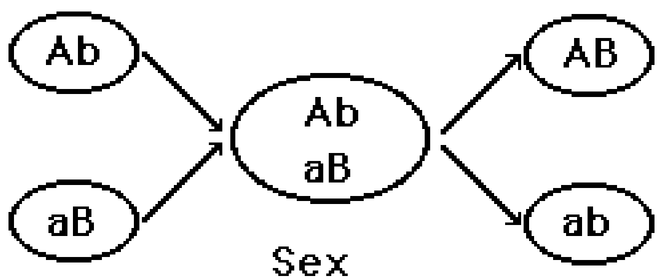
EVOLUTION OF SEX

Three questions:

1. Origins: How did conjugation, transformation, and transduction arise? How did sex with meiosis arise? VERY hard problem, no present-day taxa with obvious intermediate stages. Will require resolving base of trees, complete genomes to trace meiosis genes, detailed study of genetics of groups where mechanisms of mitosis and meiosis and syngamy are vague. Not covered.
2. Evolution of variants on sexual and asexual life cycles … e.g. parthenogenesis vs. sex, monoecy vs. dioecy, selfing vs. outcrossing … is large and active field of evolution, especially in plants. Not covered.
3. Evolutionary consequences of losing sex in eukaryotes. Our focus.

Sex



- Sex = putting genes from two different individuals into one and producing recombinant genotypes.

Genetic Consequences of Sex

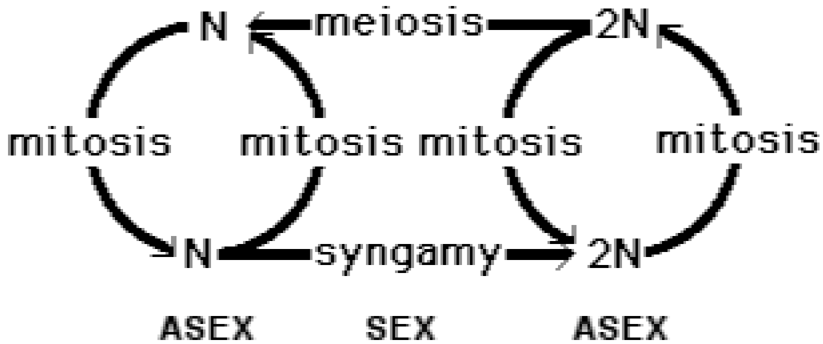
Meiosis has two effects:
- Segregation of alleles at each locus
- Recombination of alleles at two or more loci

Sex with outcrossing has two effects:
- Reduces linkage disequilibrium by combining alleles from different loci randomly to produce multi-locus genotypes
- Produces heterozygotes in diploid cells, while inbreeding produces homozygotes

Sex in Prokaryotes

It happens and can involve outcrossing: conjugation, transformation, transduction

Eukaryotic life cycles



Definition(s) for Eukaryotes

- Sex = syngamy followed by meiosis and recombination
- Sexual reproduction = sex in the course of reproduction
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Sex with outcrossing
- Amphimixis = meiosis and syngamy with at least some outcrossing → linkage equilibrium, heterozygosity

Sex with inbreeding (clonal reproduction)
- Selfing = meiosis and syngamy involving only one individual
- Automixis = meiosis with diploidy restored by fusion of two haploid products of same division or by duplication of one haploid genome

Asex
- Apomixis = reproduction by mitosis only → linkage disequilibium
- Asexual reproduction = one individual or cell produces progeny without sex

Varieties of Asexual Reproduction.

Single cells: Mitotic cell division
Multicellular organisms (e.g.)
- Binary fission
- Budding
- Parthenogenesis (via egg): apomixis or automixis

Sex is a Quantitative Trait

The effectiveness of sex is a function of
- frequency of sexual reproduction
- recombination frequency
- amount of outcrossing

Linkage equilibrium (gametic): in obligately sexual population with random mating population and allele frequencies $f(A) = p$, $f(a) = q$, $f(B) = r$, $f(b) = s$, the genotype frequencies are $f(AB) = pr$, $f(Ab) = ps$, $f(aB) = qr$, $f(ab) = qs$.

Linkage disequilibrium is deviation from equilibrium, due to linkage, mutation, random drift, selection, etc.

Variation Among Organisms

- Majority of organisms reproduce asexually a majority of the time.
- Some reproduce only asexually. (But this is hard to prove.)
- Some reproduce only sexually, but these are multicellular organisms in which the individual reproduces sexually while the cells reproduce asexually (except at end of germ line).

Evolutionary History of Meiotic Sex

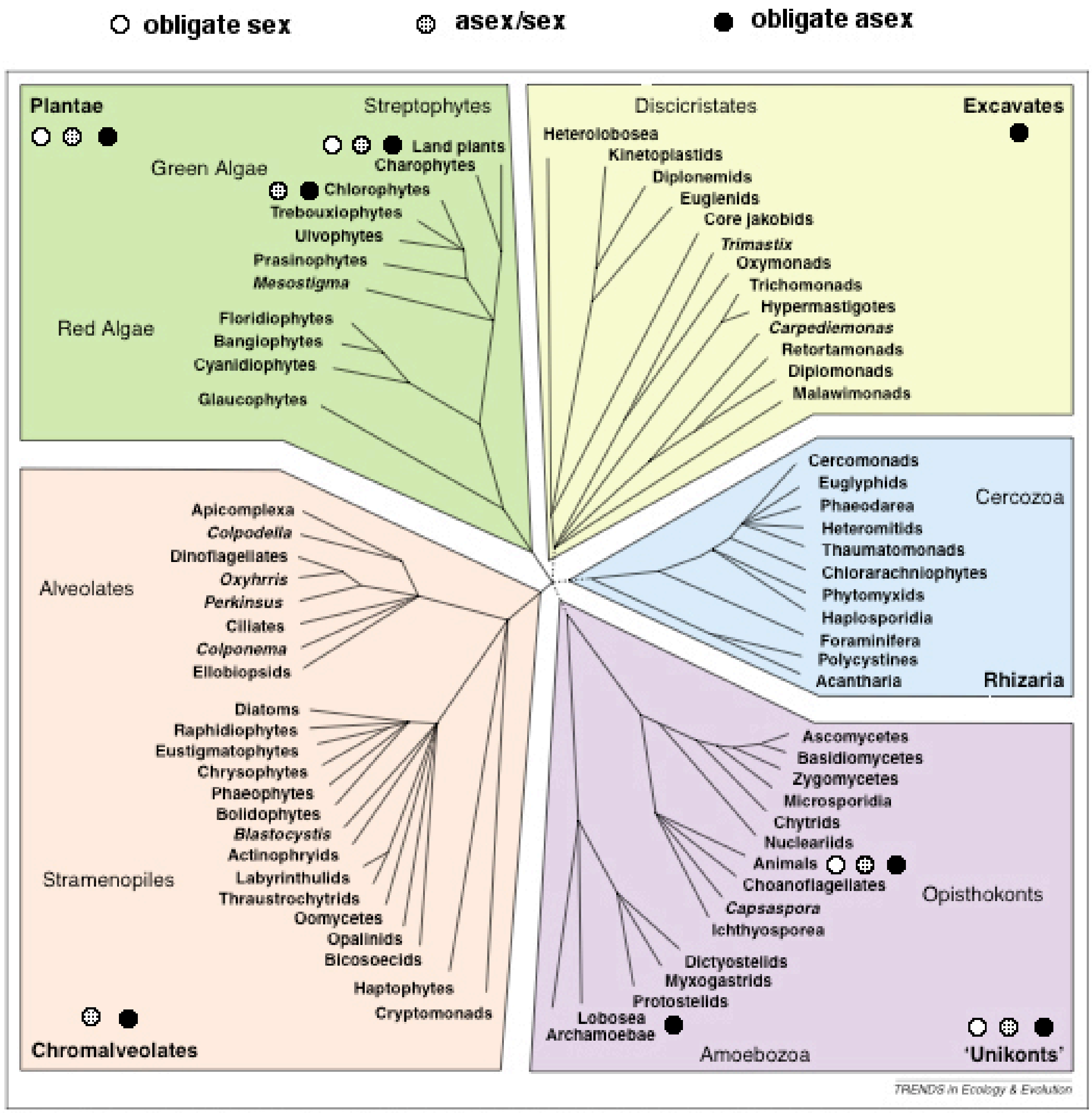


Figure 1. A tree of eukaryotes. The tree is a hypothesis composed from the various types of data discussed in the text, including molecular phylogenies and other molecular characters, as well as morphological and biochemical evidence. Five 'supergroups' are shown, each consisting of a diversity of eukaryotes, most of which are microbial (mostly protists and algae). Relationships are left unresolved (i.e. where several branches emerge simultaneously) when there is little or no evidence for the branching order. Other branches are shown dotted when there are only preliminary indications for this relationship. A handful of 'orphan' genera and two groups, Apusazoa and centrohelid Heliozoa, are not shown. There are few data from these organisms and they are not yet associated with any of these groups.

Alternating asexual reproduction by mitosis and sexual reproduction by meiosis is probably primitive, unless Excavates are basal. Most or all cases of obligate asexual organisms are cases where sex was lost secondarily.

Organelle Genomes are Usually Asexual

- Even in organisms that reproduce sexually, organelle genes are often inherited largely or entirely from only one parent (uniparental inheritance).
- In some cases where inheritance is biparental, recombination between genomes from different parents is limited.

Lose sex by:
- Loss of sex due to mutation probably most common in organisms with alternating sex/asex but may also be possible in obligate sexuals
- Hybridization and/or polyploidization in sexual animals and plants

Mutational Pressure Favors Asex

- Loss of sex due to mutation, polyploidization, and hybridization is common (except in mammals and birds, where imprinting makes it impossible) and quickly becomes irreversible due to additional mutations. S – u -> A
- Asexuals accumulate, eventually no sexuals.

Hasn't happened. Conventional wisdom:
- Most organisms reproduce sexually at least part of the time.
- Most strictly asexual lineages are twigs on the tree, with few deep branches.

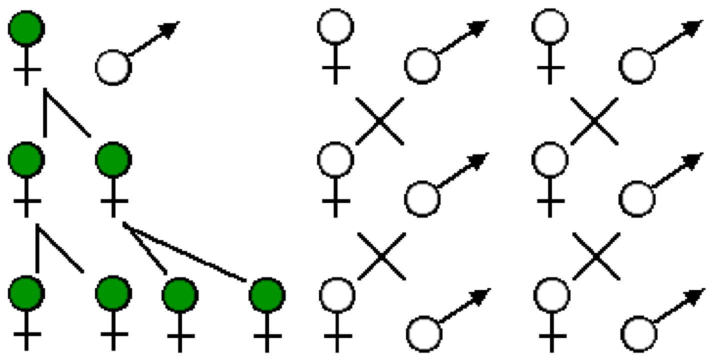
Problems:
1. Based mainly on opisthokonts and plants.
2. Few quantitative data on ages of asexuals.
3. How can we know that a species isn't having furtive, cryptic, or rare sex?

Nevertheless, the conclusion that compared to sexuals, asexual lineages are on average uncommon, short-lived, and not very speciose is probably correct for animals and plants.

Two levels of selection:

1. Asexual mutant must be fixed in population or establish a new population to produce an asexual species.

  - Asexual mutants are good colonizers, establish new populations. Asexuals over-represented among colonizing plants.
  - Asexuals can also displace sexual members of species. Mergeay (06 ProcRoySocB 273:2839): asexual *Daphnia pulex-D. pulicaria* hybrid introduced from America to Africa displaced native African *D. pulex* throughout its range. Did so in spite of "absence of genetic variation".
    - Asexual mutants have advantage because asexual reproduction is faster.
    - An oogamous organisms, asexual mutants have as much as two-fold advantage:



2. Asexual species must survive and speciate.
- Good colonizers speciate better.

This is NOT group selection, which is selection for a group within a subdivided population. Discredited specifically as explanation for origin of traits that benefit a group but are detrimental to individuals. Confusion: many people thought this meant all cases of selection above individuals are impossible … except evolutionary advantage of sex. Group selection might be involved but not necessarily.

Sex must provide compensating advantage(s) at level of individual or at level of species.

- Individual level: probability of fixation of new mutation
- Species level: net speciation rate = speciation rate – extinction rate

Some early history:

August Weismann 1889-1904 Amphimixis is source of individual variation on which natural selection can act. Brings together advantageous as well as detrimental "variations", i.e. produces new genotypes, and natural selection eliminates the less fit ones.
Problem: Mutation as well as recombination is a source of variation in genotypes. In principle mutation can produce as the same genotypes as recombination, albeit slower and less efficiently.

A. H. Sturtevant, H. J. Muller, R. A. Fisher, J. B. S. Haldane, Jim Crow, John Maynard Smith, Graham Bell, Bill Hamilton, Alex Kondrashov, et al. produced variety of hypotheses about evolutionary advantage of sex. Some predicted advantage to sex, some to asex. Joe Felsenstein introduced some order and unification.

Most General Statement About Evolutionary Advantage of Sex

Natural selection works better with sex, which facilitates
- elimination of detrimental mutations
- fixation of advantageous mutations

Evolutionary disadvantages of losing sex:

- accumulate more detrimental mutations → earlier extinction (Muller's ratchet leads to mutational meltdown)
- lose more advantageous mutations by drift →
  - less able to adapt to changing environments → higher rate of extinction
  - less able to adapt to new environments → lower rate of speciation

Simplistic example: consider two loci with two alleles: A1 and B1 are advantageous, A2 and B2 are detrimental. In asexual population, starting with genotype A1 B1, mutations occur (usually in different individuals), producing genotypes A2 B1 and A1 B2. Now selection against A2 is confounded by selection for B1, and selection against B2 is confounded by selection for A1.

Experimental Studies

Real-time lab experiments:
- Goddard et al. (2005 *Nature* 434:636-640): yeast adapt more effectively to harsh environment (37°) when they are reproducing sexually.
- Colegrave, Katz, and Bell (2002 *Evolution* 56:14 and 1743; *Nature* 420:664) experiments with Chlamydomonas showed that the rate of adaptation to a novel environment and the variance in fitness was increased by sexual reproduction.

.Evolutionary experiments:

- Lynch $$: Organelle genes have higher Ka/Ks than nuclear genes in same organisms (animals, fungi, plants)
- Paland and Lynch (2006 *Science* 311:990-992) *Daphnia pulex* asexual lineages have higher Ka/Ks than sexual lineages. Lineages appear young, maybe within species.
- Nonrecombining regions of chromosomes in otherwise sexual organisms have accumulated more detrimental mutations measured by K_a/K_s.
- Asexual bdelloid rotifers show similar K_a/K_s ratio to sexual monogonont rotifers, hence no evidence for accumulation of detrimental mutations without sex: Mark Mark Welch & Meselson (2000 *PNAS* 98:6720) nuclear genes; Birky et al. (2005 *Hydrobiologia* 546:1) mitochondrial genes. Why?
  - Compensating substitutions? No, because those would show up in K_a.
  - Lower u? Not for nuclear genes; probably not for mito genes.
  - Higher N_e due to larger N? No, mitochondrial $N_e u$ similar or smaller in bdelloids.
  - We see mainly lucky survivors that haven't accumulated many detrimental mutations?

Ancient Asexual Scandals?

Judson and Normark (1996) "Ancient asexual scandals" *TREE* 11:41-45.
Listed animals, plants, and fungi believed to be obligate asexuals and "ancient" (≥ 1 My old). Claims these "challenge current theories of sex" as well as data showing most asexual species are short-lived.

Problems:

1. Data showing most asexuals are short-lived is based mainly on their being mostly species or genera, not higher taxa. But

- Species often ill-defined
- Taxonomic level doesn't scale well with age.

2. No evidence that "ancient asexuals" are outliers on the frequency distribution of ages of asexuals.

3. Time to extinction due to Muller's ratchet depends on mutation rate to detrimental, mutations, distribution of selection coefficients of detrimental mutations, and census and effective population sizes. None of these is well-known for any asexual group.

Ecological and Other Factors

There are numerous other factors that may iintervene to make asexuals more or less successful. Most of these will be limited to taxa with a particular life style or in a particular environment, or subject to certain kinds of accidents such as the invasion of a selfish detrimental genetic element. However, they may make a big difference in specific cases.

SUUMMARY

- Primitive eukaryotic life cycle was probably alternating asexual and sexual reproduction.
- Loss of sex via mutation, polyploidization, or hybridization is common, largely irreversible, and often selectively advantageous at the individual level.
- Sexual reproduction is maintained by advantages at the species level. Loss of sex makes natural selection less effective, increasing the rate of extinction and decreasing the rate of speciation.