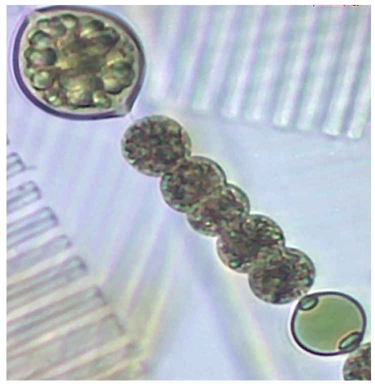
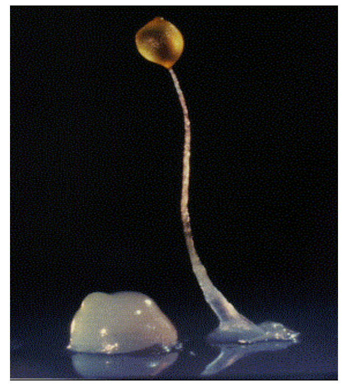
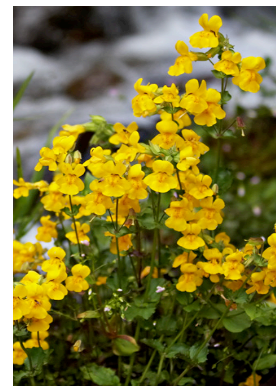
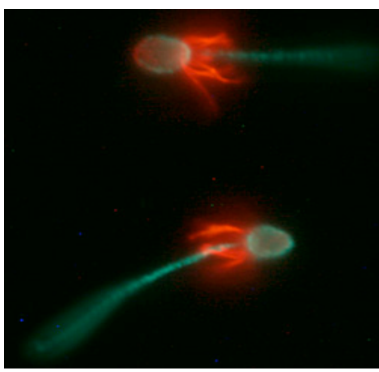
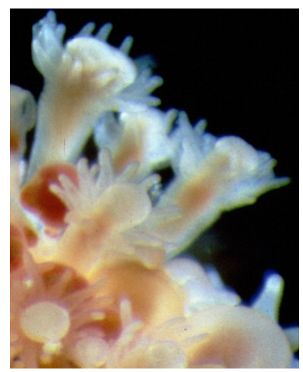
Opportunities for Defection and the Control of Defectors in Developmental and Evolutionary Transitions to Multicellularity


Rick Grosberg
Center for Population Biology
UC Davis

Richard Strathmann
Friday Harbor Labs
University of Washington

The seven major transitions

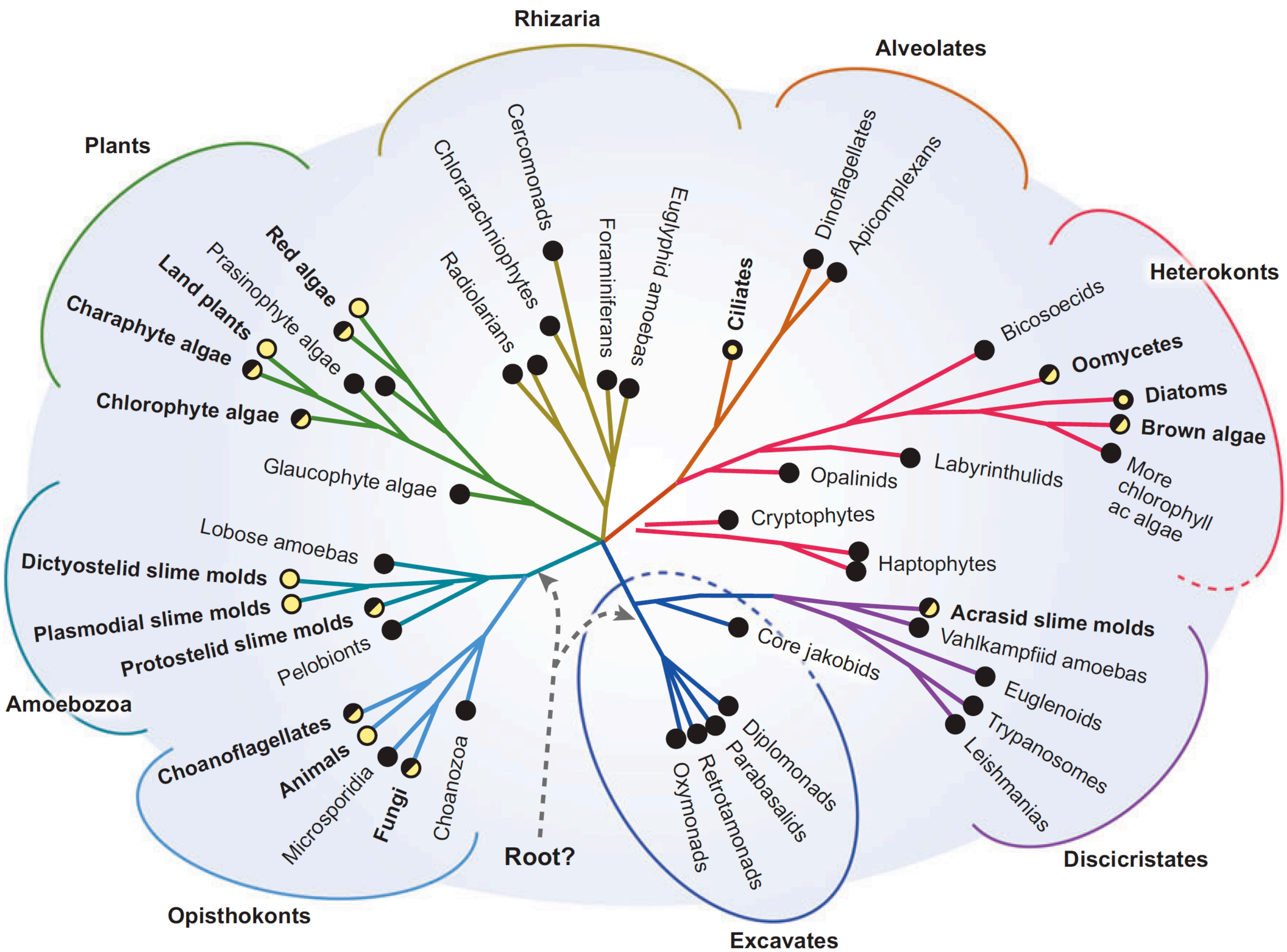
1. Compartmentalization of replicating molecules: **CELLS**
2. Coalescence of replicating molecules: **CHROMOSOMES**
3. DNA + Proteins: **GENETIC CODE & CENTRAL DOGMA**
4. Consolidation of symbiotic cells: **EUKARYOTIC CELLS**
5. Fusion of haploid gametes: **SEXUAL REPRODUCTION**
6. Associations of unicellular organisms: **MULTICELLULARITY**
7. Associations of multicellular individuals: **SOCIAL GROUPS**

Obstacles to major transitions: Why is it so hard?

- Genetic conflicts within and across levels of biological organization oppose selection favoring increased levels of biological complexity.

- Most of the major transitions are rare, or even singular.
  - How do the fitness interests of lower and higher levels of biological replication become aligned?
  - Or, what keeps selection acting on the ancestral level of biological organization (within-group selection) from disrupting the integration of the derived level?

THE EVOLUTION OF MULTICELLULARITY: Why is it so easy (in eukaryotes)?

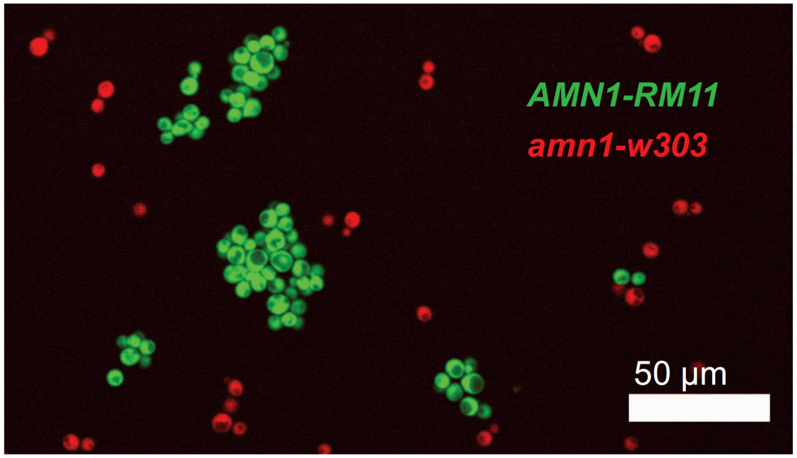


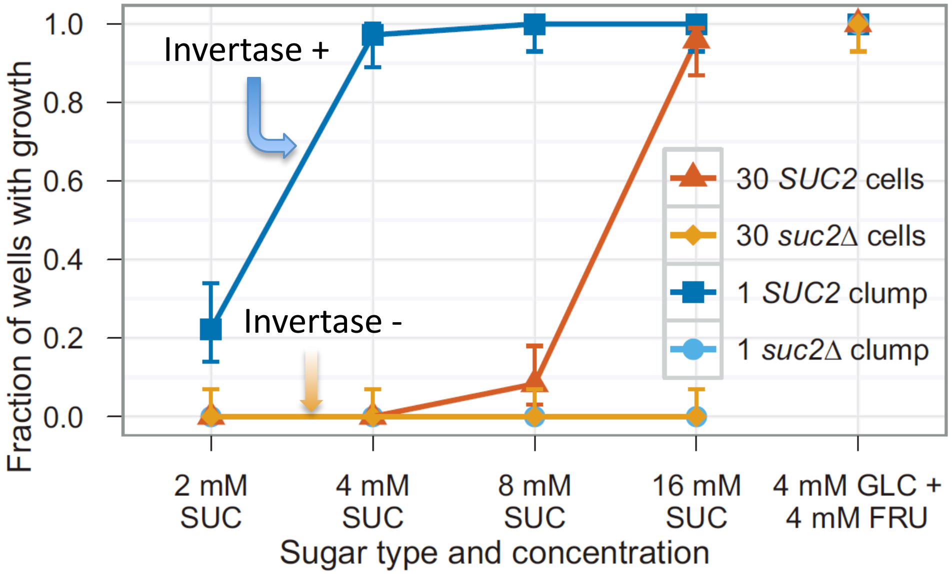
All members are multicellular
Clade contains unicellular and colonial/multicellular species
Unicellular with rare multicellular forms

Why be multicellular?

1. Cooperative feeding
2. Size-related defense against predators or competitors
3. Storage of resources
4. Functional specialization/division of labor

Sucrose breakdown by secreted invertase in yeasts: public goods and the benefits of clumping

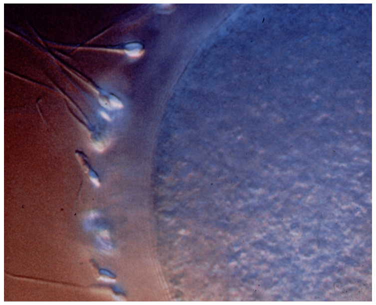


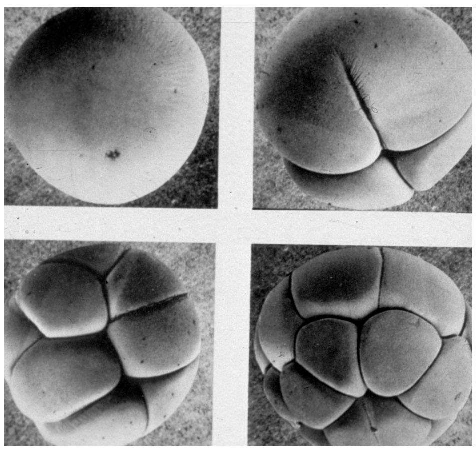


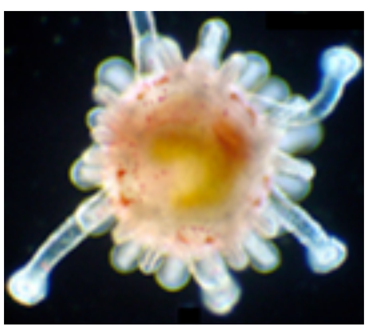
Koschwanez, Foster & Murray (2011) PLoS Biology **9**: 1-10.

How to make a multicellular organism

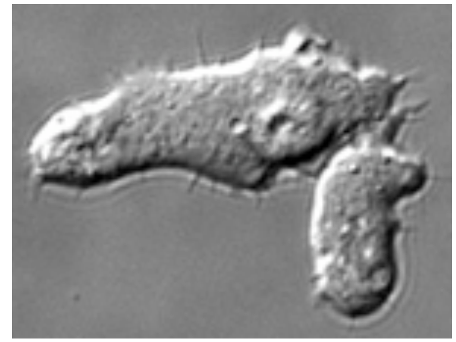
1. CLONAL (UNICELLULAR) DEVELOPMENT (staying together)

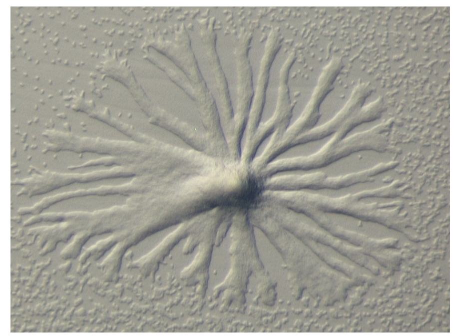


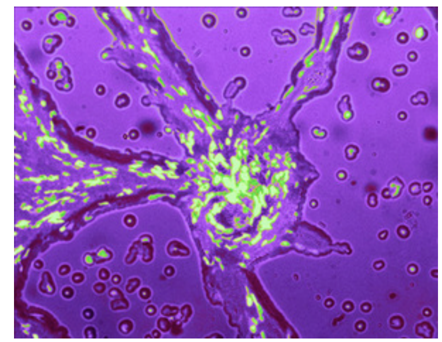


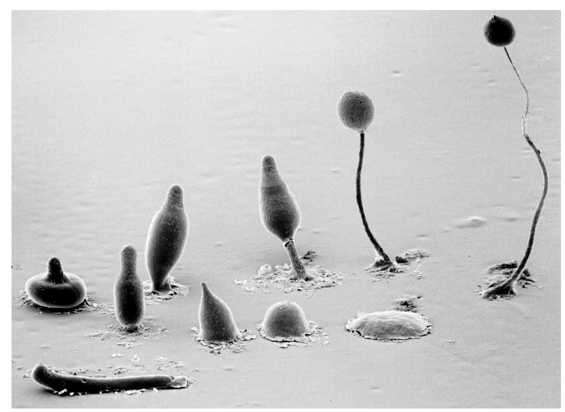


2. AGGREGATIVE DEVELOPMENT (getting together)



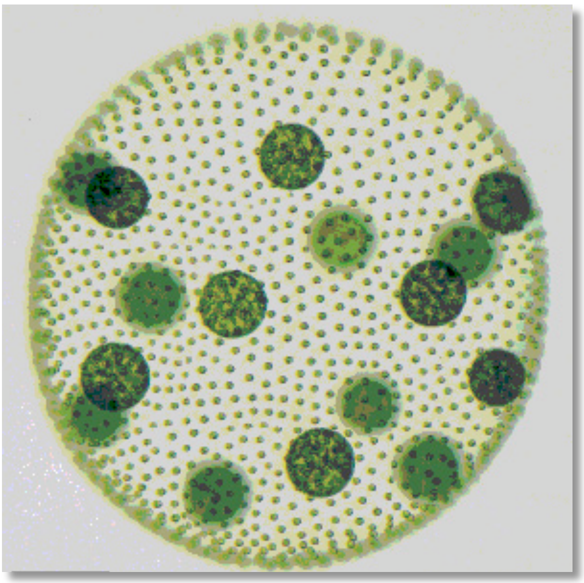


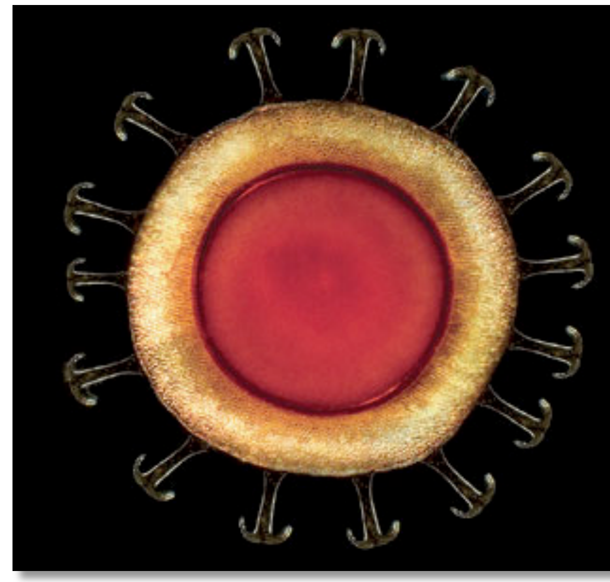




How to make a multicellular organism

3. VEGETATIVE (MULTICELLULAR) DEVELOPMENT

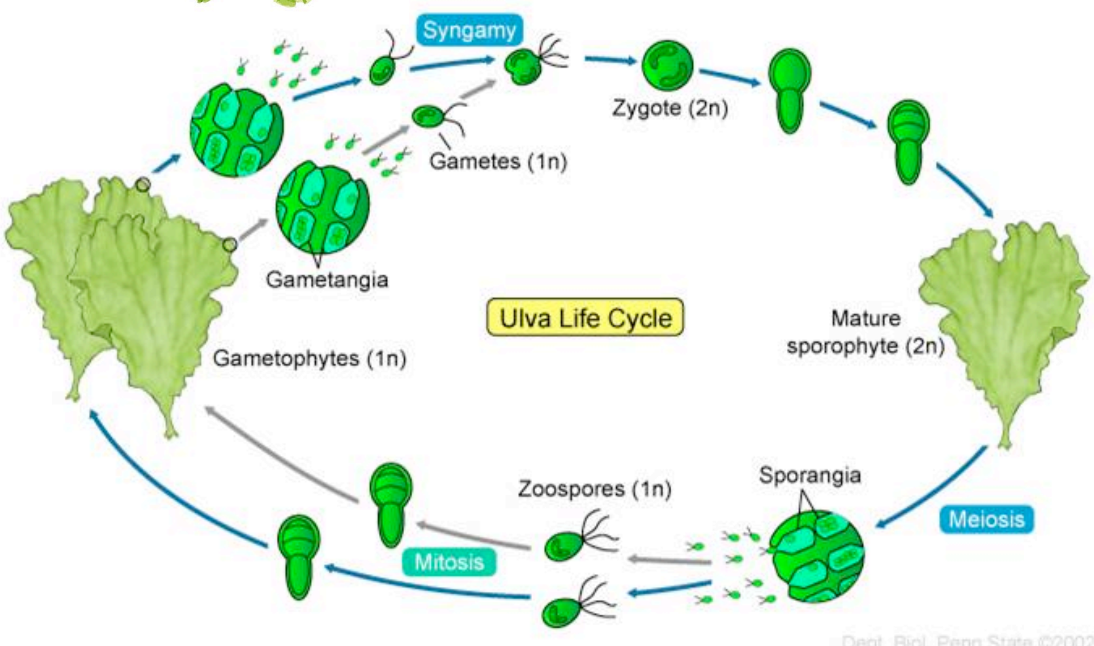


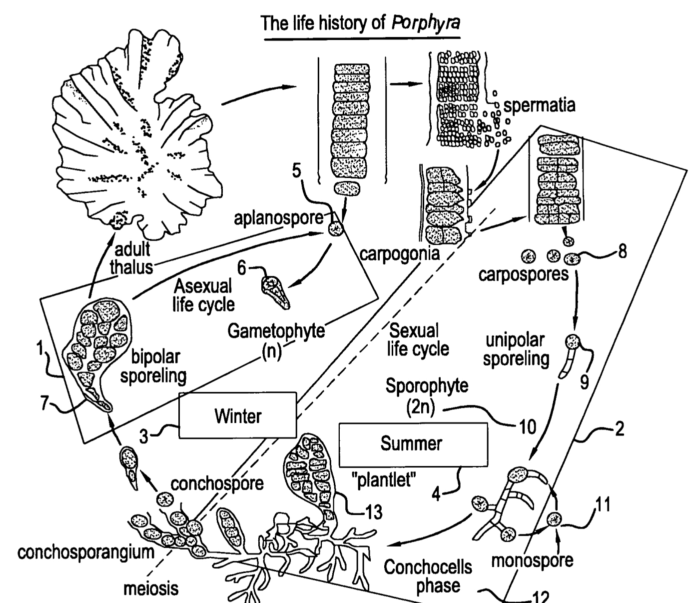


- Life cycles almost always involve regular passage through a unicellular stage (either a spore or a zygote).

How to make a multicellular organism

4. MATT'S TALK (all the other stuff)





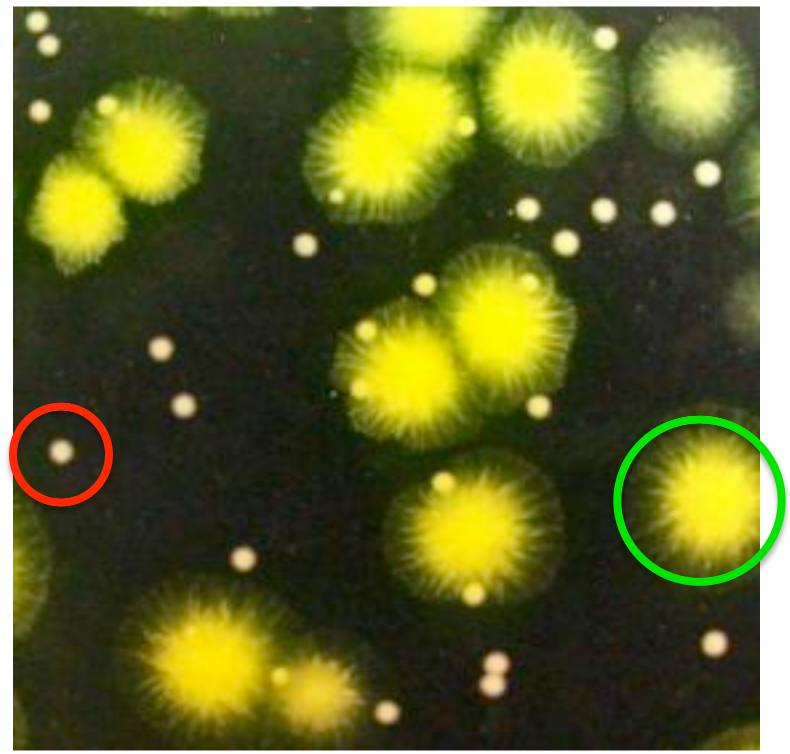
Modes of development in multicellular organisms

TAXON	UNICELLULAR DEVELOPMENT	AGGREGATIVE DEVELOPMENT
Myxobacteria	No	Yes
Cellular slime molds	No	Yes
Pseudomonads	No	Yes
Ascomycetes	Yes + Vegetative	No
Basidiomycetes	Yes + Vegetative	No
Red algae	Yes + Vegetative	No
Sponges	Yes + Vegetative	No
Cnidarians	Yes + Vegetative	No
Bryozoans	Yes + Vegetative	No
Colonial ascidians	Yes + Vegetative	No
Everyone else	Yes + Vegetative	No

Sources of genetic conflict in the multicellular transition

- Genetic conflicts arise when there is within-organism/ individual genetic variation and some variants can proliferate at the expense of others.

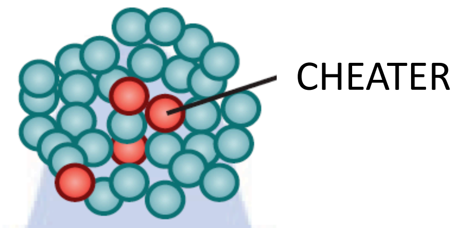
- Defector or parasitic variants (*aka* CHEATERS) can disrupt the integrity of the multicellular organism (the public good or commons) and de-stabilize the transition to multicellularity.



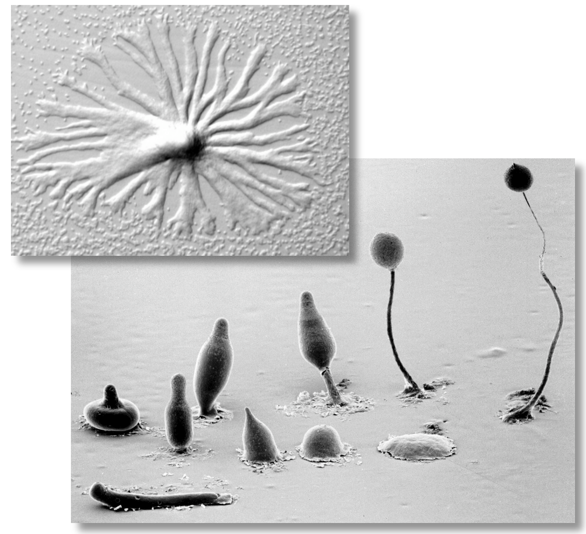
Pseudomonas aeruginosa

Where do cheaters come from?

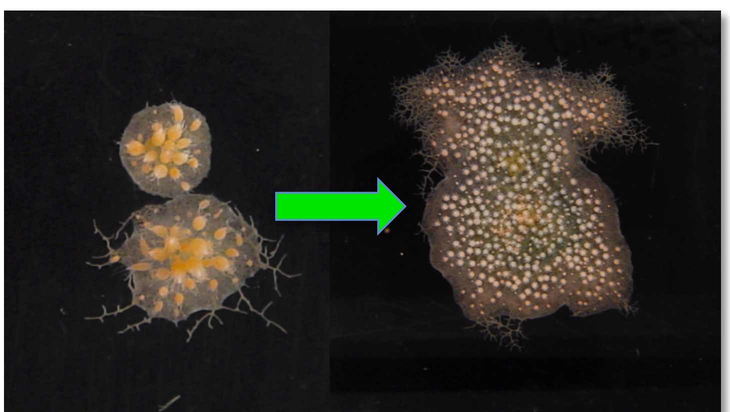
SOMATIC MUTATION

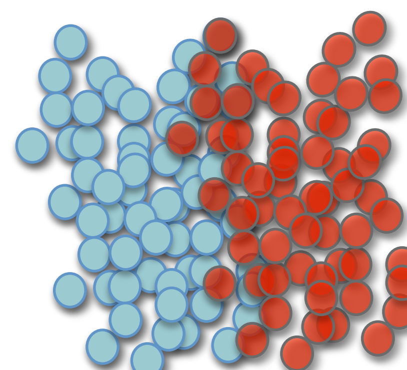


CO-AGGREGATION



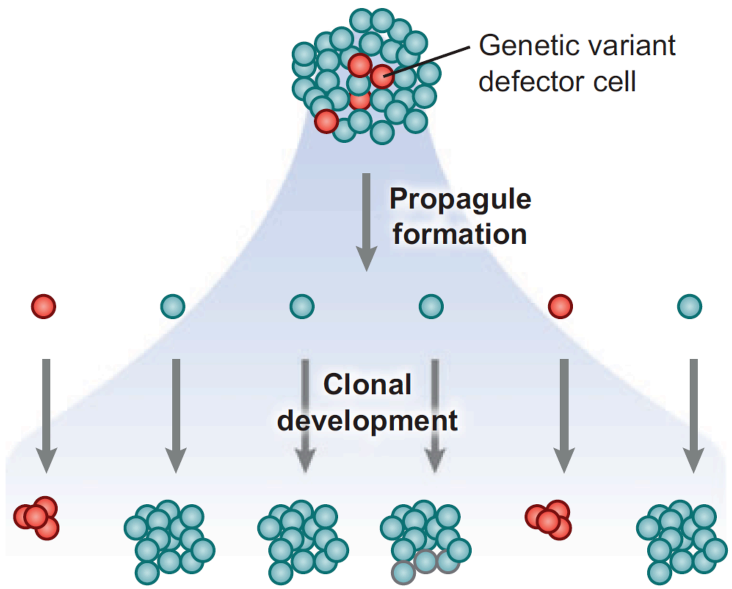
COLONY FUSION (another form of getting together)



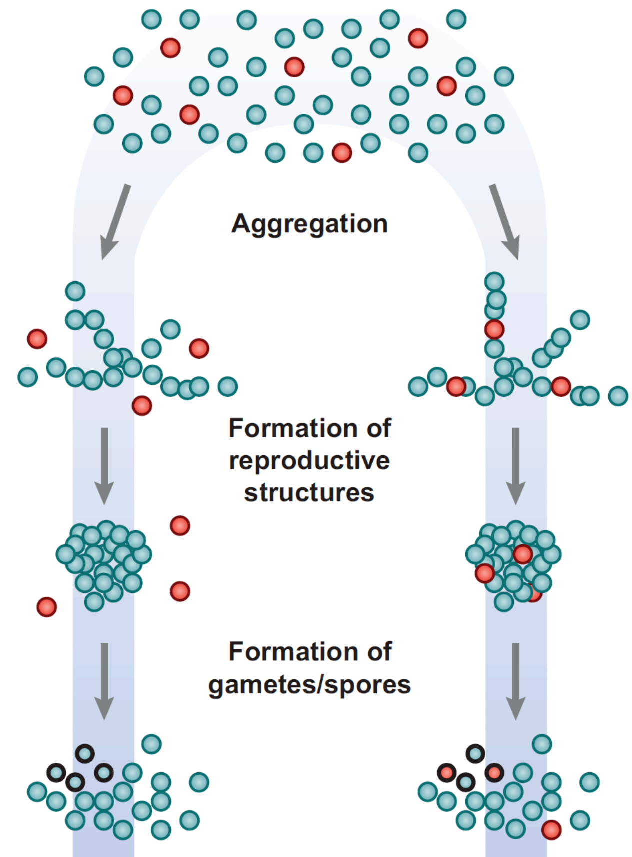


Life cycles of multicellular organisms: Fates of cheaters

CLONAL (UNICELLULAR) DEVELOPMENT
(staying together)



AGGREGATIVE DEVELOPMENT
(getting together)



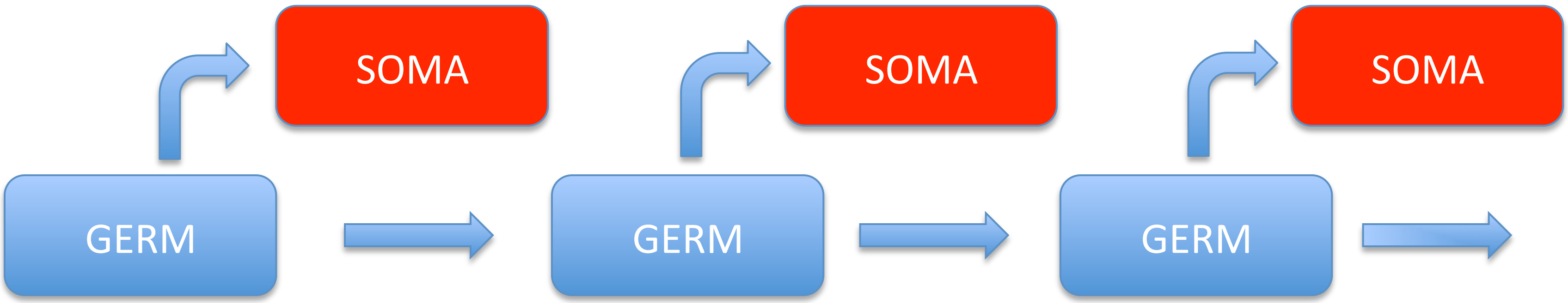
+ Policing/
Recognition

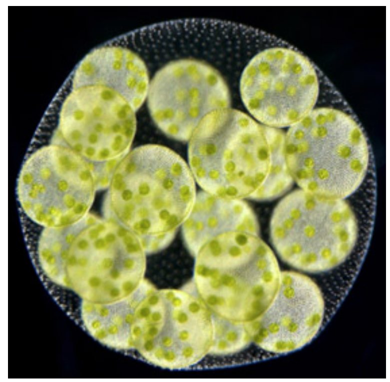
- Policing/
Recognition

Controlling cheaters

- **HUMILIATION?**
- **GERM-LINE SEQUESTRATION**
  - Buss, the “young” Michod?
- **BOTTLENECKS/UNICELLULAR DEVELOPMENT**
  - Hamilton, Maynard Smith, Dawkins, Price
- **ALLORECOGNITION/POLICING**
  - Buss, Frank, & many others

Sequestration of a germ line...



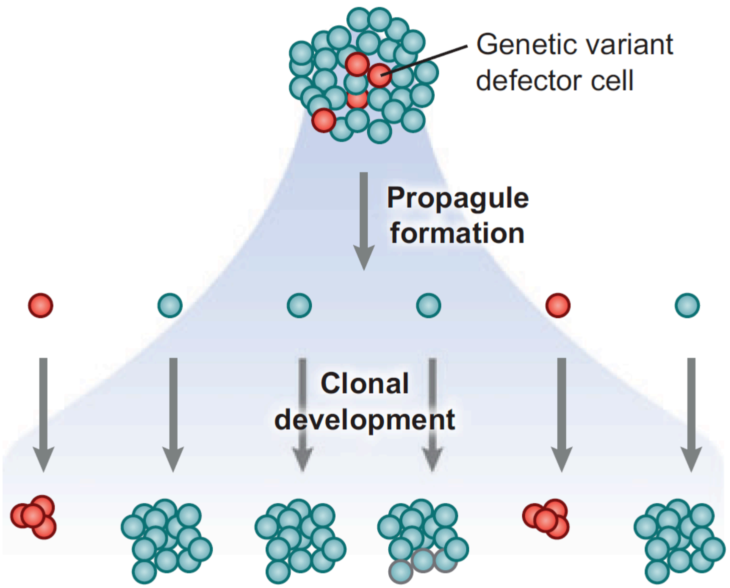


- Once a group of cells is set aside for reproduction, only mutations in that population can be transmitted to the next generation.
- (1) The earlier a germ line is sequestered, (2) the fewer cells the # of cells that initiate that line, & (3) the fewer mitotic divisions that occur in that line, the less likely it is that defector cells will arise and come to dominate the pool of gametes.

Sequestration of a germ line: problems

1. If the life cycle involves a unicellular bottleneck, cheaters would either...

- not have to pay any somatic cost of being cheaters (they always prosper)
- or find new victims each generation



2. Lots of multicellular organisms face cheaters but *don't* sequester a germ line

TAXON	CHEATERS	GERMLINE SEQUESTERED
Myxobacteria	+	No
Cellular slime molds	+	No
Pseudomonads	+	No
Ascomycetes	+	No
Basidiomycetes	+	No
Red algae	?	No
Sponges	?	No
Cnidarians	?	No
Bryozoans	?	No
Colonial ascidians	+	No

Controlling cheaters

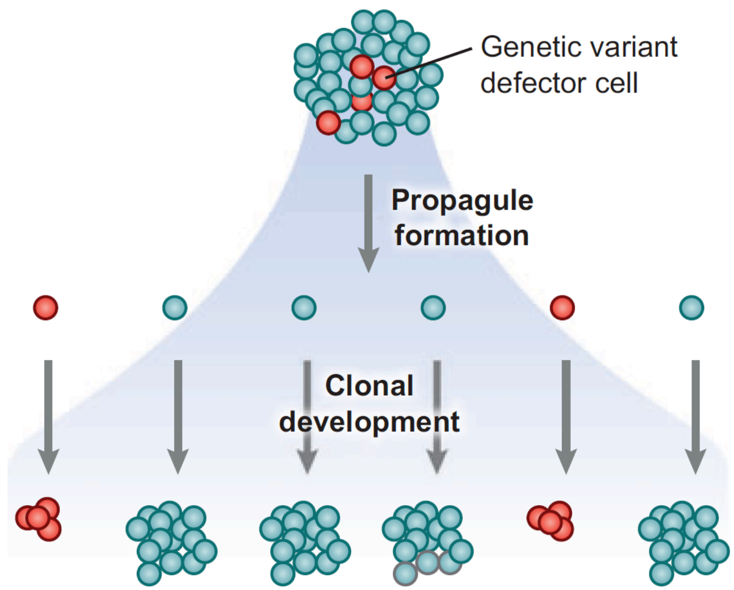
- **Sequestration of a germ line**:
  - May be very important for the evolution of complex development, but NOT multicellularity *per se*

- **Bottlenecks/Unicellular Development**:

- **Allorecognition/Policing**:

How bottlenecks control cheating

CLONAL (UNICELLULAR) DEVELOPMENT



- KIN SELECTION: Kinship reset to *r*=1 every generation.
- GROUP SELECTION: Genetic variance re-distributed EVERY generation from within to between organisms.
- How can cheaters prosper across generations (if there's any cost to cheating)?

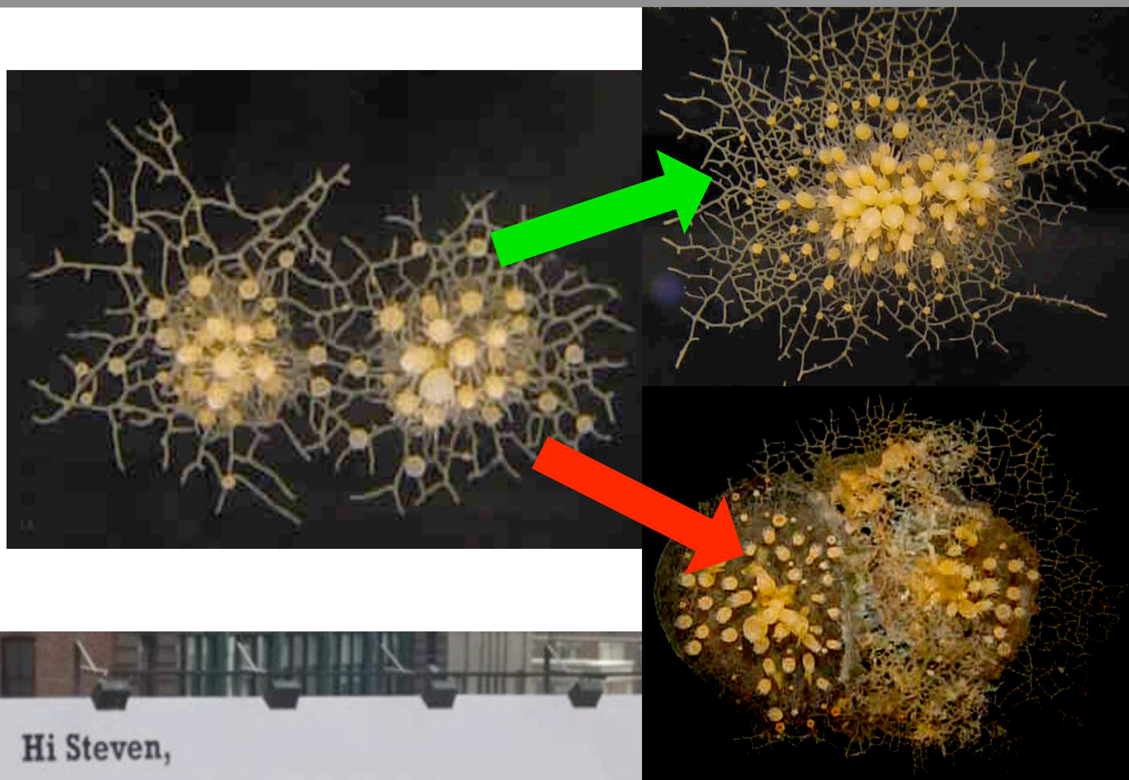
Controlling cheaters

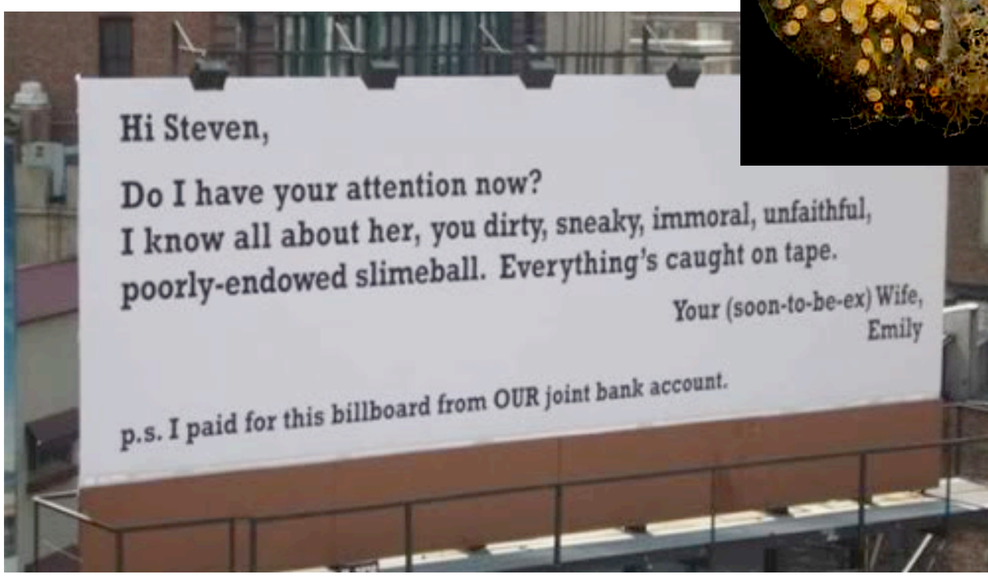
- Sequestration of a germ line
    - May be very important for the evolution of complex development & differentiation, but NOT multicellularity *per se*

- Bottlenecks/Unicellular Development
    - All multicellular organisms with ***complex development*** regularly pass through a unicellular phase
    - Promotes evolution of cooperation through clone/kin selection
    - Severely handicaps cheaters by forcing them to make it on their own each generation

- **Allorecognition/Policing**

Allorecognition/Policing (Detecting Cheaters)





Mechanisms that control cheaters

- **Sequestration of a germ line**
  - May be very important for the evolution of complex development & differentiation, but NOT multicellularity *per se*
- **Bottlenecks/Unicellular Development**
  - All multicellular organisms with ***complex development*** regularly pass through a unicellular phase
  - Promotes evolution of cooperation through clone/kin selection
  - Or, promotes cooperation by transferring within-group variance to among-group variance
  - Severely handicaps cheaters by forcing them to make a go of it on their own each generation
- **Kin recognition/Policing**
  - Limits aggregation &/or fusion to clonemates and close relatives, controlling opportunities for, & costs of, cheating
  - Widespread in taxa that have evolved societies of multicellular individuals

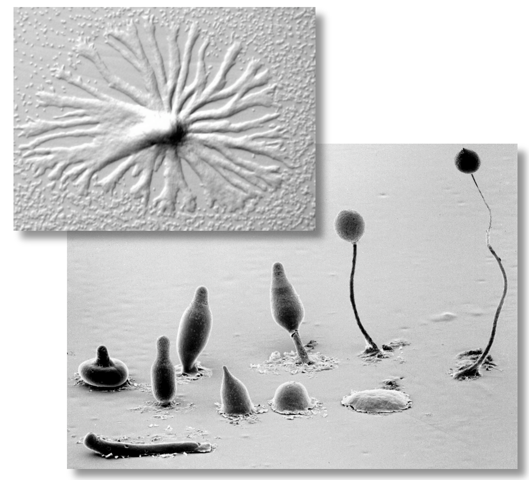
Development, defectors, & controls

TAXON	UNICELLULAR DEVELOPMENT	AGGREGATIVE DEVELOPMENT	FUSION	CHEATERS	RECOGNITION	GERMLINE
Myxobacteria	No	Yes	?	+	+	No
Cellular slime molds	No	Yes	?	+	+	No
Pseudomonads	No	Yes	?	+	?/+	No
Ascomycetes	Yes + Vegetative	No	+	+	+	No
Basidiomycetes	Yes + Vegetative	No	+	+	+	No
Red algae	Yes + Vegetative	No	+	?	+/?	No
Sponges	Yes + Vegetative	No	+	?	+	No
Cnidarians	Yes + Vegetative	No	+	?	+	No
Bryozoans	Yes + Vegetative	No	+	?	+	No
Colonial ascidians	Yes + Vegetative	No	+	+	+	No
Everyone else	Yes + Vegetative	No	-	(pathogens)	+ (social groups)	Yes

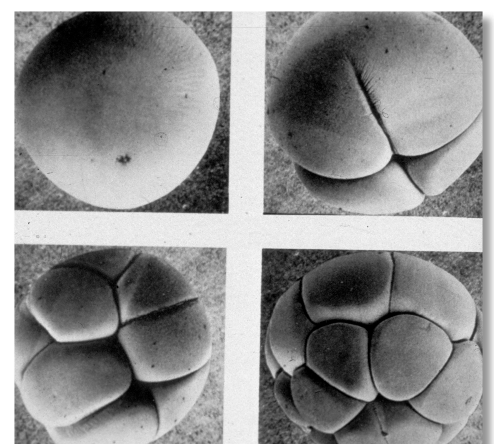
The bottom line: The transition to multicellularity

- **All multicellular organisms must control intraorganismal genetic conflicts**

- ***Multicellular organisms that develop by aggregation or fusion*** rely primarily on allorecognition or policing to limit the impacts of cheaters

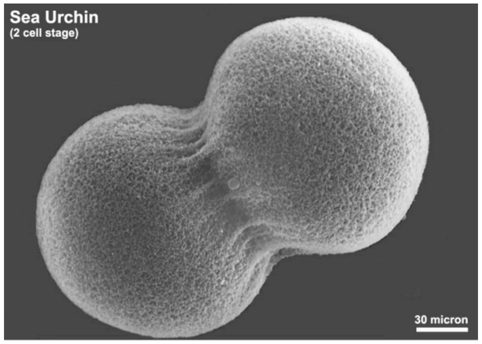


- ***Multicellular organisms that develop clonally from a unicell*** limit the impacts of cheaters through (1) kin (or group) selection and (2)allorecognition/policing



The evolution of multicellular complexity

- A unicellular bottleneck may be essential for the evolution of morphologies more complex than those observed in slime molds, *etc*.
  - ➢ Not clear why...
    - Alignment of fitness interests?
    - Epigenetic/developmental coordination?



- Allorecognition & policing favor the evolution of persistent social cooperation, especially when cooperation involves reproductive altruism

- Germ line sequestration appears to be associated with the evolution of complex multicellular organization (but NOT multicellularity *per se*)
  - Is it important distinguish among terms like *germ-soma, germ line sequestration, gametes, etc.?*