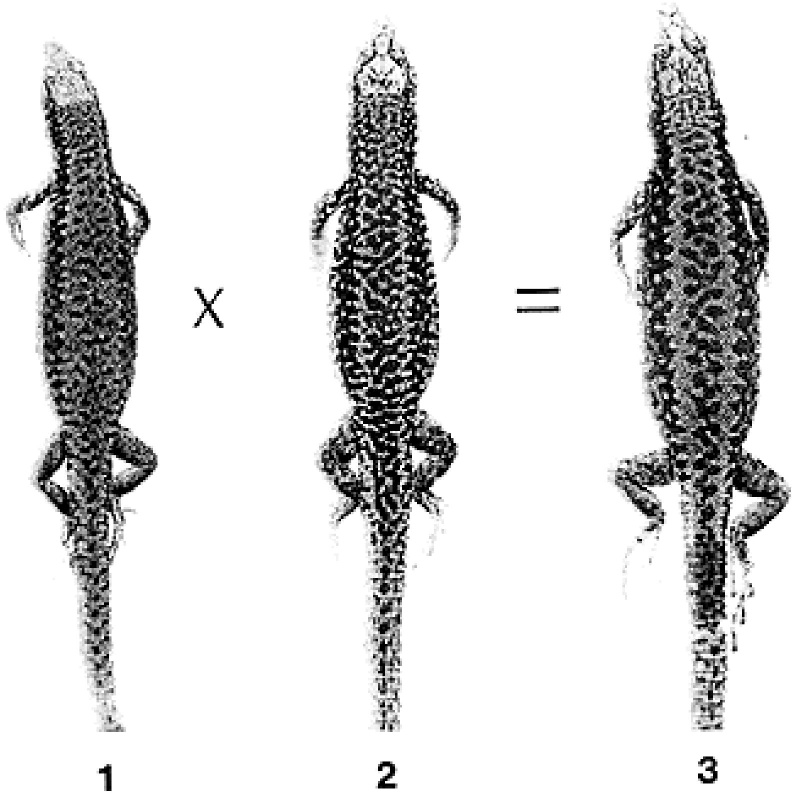


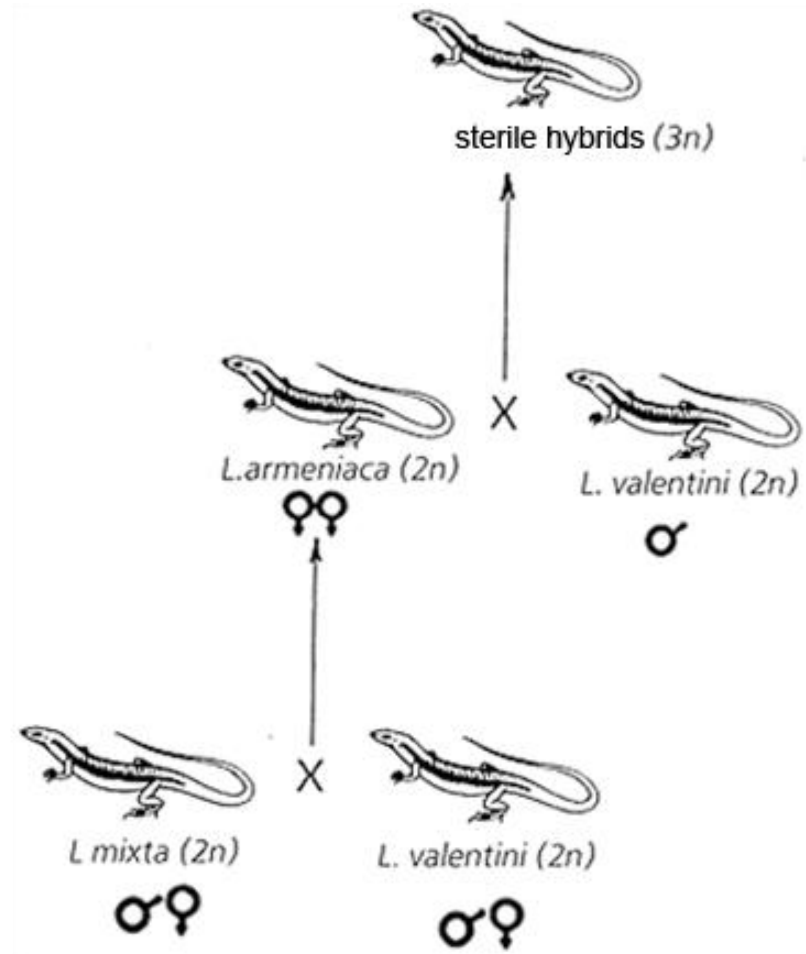
The phylogenetic origin of unisexual *Darevskia*

Darevskia unisexualis



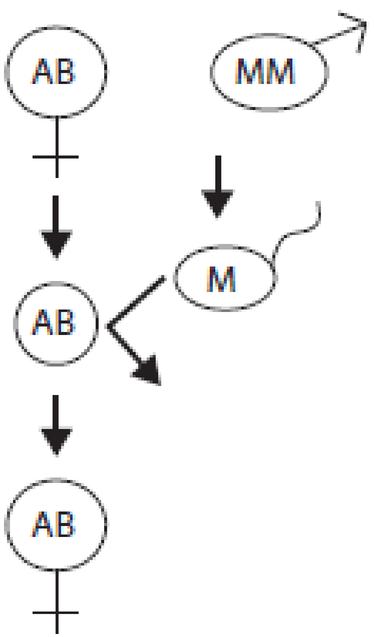
Triploidy in *Darevskia*





Gynogenesis

- Amphibian and fish eggs need to be activated by sperm prior to development.
- Unisexual fish and amphibians must be sympatric with one of the parental species.



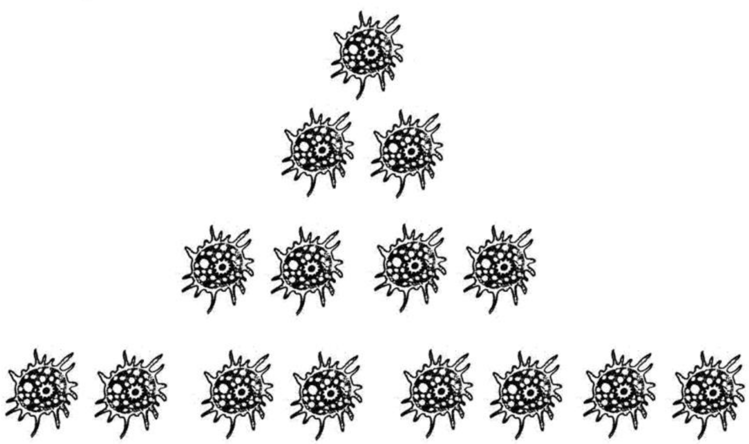
Poecilia formosa

Evolution of clonal lineages

+

two-time higher fecundity

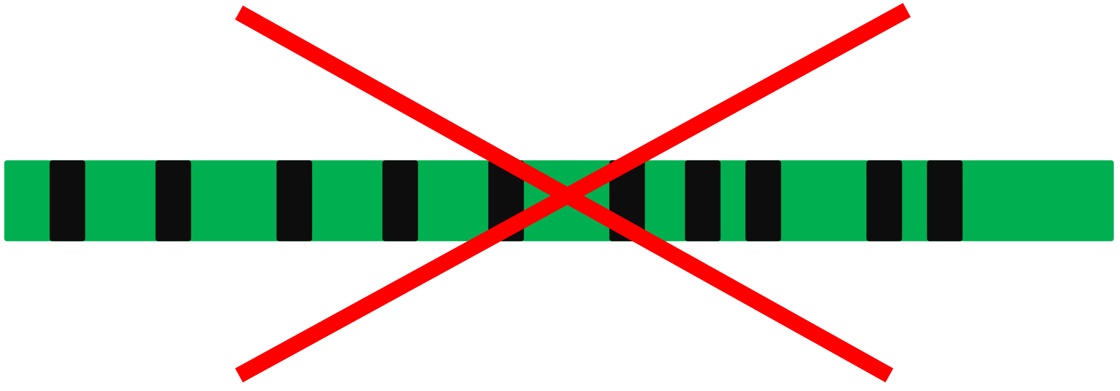
no intraspecific competition



Evolution of clonal lineages

-

Muller's ratchet

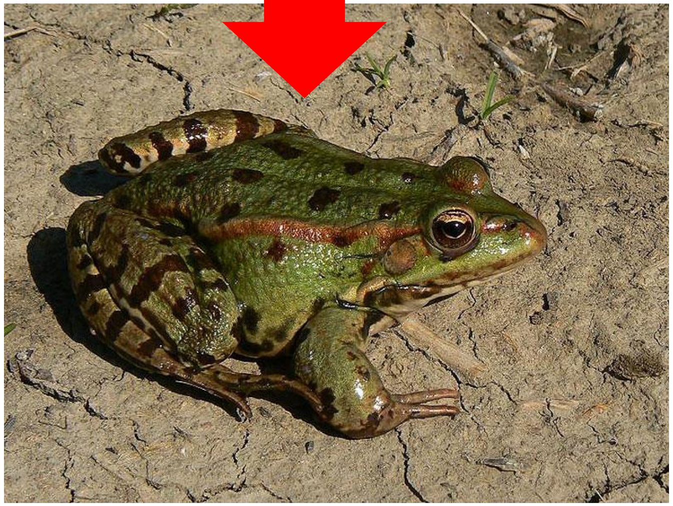


10^5

Escaping the Muller’s ratchet: hybridogenesis

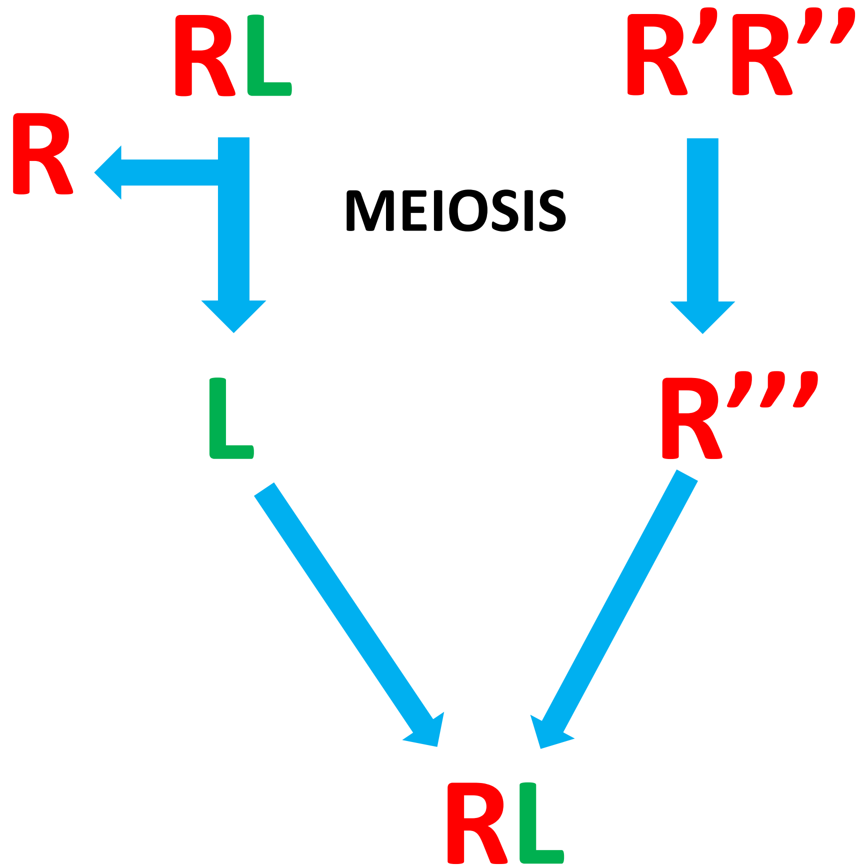
Rana ridibunda

Rana lessonae



“Rana esculenta”

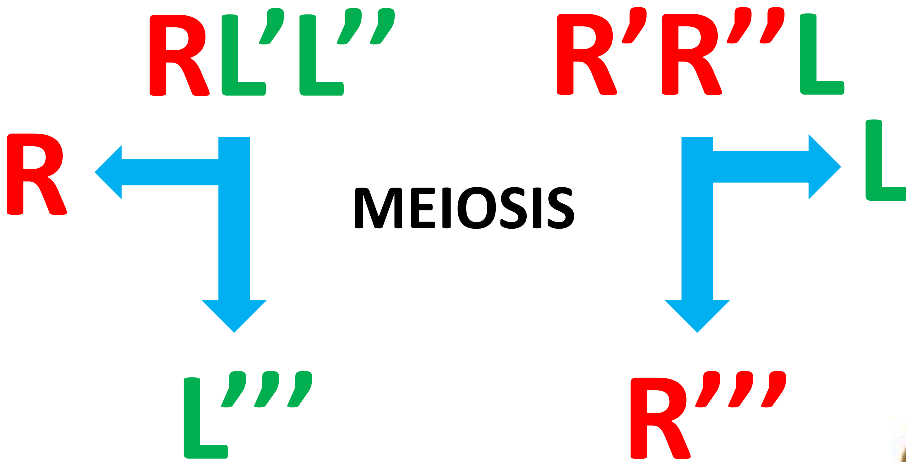
The simplest *R. esculenta* hybridogenetic system

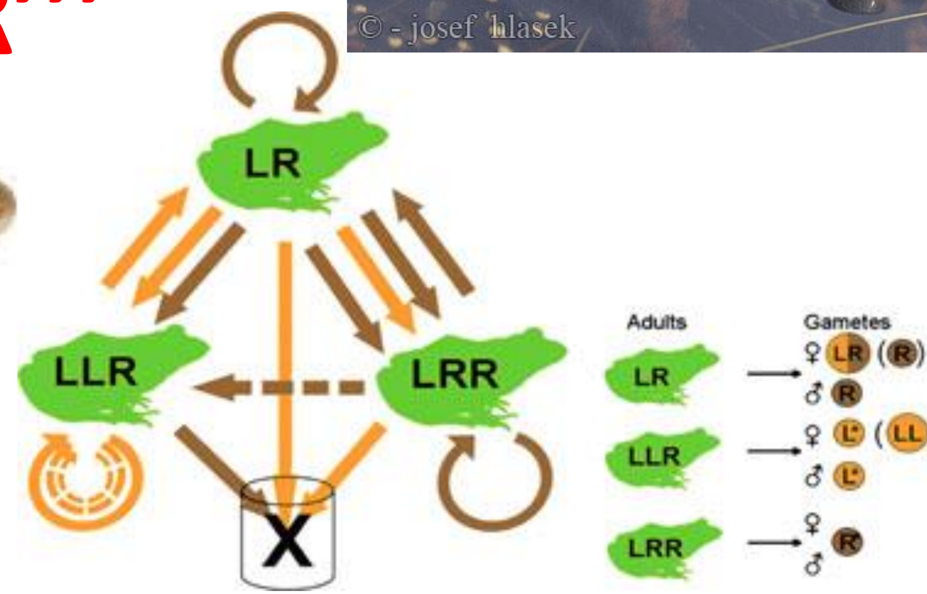


Independent genome segregation
Genome exclusion

Rana esculenta is a genomic parasite

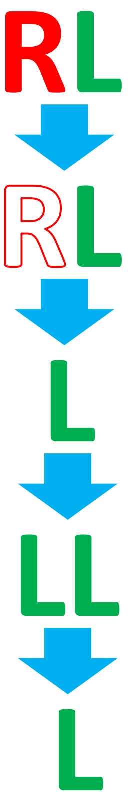
More complex *R. esculenta* hybridogenetic systems





Mechanism of genome exclusion in *R. esculenta*

- Somatic tissue
- Gonadal tissue
  - R inactivation
  - Chromosome by chromosome R loss in mitotic divisions
  - Haploid L oogonia proliferation
  - L duplication
  - Meiosis



Bufo viridis complex

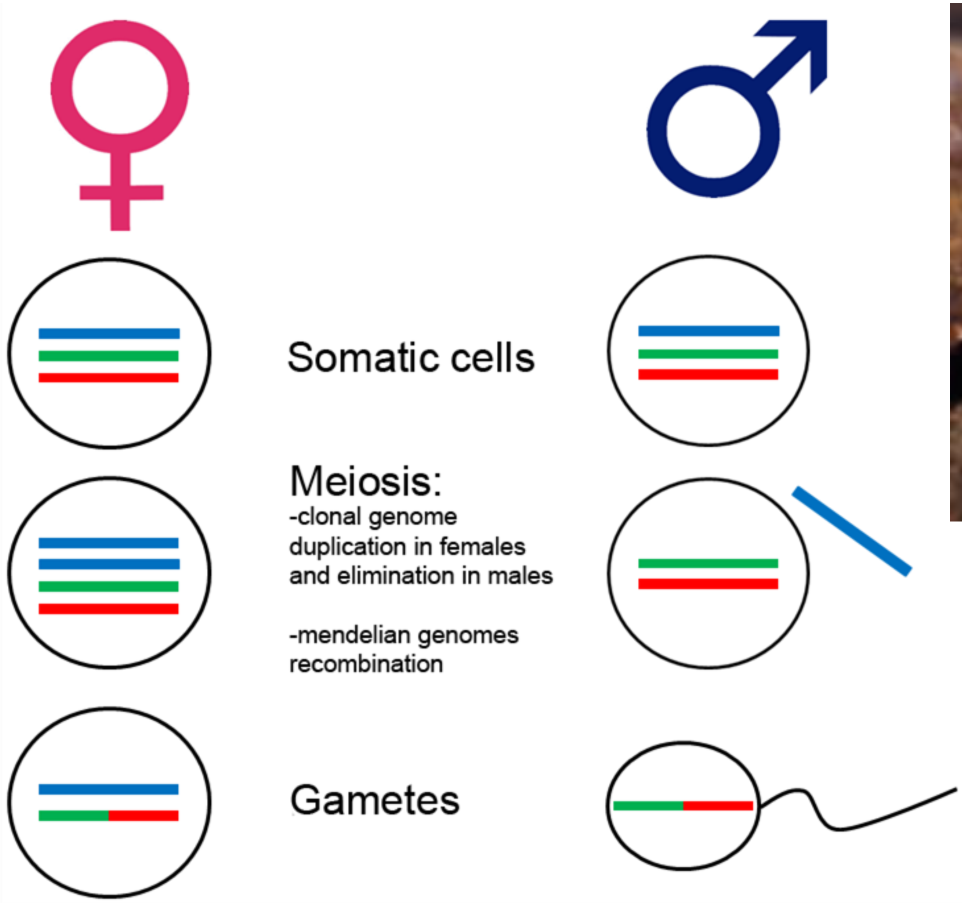
- A variety of 2n species and 3n and 4n hybrids

Bufo viridis (2n)

Bufo baturae (3n)

Bufo pewzowi (4n)

Bufo baturae: a sexually reproducing all-triploid vertebrate



Stöck et al., 2002 **Nature Genetics**

Ambystoma: the most complex hybridogenetic system known

- Species involved, from left to right (Bogart et al, 2007):
  - A. jeffersonianum
  - A. tigrinum
  - A. laterale
  - A. texanum
  - + A. barbouri (Bogart et al., 2009)

Unisexual *Ambystoma*

- Ploidy levels: 2n, **3n**, 4n, 5n.
- Genomic constitution:
  - LJ, LJTx, JLL, JJL, LJTx, LTgTx…
  - LLLJ, LJJJ, LJTgTx…

????

Kleptogenesis: a new reproductive mode for eukaryotes

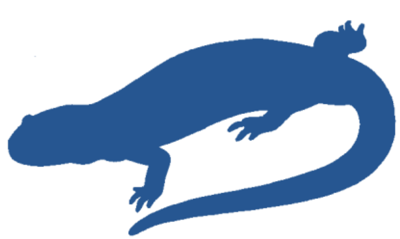
LJJ x JJ system

Eggs may be unreduced or, rarely, reduced, but the L genome is never excluded:

LJJ LJ

Each type of egg may develop gynogenetically:

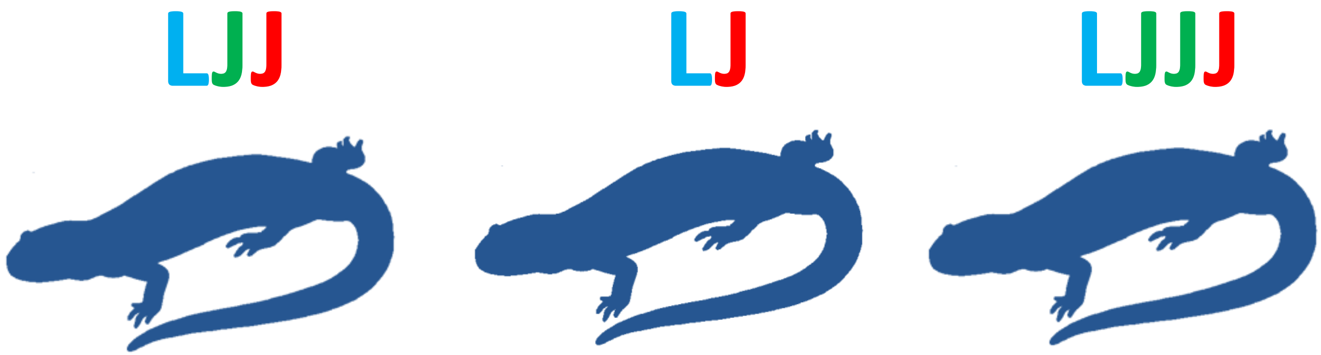
LJJ



LJ

Kleptogenesis: a new reproductive mode for eukaryotes

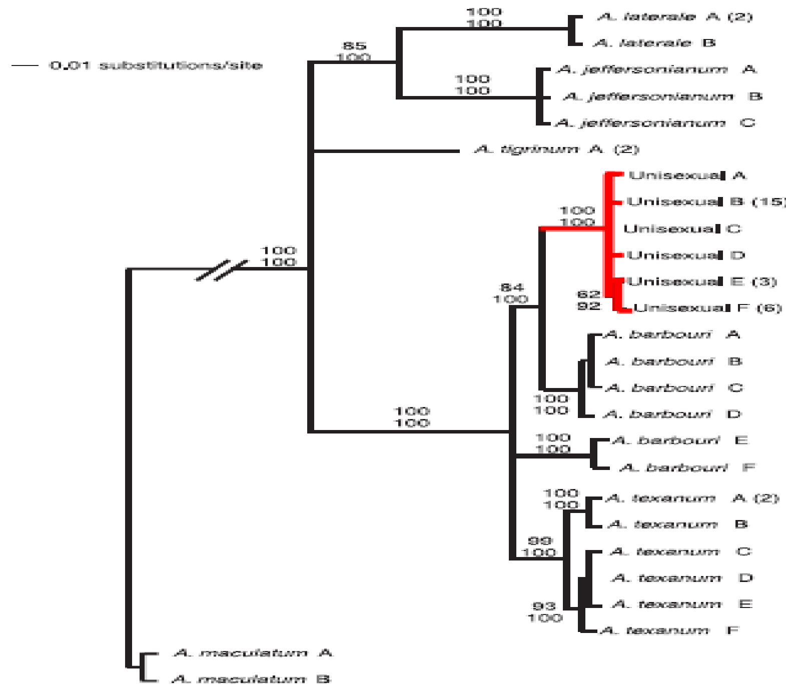
Or be fertilized with or without genome replacement:



Thus, there are no old clonal genomes. The genomes are shifted every several generations.

The origin of unisexual *Ambystoma*

All unisexual *Ambystoma* originate from a single *A. barbouri* female, which lived 2,4-3,9 MYA.



A. barbouri is not involved in most present systems!

Evolutionary perspectives of hybridogenetic lineages

- *R. esculenta* systems may be stable and independent due to the presence of triploids, which produce recombinant R and L genomes.

Evolutionary perspectives of hybridogenetic lineages

- In *B. baturae*, a clonal genome even does not have its own carrier. As it does not recombine, it may degenerate and be lost, making *B. baturae* a normal diploid.

Evolutionary perspectives of hybridogenetic lineages

- Unisexual *Ambystoma* may succeed and persist for millions of generations, but these are obligate genomic parasites and can not exist without host species.

Unanswered questions and research perspectives

- What are the mechanisms of independent genome segregation?
- What are the mechanisms of multiple parallel origin of parthenogenetic hybrids in the same lineages?