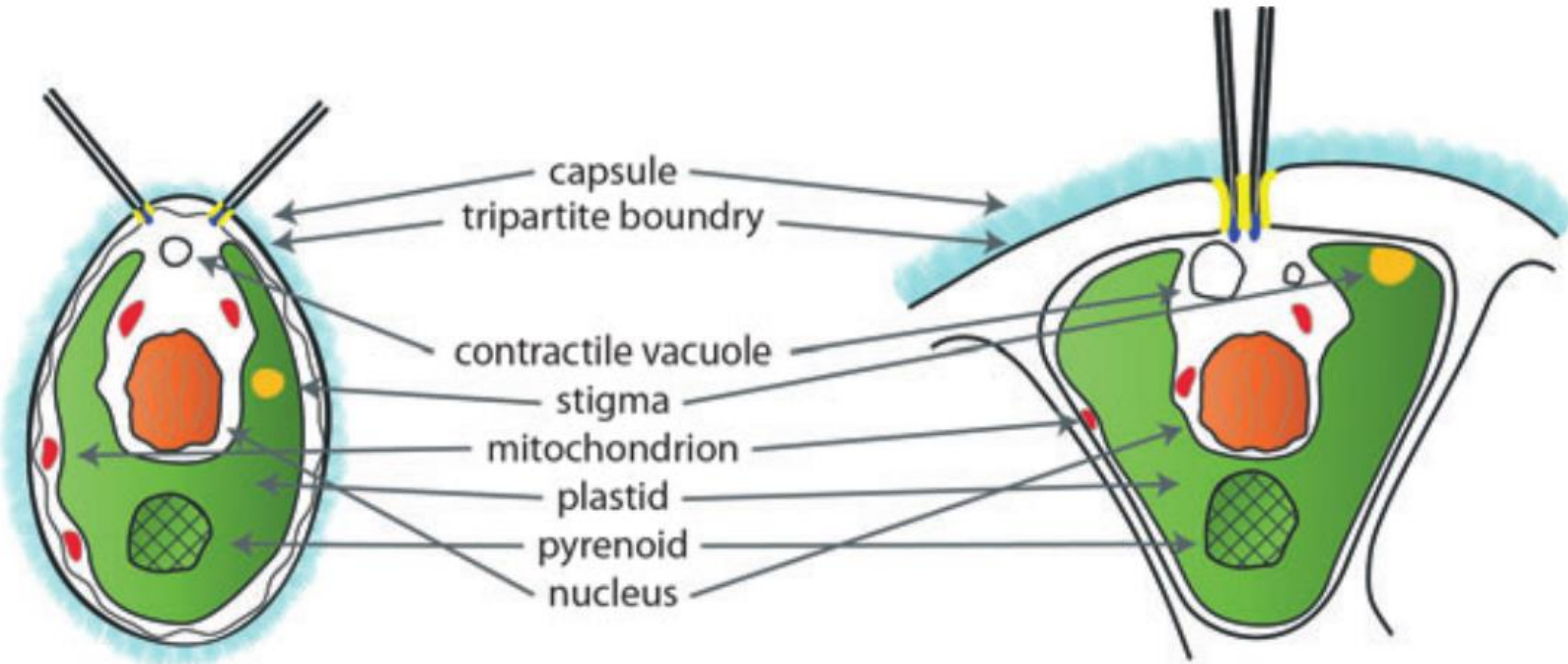
Volvocacean unicell structure

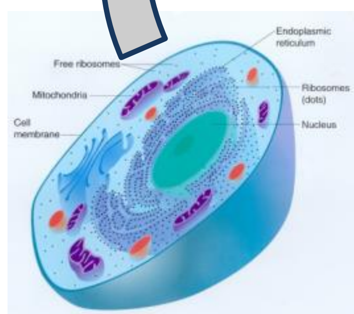


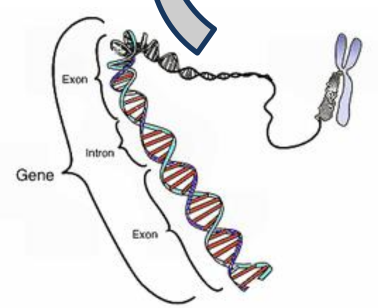
Coleman 2012. J. Phycology.

Acknowledgments

NASA
NSF
ARIZONA

Hierarchy of Darwinian individuals



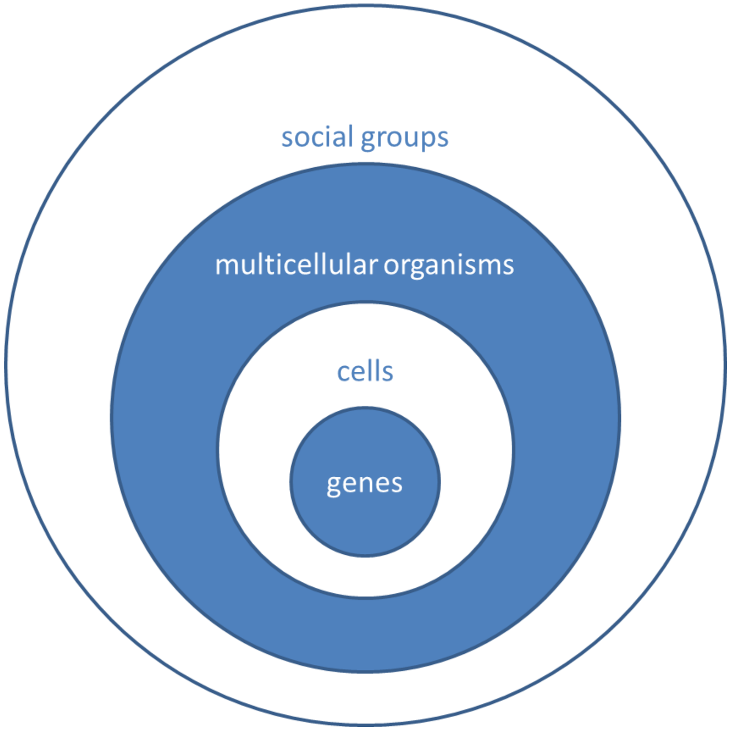


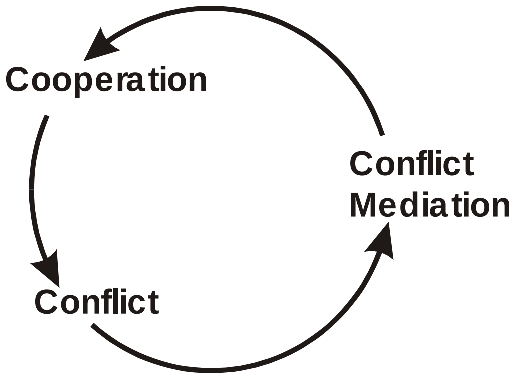
Variation

Reproduction

Heritability

Slide credit D. Shelton


social groups
multicellular organisms
cells
genes


Cooperation
Conflict
Mediation
Conflict

Challenge for evolutionary theory

- how groups of reproducing individuals become reproducing individuals and acquire fitness
- How do groups become individuals

Darwinian properties

- Darwin (1856)
  - "Struggle to survive and reproduce"
  - Variation in ability to undertake the "struggle"
  - Offspring resemble parents
- Lewontin (1970)
  - Variation
  - Fitness differences
  - Heritability
- Maynard Smith (1988)
  - Multiplication
  - Variation
  - Heredity
- Heritable variation in fitness

➢ How can Darwinian properties arise in entities that do not possess them?

Theory of population genetics

- Concerns frequencies and probabilities of genes
- What do we count?
- Individuals
- How can we use the theory of population genetics to explain the origin of individuals?

Multi-level selection theory

	Organism (i)	Group (s)	Total Population
Number of Genes	2	$2N_s$	$N = 2\sum_s N_s$
Frequency	$q_{i,s} = 0, \frac{1}{2}, 1$	$q_s = \frac{1}{N_s}\sum_{i=1}^{i=N_s} q_{i,s}$	$q = \frac{1}{N}\sum_s N_s q_s$
Fitness	$W_{i,s}$	$\overline{W_s} = \frac{1}{N_s}\sum_{i=1}^{i=N_s} W_{i,s}$	$\overline{W} = \frac{1}{N}\sum_s N_s \overline{W_s}$
New Frequency	$q_{i,s}$	$q_s' = \frac{1}{N_s \overline{W_s}}\sum_{i=1}^{i=N_s} q_{i,s} W_{i,s}$	$q' = \frac{1}{N'}\sum_s N_s' q_s'$
Change in Frequency	$\Delta q_{i,s} = 0$	$\Delta q_s = q_s' - q_s$	$\Delta q = q' - q$

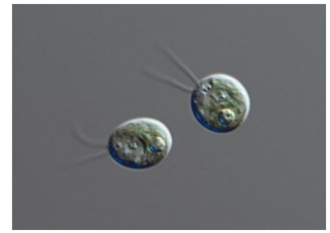
Questions

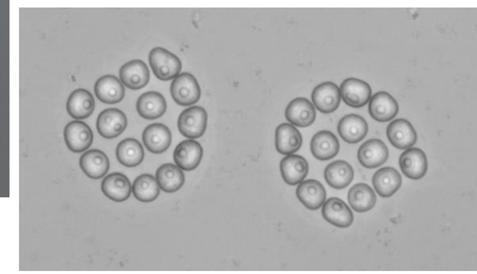
- Why does cellular selection (selection between competing cell lineages in an organism) not disrupt selection at the level of the cell group or organism
- Can selection at the group level lead to adaptations that reduce competition among cells and enhance cooperation among cells?
  - Conflict mediators: Germ/Soma, spore, PCD
- How can Darwinian properties arise in entities that do not possess them?
- Can we use the theory of population genetics to explain the origin of individuals?
- How do groups of individuals become individuals?

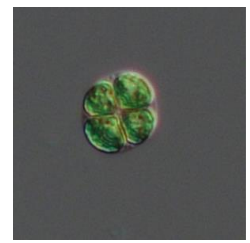
Approaches

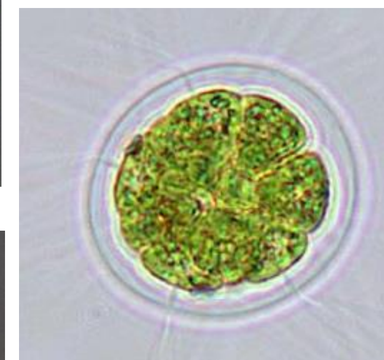
- Mathematical models
  - population genetics and ecology
- Volvocine green algae
  - Comparative biology
  - Genomics
  - Experiments
  - Cell biology?
- Philosophical analysis

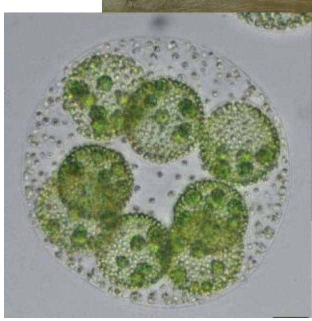
Volvocine algal species have diverse, but simple forms

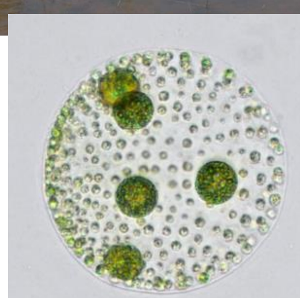


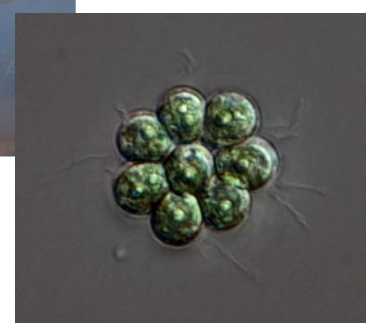


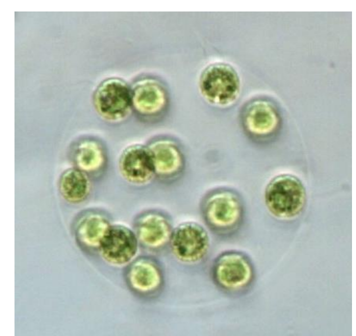












Slide credit D. Shelton

Levels of selection

- Abstract nature of Darwin's conditions
- Hierarchical organization of the living world
- Population structure
- Altruism
  - Organismal adaptations speak to the power of selection on organisms. However, traits, like altruism, exist which are not advantageous to organisms
  - Altruism illustrates an important aspect of fitness in structured populations. Effects of a trait may be different at different levels.
  - Cancer

Group selection debate

Synchronic

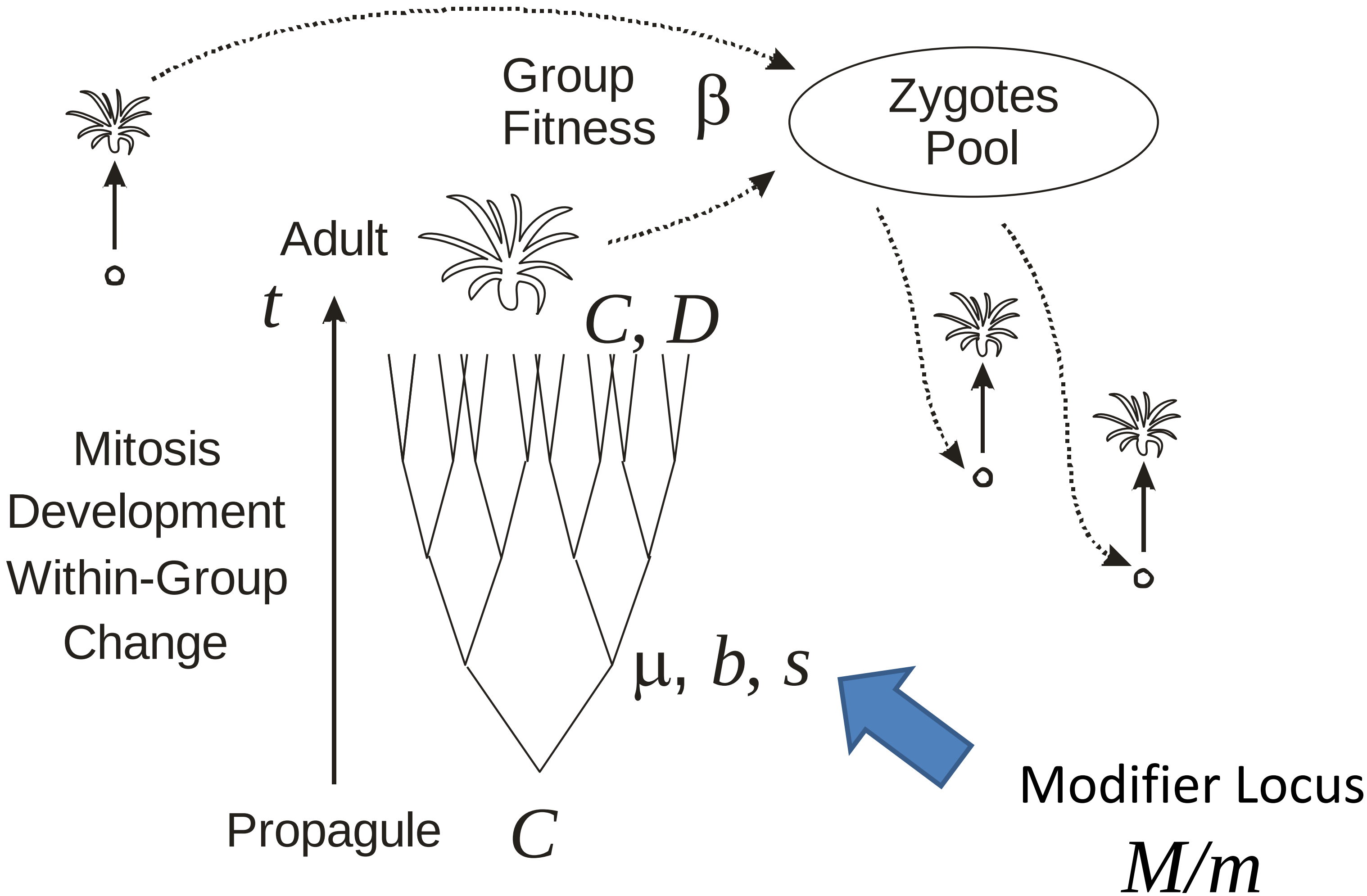
- At what level in the hierarchy is selection acting?
- Takes the hierarchy of life for granted
- The hierarchy of life is a product of evolution

Diachronic

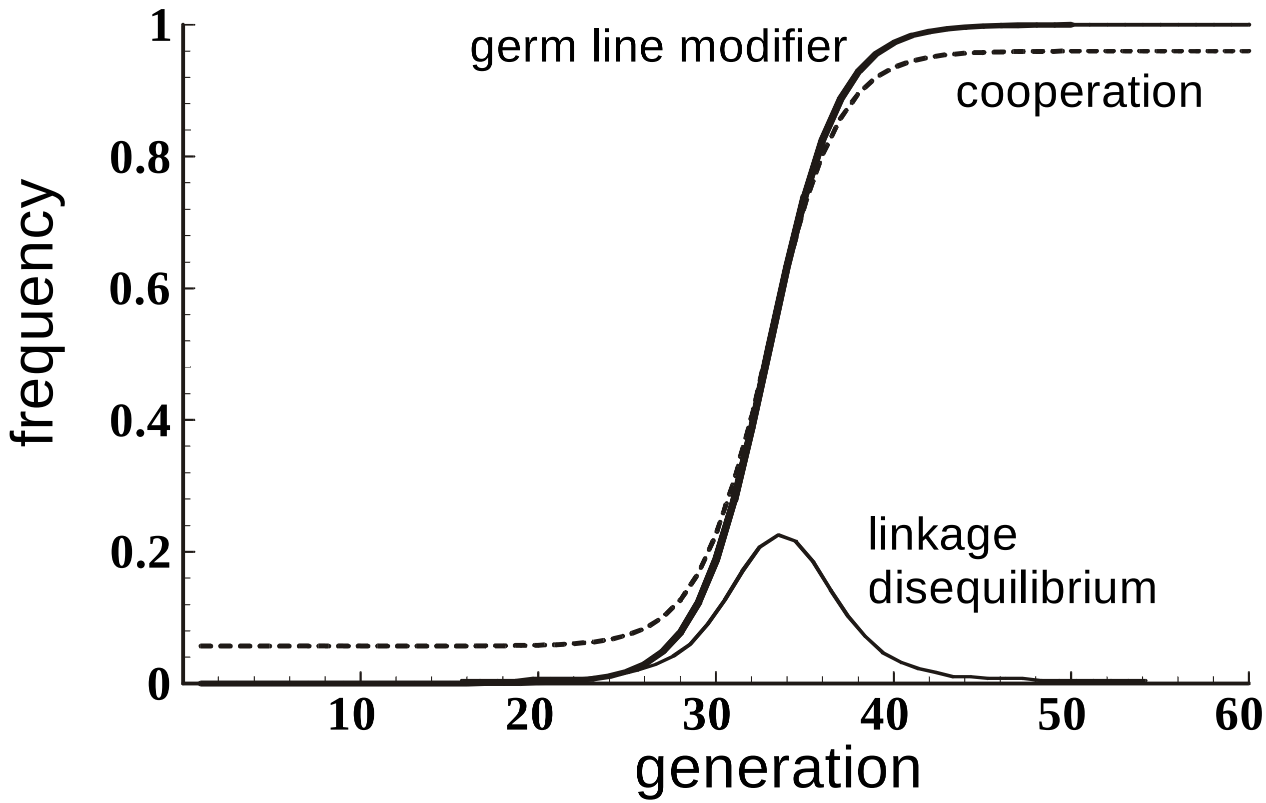
- How did the levels in the hierarchy of life evolve?
- Renewed sense of urgency
- Multicellular organisms didn't always exist
- Originate as groups of cells
- So whether or not group selection exists today, it must have existed in the past

- Credit: S. Okasha

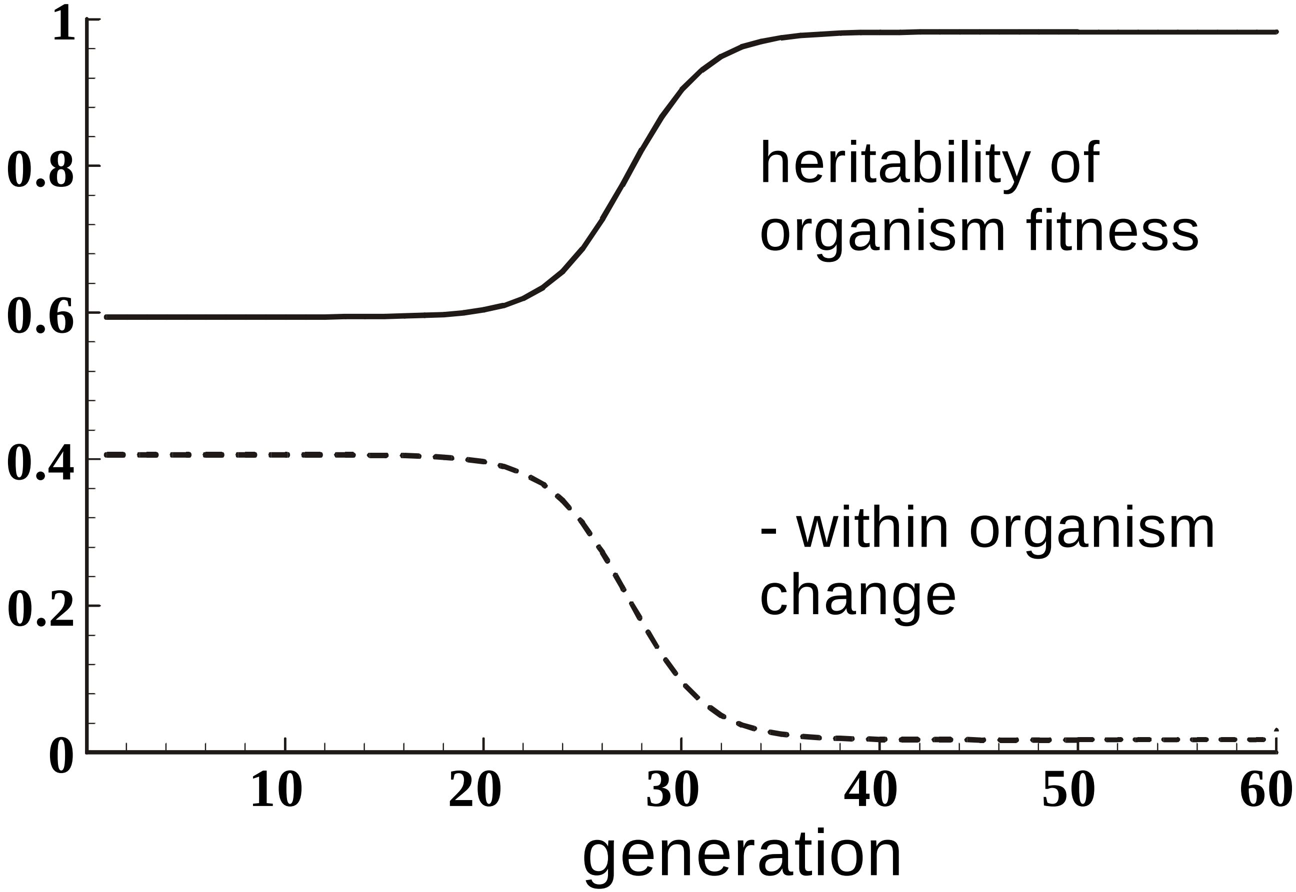
Multi-level selection of development



Level of Cooperation Increases During Evolutionary Transition

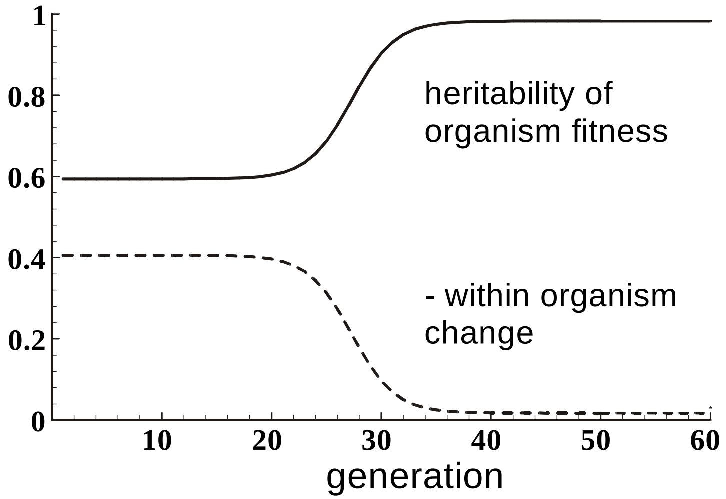


Heritability of fitness increases during evolutionary transition

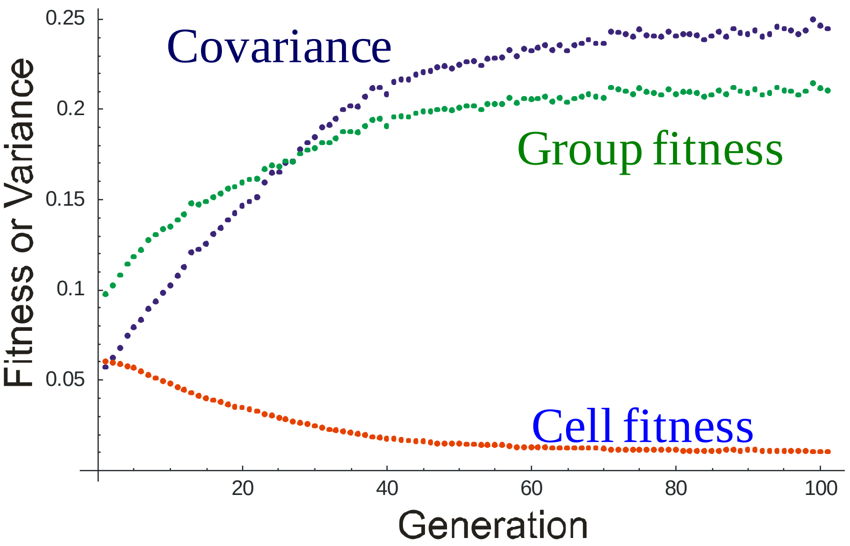


Transfer of fitness during ETI

Conflict mediator model



Division of labor model



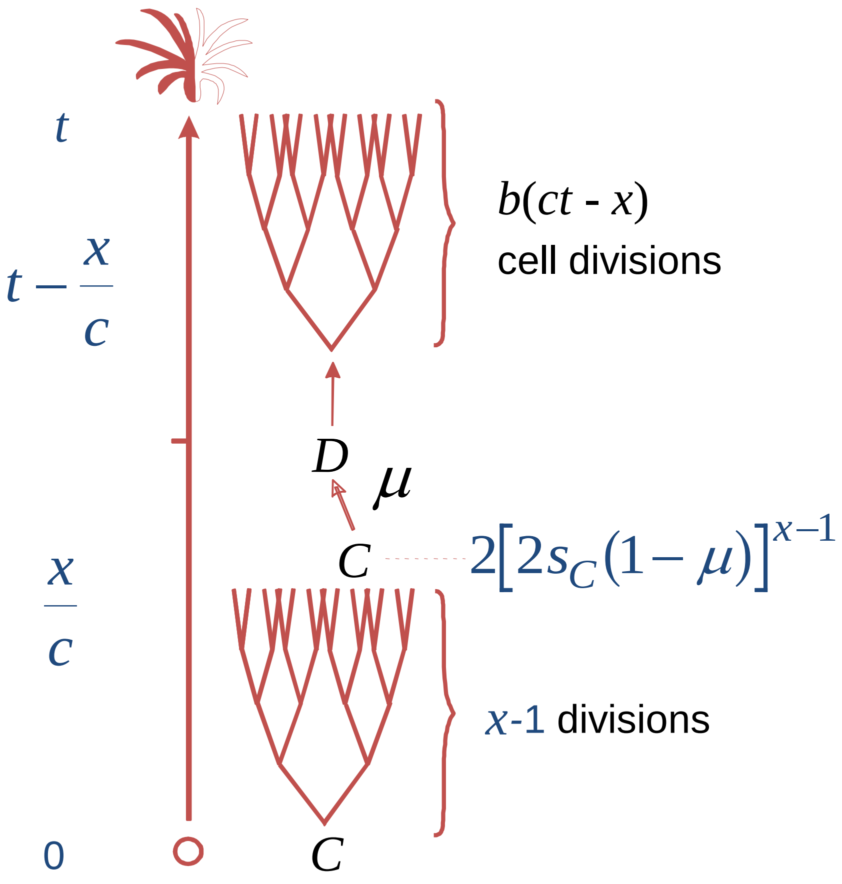
Conflict Mediators
Cell to Organism Transition

- Kinship
  - Zygote stage
  - Result: levels of cooperation still low
- Mutation rate
- Self-policing
- Parental control
- Programmed cell death
- Determinate size
- Sex
- Germ soma (G/S)

Some detail slides follow

Jump to “Steps to multicellularity”?

Calculation of the adult



$$k_{DC}=\sum_{x=1}^{ct}2\left[2s_C(1-\mu)\right]^{x-1}\mu s_D\left[2s_D\right]^{b(ct-x)}$$

Population Genetics
Two-locus Modifier Equations

$$x_1'\bar{W} = \left(x_1 - rG\right) W_1 \frac{K_{11}}{K_1}$$

$$x_2'\bar{W} = \left(x_2 + rG\right) W_2 \frac{K_{22}}{K_2}$$

$$x_3'\bar{W} = \left(x_3 + rG\right) W_3 + \left(x_1 - rG\right) W_1 \frac{K_{31}}{K_1}$$

$$x_4'\bar{W} = \left(x_4 - rG\right) W_4 + \left(x_2 + rG\right) W_2 \frac{K_{42}}{K_2}$$

Linkage Disequilibrum

$$G = x_1 x_4 - x_2 x_3$$

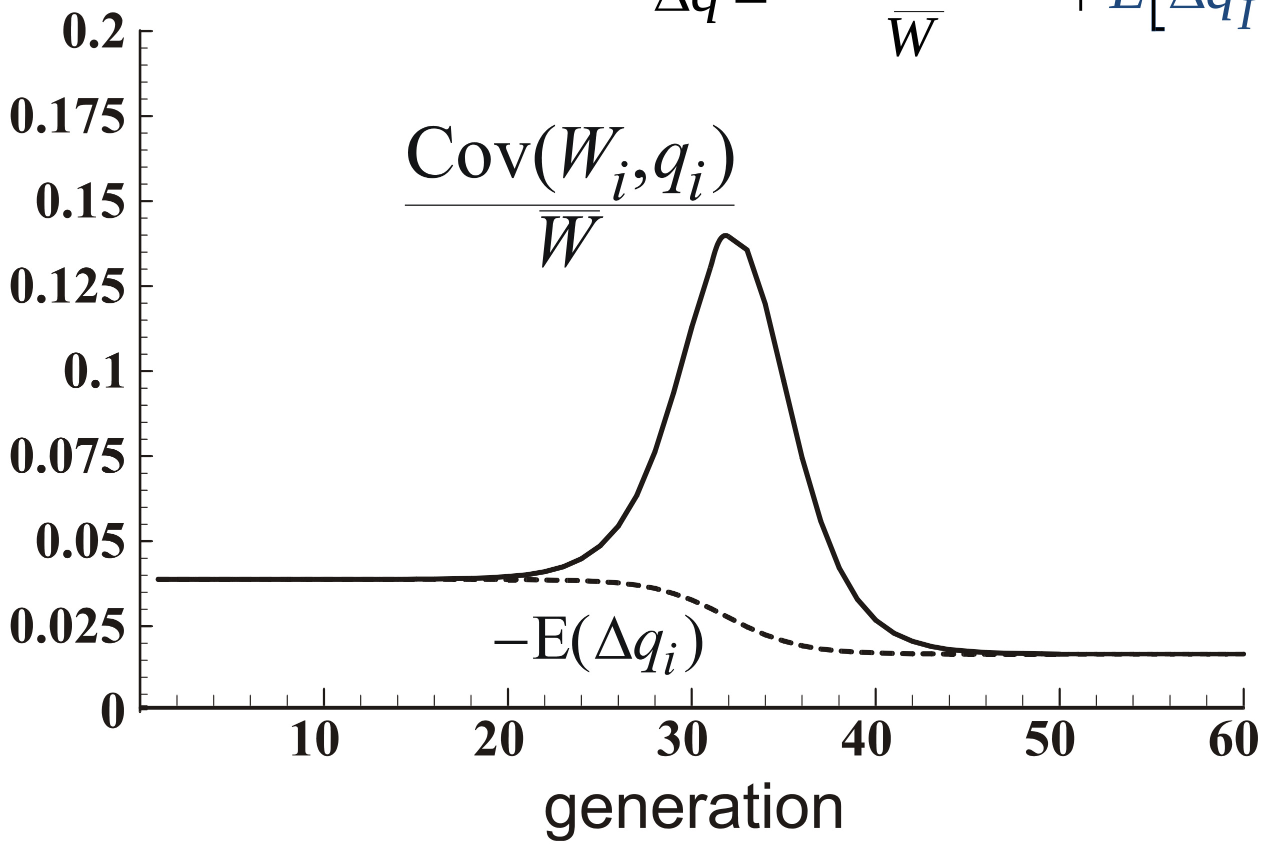
$$\bar{W} = (x_1 - rG)W_1 + (x_2 + rG)W_2 + (x_3 + rG)W_3 + (x_4 - rG)W_4$$

Evolutionary Equilibria (G=0)

Eq.	Alleles		Description	Interpretation
1	*D*	*m*	no cooperation; no modifier	*Single cells*, no organism
2	*D*	*M*	no cooperation; modifier fixed	Not of biological interest, never stable
3	*C*,*D*	*m*	polymorphic for cooperation and defection; no modifier	*Group of cooperating cells*: no higher level functions
4	*C*,*D*	*M*	polymorphic for cooperation and defection; modifier fixed	*Individual organism*: integrated group of cooperating cells with higher level function mediating within organism conflict

Group Fitness Covariance

$$\Delta q = \frac{Cov\left[W, q_I\right]}{\overline{W}} + E\left[\Delta q_I\right]$$

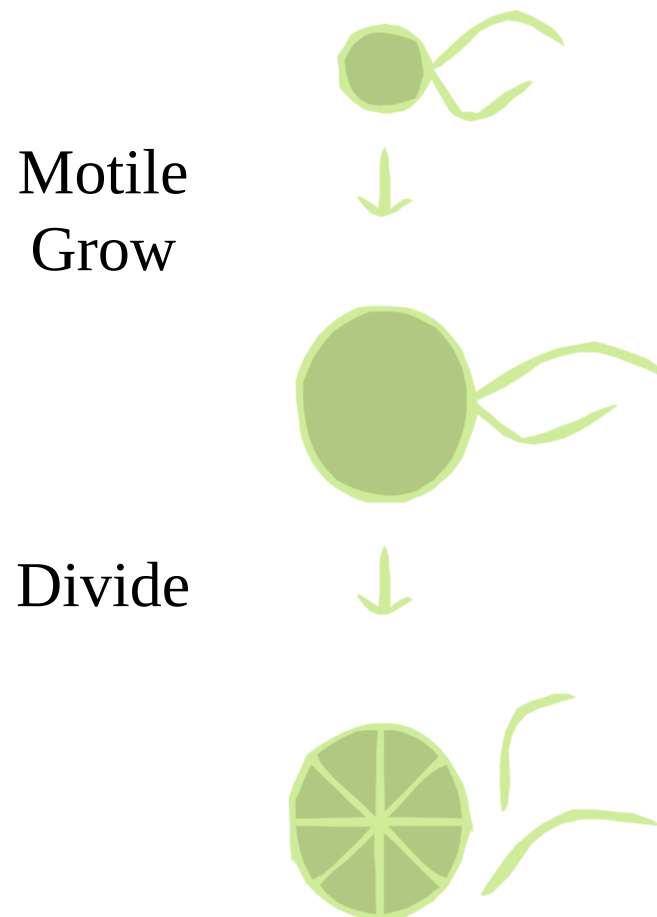


Steps to multicellularity

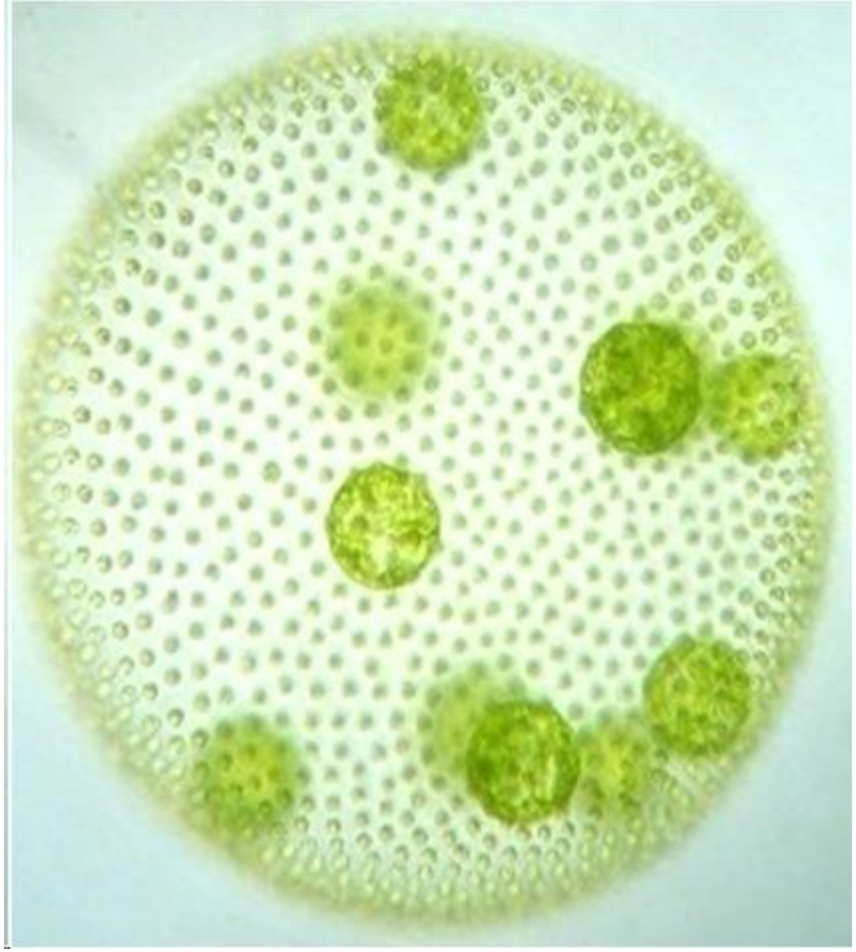
MULTICELLULARITY

Life as a single cell

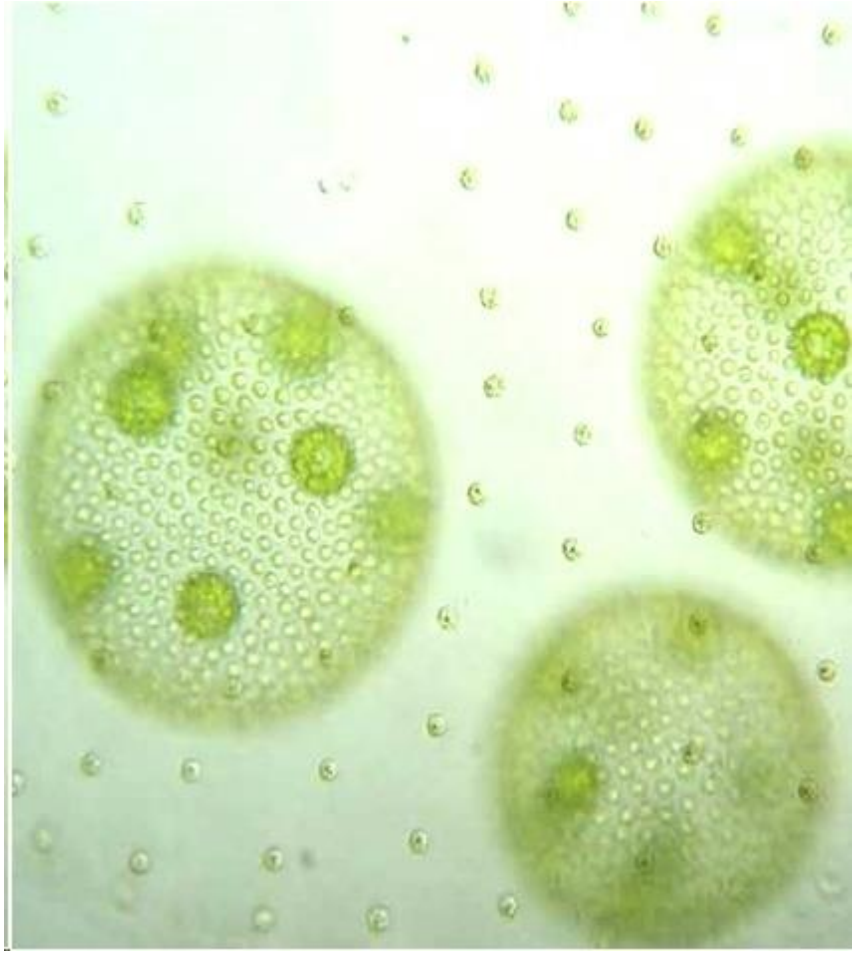
- Advantages
  - Surface/Volume
  - Immediate & effective interaction with environment
  - Fast generation time
- Problem
  - Single cell has to do everything
  - Trade-offs
    - Can’t swim and divide at the same time
- Answer
  - Division of labor



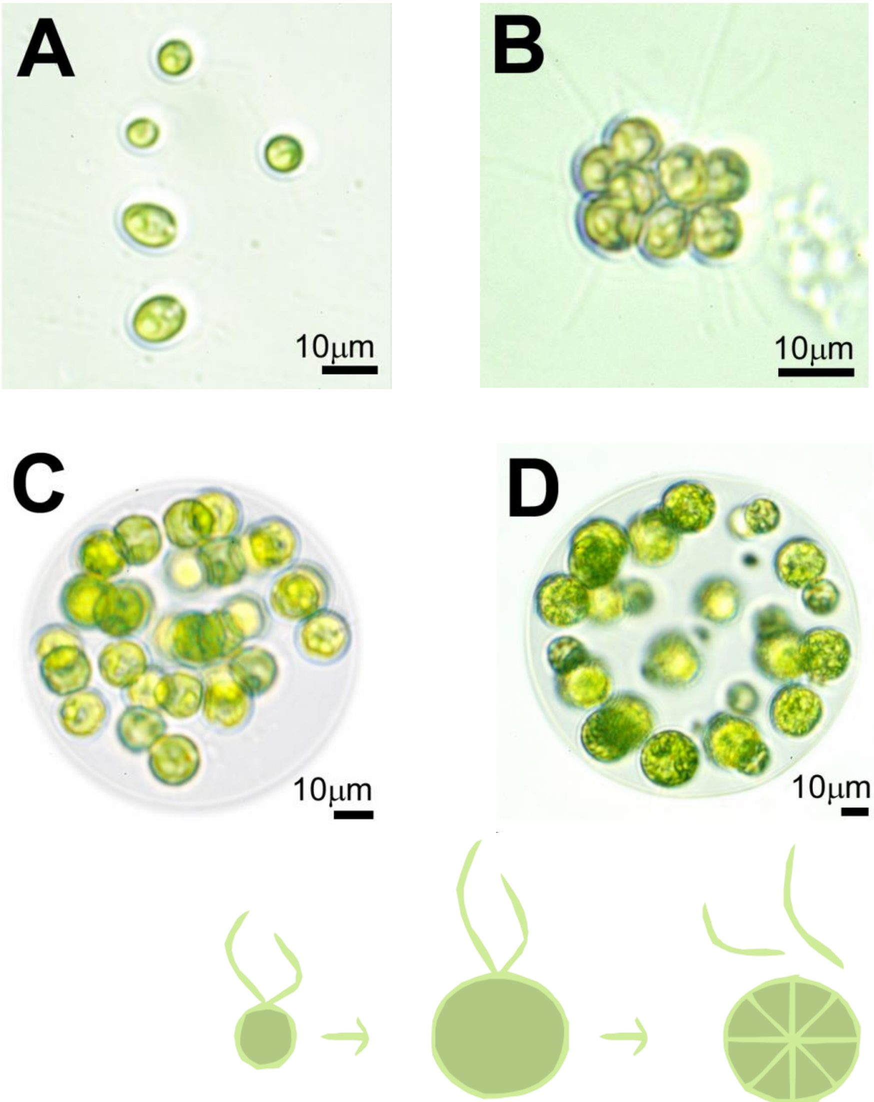
Division of labor: *Volvox carteri*

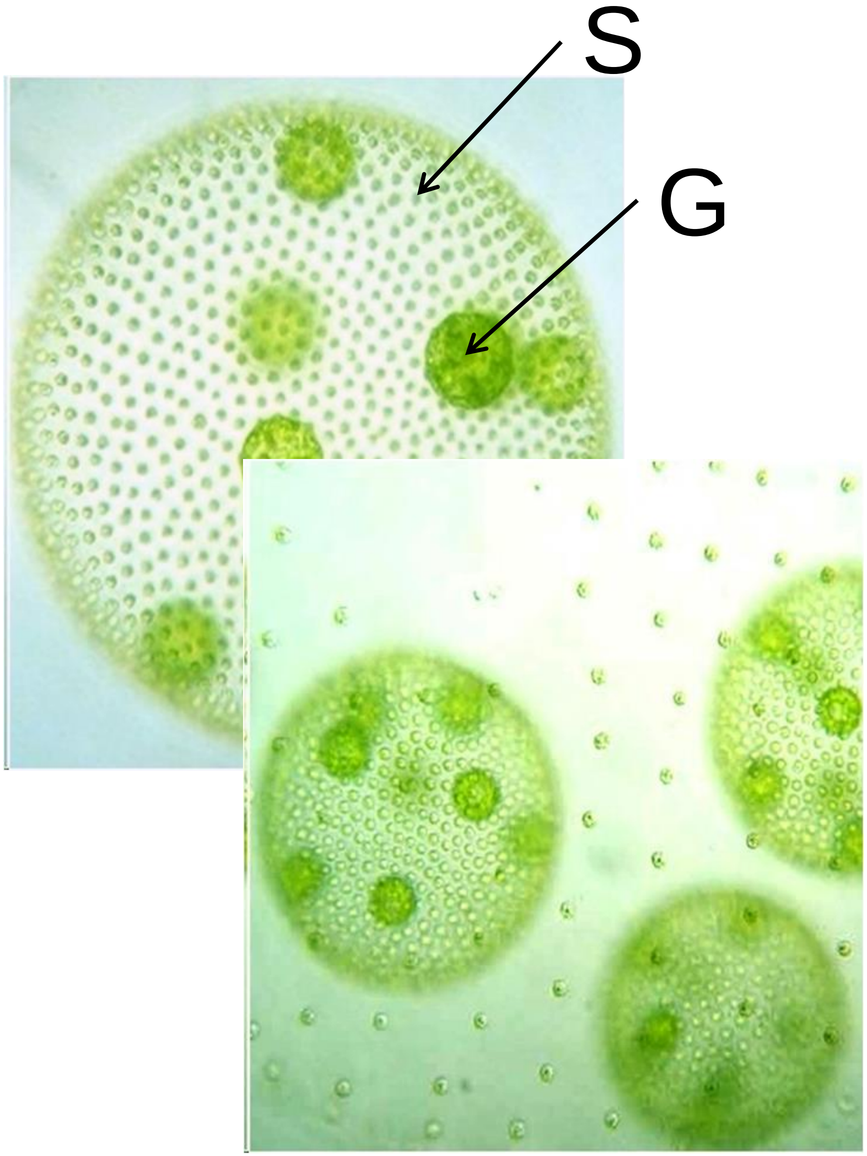


Juvenile



Mother with babies inside





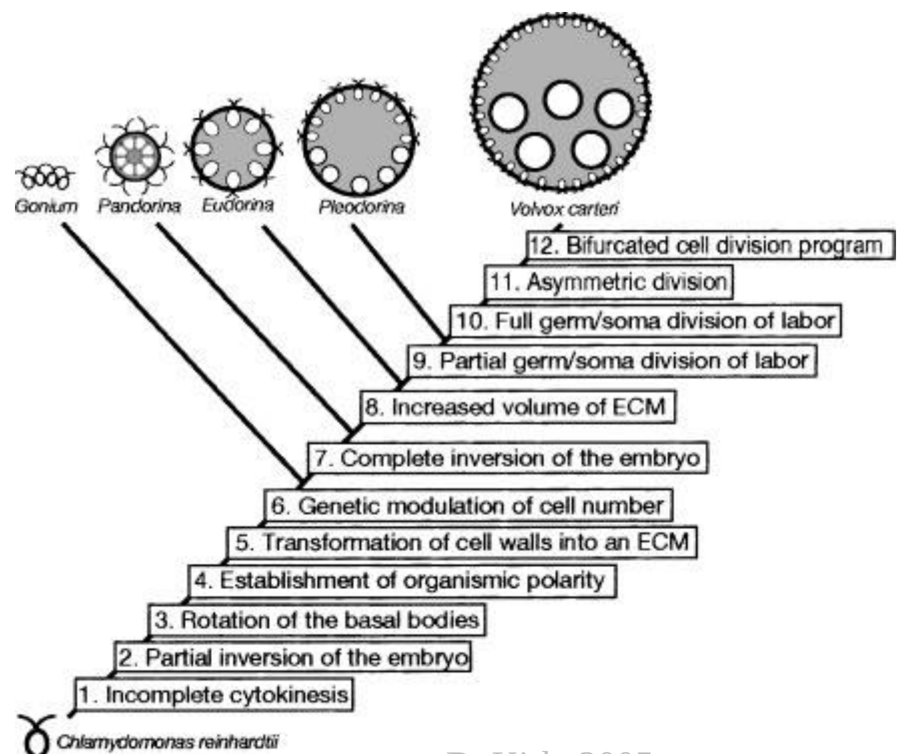
- Individuality depends on G/S division of labor
- Multiple vs. binary fission

Multicellularity is a complex trait

•Darwin: *Reduce jump in complexity to a set of possible steps each advantageous*

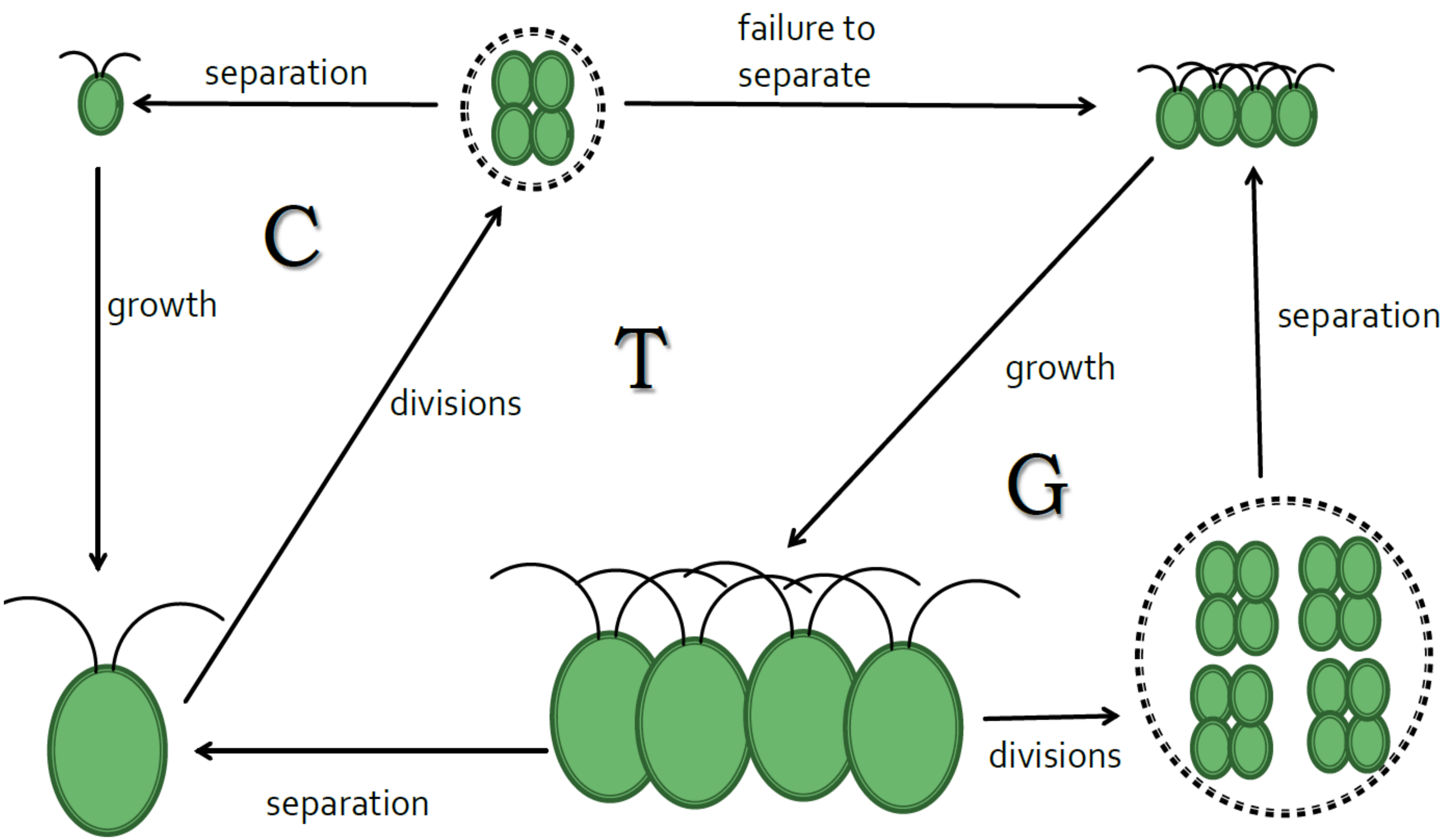
- Multi-level selection
  - Group formation
  - Cellular cooperation
  - Increased integration
  - Groups increase in size
  - Conflict mediation
  - G/S specialization
  - Group becomes indivisible, an individual

- Developmental steps

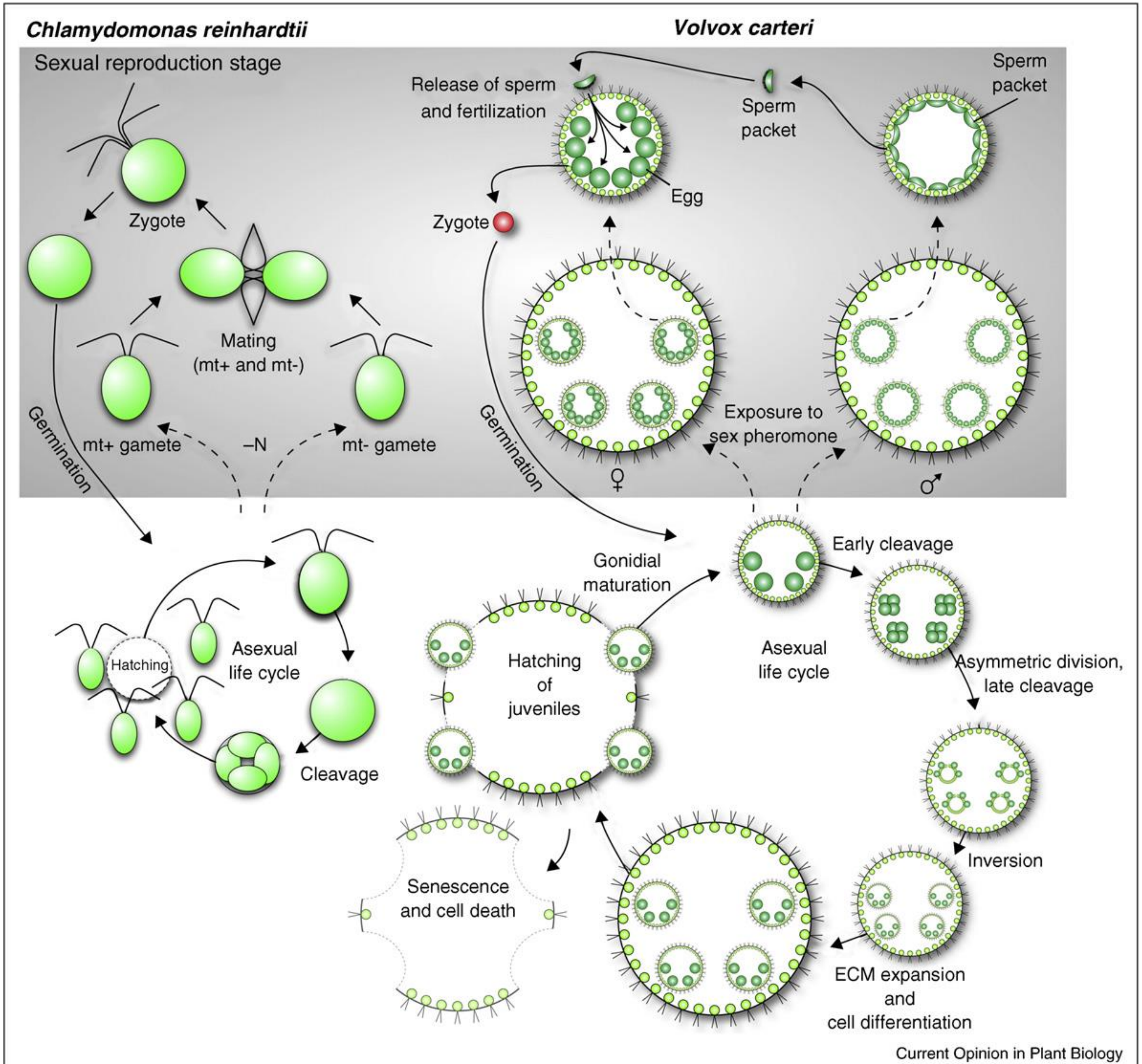


•D. Kirk. 2005

Steps to multicellularity – group life cycles



•Credit D. Shelton



•From
Nishii and Miller 2010

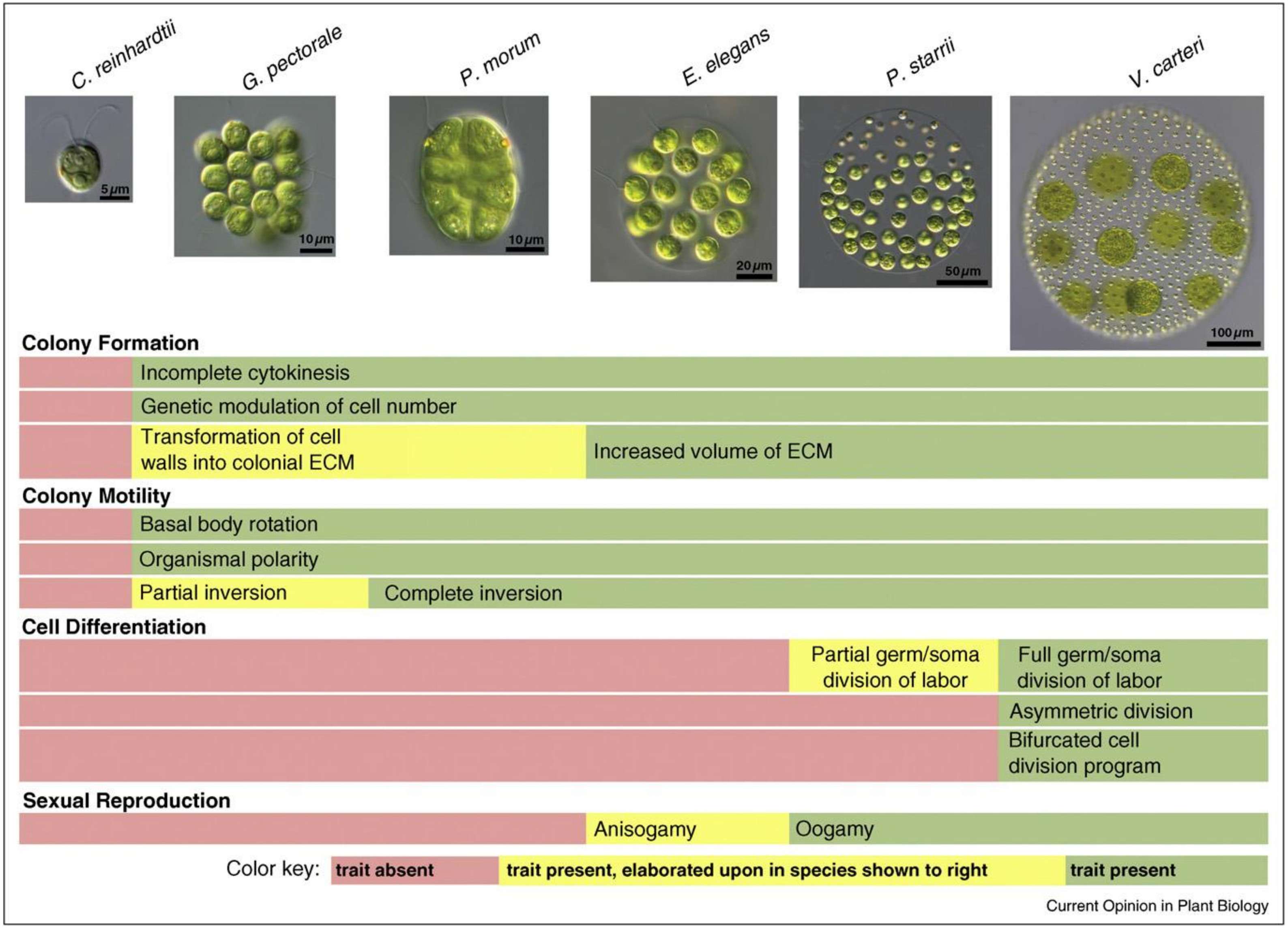
Table 1

Developmental traits that evolved in the volvocine algae[a]

Developmental traits	Description
Incomplete cytokinesis	Modified version of the *Chlamydomonas* multiple-fission cell division program, that leaves cells connected by cytoplasmic bridges at least through embryogenesis and therefore permits colony formation.
Partial embryo inversion (*Gonium*)	A reversal of cell-sheet curvature that occurs after cleavage to re-position flagellar ends of cells from the concave to the convex surface.
Full embryo inversion (in spheroidal volvocine species)	A reversal of sheet curvature whereby the embryo turns 'inside out', that occurs after cleavage and repositions flagellar ends from the interior to the exterior surface.
Basal body rotation	Reorientation of basal bodies that alters the 180° rotational symmetry they initially have after cell cleavage; occurs in 12 peripheral cells of the 16-cell *Gonium* colony and in all flagellated cells of spheroidal volvocine species, permitting flagella to beat in parallel, instead of backstroke fashion as they do in *Chlamydomonas*.
Organismal polarity	Refers to central/peripheral cell differences (*Gonium*; see above), and to anterior/posterior differences in features such as cell size and/or location of terminally differentiated somatic cells (spheroidal species).
Transformation of cell wall into ECM	Conversion of the homolog of the outer of two *Chlamydomonas* cell wall layers into either a connecting layer (*Gonium*) or boundary layer (spheroidal species) that holds all cells of the colony together.
Increased volume of ECM (*Eudorina*, *Pleodorina* and *Volvox*)	Expansion of the region that is homologous to the inner cell wall layer of *Chlamydomonas*.
Genetic modulation of cell number	Refers to the fact that maximum number of cell divisions is dependent on genetic factors, not environmental ones.
Partial germ-soma division of labor (in all species of *Pleodorina* and most species of *Volvox*)	Some cells express both somatic and gonidial fates, while others express only the somatic fate. All cells first differentiate as biflagellate somatic cells, but only a subset (located in the anterior region) remains differentiated, while all others de-differentiate and become gonidia.
Complete germ-soma division of labor (some *Volvox* species)	Every cell expresses a single fate, developing either as a somatic cell or as a gonidium.
Asymmetric division (a few *Volvox* species including *V. carteri*)	Unequal cleavage of a subset of blastomeres that generates large gonidial precursor cells.
Bifurcated cell division program (a few *Volvox* species including *V. carteri*)	In the species that generate large gonidial initials through asymmetric cell division, those gonidial precursor cells withdraw from cleavage after the 8th embryonic cleavage stage while all other cells (somatic initials) undergo 3–4 additional rounds of cell division.
Anisogamy (*Eudorina*)	Production of motile and unequal-sized gametes.
Oogamy (*Pleodorina* and *Volvox*)	Production of large immotile eggs and small motile sperm.

[a] Based on Kirk, 2005 (6).

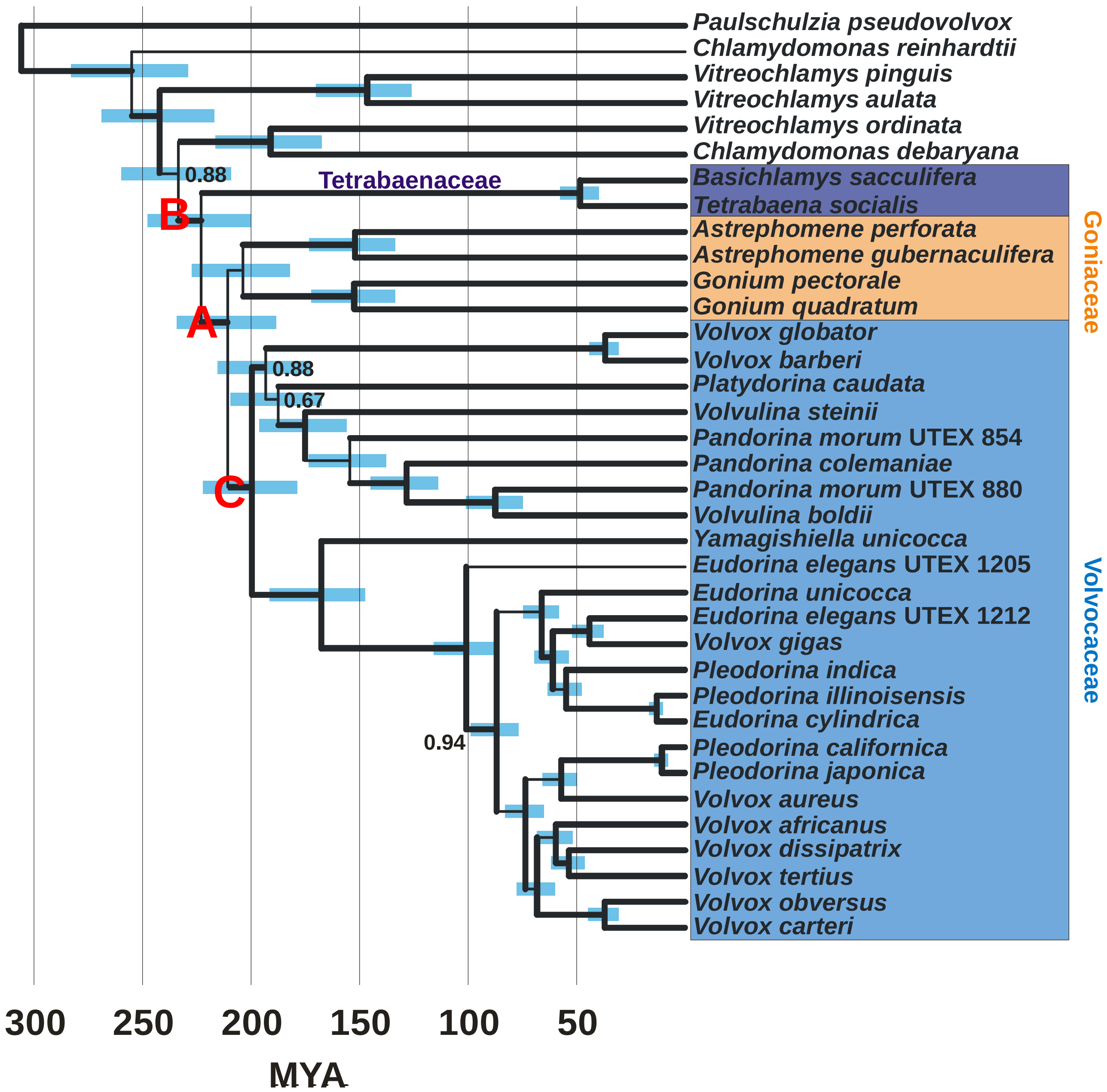
•From Nishii and Miller 2010

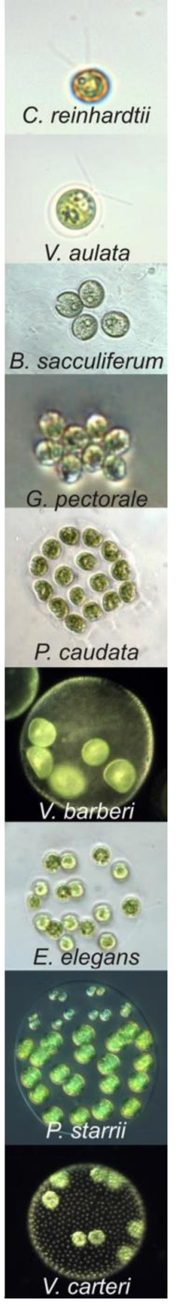


•From Nishii and Miller 2010

Steps to multicellularity

DEVELOPMENT

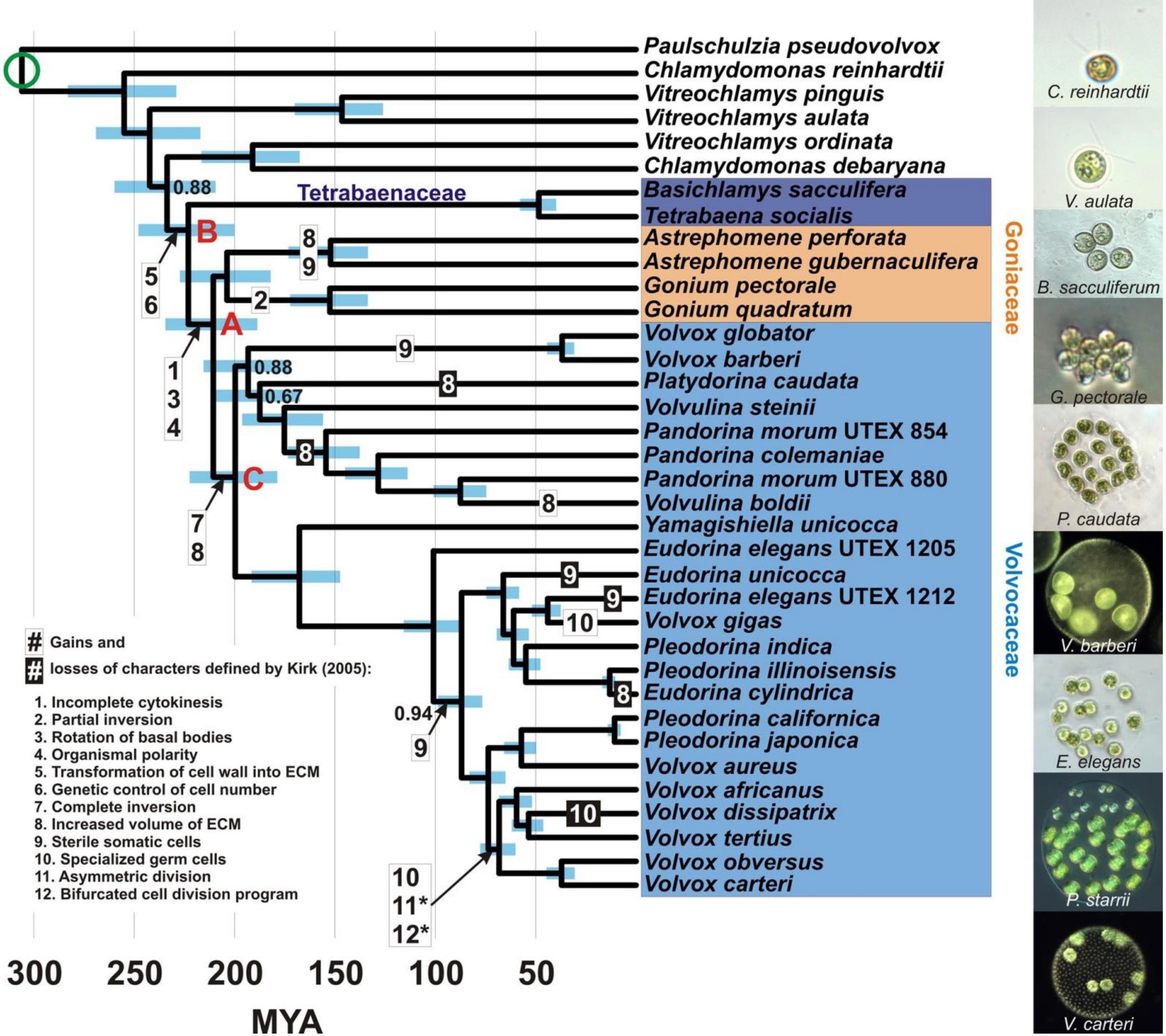




•Credit
M. Herron

Herron, M. D., et al. 2009. Triassic origin and early radiation of multicellular volvocine algae. *PNAS*, USA 106: 3254-3258

Herron, & Michod. 2008. Evolution of complexity in volvocine algae: transitions in individuality through Darwin's eye. *Evolution*. 262: 436-451



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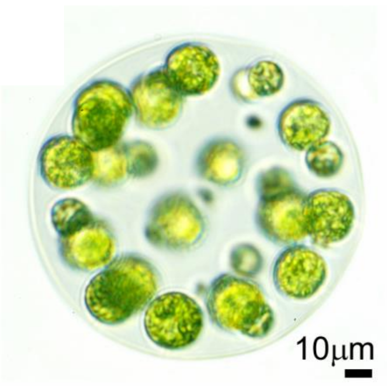
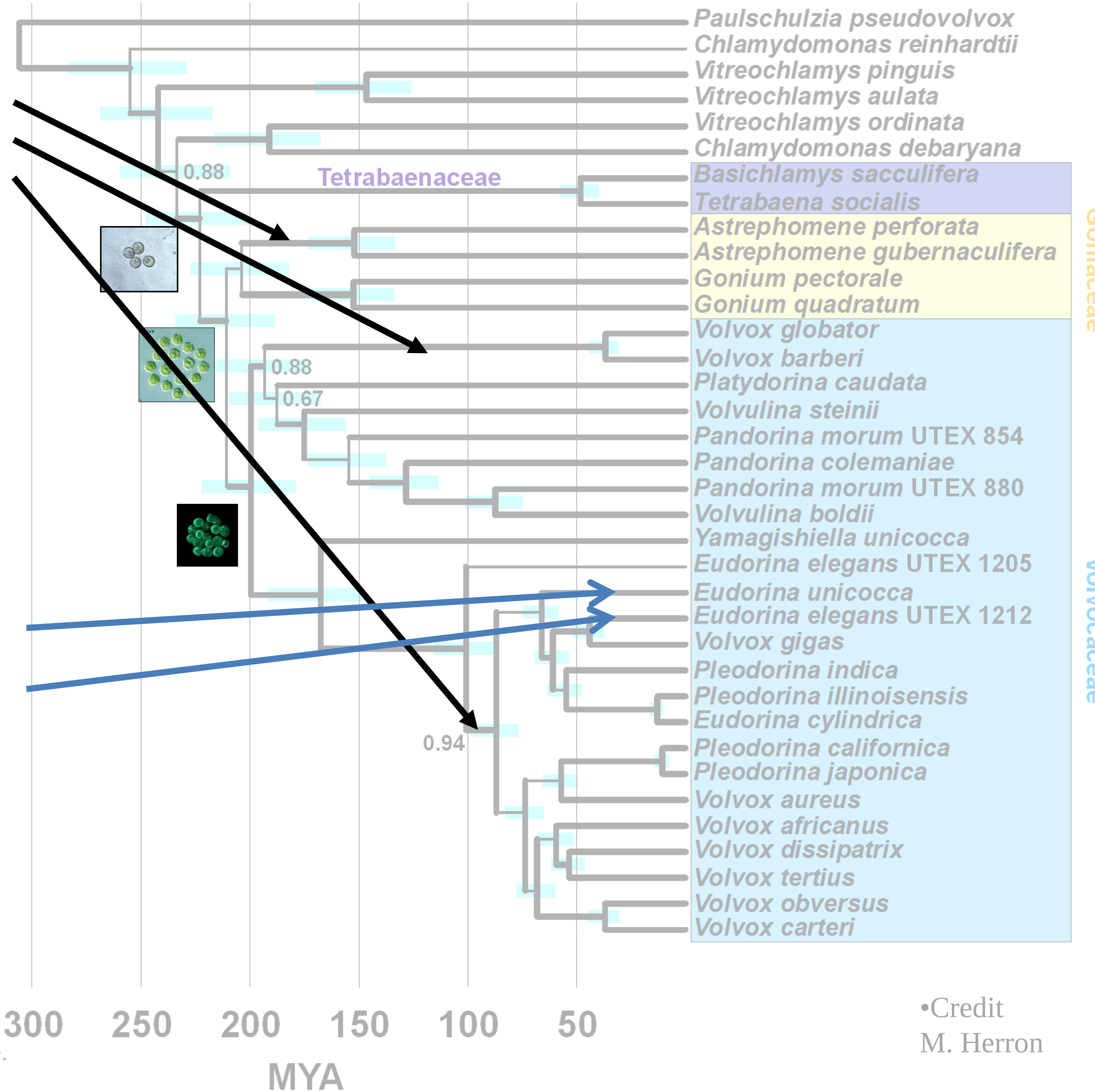
+ Sterile soma

- Sterile soma





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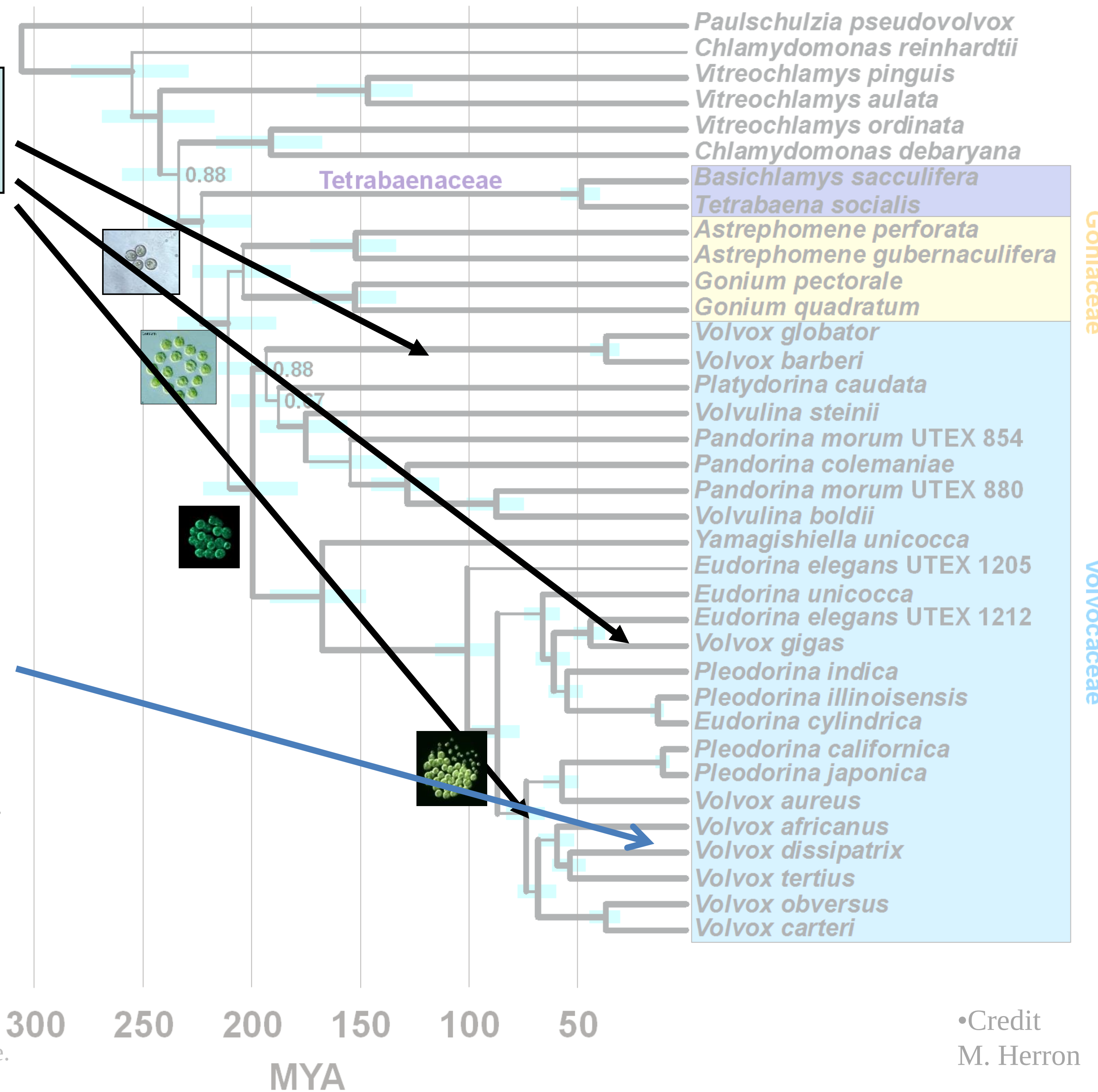
•Credit M. Herron

+ Specialized reproductive cells (germ)

- Specialized reproductive cells (germ)



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Herron, M.D. and R. E. Michod. 2008. Evolution of complexity in the volvocine algae: transitions in individuality through Darwin's eye. *Evolution*. 262: 436-451

•Credit M. Herron

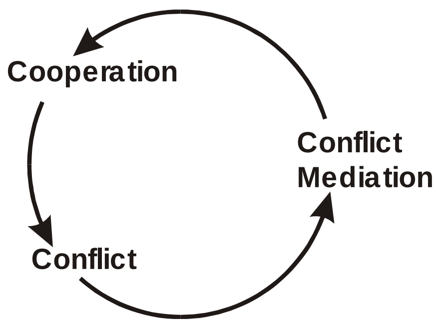
•Key innovation

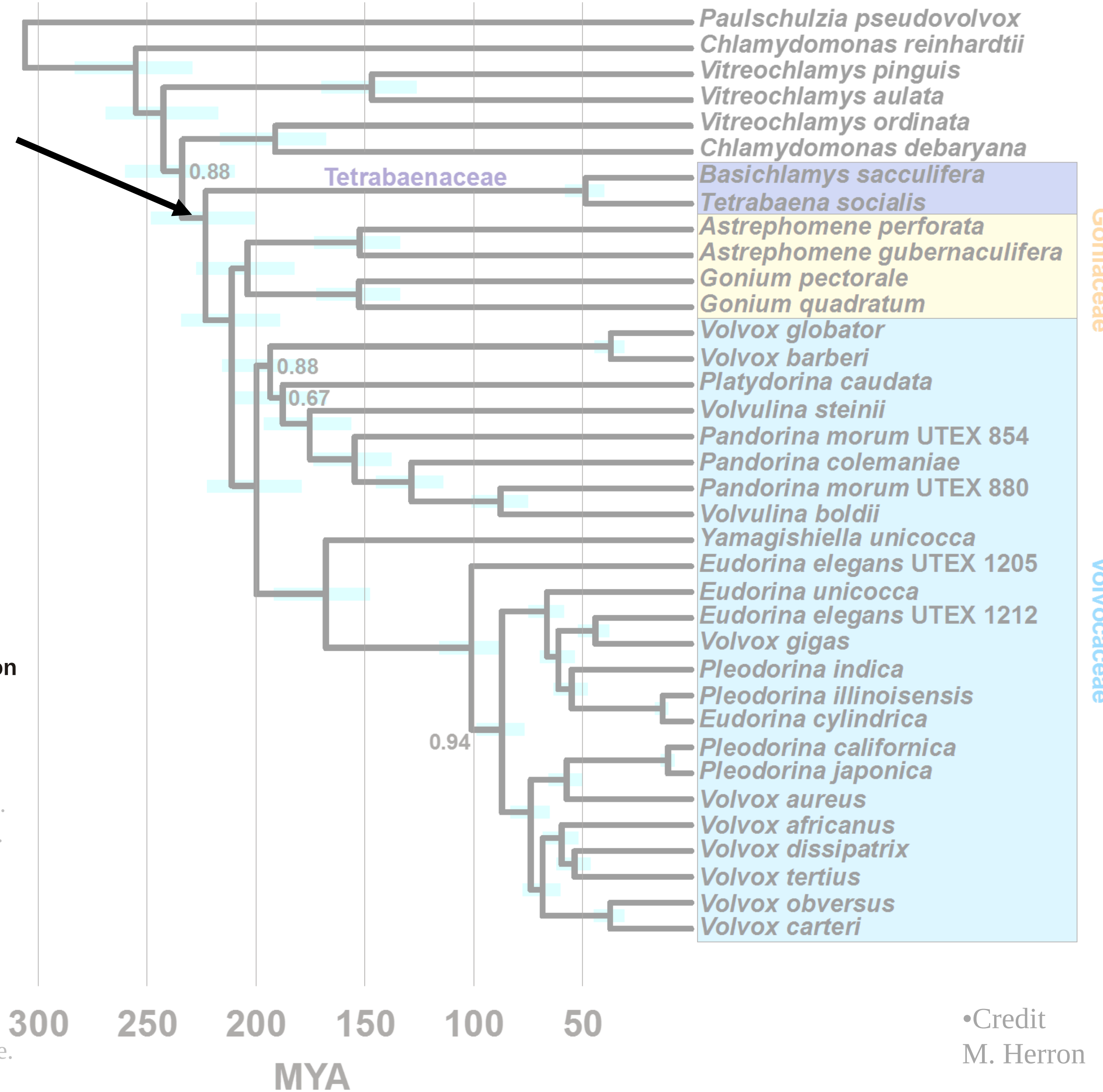
Transformation of cell wall into extracellular matrix

Genetic control of cell number

Cooperation = ECM

Conflict mediation= genetic control of cell number





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•Credit M. Herron

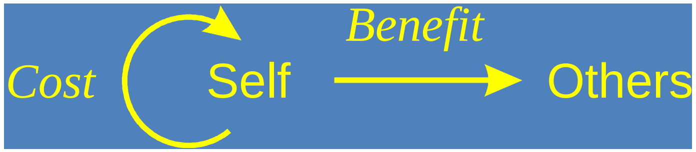
Conclusions

- The first and only complete timeline of an ETI
- Triassic origin of multicellular *Volvox*
- Early rapid radiation of multicellular volvocine algae
- Stasis of certain body forms
- Not progressive march to multicellularity but multiple gains and losses of key traits
- Phylogeny does not recapitulate ontogeny
- Multiple origins of specialized cells
  - Soma (reproductive altruism)
  - Germ (reproductive specialization)
- Early cycle of cooperation and conflict mediation
- Second cycle relating to soma and reproductive altruism

Fitness trade-offs and altruism and cheating in *Volvox*

REPRODUCTIVE ALTRUISM

Altruism

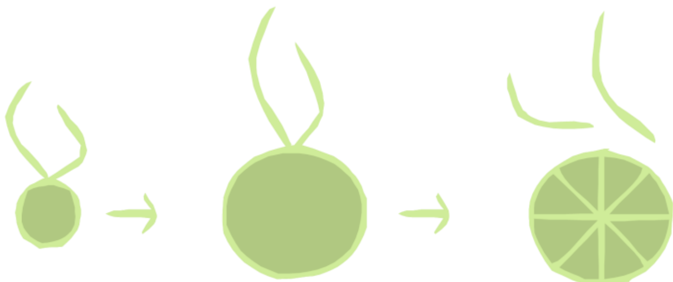


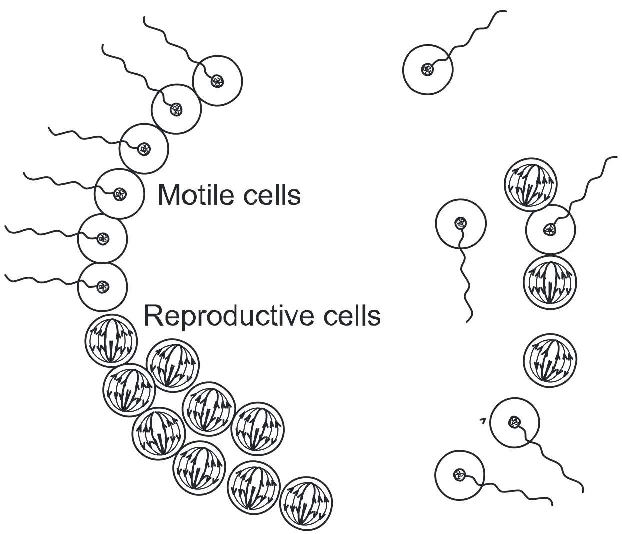
- Widely appreciated to be the central problem of social behavior

- Fundamental to evolutionary transitions in individuality
- Transfers fitness from lower to higher level
  - Costs reduce fitness at lower level
  - Benefits increase fitness at higher level

Cell Behavior	Level of Selection	
	Single cell	Cell group
Defection	+ replicate faster	- less functional
Cooperation	- replicate slowly	+ more functional

Fitness trade-offs → Altruism

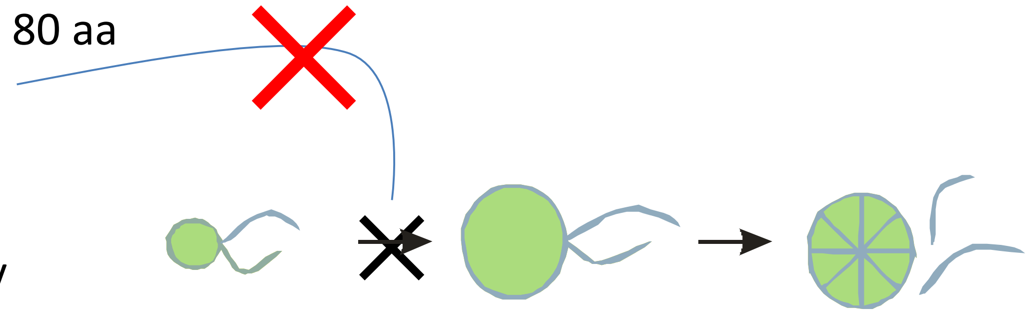


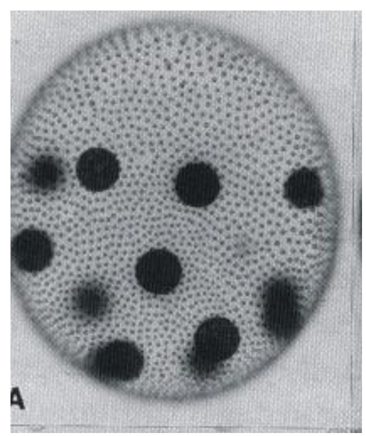


- Cells (lower level)
  - Two functions
    motile ➔ reproductive
  - Cells grow large and divide while losing flagella
  - Fitness trade-off between reproduction and motility
- Colony (higher level)
  - Motility & reproduction
  - Flagella = altruism

Altruism & cheating in *Volvox*

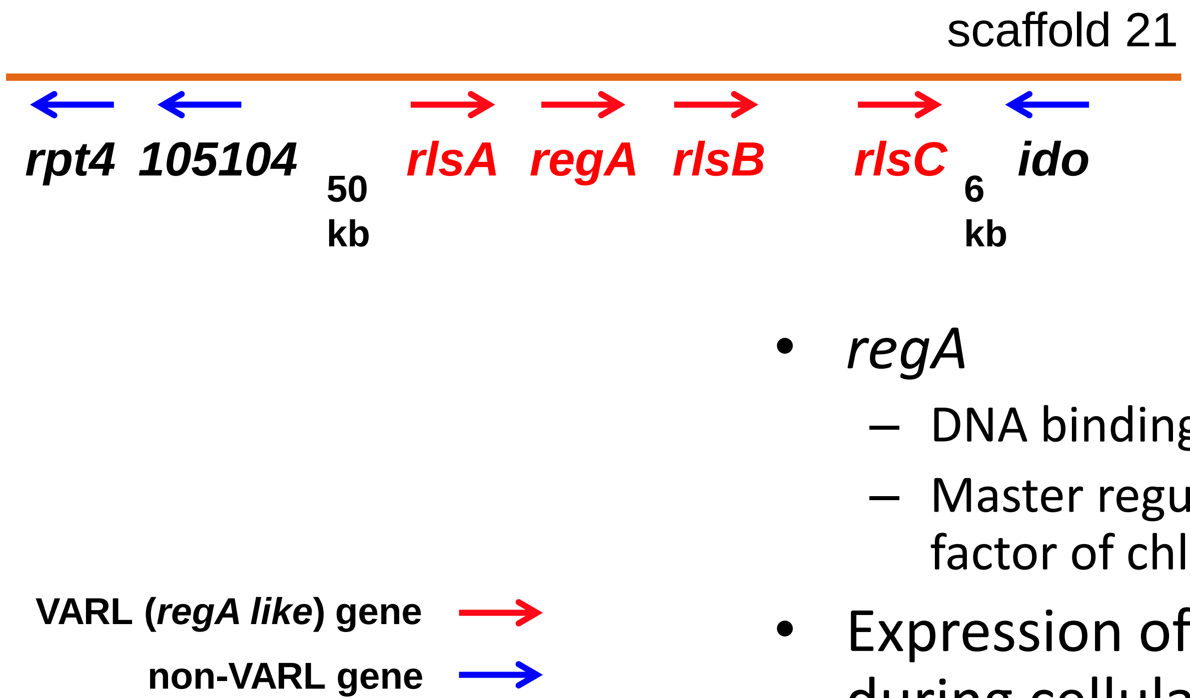
- *regA*
  - Master regulator transcription factor of chloroplast biogenesis
  - DNA binding SAND domain 80 aa
  - Keeps somatic cells small by starving them
  - Altruistic gene
  - Expressed developmentally
  - Selfish mutants, “reg” = regenerator





Pictures from Kirk, D. 1998

regA gene family in *V. carteri*



- *regA*
  - DNA binding SAND domain 80 aa
  - Master regulator transcription factor of chloroplast biogenesis
- Expression of gene family peaks during cellular differentiation
- Tandem duplications of *rlsD*
- *rlsD* ortholog of *Chlamy RLS1*

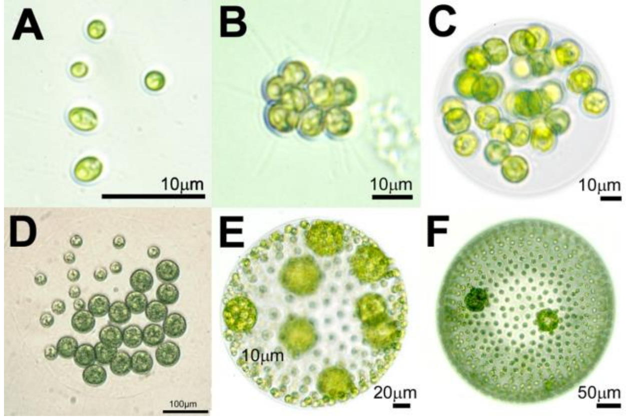
•Credit P. Ferris

Can the evolution of *regA* be traced back to the undifferentiated or unicellular ancestors? If so, what was its function?

EVOLUTION OF REGA GENE FAMILY

Approach and Methodology

- Genomics
  - *Chlamydamonas*
  - *Volvox carteri*
  - *Gonium* (submitted)
  - *Pleodorina* (in prep)

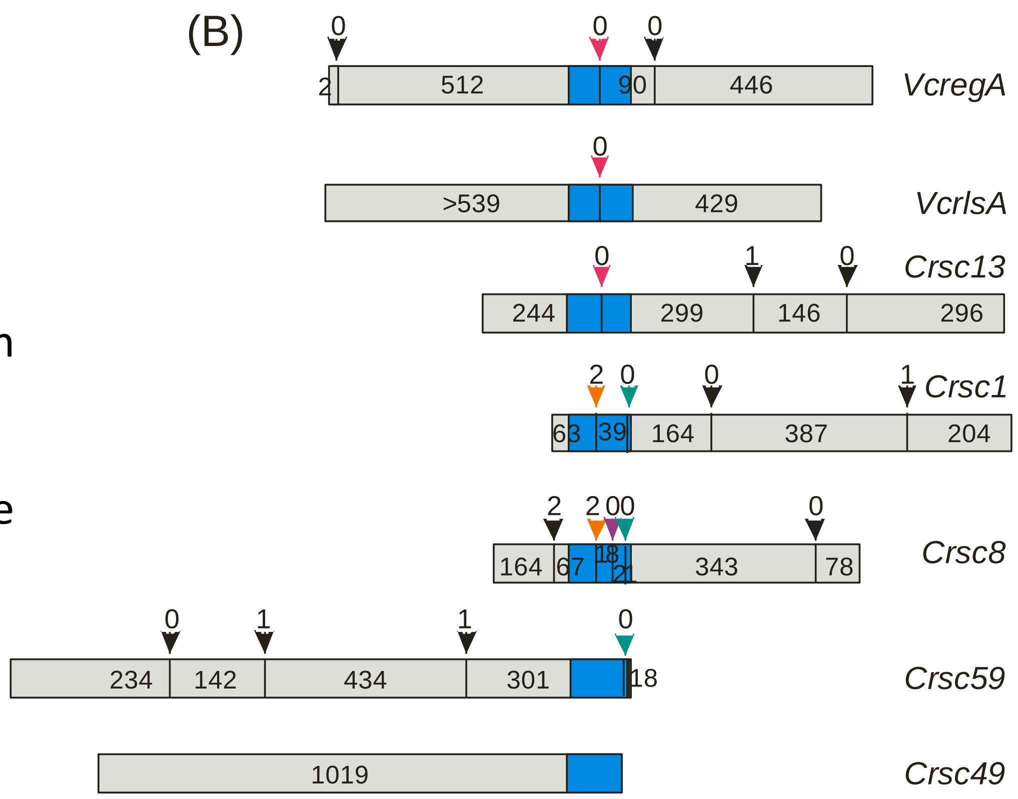


Picture credit: C. Solari and M. Herron

- PCR
  - Use degenerate primers for genomic PCR to clone portions of *regA* family VARL genes in diverse volvocine species
  - Create hybridization probes from the PCR clones and screen cosmid libraries from the two species
  - Sequence cosmids

Origin of *regA*: Search for *regA*-like genes in a uni-cellular relatives

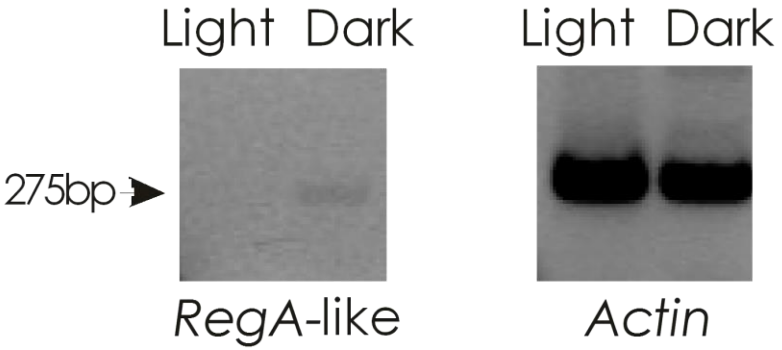
- Search *C. reinhardtii* genome
- Multigene family of *regA*-like genes
- Widely diverged except for a conserved 80-aa VARL region similar to SAND domain which functions in DNA binding and transcriptional control
- Gene in unicell co-opted to be *regA*?
- Why should a unicellular organism suppress its own reproduction?
- Life history perspective



Nedelcu A.M., Michod R.E. (2006). The evolutionary origin of an altruistic gene in *Volvox carteri*. *Molecular Biology and Evolution*. 8:1460-1464.

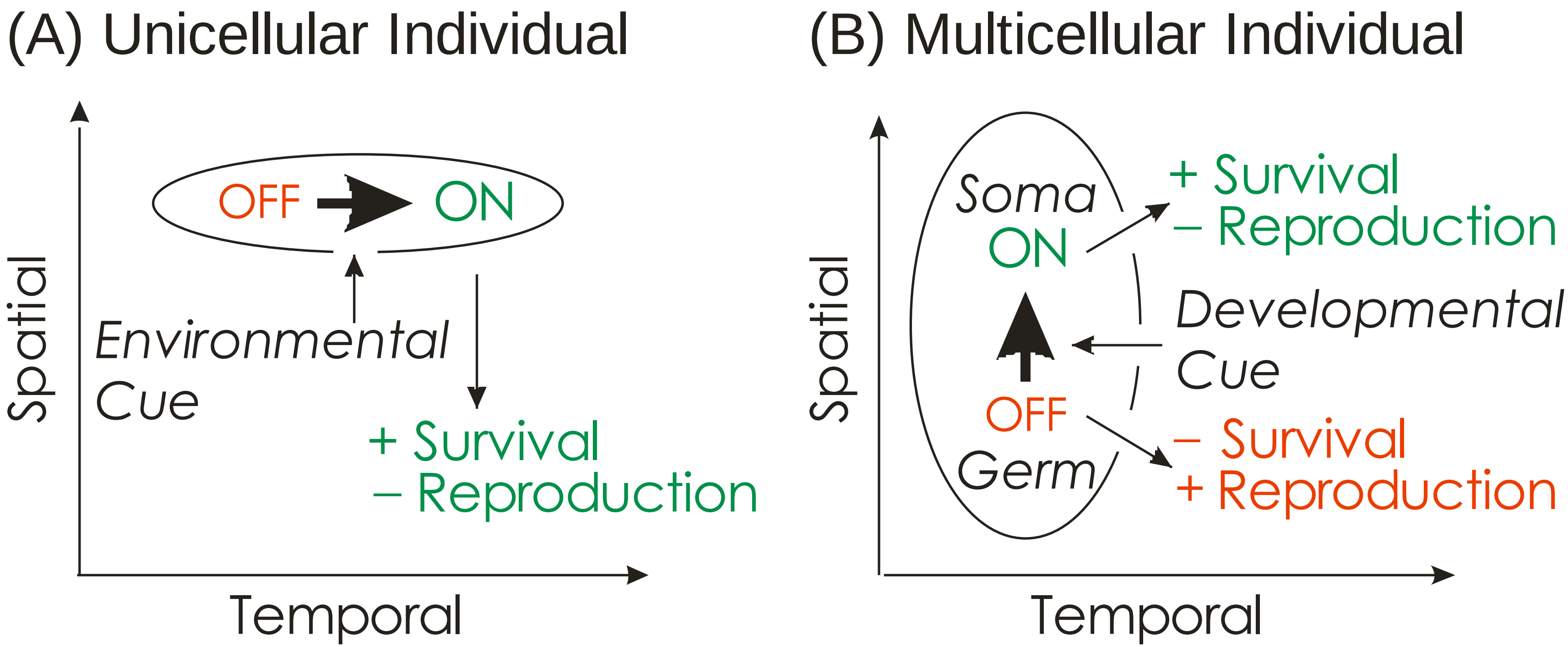
In what environments should reproduction be suppressed?

- Expressed? No ESTs similar. Pseudogene?
- Chloroplasts needed for growth & reproduction
- Why invest in chloroplasts in dark?
- *RegA*-like on in dark
- Gene for chloroplast protein off in dark



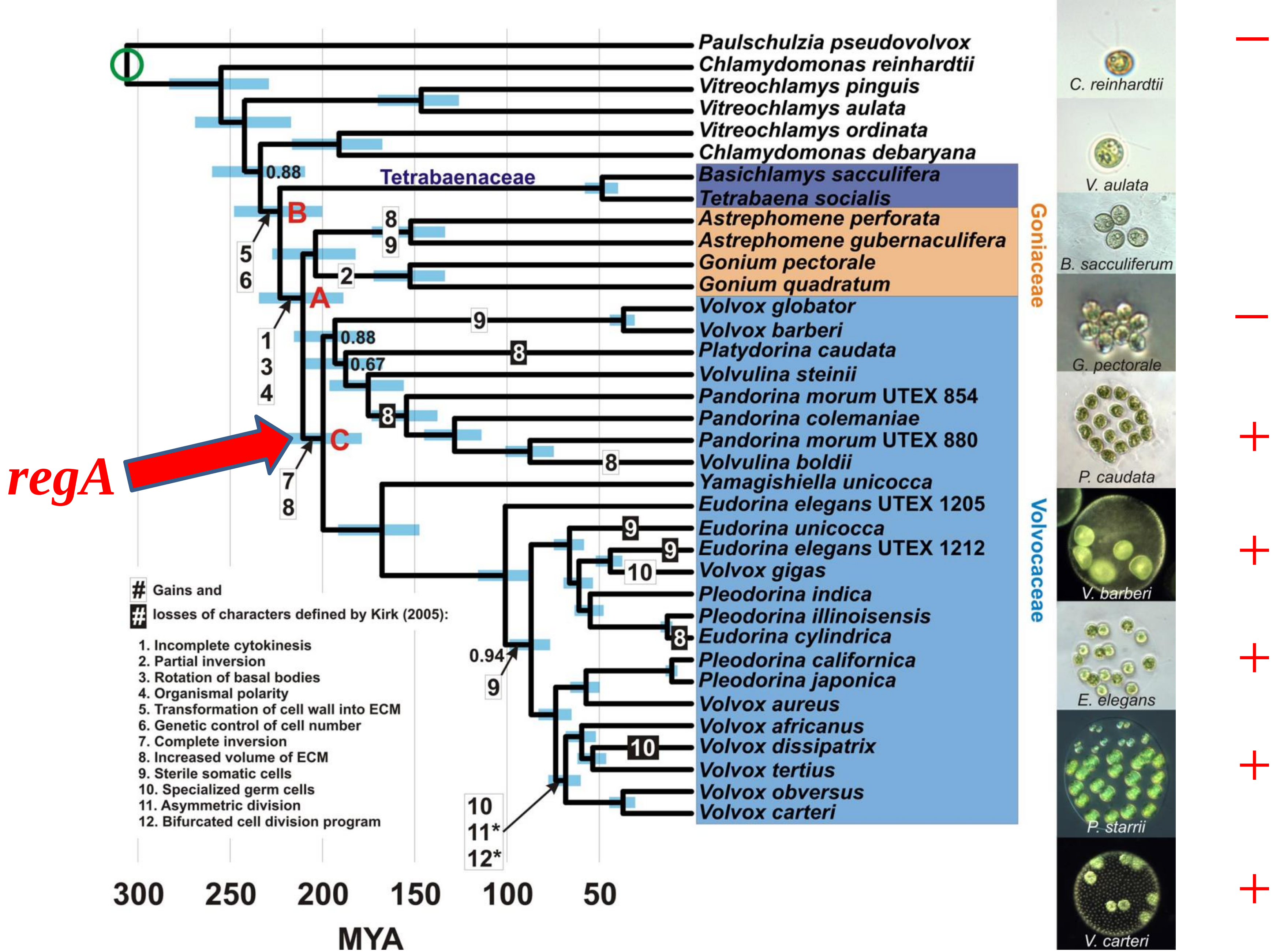
Nedelcu A.M., Michod R.E. (2006). The evolutionary origin of an altruistic gene in *Volvox carteri*. *Molecular Biology and Evolution*. 8:1460-1464.

Hypothesis: Gene for reproductive altruism originates via co-option of life history gene



"Spatial" means within a cell group

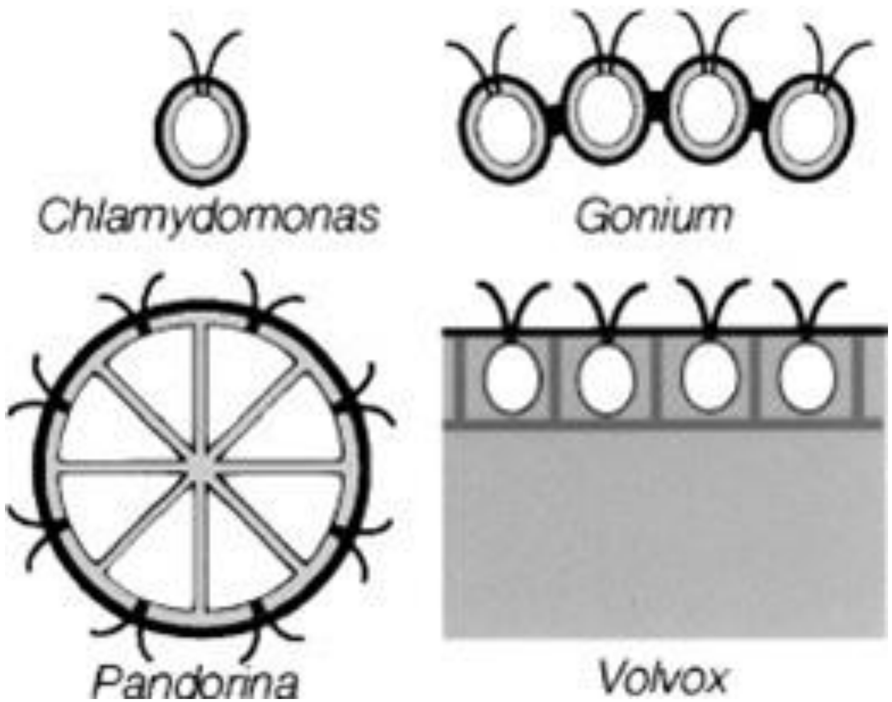
Nedelcu A.M., Michod R.E. (2006). The evolutionary origin of an altruistic gene in *Volvox carteri*. *Molecular Biology and Evolution*. 8:1460-1464.



Herron, M. D., et al. 2009. Triassic origin and early radiation of multicellular volvocine algae. *PNAS*, USA 106: 3254-3258

Herron, & Michod. 2008. Evolution of complexity in volvocine algae: transitions in individuality through Darwin's eye. *Evolution*. 262: 436-451

Commitment to Group Living



Picture Credit: D. Kirk. 2005

Conclusions

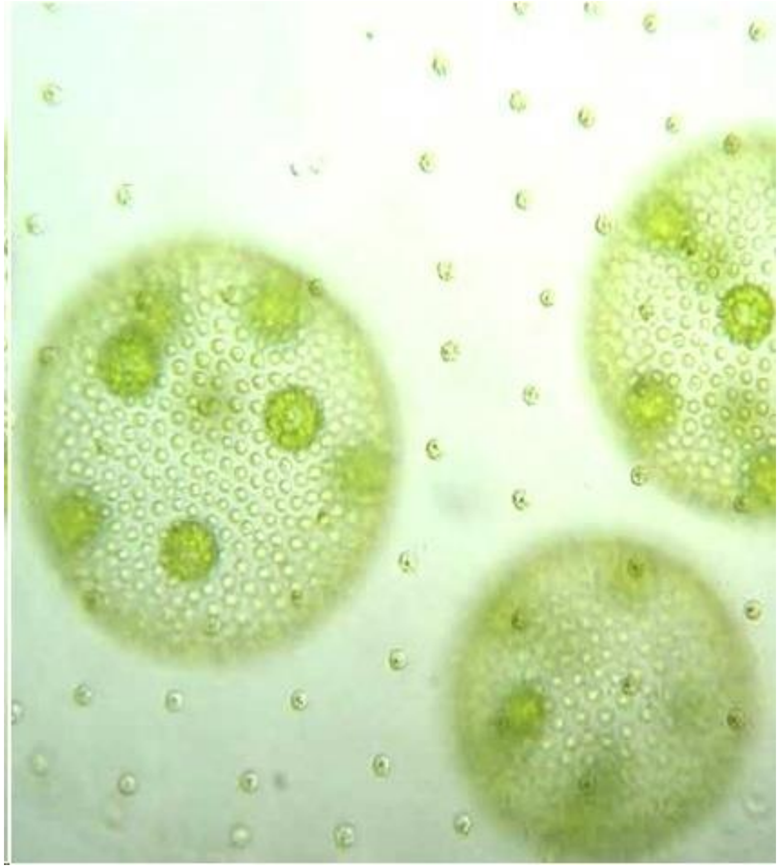
- Species have genetic basis for soma, but don’t have soma
  - Lack greater individuality & complexity that soma could create
- Species may lose soma but retain genetic basis
  - Soma is reversible
- What are *regA*-like genes doing in species without soma?
  - Involved in group life cycle?
- Soma evolved through changes in the genotype-phenotype map
  - Zach Grochau-Wright: *regA* transformation experiments

Life History Evolution

COST OF REPRODUCTION

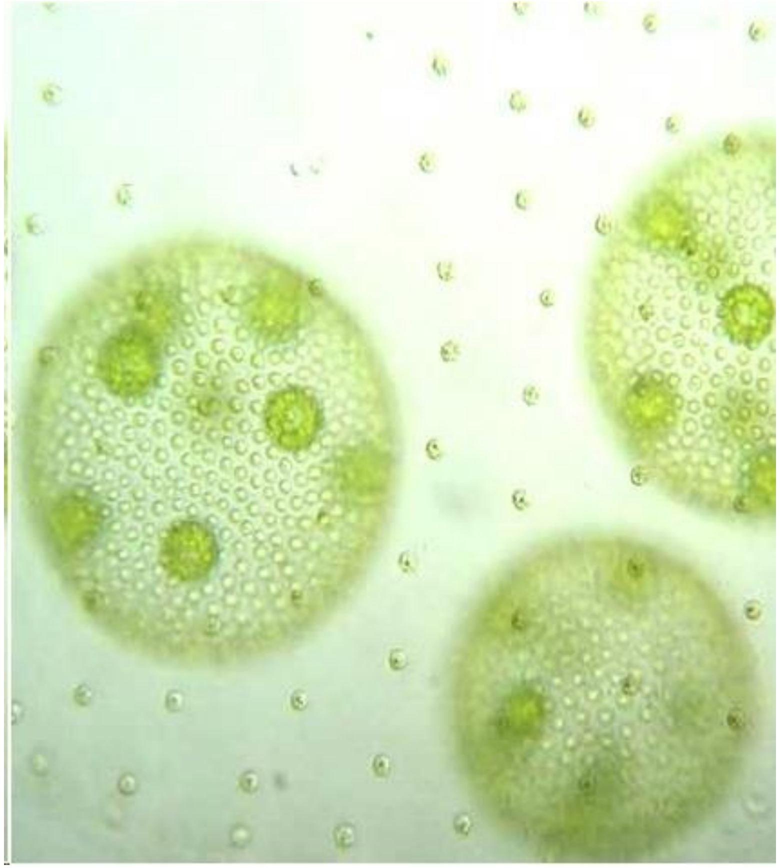
Cooperation: How? and why?

- <u>How</u> can a gene for reproductive altruism arise?
  - Co-option of life history gene
- <u>Why</u> does reproductive altruism evolve?
  - Kin selection
  - Reproductive altruism only in the larger species
  - Costs of larger size

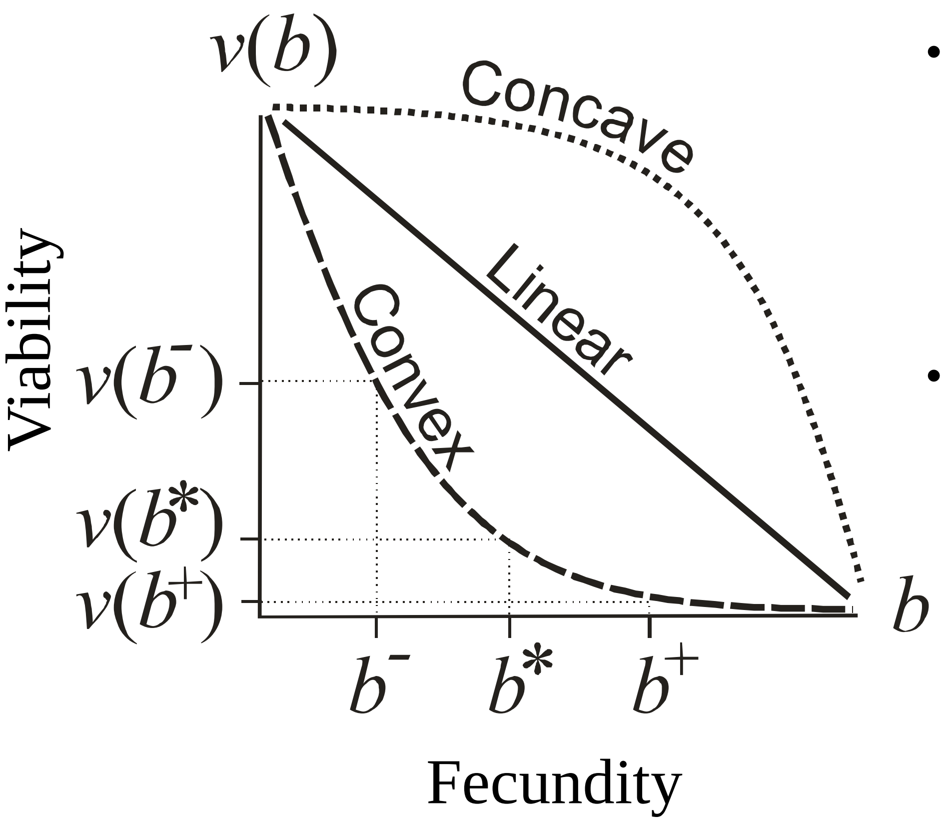


Cost of reproduction to survival increases with colony size

- Survival = flagellar action
  - Motility
  - Mixing
- Assume bigger is better, but there are costs
- Costs of reproduction to survival
  - Hydrodynamic drag
  - Flagellation constraint
    - Cannot be motile and reproduce
    - > 32 cells
- Costs paid by soma



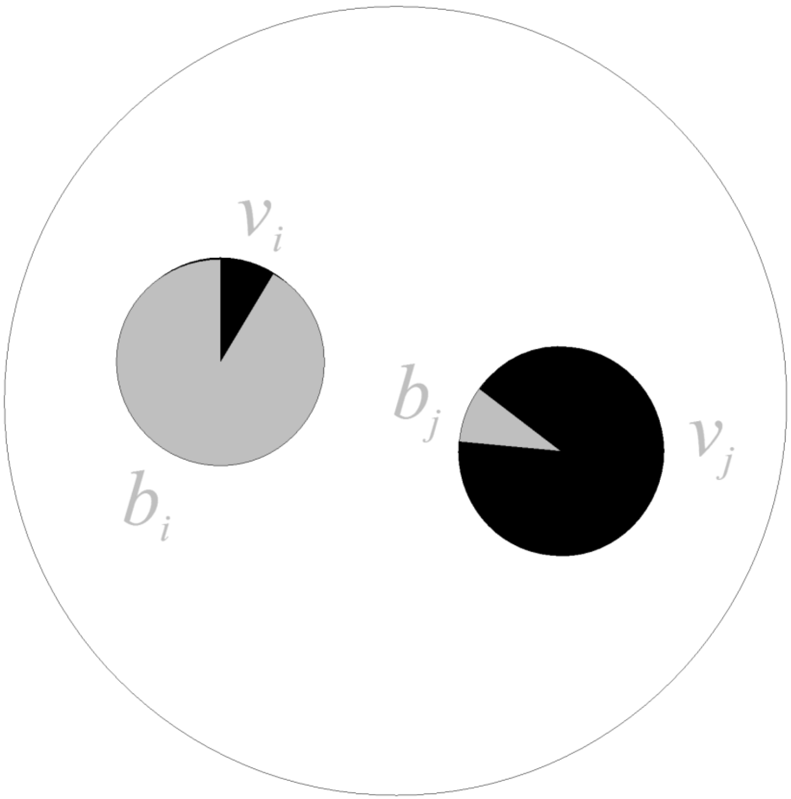
Specialization Depends on Curvature of Trade-off Function



- Linear
  - Same return no matter what effort
- Concave
  - Increasing viability cost
  - 2 cells with different fecundities that jointly adjust their fecundity to be in the middle maintain the same fecundity for the group but increase group viability
- Convex
  - Decreasing viability cost
  - 2 cells that jointly increase and decrease their fecundity by the same amount maintain the same fecundity for the group but increase group viability

$$v\left(b^{-}\right)+v\left(b^{+}\right)>2v\left(b^{*}\right)$$

Good Team



- Group advantage emerges from variance in fitness components at lower level
- First integrative effect
- Generalized into "covariance effect"

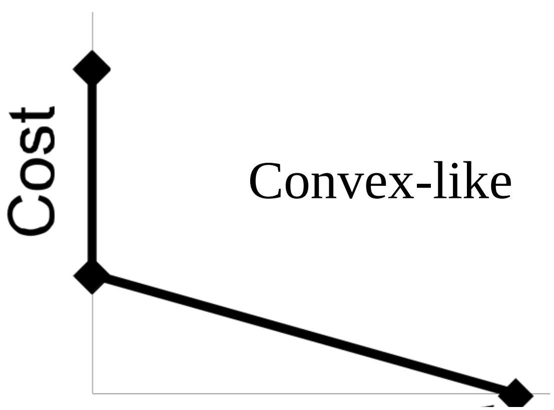
Michod RE (2006) The group covariance effect ….
Proc Natl Acad Sci USA 103: 9113–9117.

Initial cost of reproduction to flagellar force in *V. carteri* mutants

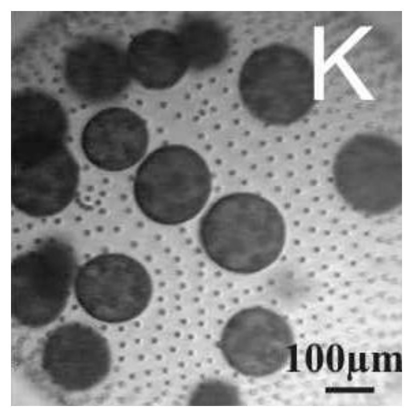
Forms	PIC	Colony	N	Change	*f* (dynes)
wt	K	G/S	2202		8.0 x 10^{-8}
regA$^-$	L	G/GS	239	235S→GS	4.9 x 10^{-8}

Credit: C. Solari

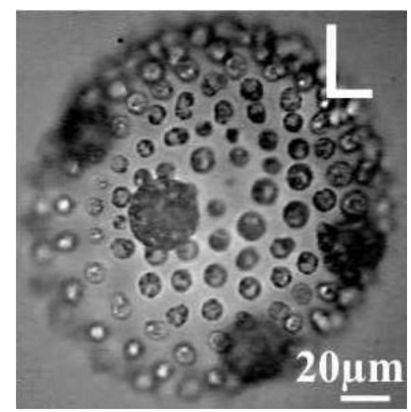
viability



fecundity



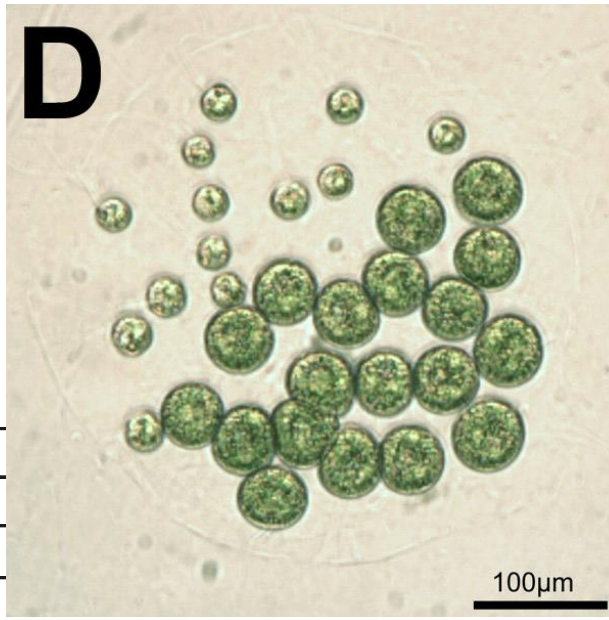
wild type



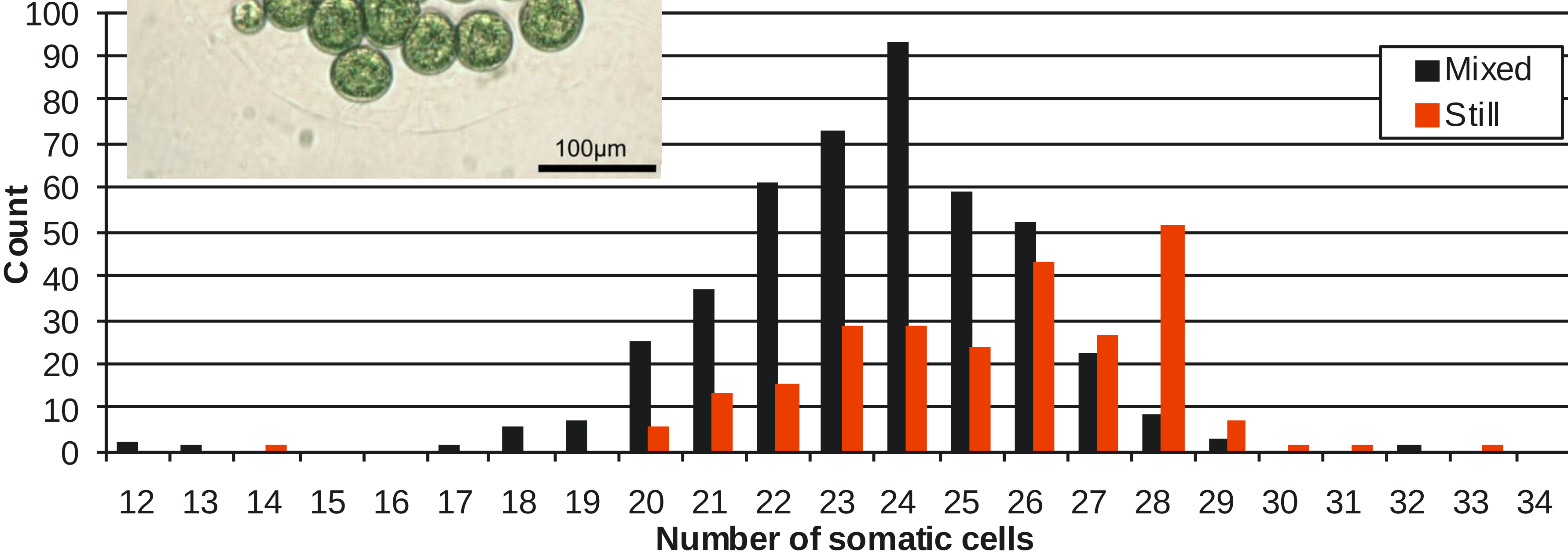
regA-

Michod, R.E. 2007. Evolution of individuality during the transition from unicellular to multicellular life. *PNAS*.104: 8613-8618.

Artificial selection on body size

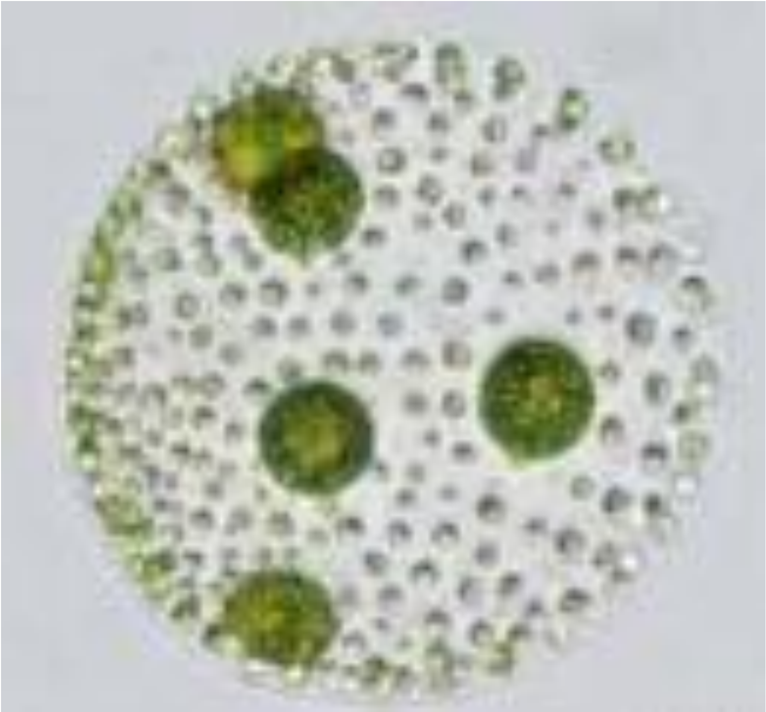


- Trade-off acute > 32 cells
- *P. starrii*
- 64 celled colonies



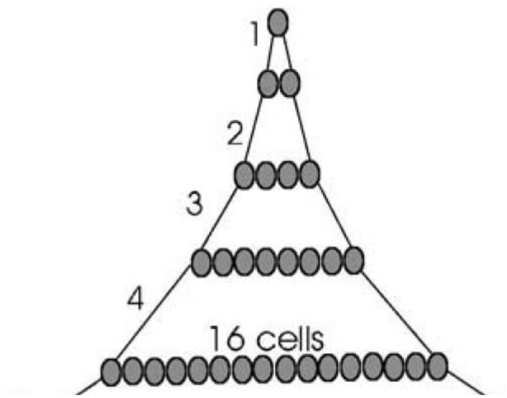
•Credit M. Herron

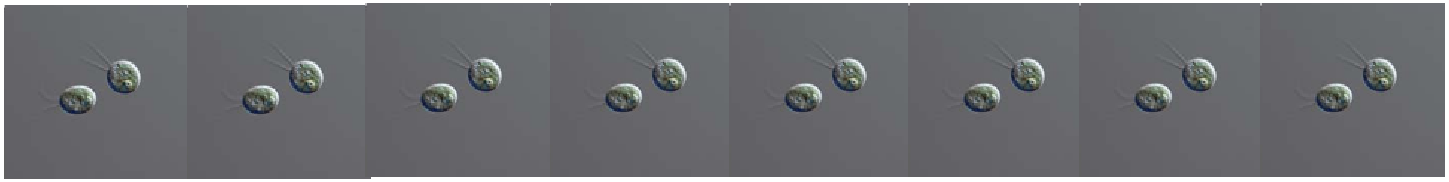
Evolutionary transition in individuality (ETI)



Slide credit D. Shelton

Cell division …



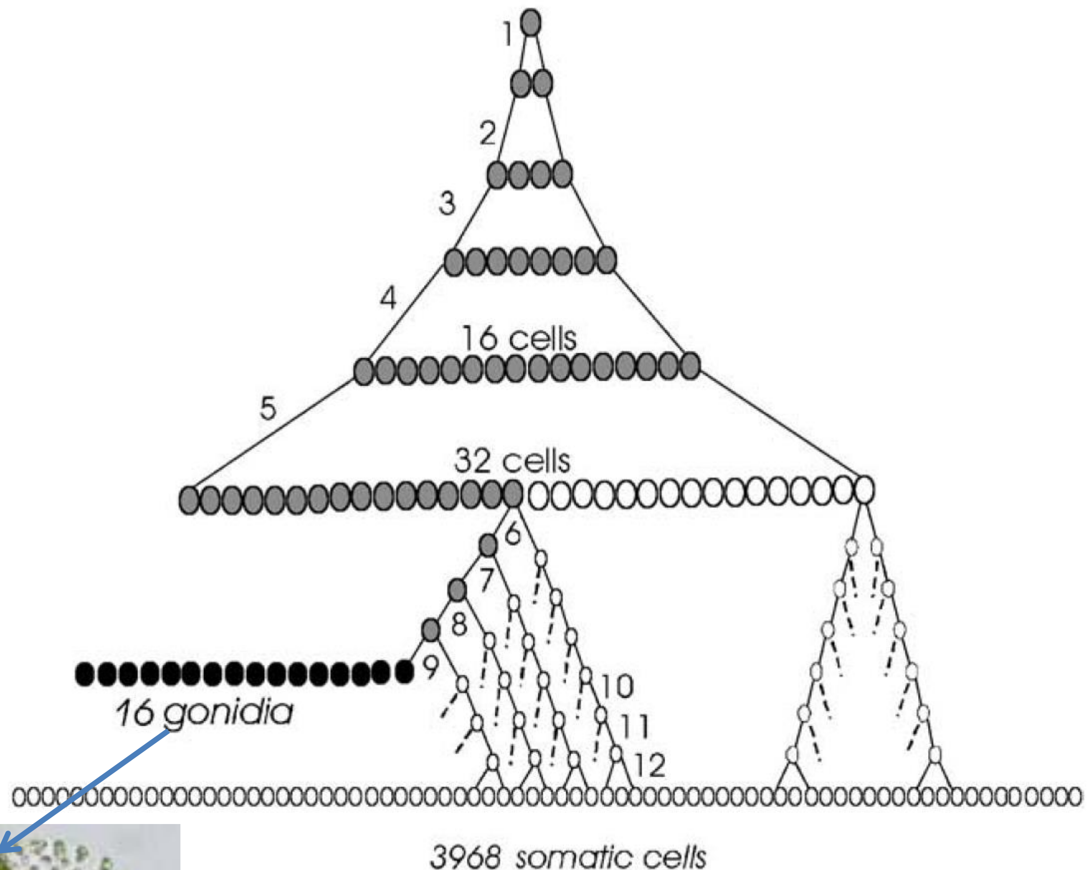


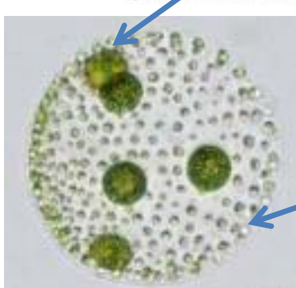
- ... makes offspring cells
- Cell division for reproduction

•Michod, R. E., A. M. Nedelcu, and D. Roze. 2003. Cooperation and conflict in the evolution of individuality IV. Conflict mediation and evolvability in Volvox carteri. *BioSystems* 69:95-114.

Slide credit D. Shelton

Cell division becomes part of organism reproduction

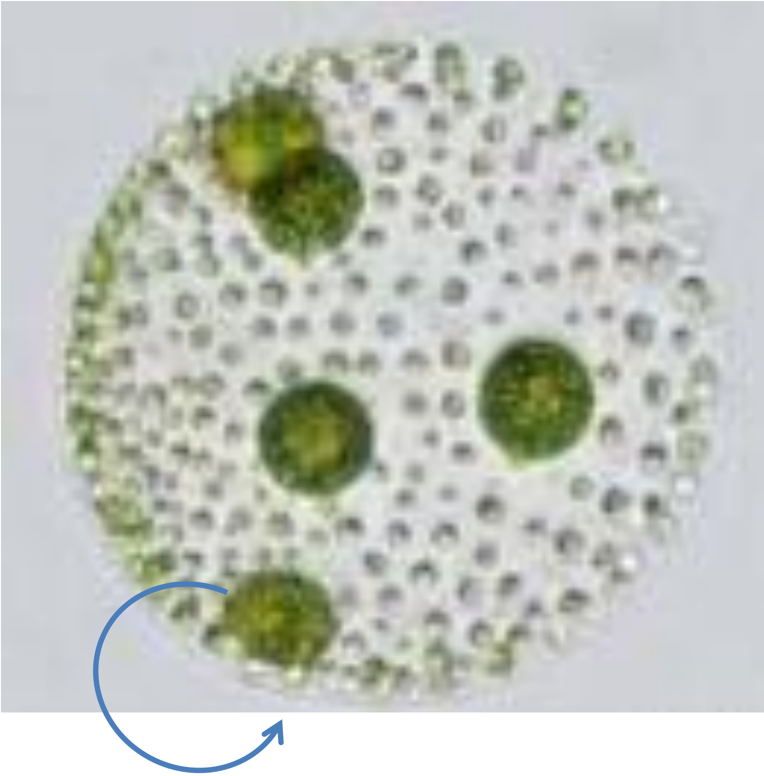




Slide credit D. Shelton

•Michod, R. E., A. M. Nedelcu, and D. Roze. 2003. Cooperation and conflict in the evolution of individuality IV. Conflict mediation and evolvability in Volvox carteri. *BioSystems* 69:95-114.

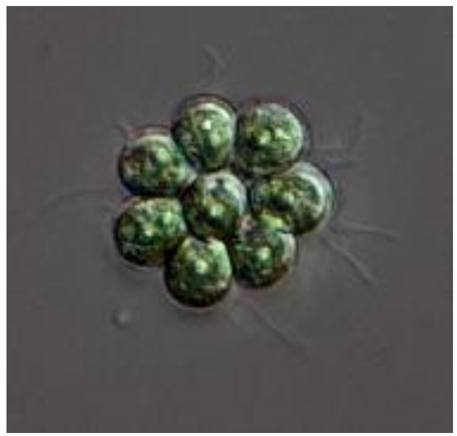
Changing role of cell divisions

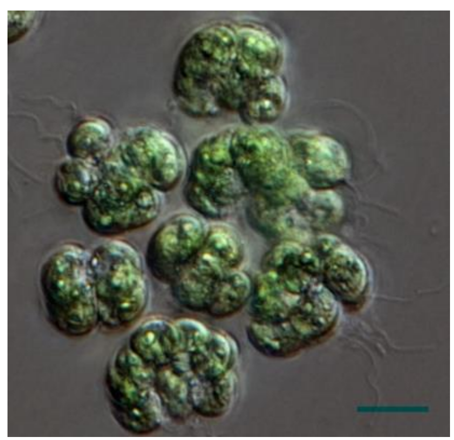


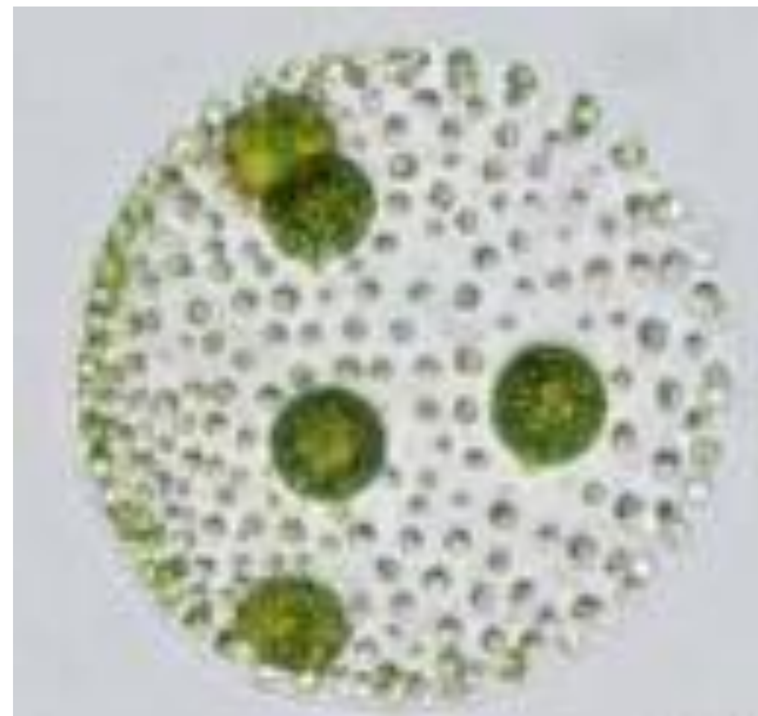
- Cell division for growth of multicellular organism
- Cell division coupled to group reproduction

Slide credit D. Shelton

Changing role of cell divisions: volvocine intermediates

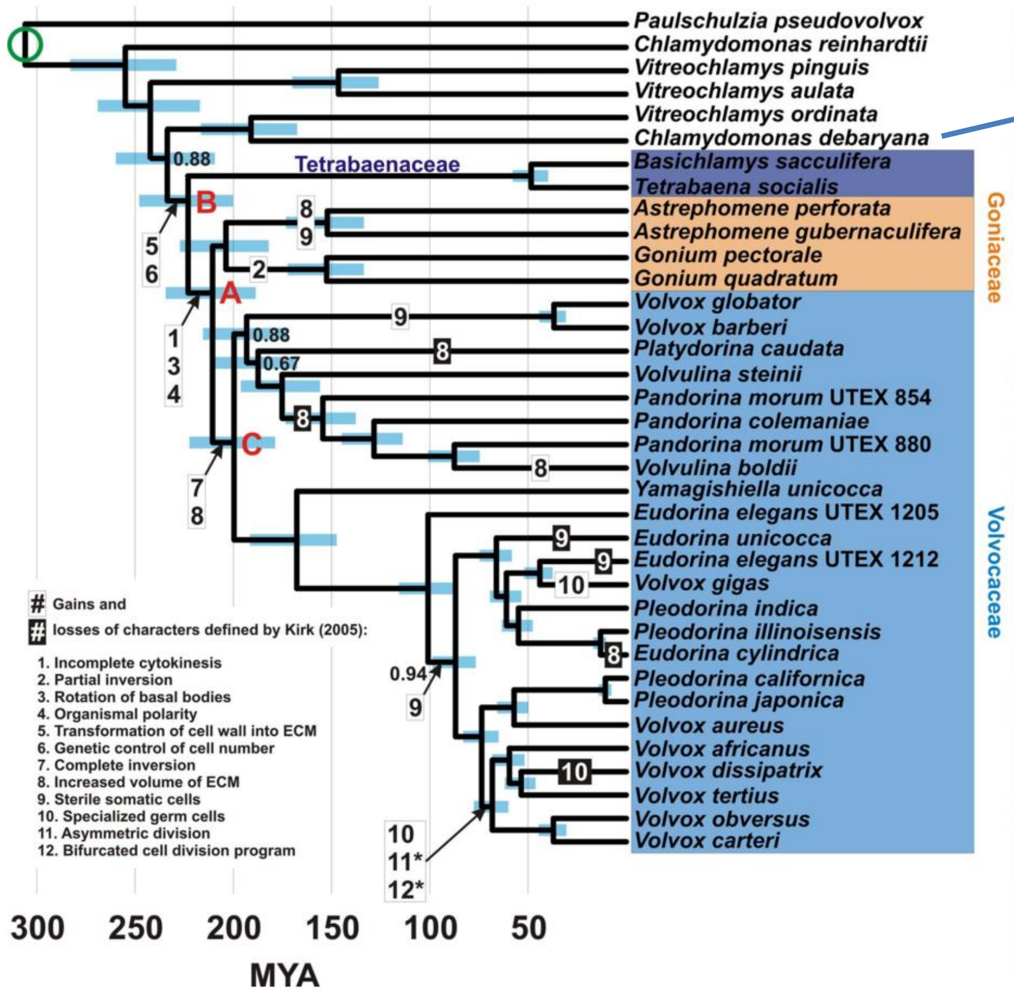


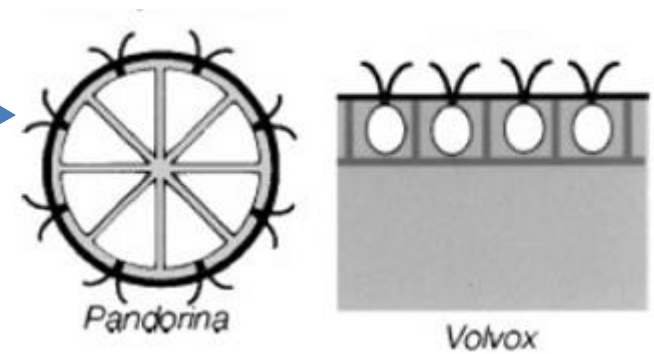




Slide credit D. Shelton

Changing role of cell divisions: volvocine intermediates



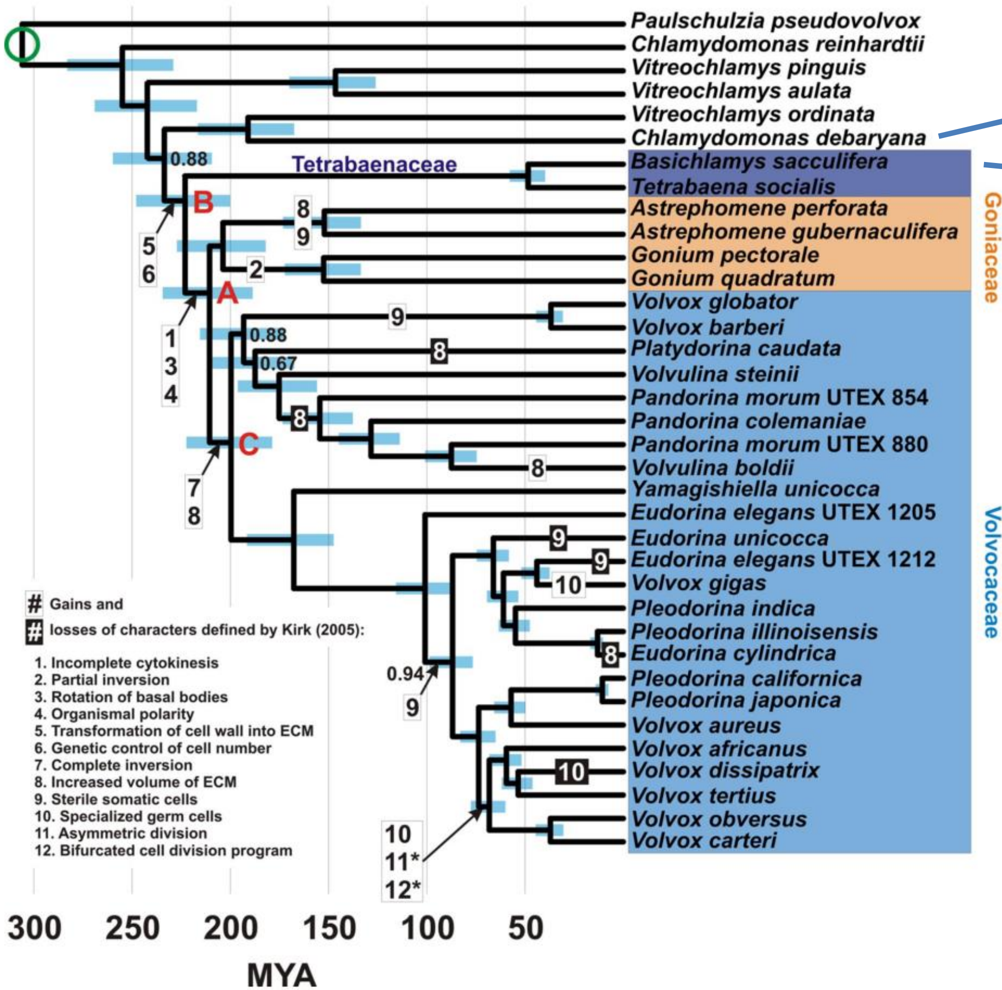


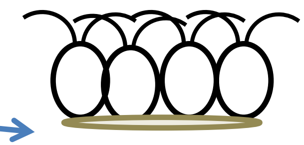
- Kirk, D.L. (2005) A twelve-step program for evolving multicellularity and a division of labor. Bioessays 27, 299–310

- Herron, M. D., Hackett, J. D., Aylward, F. O., & Michod, R. E. (2009). Triassic origin and early radiation of multicellular volvocine algae. Proceedings of the National Academy of Sciences, USA, 106(9), 3254-3258.

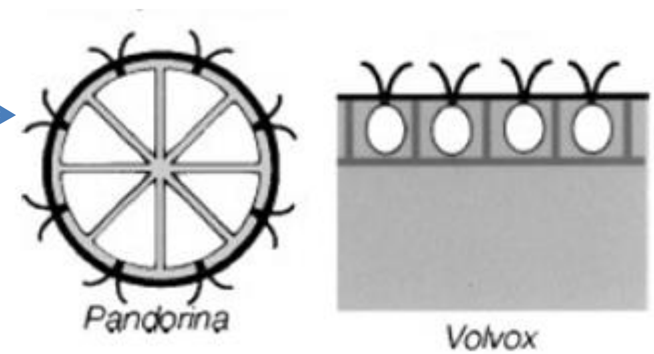
Slide credit D. Shelton

Changing role of cell divisions: volvocine intermediates





•*Basichlamys*



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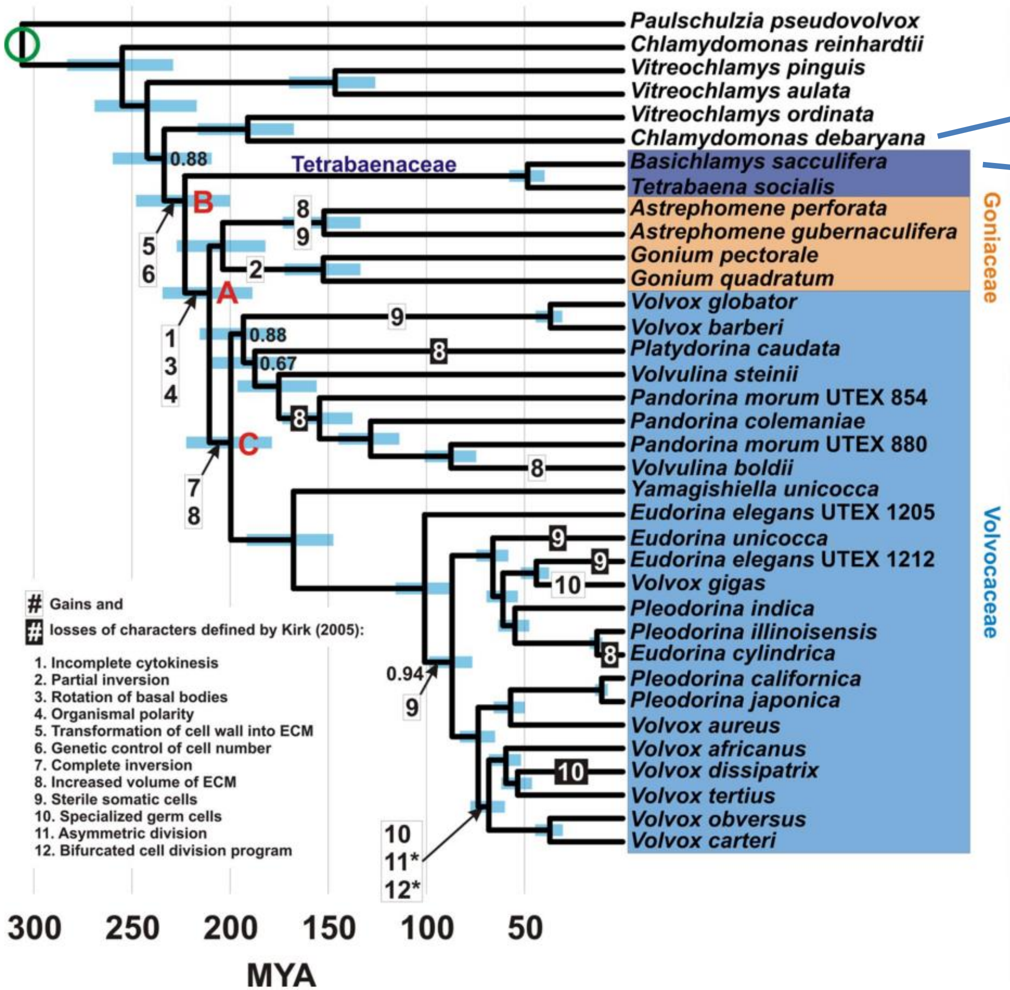
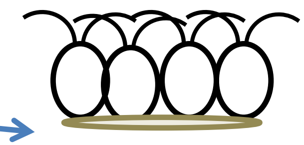
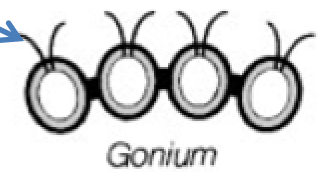
Slide credit D. Shelton

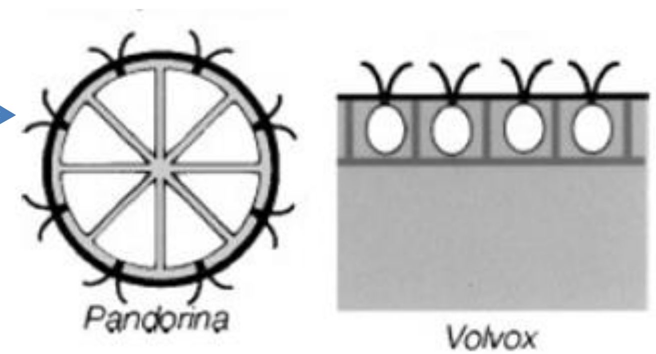
Changing role of cell divisions: volvocine intermediates





Basichlamys





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Slide credit D. Shelton

Overarching motivation and question

- Evolution of life cycles in the “simplest” volvocine algae is a window into how reproduction can shift from a lower to a higher level of organization

- How did the cell cycle and its regulation change in the early evolution of colonial volvocines?

Slide credit D. Shelton

How do groups acquire the capacity to reproduce other groups?

ORIGIN OF A GROUP LIFE CYCLE

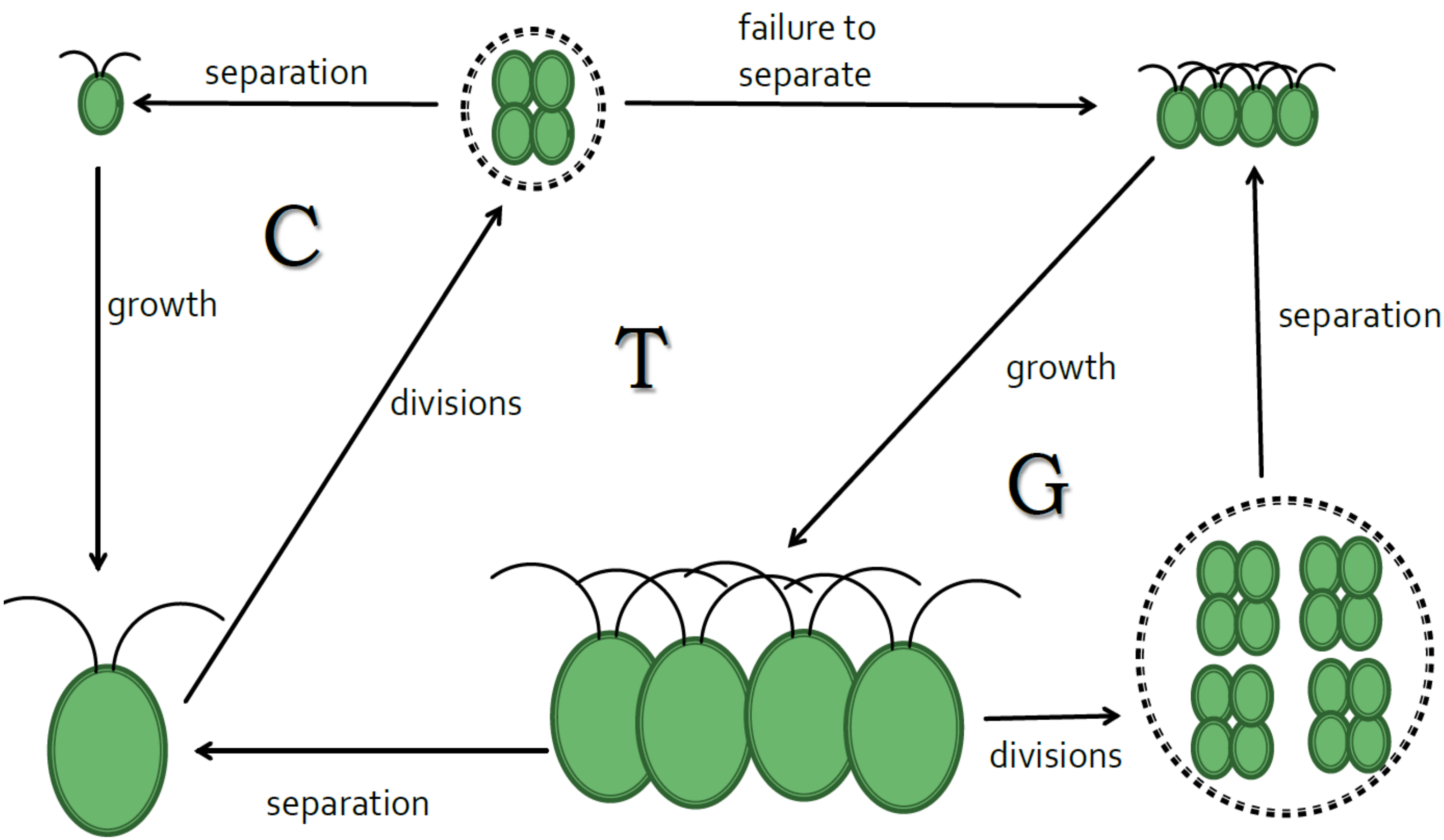
Origin of group reproduction

- Maynard Smith and Szathmáry (1995):
  - *entities that were capable of independent replication before the transition can replicate only as part of a larger whole after it*
- Thus reproduction at the group level is a central issue for the emergence of a new level of individuality
- How can groups acquire the capacity to reproduce?
- Origin of a group life cycle

Chicken-egg problem with origin of group reproduction

- Traits related to reproduction at the group level often appear both to be a result of and a prerequisite for natural selection at the group level
- Paul Rainey: *how can the first groups evolve by natural selection, given that the first groups are seemingly unable to participate in the process of evolution by natural selection, because they are unable to leave offspring?*

Steps to multicellularity – life cycles

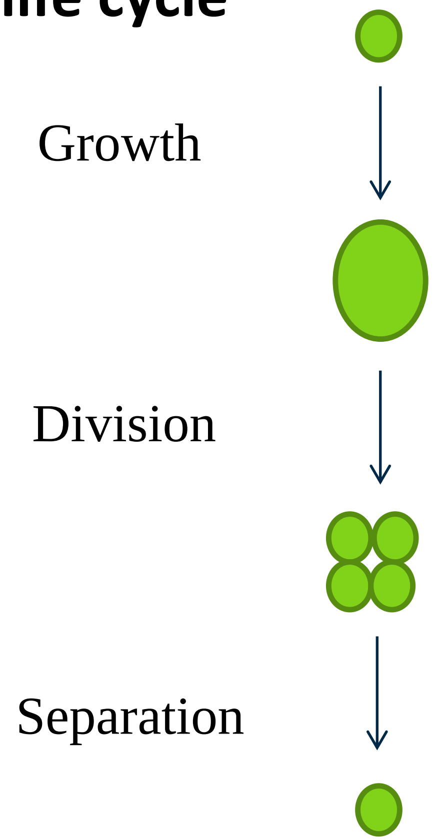


•First steps: 1) Failure of separation, 2) Change in order of life cycle stages

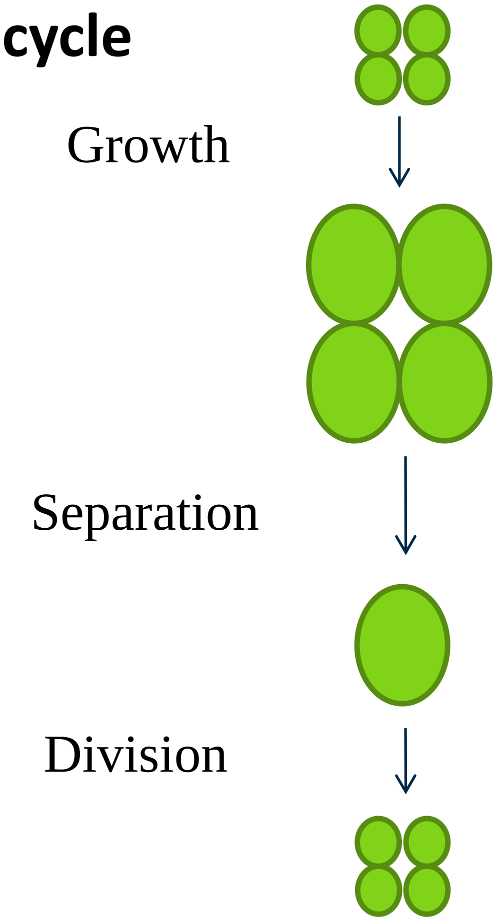
•Credit D. Shelton

Volvocine life cycles

Cell life cycle



Simplest
Group life cycle



- First steps: 1) Failure of separation, 2) Change in order of life cycle stages

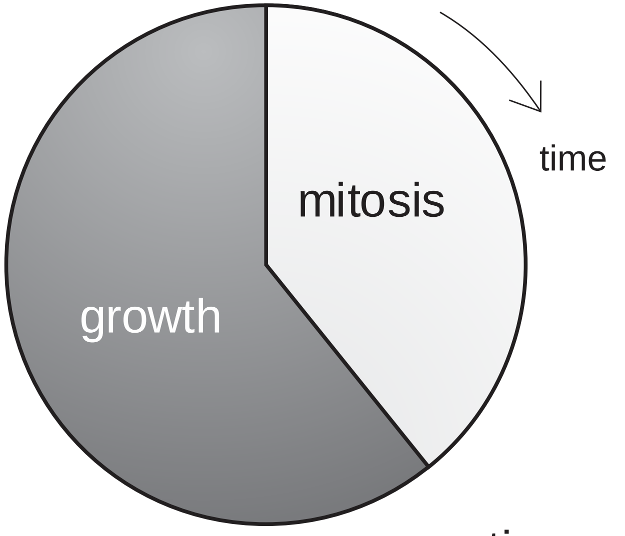
Two traits

- Features that facilitate the emergen p group structure are already present in unicells – cell cyc
- Group structure emerges
- "Group-specific adaptations" evolve t_g
  - Traits that were already subject to selection in the unicellular context affect performance in group
  - In group context these traits take on new group-specific values different than the values in unicells
- These group-specific adaptations lead to selective pressure for increased cohesiveness or regularity of the group structure (traits are maladaptive if cells leave the group)
- Further evolution of group-specific life cycle adaptations as group selection on cohesive groups is now established

Shelton, D. & R. E. Michod. 2014. Biological Theory.

Cell cycle to group life cycle

- Cell Cycle
  - Growth
    - G1
  - Division
    - DNA synthesis
    - Mitosis
  - Separation
- Hypothesis
  - Cell cycle involves a cell-group stage
  - Failure of separation
  - “Group specific adaptations”



Maliet, O. D. Shelton & R.E. Michod. 2015. Proc. Royal Soc. Biol. Letters.

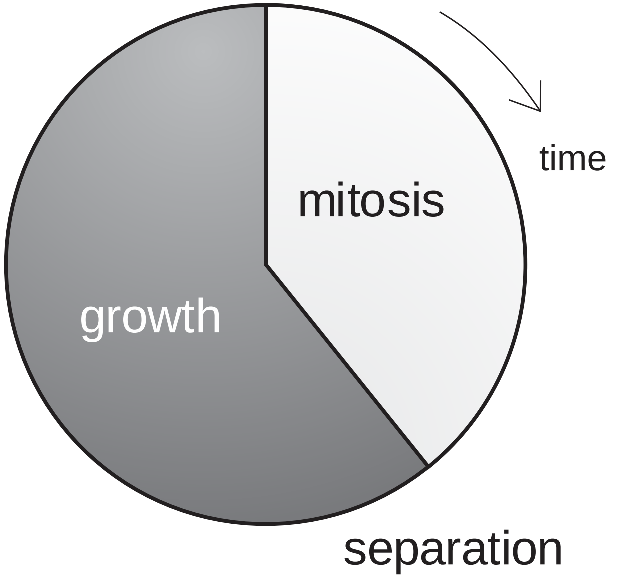
Time?

- Skip next two slides on model details

Model

- Fitness = $r = \frac{\ln(fecundity \text{ x } survival)}{generation\ time}$
- Fecundity
  - Size $V(t)$
  - Growth rate = $\partial_t V(t) = kV(t)^b$
- Survival = $S(t) = e^{-mt}$
- Generation time = $t_g + t_m$
- Trade-off:

  Increase t_g, good for fecundity, bad for survival



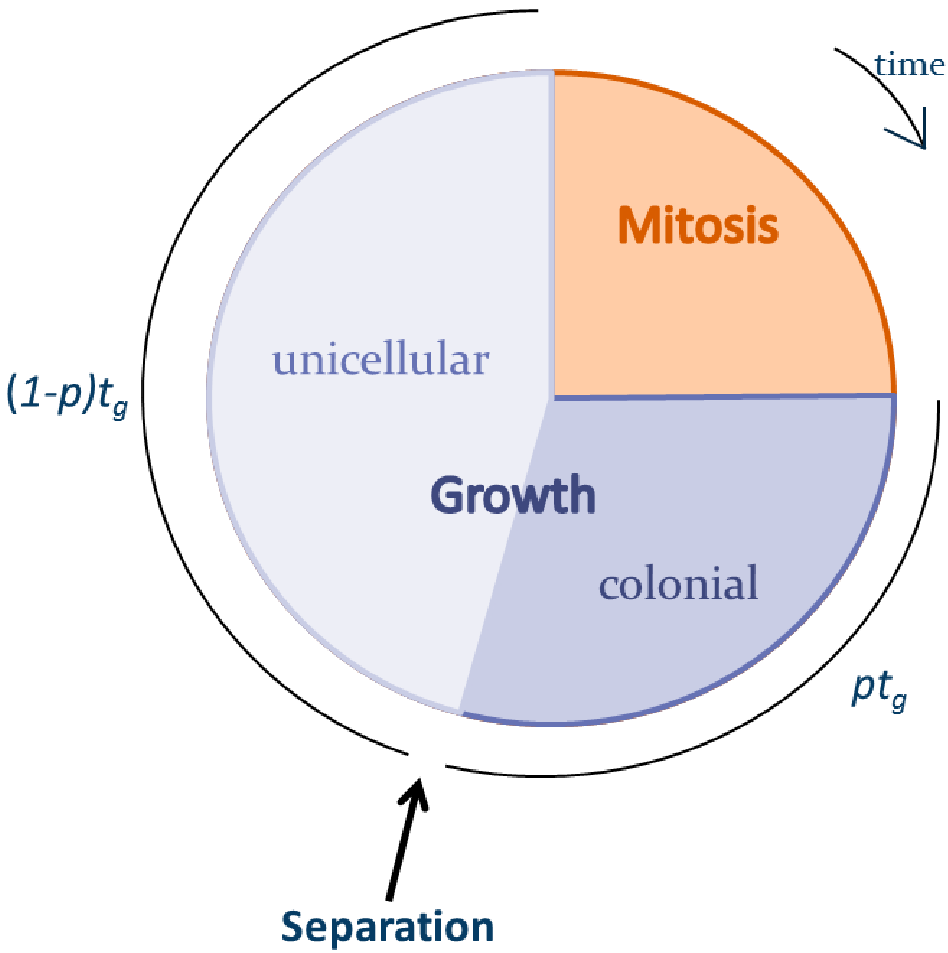
Maliet, O. D. Shelton & R.E. Michod. 2015. Proc. Royal Soc. Biol. Letters.

Additional model terms

parameter name	interpretation in model B	constraints on the parameter value
p	proportion of growing time spent in a group (heritable trait)	$0 \leq p \leq 1$
t_g	time allowed for growth (heritable trait)	$0 \leq t_g$
$r(p,t_g)$	intrinsic rate of increase for the population of individuals characterized by a given value of p and t_g	$r = \frac{\ln(fecundity \times survival)}{generation\ time}$
t_m	time needed for other life events (e.g. mitosis)	$0 < t_m$
c_0	initial size of a cell	
b	exponent in the expression of the metabolic rate	b is typically ¾
k	growth rate for unicells	
K	Characteristic time for cell growth for unicells	$K = \frac{k}{(1-b){c_0}^{1-b}}$
α	effect of group-living on the growth rate	$0 \leq \alpha \leq 1$
m	death rate for unicells	
β	effect of group-living on the death rate	$0 \leq \beta \leq 1$

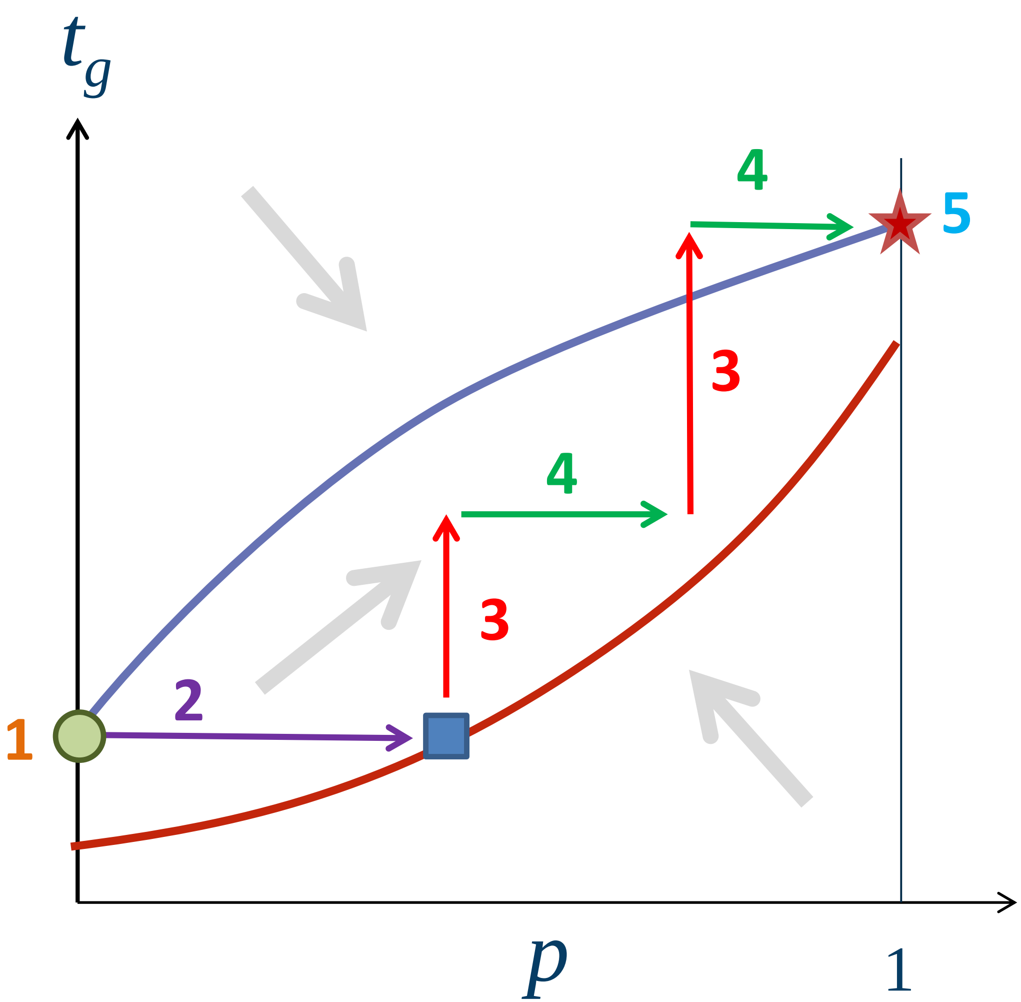
Maliet, O. D. Shelton & R.E. Michod. 2015. Proc. Royal Soc. Biol. Letters.

Continuous evolution of p allows a change in order of cell cycle stages



Maliet, O. D. Shelton & R.E. Michod. 2015. Proc Royal Soc. Bio. Letters.

Evolution of a group life-cycle



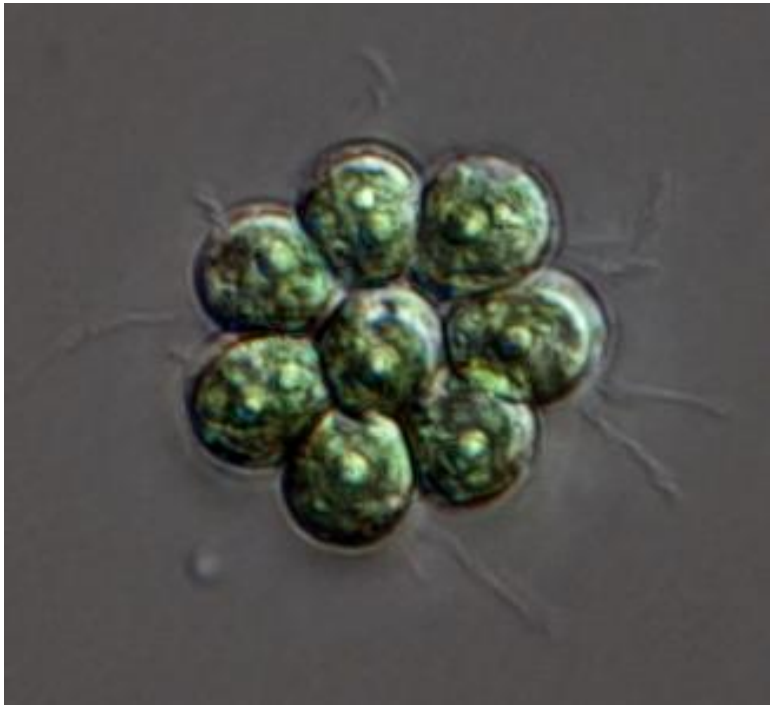
1. *Transient group stage*
2. *Group structure emerges, p* > 1
3. *Group-specific adaptation in traits already subject to selection, t_g* evolves
4. *Selective pressure for increased cohesiveness, p* increases
5. *Further evolution of group-specific adaptations as group life cycle is now established*

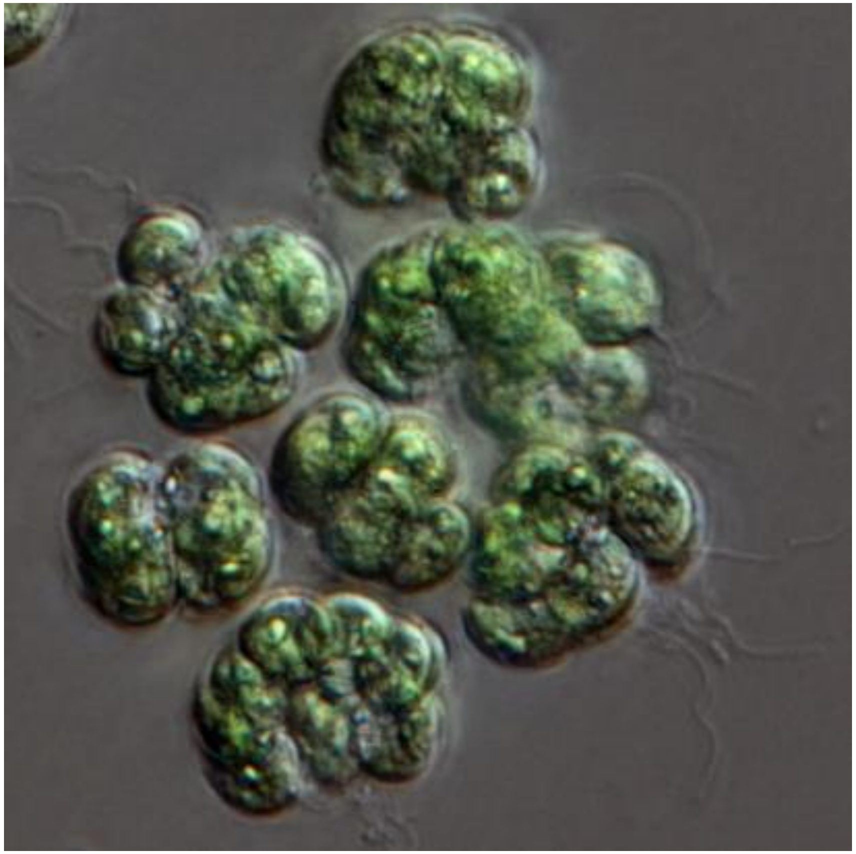
legend

- Solutions of $\partial_{t_g} r = 0$
- Solutions of $\partial_p r = 0$
- Fitness gradient direction
- Fitness maximum for p=0
- Fitness maximum with fixed t_g
- Fitness global maximum

Maliet, O. D. Shelton & R.E. Michod. 2015. Proc. Royal Soc. Biol. Letters

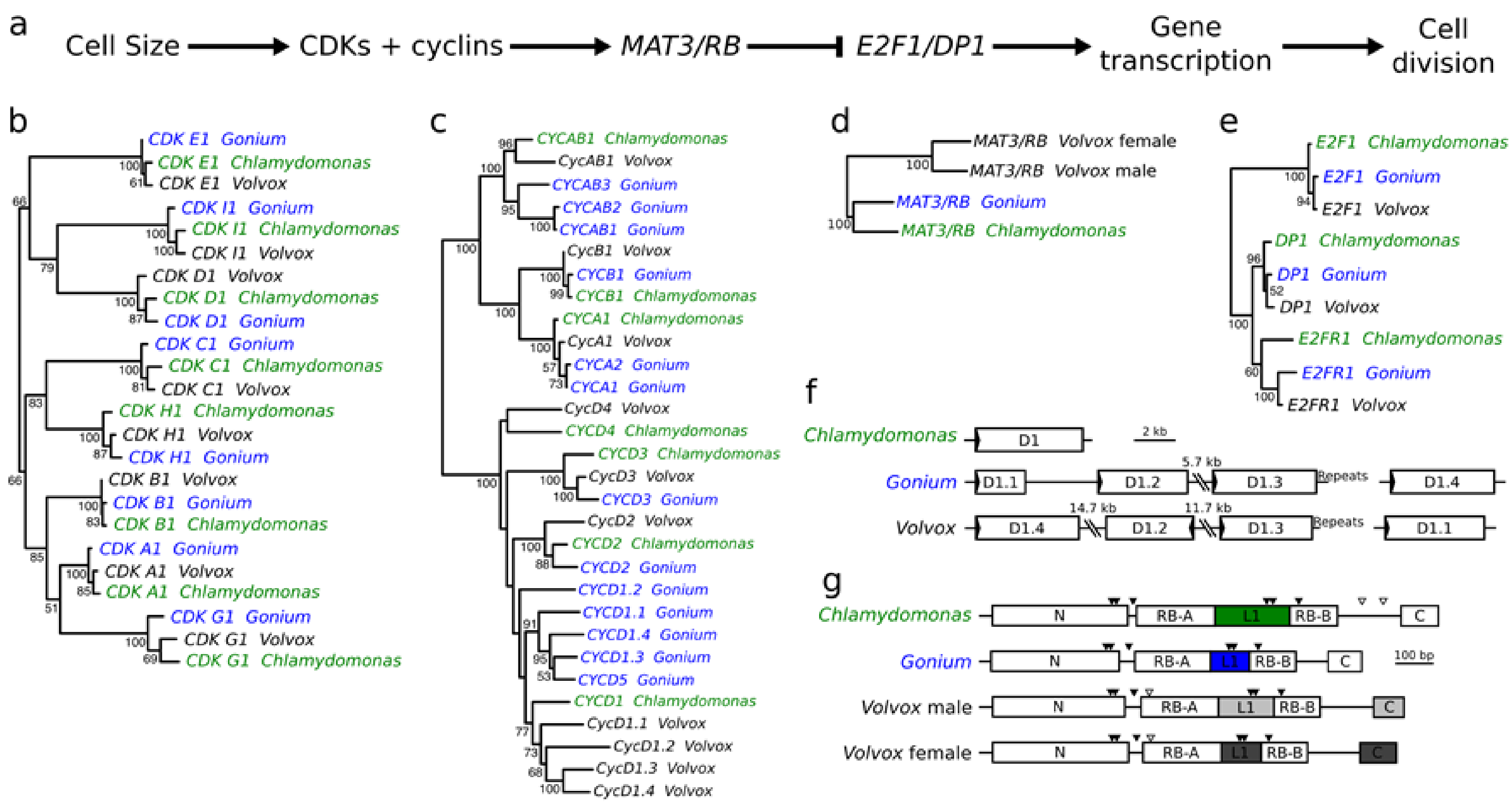
Gonium pectorale





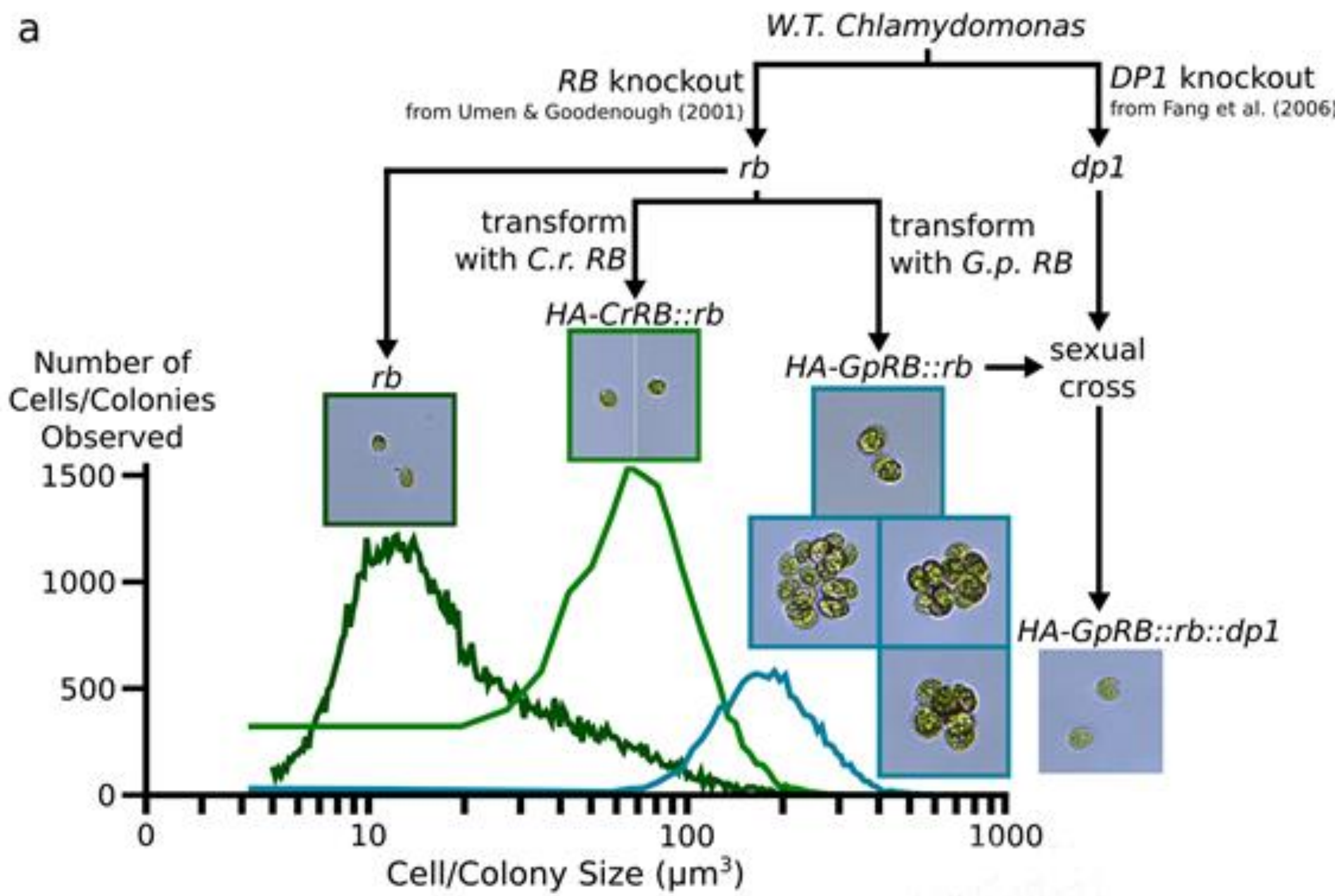
Picture credit: Shelton, D.

Gonium genome – cell cycle genes



Brad Olson, Erik Hanschen and Tara Marriage lead investigators

Gonium RB gene causes cell groups in *Chlamydomonas*



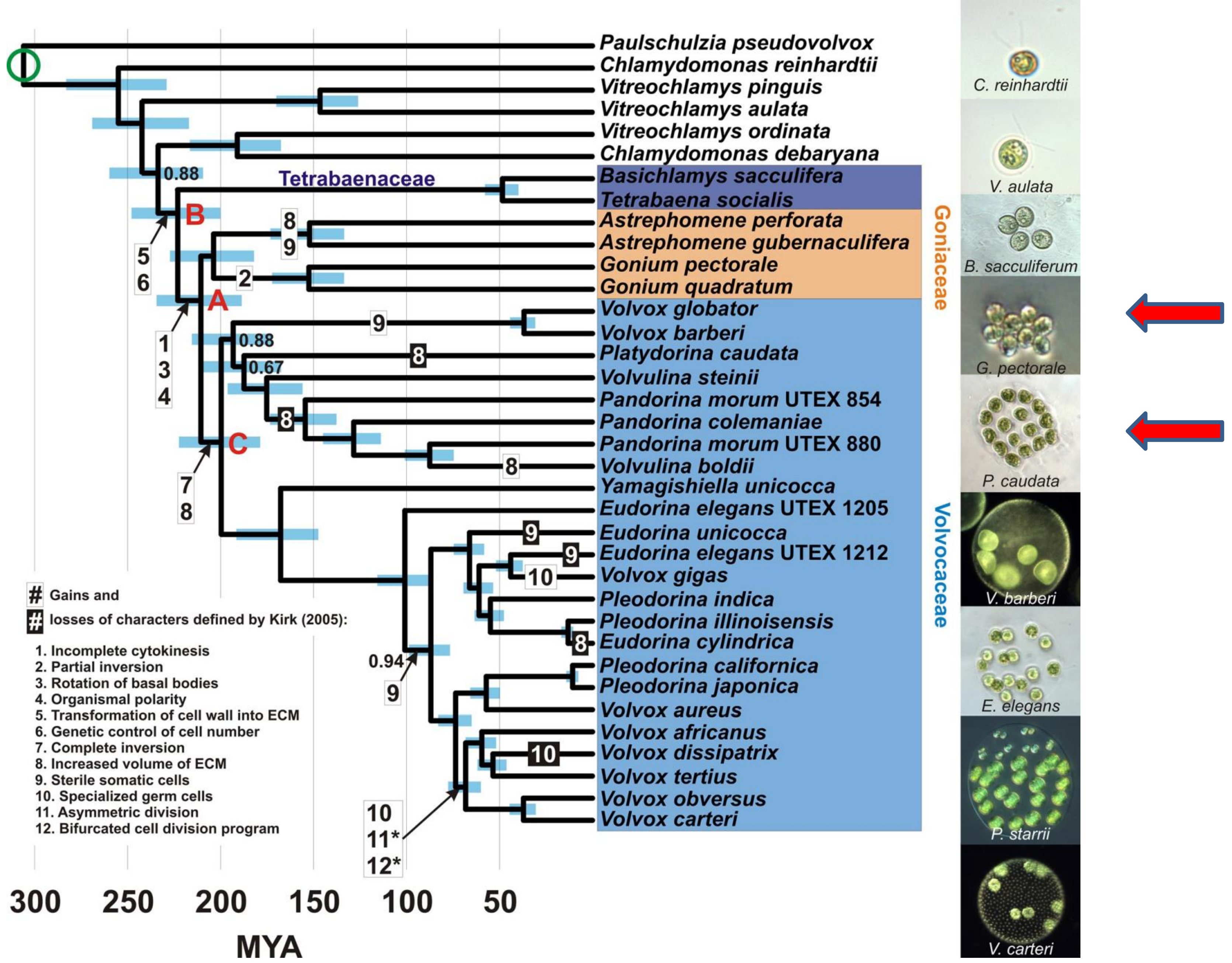
Brad Olson, Erik Hanschen and Tara Marriage lead investigators

Evolutionary transitions

INDIVIDUALITY

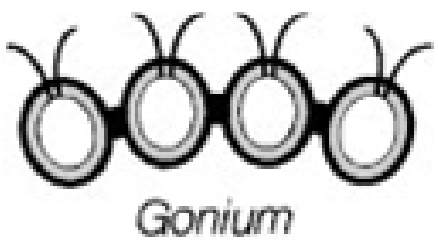
Individuality

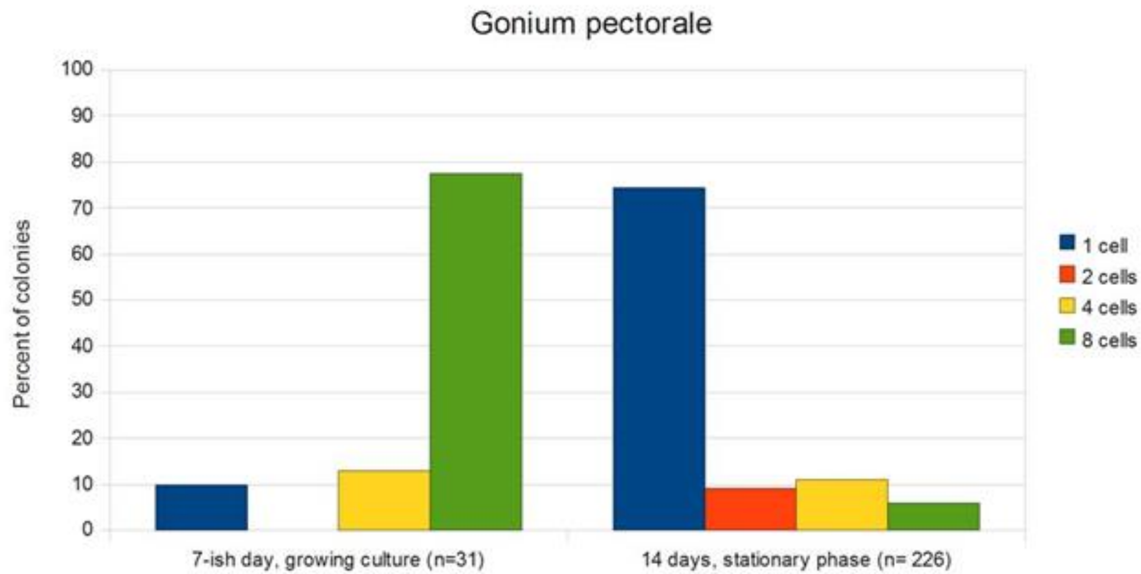
- Individuality concepts
  - Indivisibility
  - Distinctness
  - Homogeneity
  - Physiological unity
  - Integration of components
  - A level of selection and adaptation
    - stable
    - cooperation and conflict mediation
    - specialization of members at fitness components of group
- Individuality appears in grades in volvocine algae

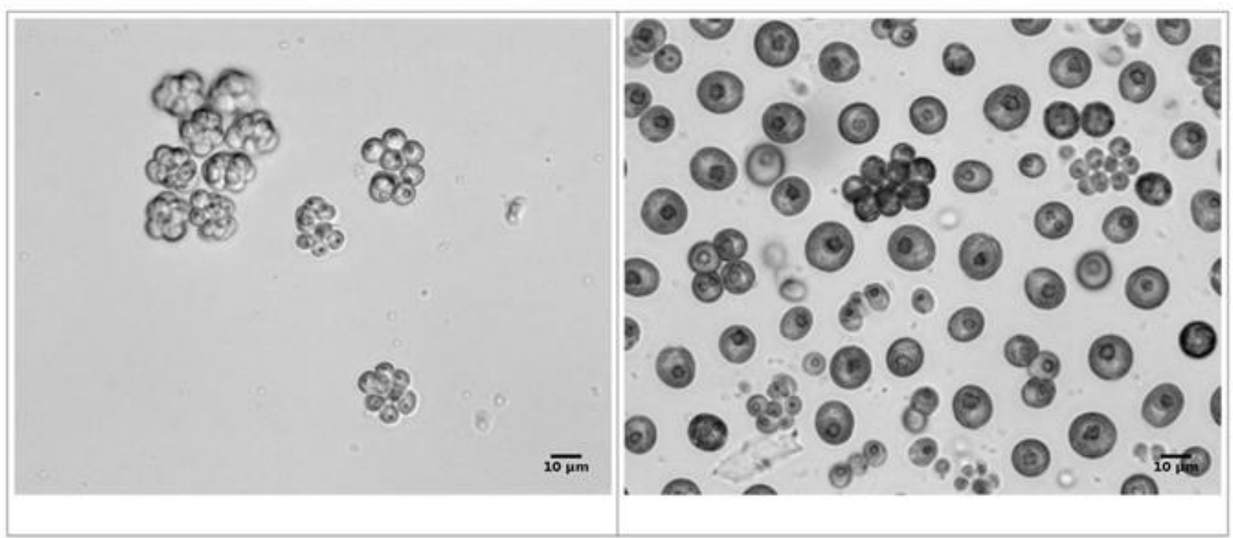


Herron, M. D., et al. 2009. Triassic origin and early radiation of multicellular volvocine algae. *PNAS*, USA 106: 3254-3258
Herron, & Michod. 2008. Evolution of complexity in volvocine algae: transitions in individuality through Darwin's eye. *Evolution*. 262: 436-451

Low Individuality

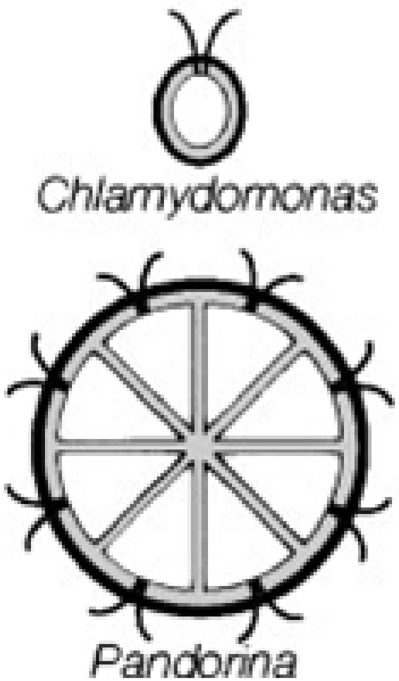


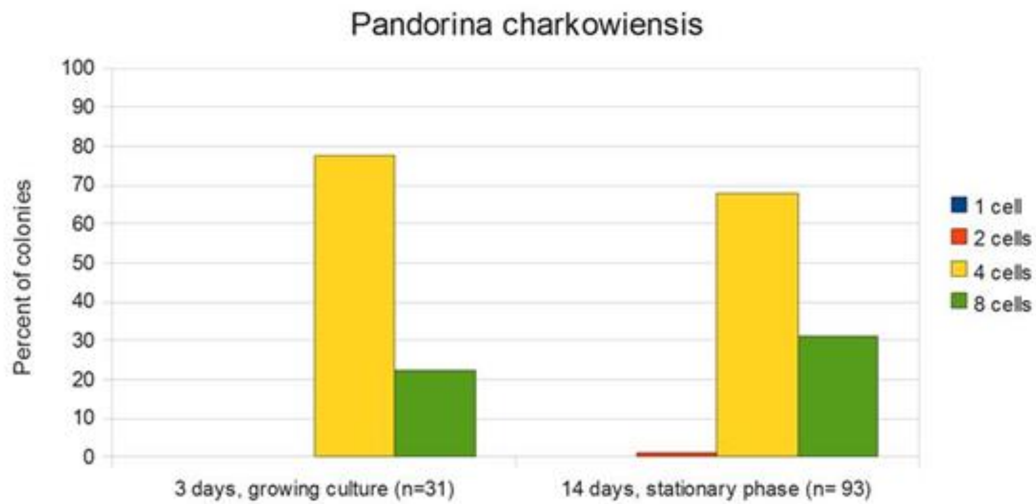


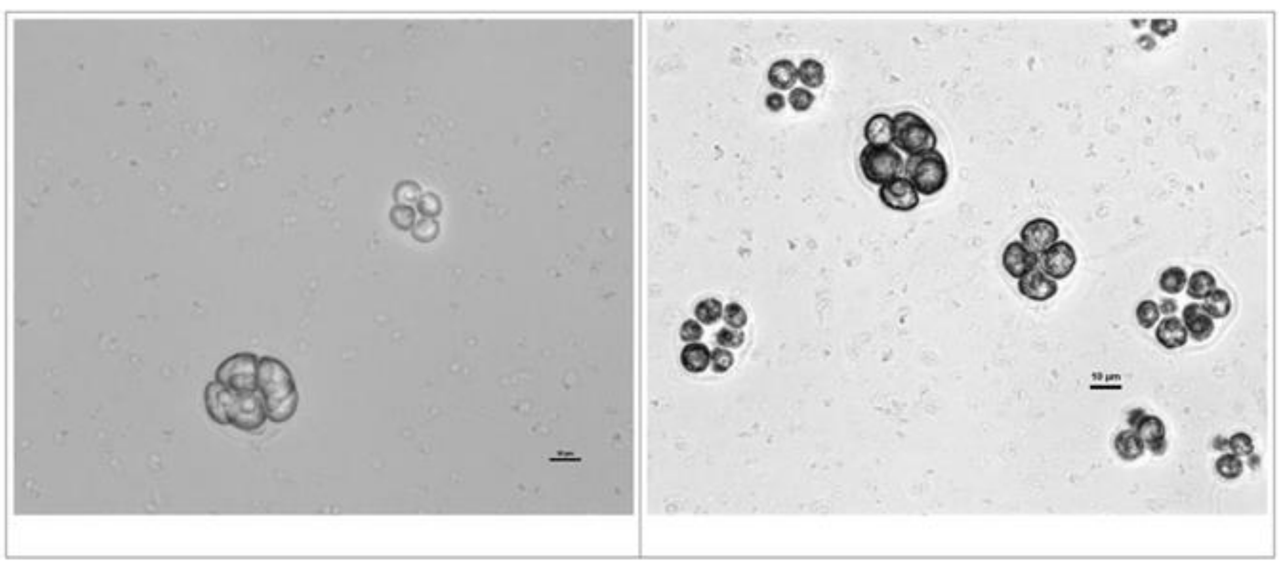


Credit: D. Shelton

High Individuality





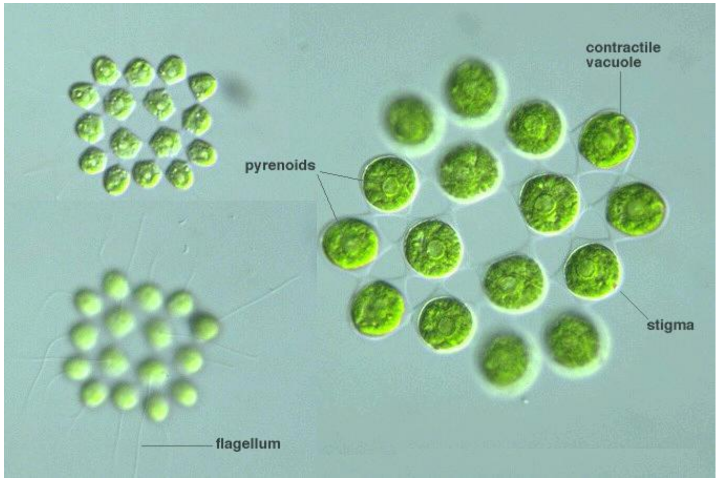


Credit: D. Shelton

Is *Gonium* an Individual?

For

- Functional integration
  - Group specific adaptations
- Level of selection
- Focus of interest



Against

- Group fitness not decoupled from cell fitness
- Group fitness is average of cell fitness
- Group state is plastic response to environmental conditions

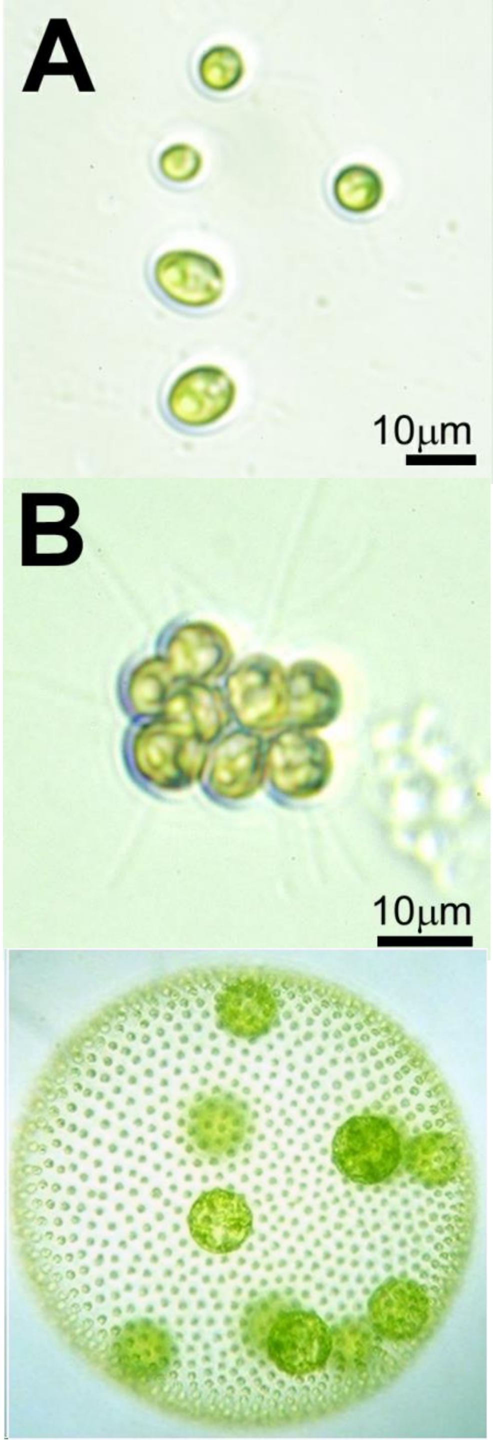
➢ Has elements of MLS1 and MLS2

PROTEIN SYSTEMS BIOLOGY OF AN EVOLUTIONARY TRANSITION IN INDIVIDUALITY

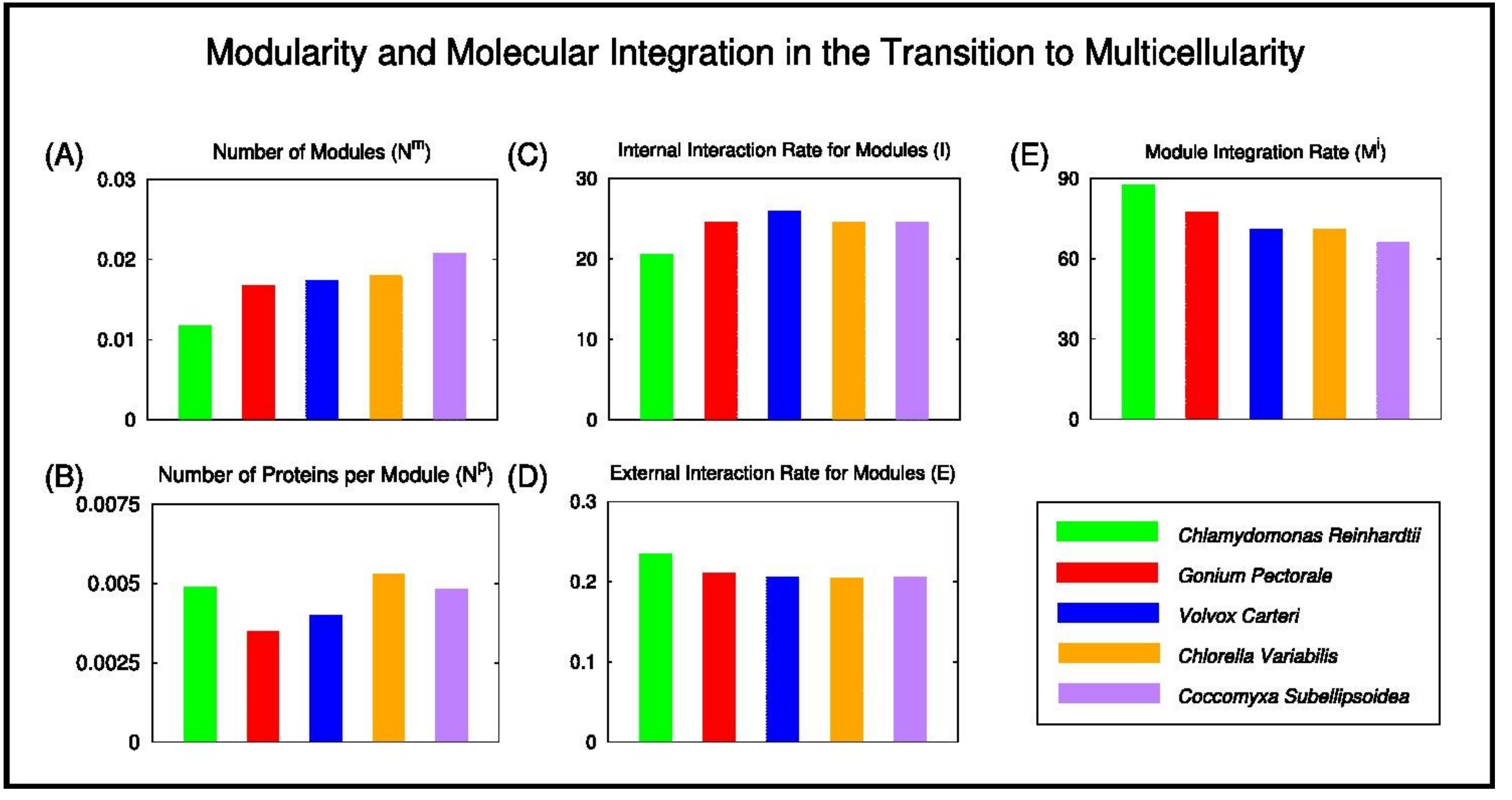
Approach

- Genomes of *Chlamy*, *Gonium*, *Volvox*
- Encoded protein interactions predicted by MP-PIPE using an experimentally verified reference database from *Arabidopsis*.
  - http://online.kitp.ucsb.edu/online/multicell_c13/
- Quantify modularity and integration
  - Order Statistics Local Optimization Method (OSLOM) method (v. 2.5)
  - http://www.oslom.org/

A.Schoenrock, F.Dehne, P.M. Durand *et al* in prep.



Modularity and molecular integration



A.Schoenrock, F.Dehne, P.M. Durand et al in prep.

Evolution of multicellularity involves an increasing number of more complex but less connected modules

- Makes sense when we view cells from a whole versus part perspective.
- When present as a unicellular organism, the cell is the individual and so can be an integrated whole. Its modules may be highly interconnected as “it,” the cellular individual, does not perform as part of another system.
- However, when present in a multicellular individual, cells become parts of another whole, the multicellular individual, and so cannot be highly interconnected as different cells must perform different functions in different contexts.
- The modules become less connected during an ETI because the unit in which they must function, the cell, is now a part of a larger system, the multicellular individual.

A.Schoenrock, F.Dehne, P.M. Durand et al in prep.

CONCLUSIONS

Reorganization of fitness

- Definition of
  - Transfer of fitness from lower to higher level
  - Lower levels specialize in fitness components of higher level
  - Heritability of fitness emerges at higher level.
- Means of
  - Fitness trade-offs
  - Group specific cell adaptations
  - Germ-soma specialization
  - Cooperation, conflict & conflict mediation
- Consequences of
  - Transfer of fitness from lower to higher level
  - Individuality at the new higher level
  - Increased Functionality and complexity
  - Evolvability at new level.

How does a group become an individual?

- How?
  - Life history genes in uni-cells co-opted for reproductive altruism in group
  - Altruism and cell specialization trade fitness from lower to higher level
  - Cell cycle evolves in group context
  - Germ soma specialization
- Why?
  - Trade-off between reproduction and survival
  - Trade-off becomes convex with increasing size
  - Increasing cost of reproduction selects for specialization and soma
  - Group specific adaptations of the cell selects for cohesion of the group
- General Points
  - Kinship
    - Important, not sufficient
    - Reproductive altruism and individuality arises in only the larger species
  - Individuality is an evolutionarily labile trait in this group

A Darwinian approach to complexity

- Fitness and its reorganization during ETIs
- Steps from unicellular to multicellular
  - Multi-level selection
  - Development
  - Life cycle stages
- Darwinian principles explain a large jump in a level of complexity and the evolution of new kinds of individuals

GROUP LIVING

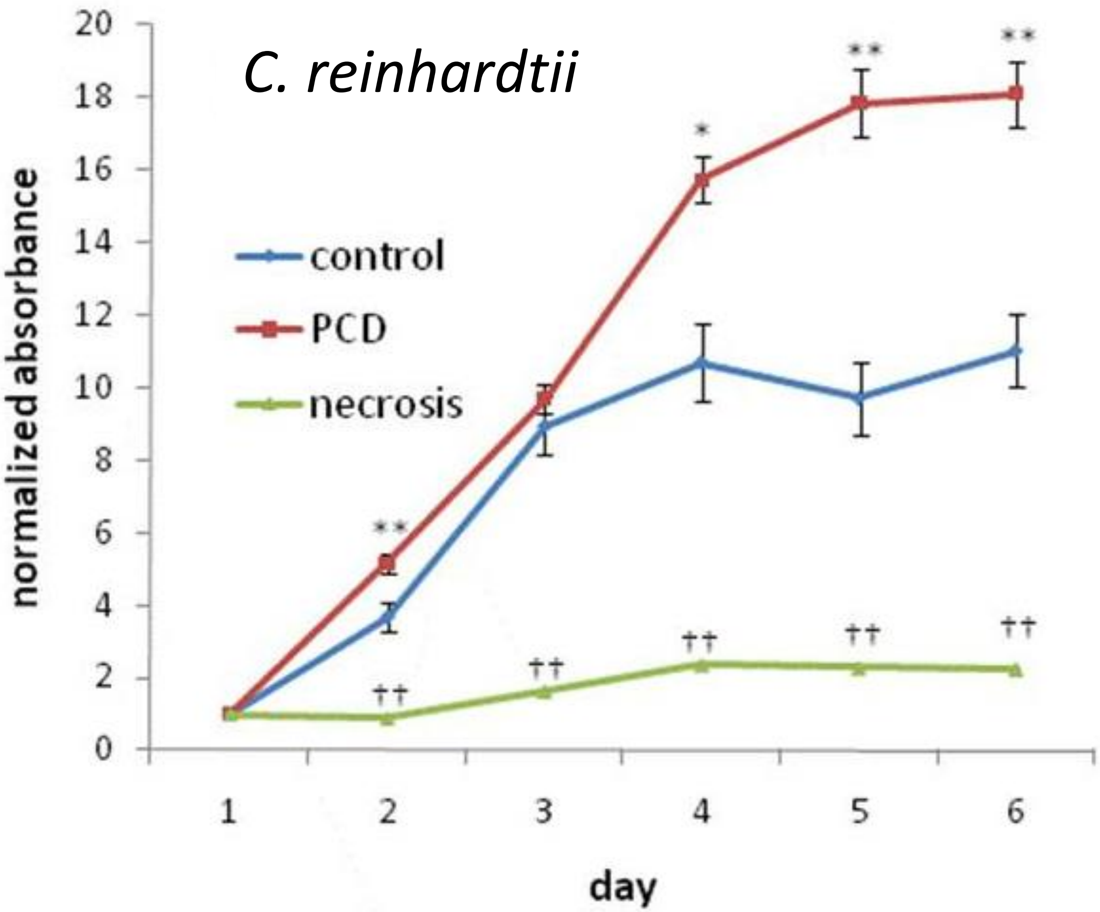
Groups – Coping with death

- External factors
  - Traumatic, injury, disruption of cell membrane,
  - Necrosis

- Internal program
  - PCD
  - DNA laddering
  - Apoptotic bodies
- Adaptive significance in multicellular organisms
- Unicells?

- Necrosis is a barrier to group living

How an organism dies affects it neighbor's fitness



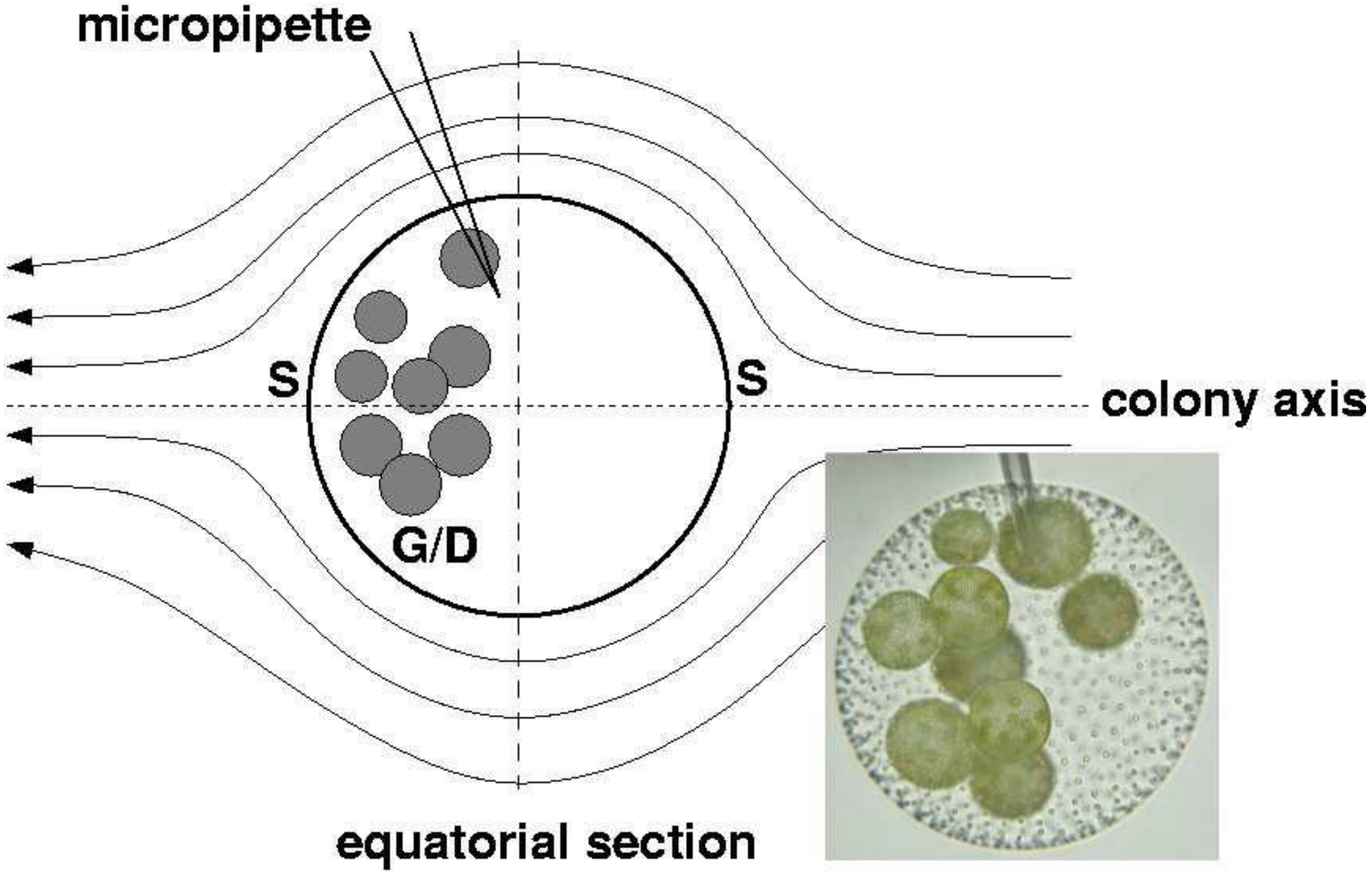
•Durand, P.M. et al. *Am Nat*, 2011. Durand, P.M. et al. *Biology Letters*, 2014.

Group Living: Transport Problem

- Problems of group living
  - Surface to volume ratio
  - Locally compact group
    - Get resources in
    - Get wastes out
- Transport problem increases with size
- Flagellar activity
  - Motility
  - Mixing (transport of metabolites and waste)

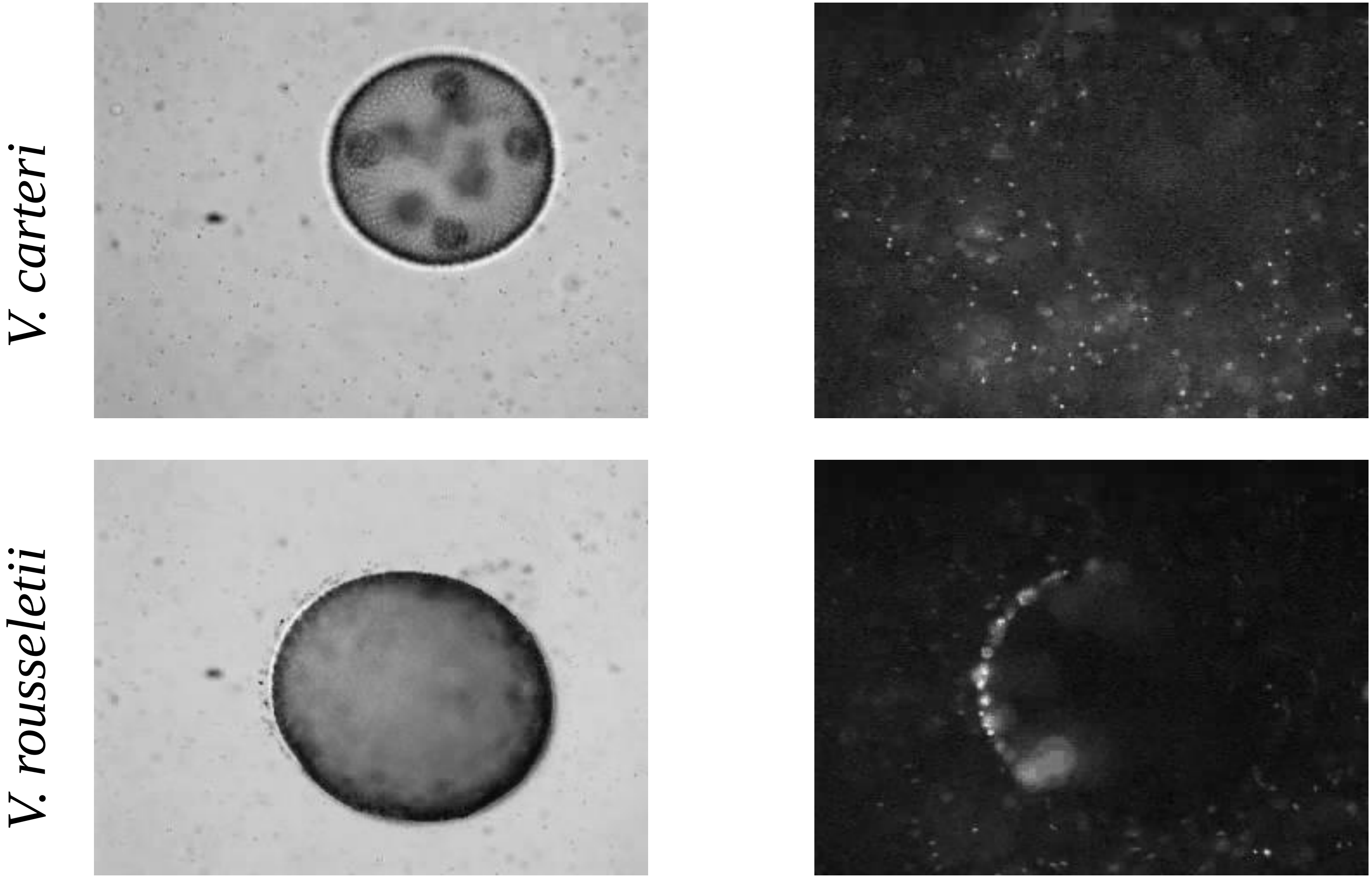
•Solari, C. A., J. O. Kessler, and R. E. Michod. 2006. A hydrodynamics approach to the evolution of multicellularity: Flagellar motility and cell differentiation in volvocalean green algae. *Am. Nat.* 167:537-554. Solari, C. A., S. Ganguly, J. O. Kessler, R. E. Michod, and R. E. Goldstein. 2006. Multicellularity and the functional interdependence of motility and molecular transport. *PNAS*, USA. 103:1353-1358.

Volvox on a stick

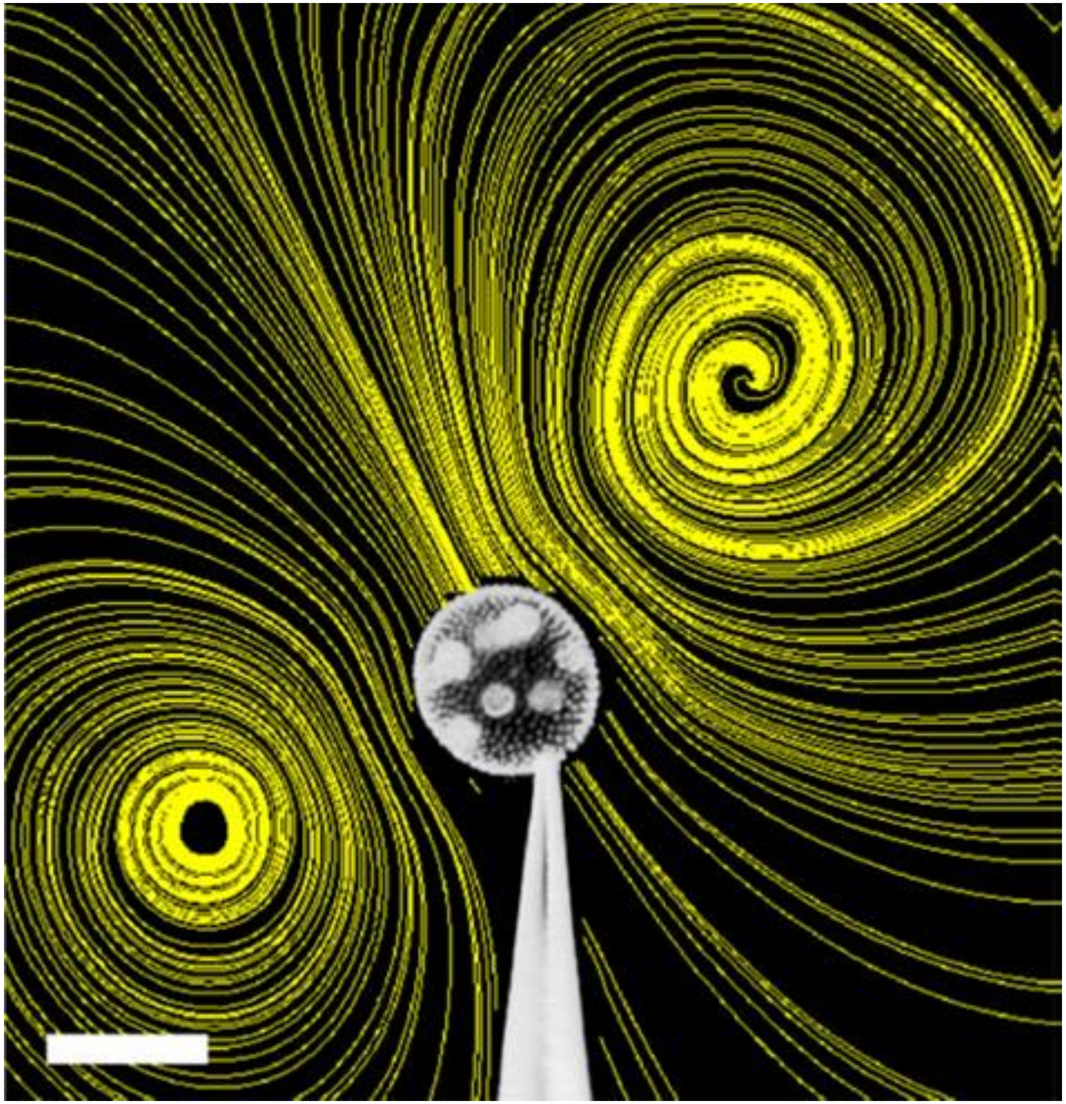


•Solari, C. A., J. O. Kessler, and R. E. Michod. 2006. A hydrodynamics approach to the evolution of multicellularity: Flagellar motility and cell differentiation in volvocalean green algae. *Am. Nat*. 167:537-554. Solari, C. A., S. Ganguly, J. O. Kessler, R. E. Michod, and R. E. Goldstein. 2006. Multicellularity and the functional interdependence of motility and molecular transport. *PNAS*, USA. 103:1353-1358.

Groups – Transport problem



•Solari, C. A., J. O. Kessler, and R. E. Michod. 2006. A hydrodynamics approach to the evolution of multicellularity: Flagellar motility and cell differentiation in volvocalean green algae. *Am. Nat.* 167:537-554. Solari, C. A., S. Ganguly, J. O. Kessler, R. E. Michod, and R. E. Goldstein. 2006. Multicellularity and the functional interdependence of motility and molecular transport. *PNAS*, USA. 103:1353-1358.



•Solari, C. A., J. O. Kessler, and R. E. Michod. 2006. A hydrodynamics approach to the evolution of multicellularity: Flagellar motility and cell differentiation in volvocalean green algae. *Am. Nat*. 167:537-554. Solari, C. A., S. Ganguly, J. O. Kessler, R. E. Michod, and R. E. Goldstein. 2006. Multicellularity and the functional interdependence of motility and molecular transport. *PNAS*, USA. 103:1353-1358.