Origins of Sexual Reproduction

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What is sexual reproduction?
What is sexual reproduction?

Summary

- what is sexual reproduction?
- the historical sequence
  - bacterial 'mitosis'
  - bacterial recombination
  - mitosis
  - syngamy
  - meiosis
  - mating types
  - anisogamy
The historical sequence

- sexual reproduction involves many different phenomena
- the historical sequence of evolutionary events probably was
  - asexual reproduction (binary cell division, mitosis)
  - limited recombination in bacteria
  - syngamy (fusion between genetically dissimilar cells)
  - meiosis (separation of genetic material, with segregation and recombination)
  - mating types
  - anisogamy, sexual selection, and gender differences
- when we think about sexual reproduction, we usually think of organisms that have gone through this entire sequence of events
- but this does not help us to understand where the origins of sexual reproduction are

Bacterial ‘mitosis’

- cell division by bacterial ‘mitosis’ in prokaryotes

from Fogel & Waldor 2006
Bacterial recombination

- plasmids can be transferred from one bacterium to another during bacterial conjugation
- the ability to fuse with other cells often stems from the exchanged genetic material itself
- could bacterial conjugation be of parasitic origin?

![Diagram of bacterial conjugation process](image)

Mitosis

- cell division by mitosis in diploid eukaryotes

![Diagram of mitosis process](image)
Syngamy

• during syngamy two haploid cells fuse completely
• this brings together genetic material (and information) of two (usually) different individuals
• requires a process that allows this information to be separated again in a coordinated and fair way

Meiosis

• a direct comparison between meiosis and mitosis
Did syngamy or meiosis evolve first?

- endomitosis and one-step meiosis occur in some single-celled eukaryotes
  - advantageous in variable environments
    - diploidy may facilitate DNA repair
    - haploidy may allow faster growth
  - one-step meiosis may use repair mechanisms
    - initially, the resulting recombination probably offered little advantage

DNA repair and recombination

- DNA repair of double-strand breaks uses mechanisms that are similar to those used during DNA recombination
- such repairs either lead to gene conversion (non-crossover) or to recombination (crossover)
- so recombination may have originated from DNA repair

FIGURE 3. The double-strand break repair model. Recombination is initiated by a double-strand break in one chromatid, called A, which is enlarged by exonucleases so as to form a gap with 3’ single-stranded ends (1). One of the free 3’ ends then invades a homologous region on the other intact chromatid, called B, forming a small joint molecule (2). This joint molecule will be enlarged by repair synthesis (dashed lines) primed by the invading 3’ end, it may then reach a length larger than the size of the gap (3). This process partially regenerates chromatid A as a single strand at the gap site (4). Repair synthesis can now fill the gap, using the 3’ end as a primer. Thus, a double-stranded gap can be repaired by two rounds of repair synthesis. (After Szostak et al., 1983)
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- syngamy evolves
  - maybe due to advantage of hybrid vigour (heterosis) or selfish genetic elements
  - here, recombination may offer advantages

from Maynard Smith & Szathmáry 1995
Selfish genetic elements and the evolution of sex

- In an asexual species, a selfish genetic element (SGE) can only spread within the genome of its current host
  - Harming the host is also bad for the SGE itself
- The SGE benefits from inducing its host to fuse with another cell
  - And to thereby spread to the other cell's previously uninfected genome
- The resulting diploidy may actually be good for the fused host cells, because it allows DNA repair and can lead to heterosis
- But the SGE only benefits if the host cells eventually divide again
- And division may also allow the host to get rid of mutations
  - Via segregation and recombination
- SGEs may have been important at the origin of sexual reproduction
  - But they are probably not responsible for its current maintenance

Meiosis: segregation and recombination

- Segregation increases with chromosome number (but recombination also works)
- Chromosome number varies dramatically
  - E.g., from $n=1$ in *Parascaris* nematodes to $n=127$ in *Eupagurus* hermit crabs
- Taxa with uniform chromosome numbers
  - E.g., $n=13$ in most dragonfly species and $n=18$ in most snake species
- Taxa with variable chromosome numbers
  - $2n=7$ in males and $2n=6$ in females of *Muntiacus muntjac vaginalis* and $2n=46$ in *Muntiacus reevesi*

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15 following Hickey & Rose in Michod & Levin 1988

16 from Stearns & Hoekstra 2005
Did syngamy or meiosis evolve first?

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  - Advantageous in variable environments
    - Diploidy may facilitate DNA repair
    - Haploidy may allow faster growth
  - One-step meiosis may use repair mechanisms
    - Initially, the resulting recombination probably offered little advantage

- Syngamy evolves
  - Maybe due to an advantage of hybrid vigour (heterosis) or selfish genetic elements
  - Here, recombination may offer advantages

- Two-step meiosis evolves
  - May limit the spread of sister-killer alleles

Sister-killer alleles

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Maynard Smith & Szathmáry 1995

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Following Haig & Grafen 1991
Sister-killer alleles

2-step meiosis

1-step meiosis

kill here

or kill here

reductional division (no recombination)

or

equational division (with recombination)

following Haig & Grafen 1991

So much has already happened and still no real ‘sex’

- mitosis
- two-step meiosis
- segregation and recombination
- syngamy
Mating types

- Initially gametes were probably isogamous and could fuse with all other conspecific gametes (including self gametes)
  - But if the aim is to exchange genes, then selfing is not helpful
- This may have selected for the evolution of an incompatibility system based on mating types
  - Avoid fusing with yourself by avoiding to fuse with cells that carry the same mating type
- Having many mating types would allow fusing with gametes from many partners
- But surprisingly, we often find that there are only two mating types (usually called plus and minus)
  - This means that every second cell one encounters is an unsuitable fusion partner!

Mating types

- Genomic conflict with cytoplasmic genetic elements, such as mitochondria and chloroplasts, may explain why there are often only two mating types
- A possible solution is uniparental inheritance of these cytoplasmic genetic elements
  - Usually only from one mating type
- For example, in *Chlamydomonas* the mitochondria are inherited by the ⊖ and chloroplasts are inherited by the ⊗ mating type

Modified from [http://biodidac.bio.uottawa.ca](http://biodidac.bio.uottawa.ca)
Mating types

• a simple route to evolving two mating types

![Diagram showing the evolution of mating types](image)

Fig. 9.4 The origin of + and − mating types (after Hoekstra, 1987). (a) Gene A specifies a surface protein not concerned with cell fusion. (b) Gene B specifies a protein causing cell fusion: any cell will fuse with any other. (c) Loss mutations, $A \rightarrow a$ and $B \rightarrow b$, produce two mating types, each of which will fuse only with the other (or with the ancestral $AB$, while that still exists). At this stage there will be selection for tight linkage between loci $A$ and $B$, because recombinant $ab$ genotypes cannot fuse. During the initial spread of $AB$ and $ab$, there would have to be a selective advantage in not fusing with one’s own type, probably through the covering up of deleterious mutations: there would also be selection maintaining approximate equality of frequency between the two types.

from Maynard Smith and Szathmary 1995

Mating types

• hypotrich ciliates have two kinds of sexual processes
  • conjugation with multiple mating types, but without the exchange of any cytoplasm
  • complete fusion of cells with only two mating types

![Phase-contrast image of a hypotrich](image)
Anisogamy: the origin of male and female

- sexual reproduction involves the fusion between two haploid germ cells to form a diploid zygote
- sex can occur via isogamy or anisogamy
  - from the Greek 'iso-' (=equal), 'anisos' (=unequal), and 'gamos' (=marriage)
- the organisms that we are most familiar with are all anisogamous
- but both types exist even today within, for example, the green algae
  - isogamy is almost certainly the ancestral condition in Eukaryota

modified from http://biodidac.bio.uottawa.ca

Anisogamy: the origin of male and female

- the male sex makes many small germ cells and the female sex makes fewer large germ cells
  - so the ‘male’ and ‘female’ sexes actually only exist in anisogamous species
  - → sexual reproduction does not require the ‘sexes’!!

eggs and sperm of Drosophila bifurca

from Bjork & Pitnick 2006
Anisogamy: the origin of male and female

* evolution of anisogamy
  * disruptive selection can lead to the evolution of a cell type that specialises in swimming (small) and another that specialises in providing energy (large)
  * the next step is selection against fusion between two small cells (because they have low viability)
  * and fusions between large cells are rare (so specialising in such fusions would be disadvantageous)
  * the small cells (or the individuals making them) compete for access to the large cells (or the individuals making them)
  * ➔ sexual selection

**Figure 2.2** Selection on gamete and zygote size.
(a) The gamete size-number trade-off, that results when a constant amount of resource, $R$, is divided between $n$ equal-sized gametes: $4n^2/3 = R/n$. (b) The relationship between zygote fitness and zygote size is assumed in the PBS model (Park et al. 1972), zygote fitness, $W_z = zygote\ size, m_z$. More realistically, the relationship between zygote fitness and zygote size may be (c) sigmoidal, or (d) have zero survival below some finite size, above which survival is decelerating. (We include curves of the form shown in (d) within the expression “more or less sigmoidal” because the consequences for the evolution of anisogamy are qualitatively the same as for a sigmoidal survival curve; Bulmer & Parker 2002.)
Anisogamy: the origin of male and female

- the male sex can be viewed as a parasite of the investment made by the female sex
  - the evolution of anisogamy involves ‘a primordial sexual conflict’ (Parker 1979)
- the evolution of anisogamy also represents the origin of the twofold cost of sex
  - the ‘main’ cost of sexual reproduction only appears after the evolution of anisogamy, so sex initially may not have needed a big advantage

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  - anisogamy
Literature

• Mandatory Reading

• Suggested Reading

• Books