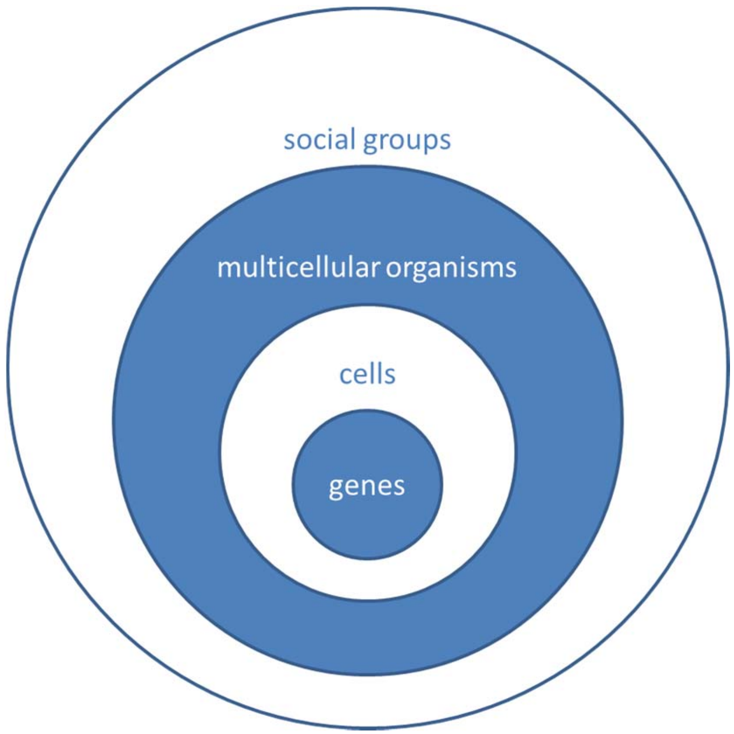
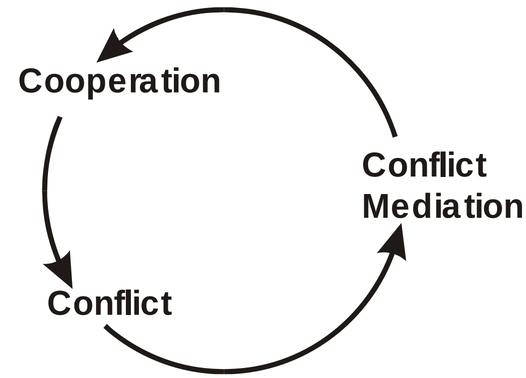
Rick Michod, Univ. Arizona





Evolutionary transitions in individuality

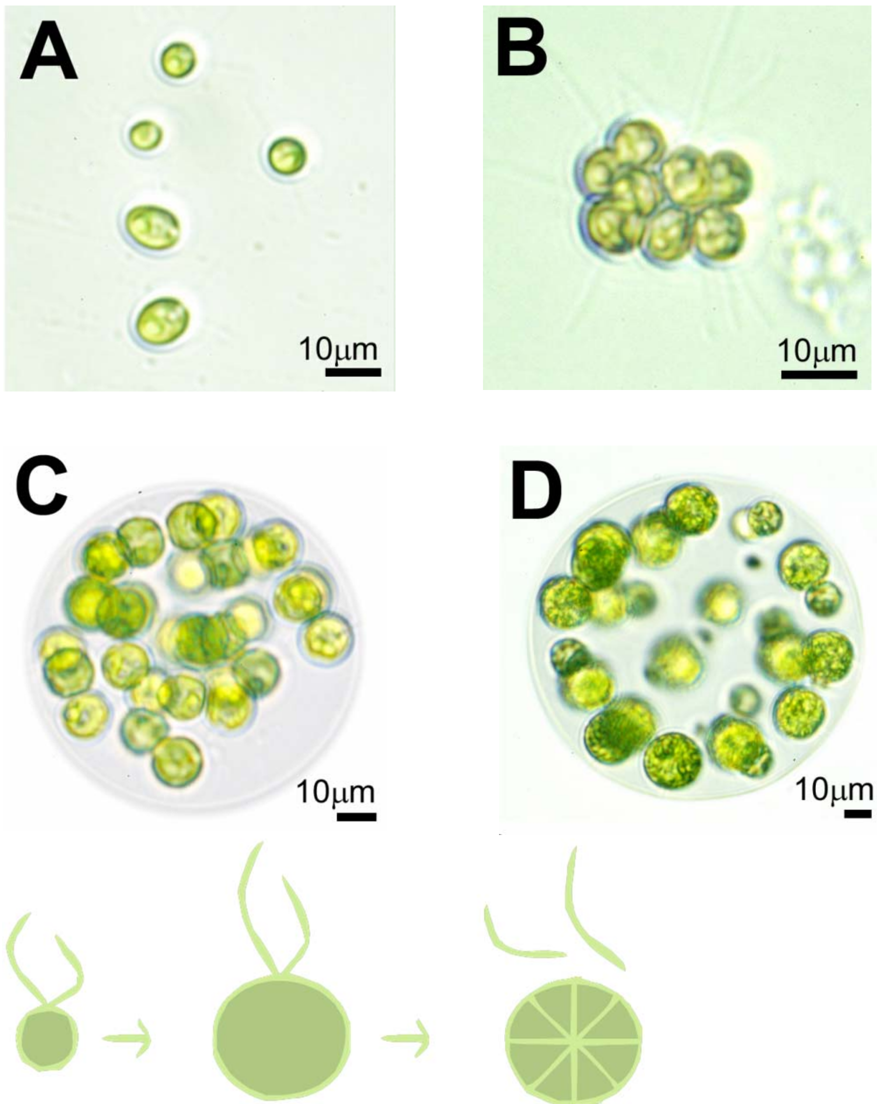
HOW & WHY DO GROUPS OF INDIVIDUALS EVOLVE INTO NEW KINDS OF INDIVIDUALS?

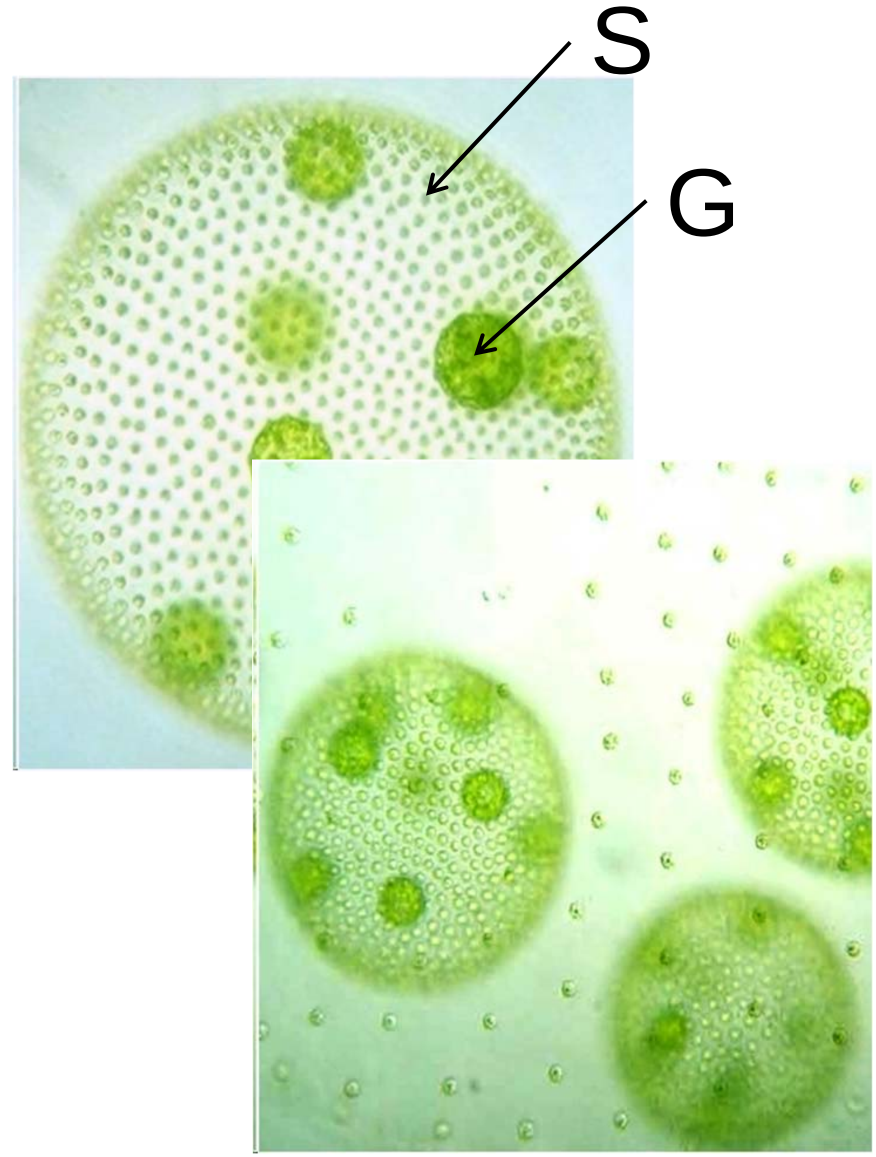
Feb 5, 2013

KITP Multicell13 Conference

Steps to multicellularity

MULTICELLULARITY





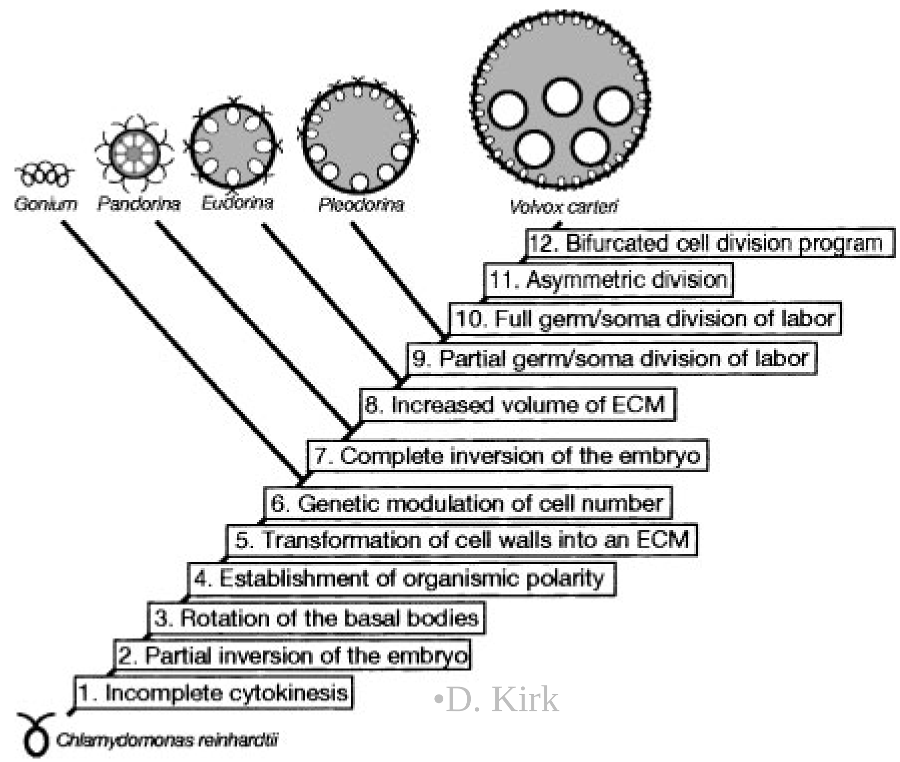
- Individuality depends on G/S division of labor
- Multiple vs. binary fission

Multicellularity is a complex trait

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

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

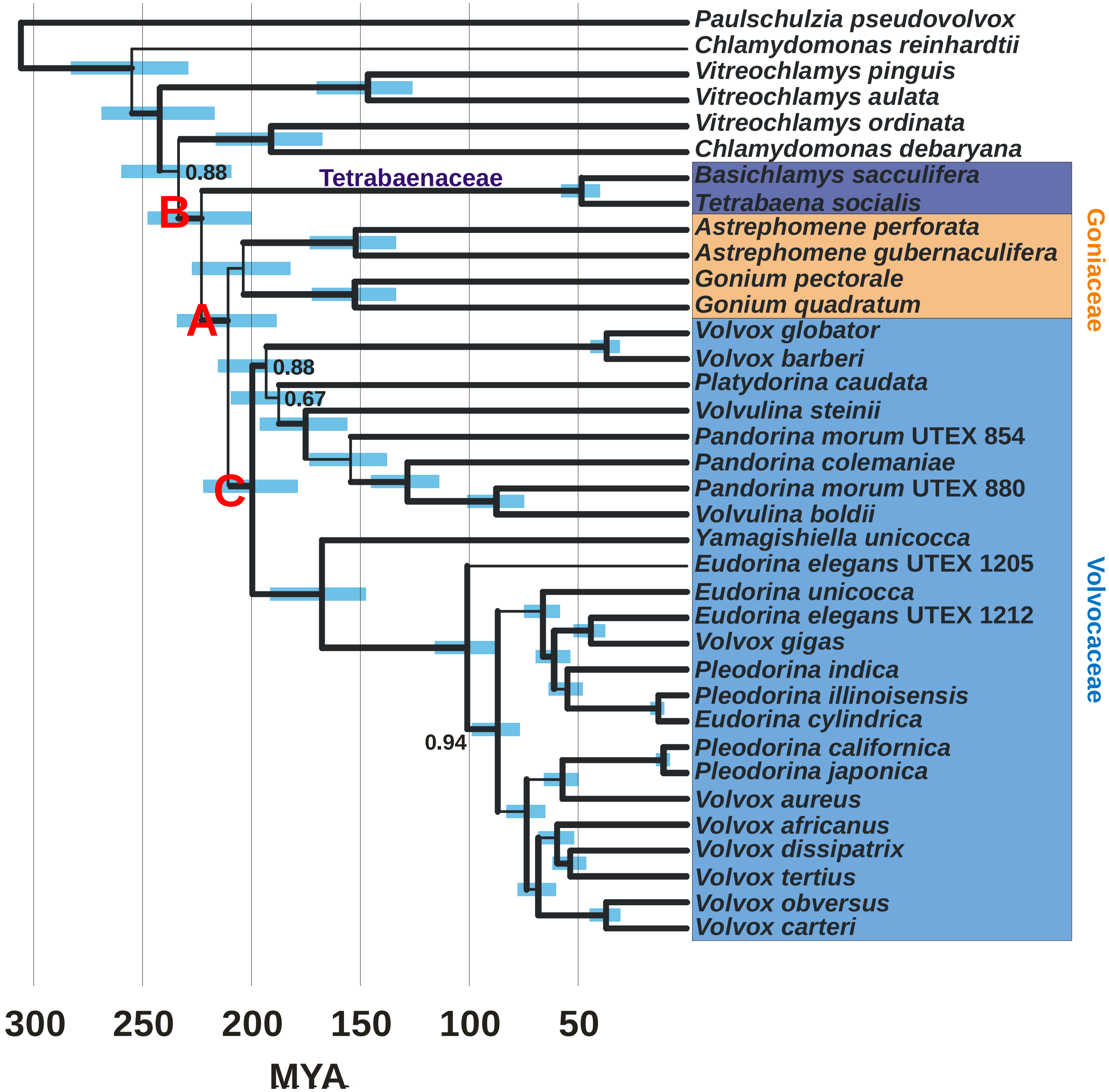
- Developmental steps

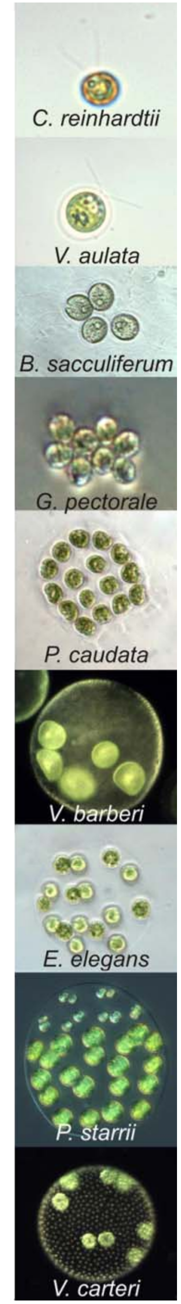


•D. Kirk

Steps to multicellularity

DEVELOPMENT

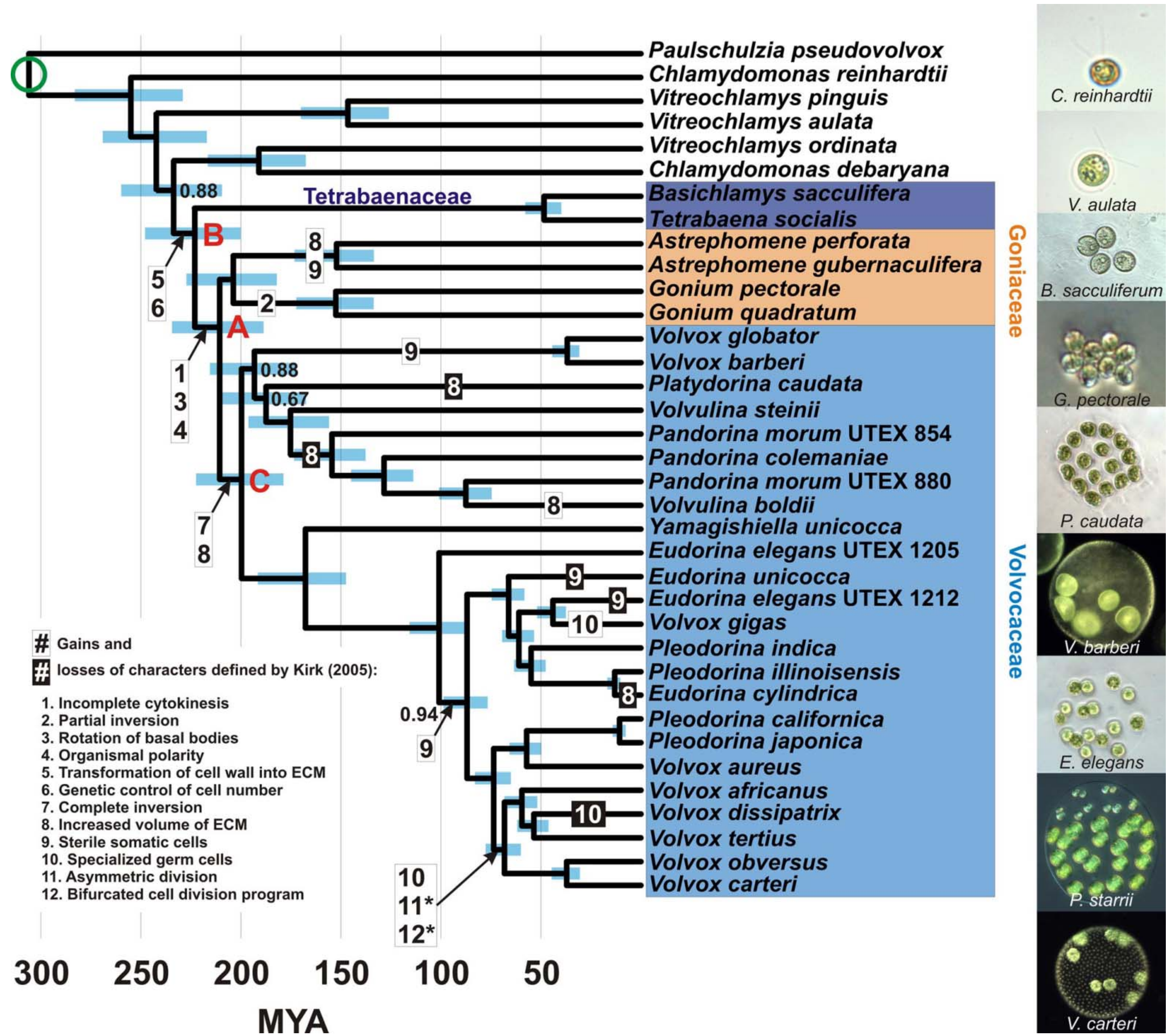




•Credit M. Herron

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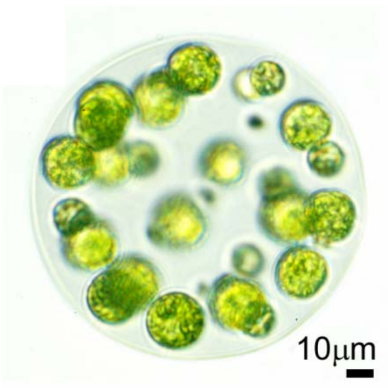

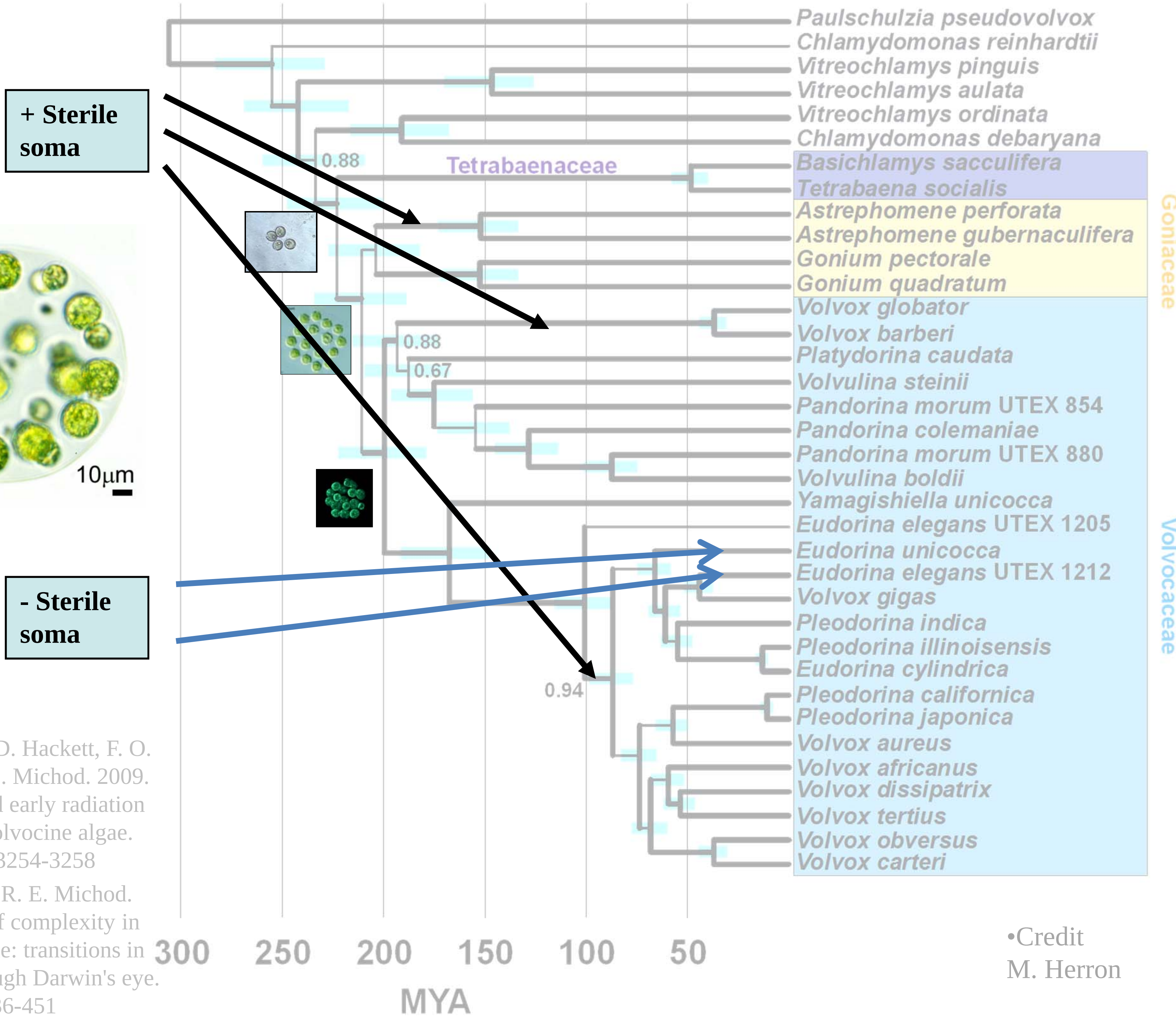

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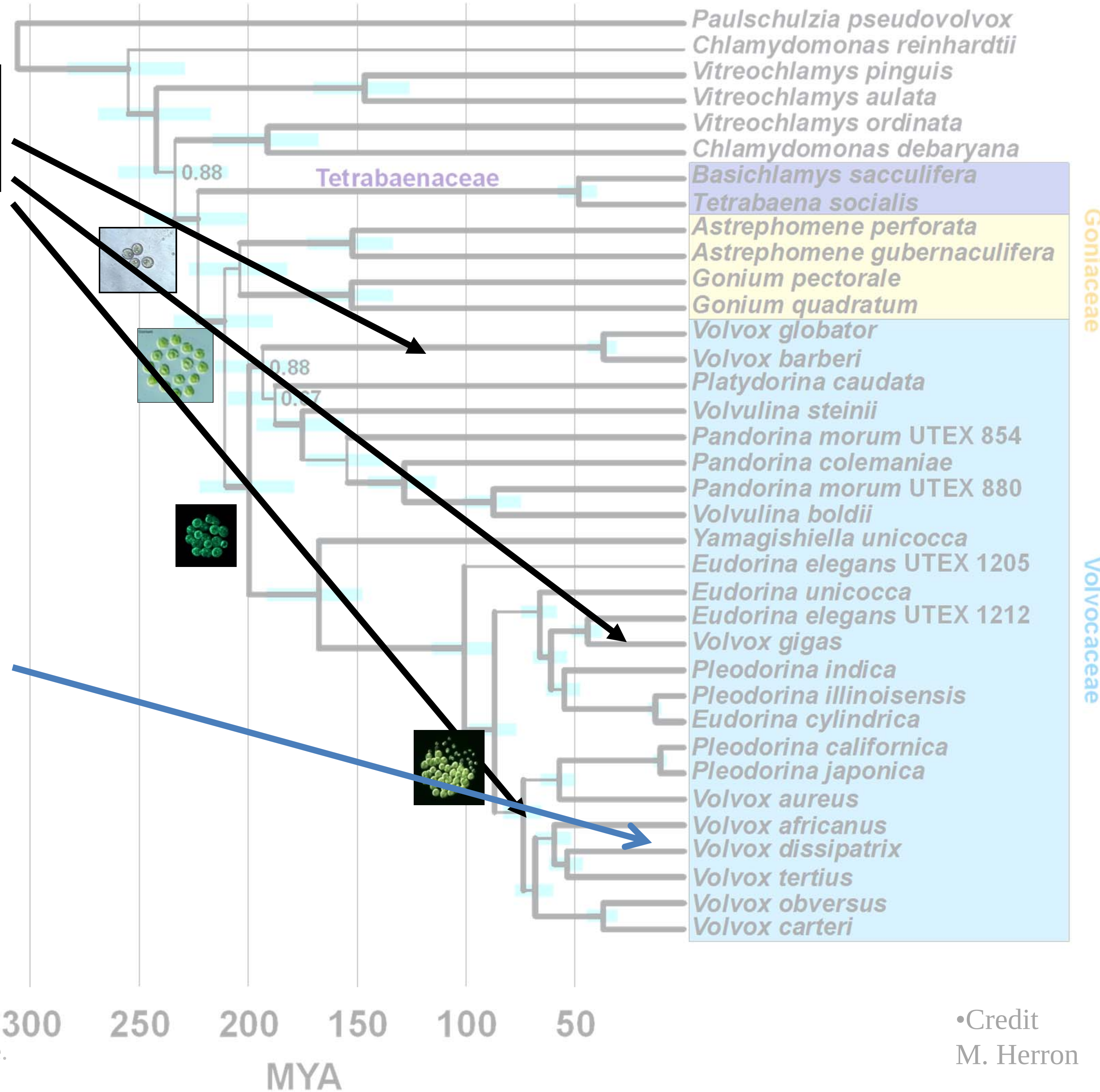
•Credit M. Herron

+ Specialized reproductive cells (germ)

- Specialized reproductive cells (germ)



Herron, M. D., J. D. Hackett, F. O. Aylward, and R. E. Michod. 2009. Triassic origin and early radiation of multicellular volvocine algae. *PNAS*, USA 106: 3254-3258

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

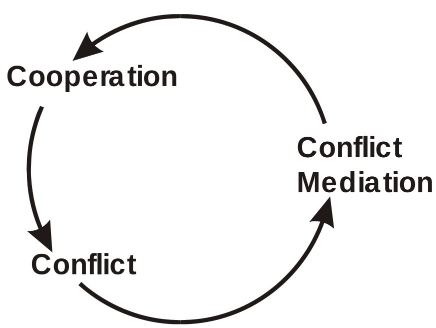
•Key innovation

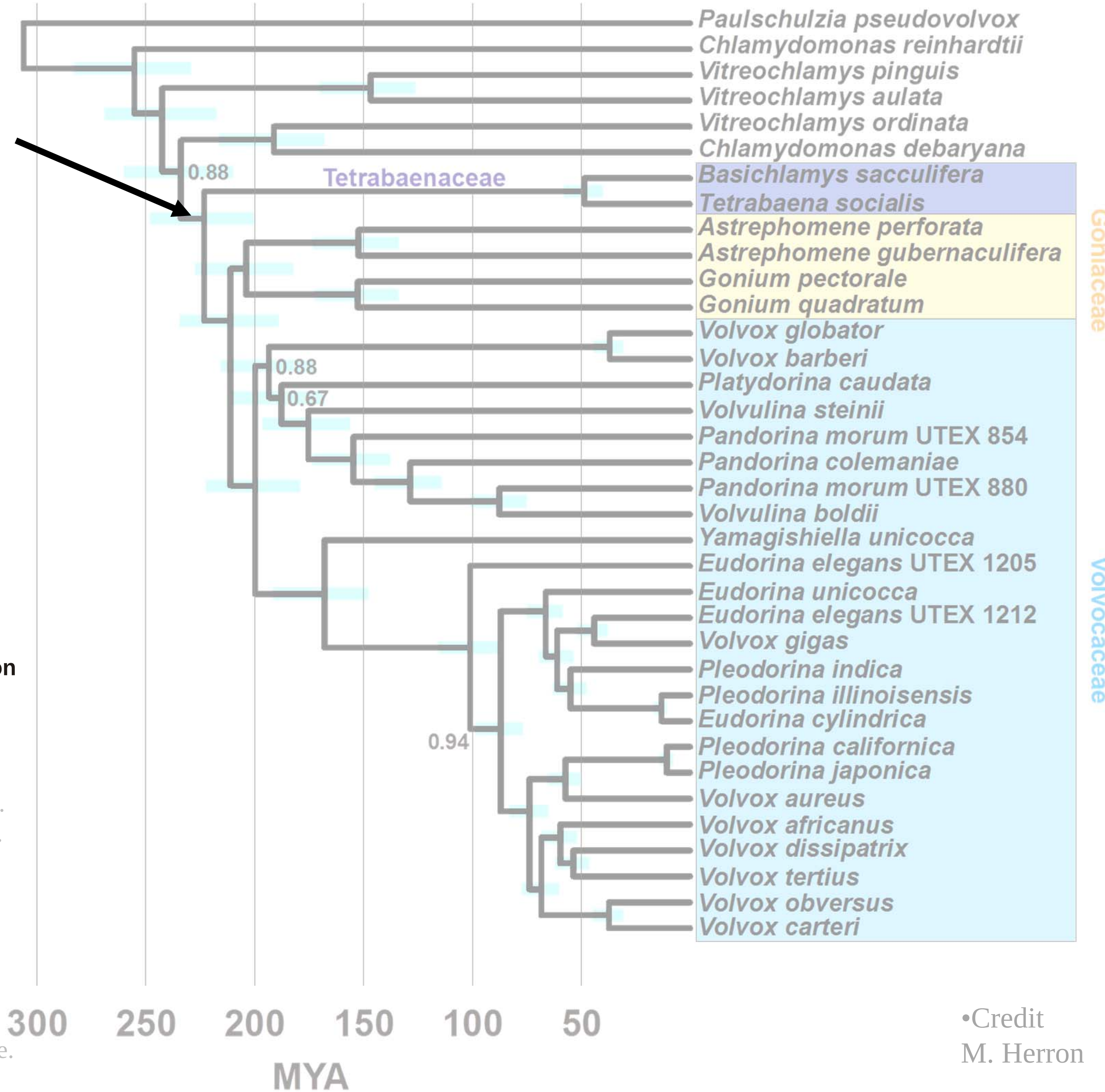
Transformation of cell wall into extracellular matrix

Genetic control of cell number

Cooperation = ECM

Conflict mediation= genetic control of cell number





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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

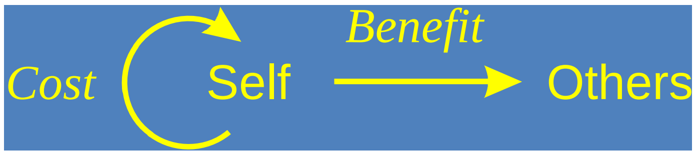
Conclusions

- 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

REPRODUCTIVE ALTRUISM

Altruism

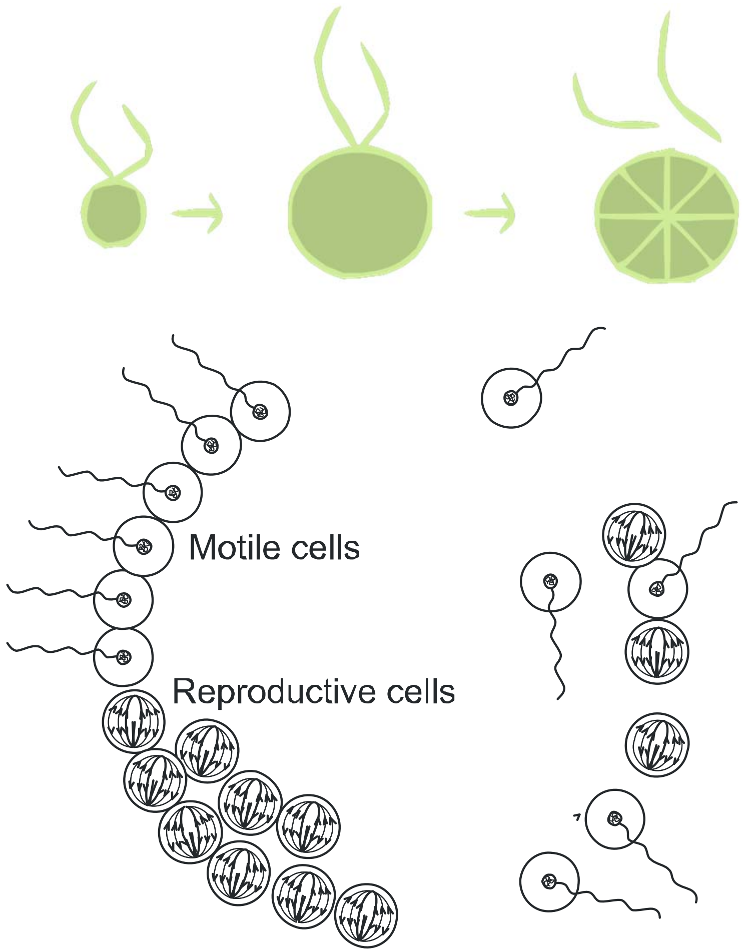


- Widely appreciated to be the central problem of social behavior

- Fundamental to evolutionary transitions in individuality
- Trades fitness between levels
  - 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

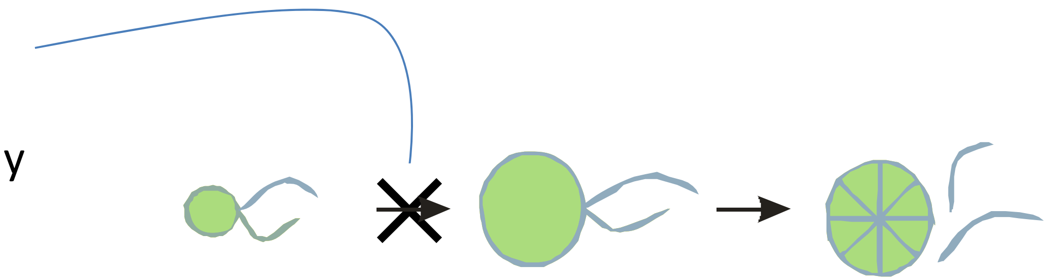
Fitness trade-offs → Altruism



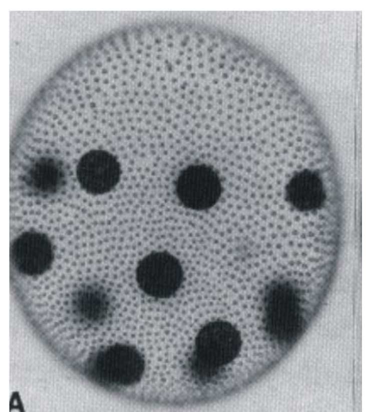
- Ancestral state
  - Two functions
    motile ➔ reproductive
  - Cells grow large and divide while losing flagella
- Fitness trade-offs
  - Motility & reproduction
  - Flagella = altruism

Reproductive altruism & cheating in *Volvox*

- *regA*
  - Keeps somatic cells small by starving them
  - Expressed developmentally
  - Altruistic gene
  - Selfish mutants



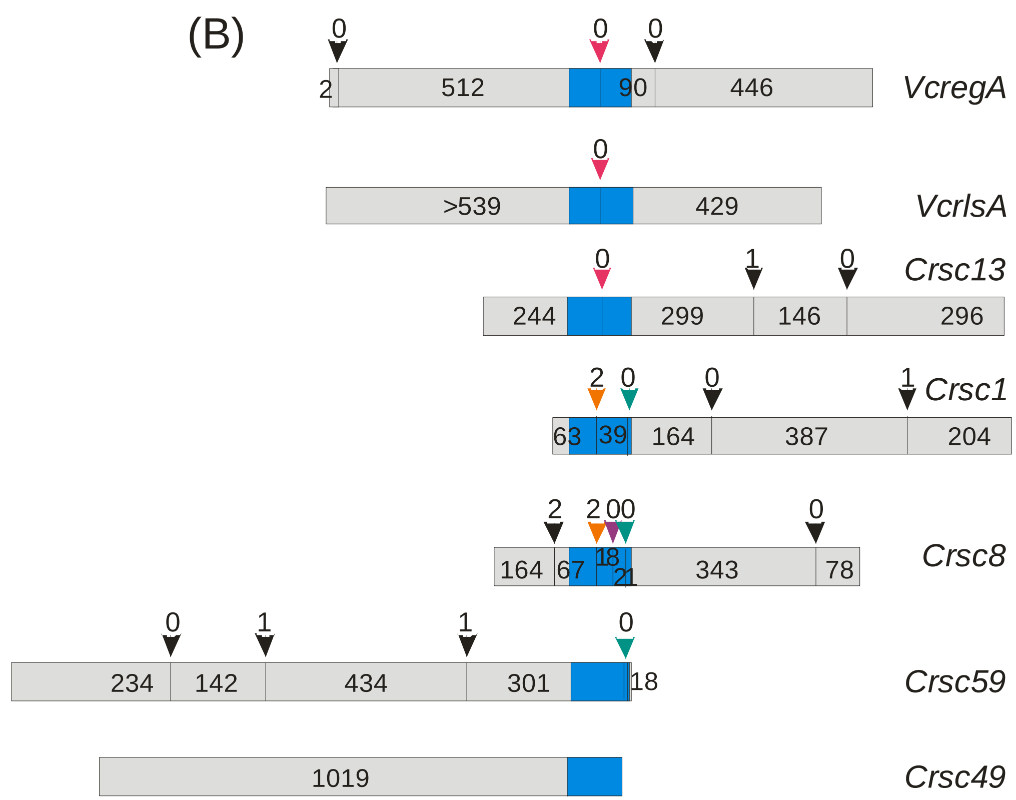
- Origin of *regA*?
  - Can the evolutionary origin of *regA* be traced back to the unicellular ancestors of this group?
  - If so, what was its role?



Kirk, D. 1998

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

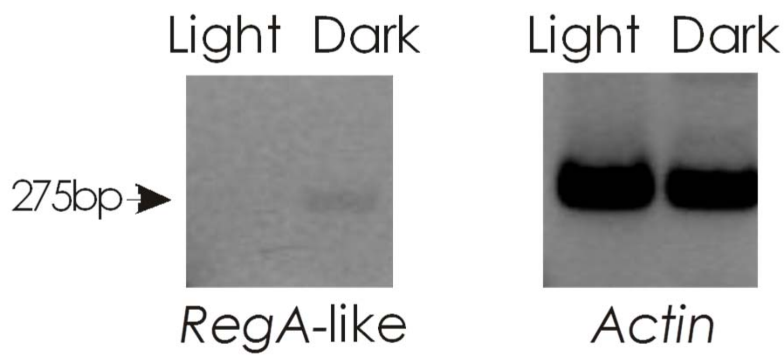
- Search *C. reinhardtii* genome
- Multigene family
- Widely diverged except for a conserved 80-aa VARL region similar to SAND domain which functions in DNA binding and transcriptional control
- Gene co-opted to be *regA*?
- Why should a unicellular organism suppress its own reproduction?
- Life history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

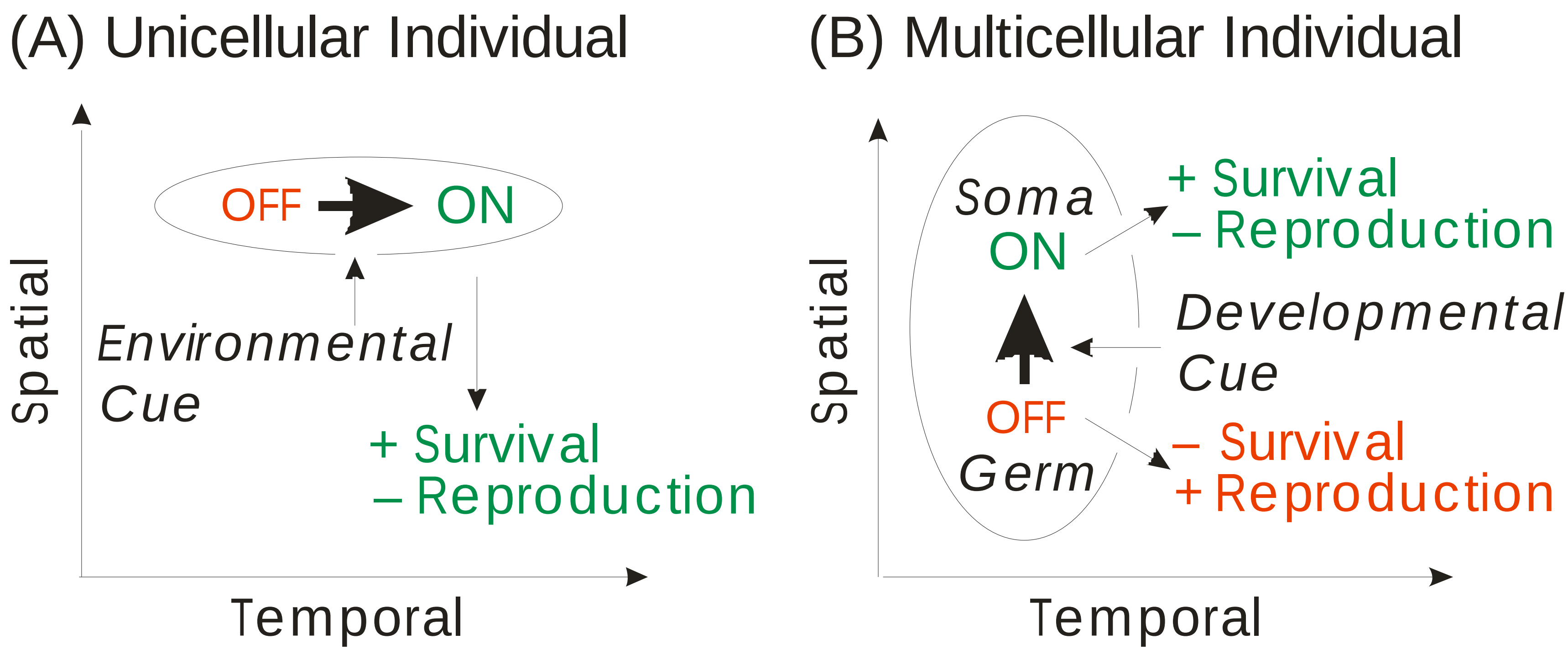
In what environments should reproduction be suppressed?

- 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.

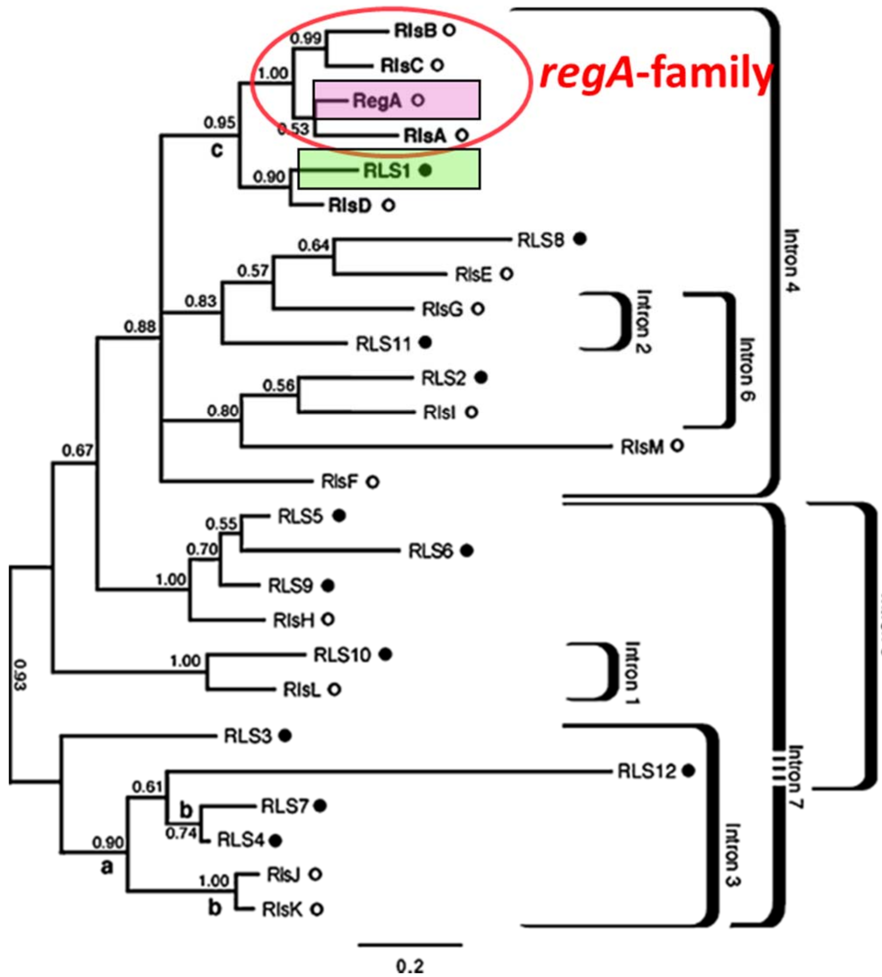
Hypothesis: Altruistic gene originates via co-option of life history gene



"Spatial" means within a cell group

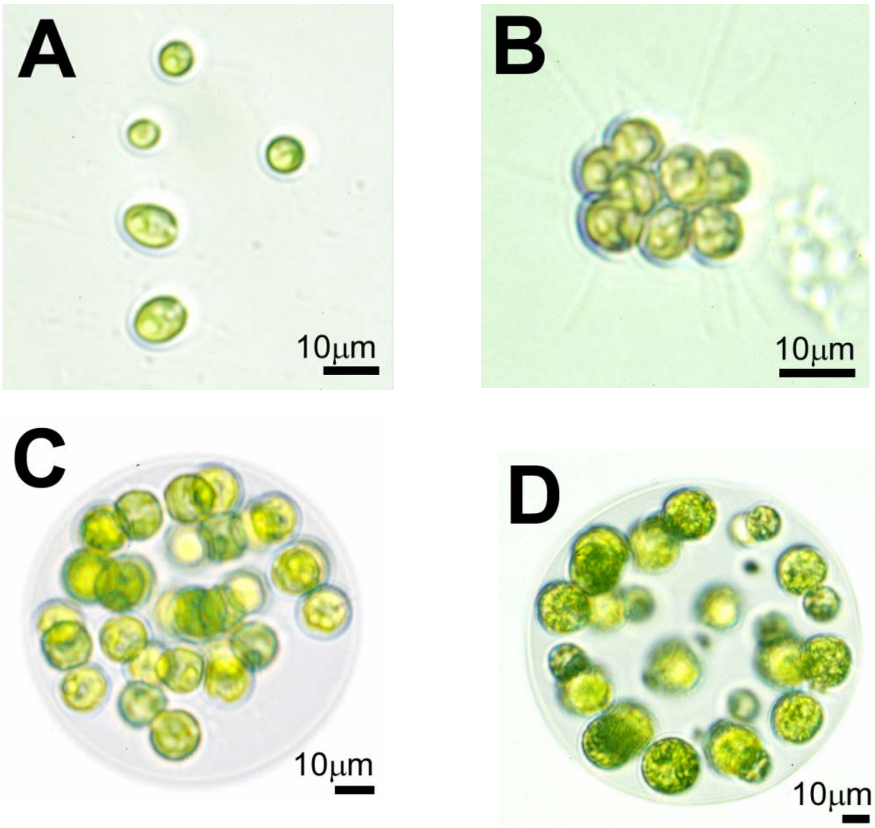
Nedelcu A.M., Michod R.E. (2006). The evolutionary origin of an altruistic gene in *Volvox carteri*. *Molecular Biology and Evolution*. 8:1460-1464.

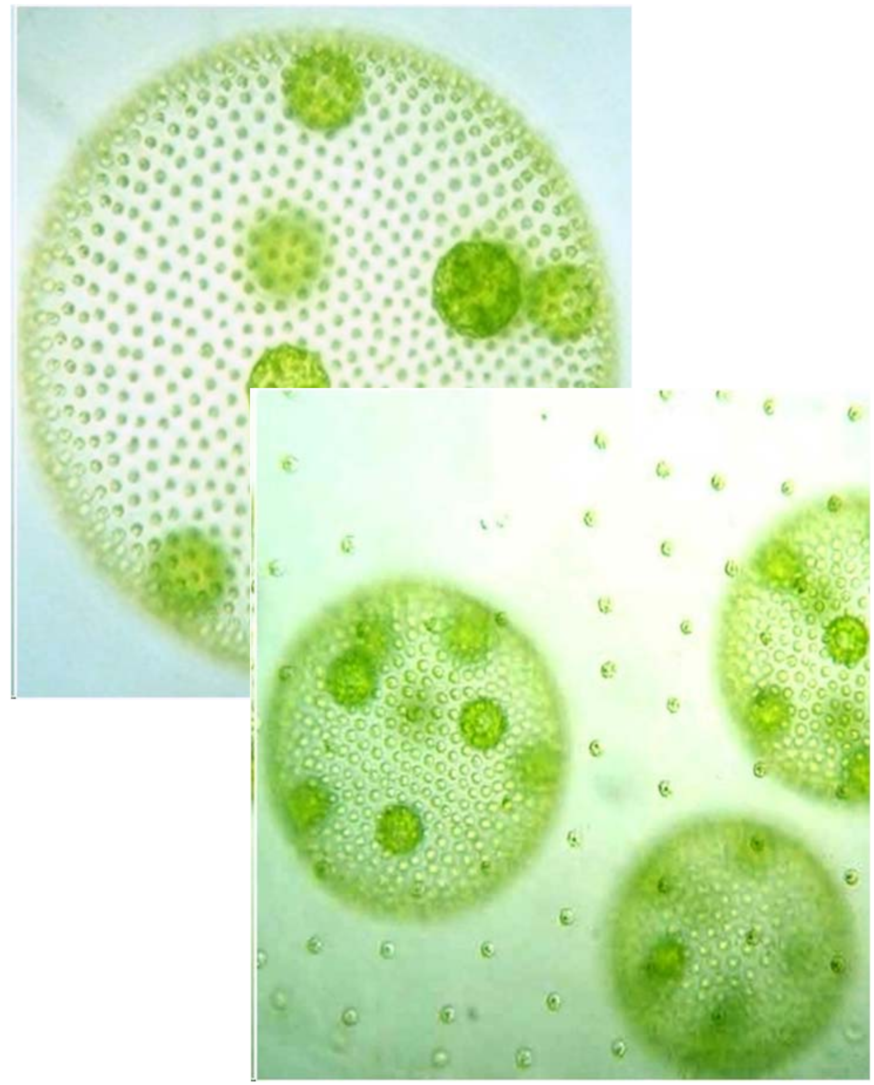
Chlamydomonas and *Volvox*
VARL domain tree



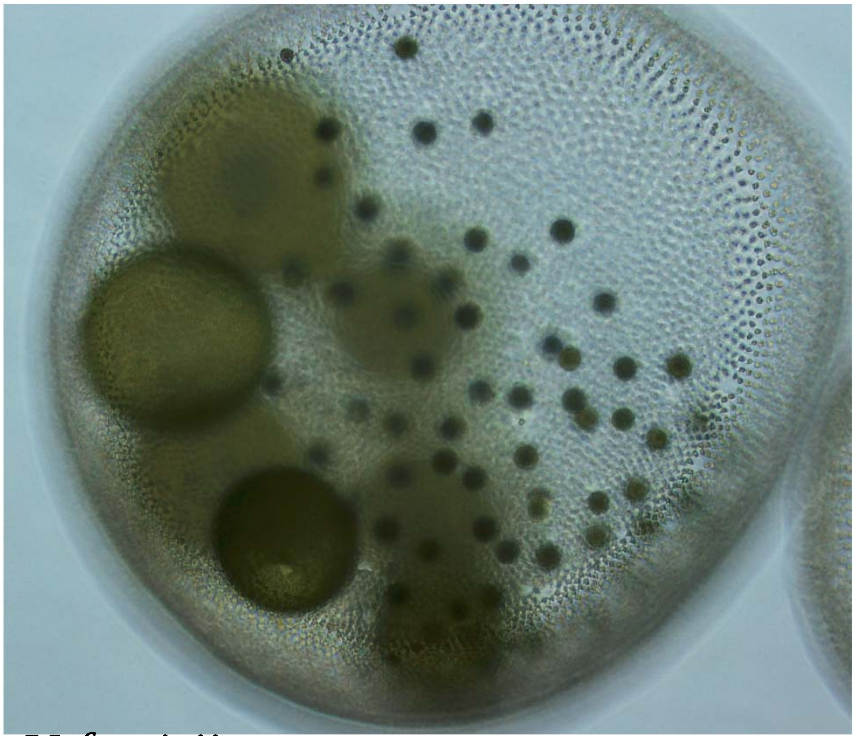
•Duncan, et al. The VARL gene family and the evolutionary origins of the master cell-type regulatory gene, regA, in Volvox carteri. J Mol Evol 65:1-11

Search *regA*-like genes in diverse volvocine taxa





V. ferrisii and *V. gigas*

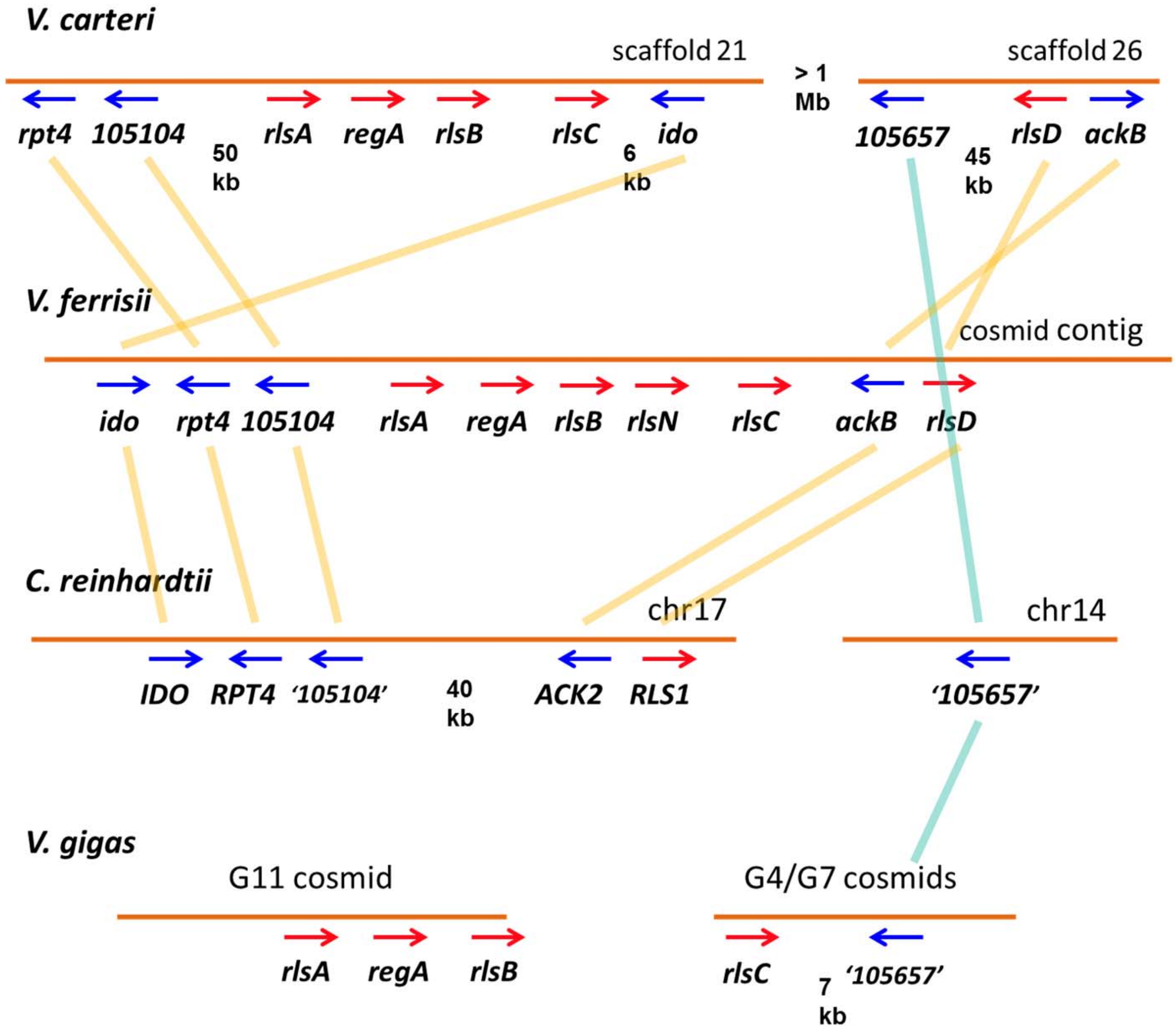


V. ferrisii picture credit: D. Shelton

- *V. carteri*
  - Multiple fission
  - Unequal cleavage: G/S
- *V. gigas* (60 million ya)
  - Multiple fission
  - Equal cleavage: G/S
- *V. ferrisii* (200 million ya)
  - Binary fission
  - Equal cleavage: G/S

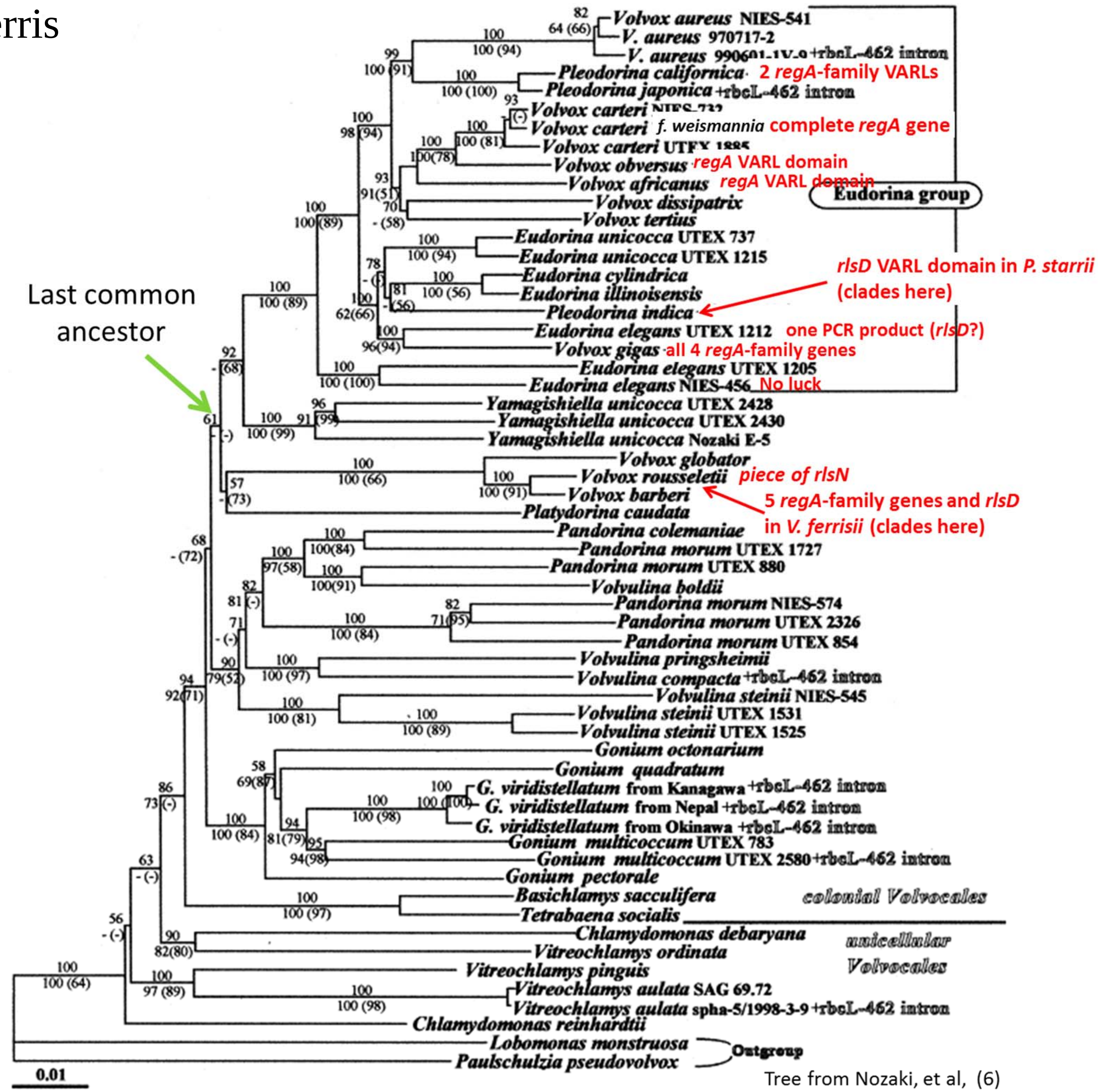
➢ Poster by P. Ferris (named after *V. ferrisii*) on *regA* genes

RegA-family genes are syntenic



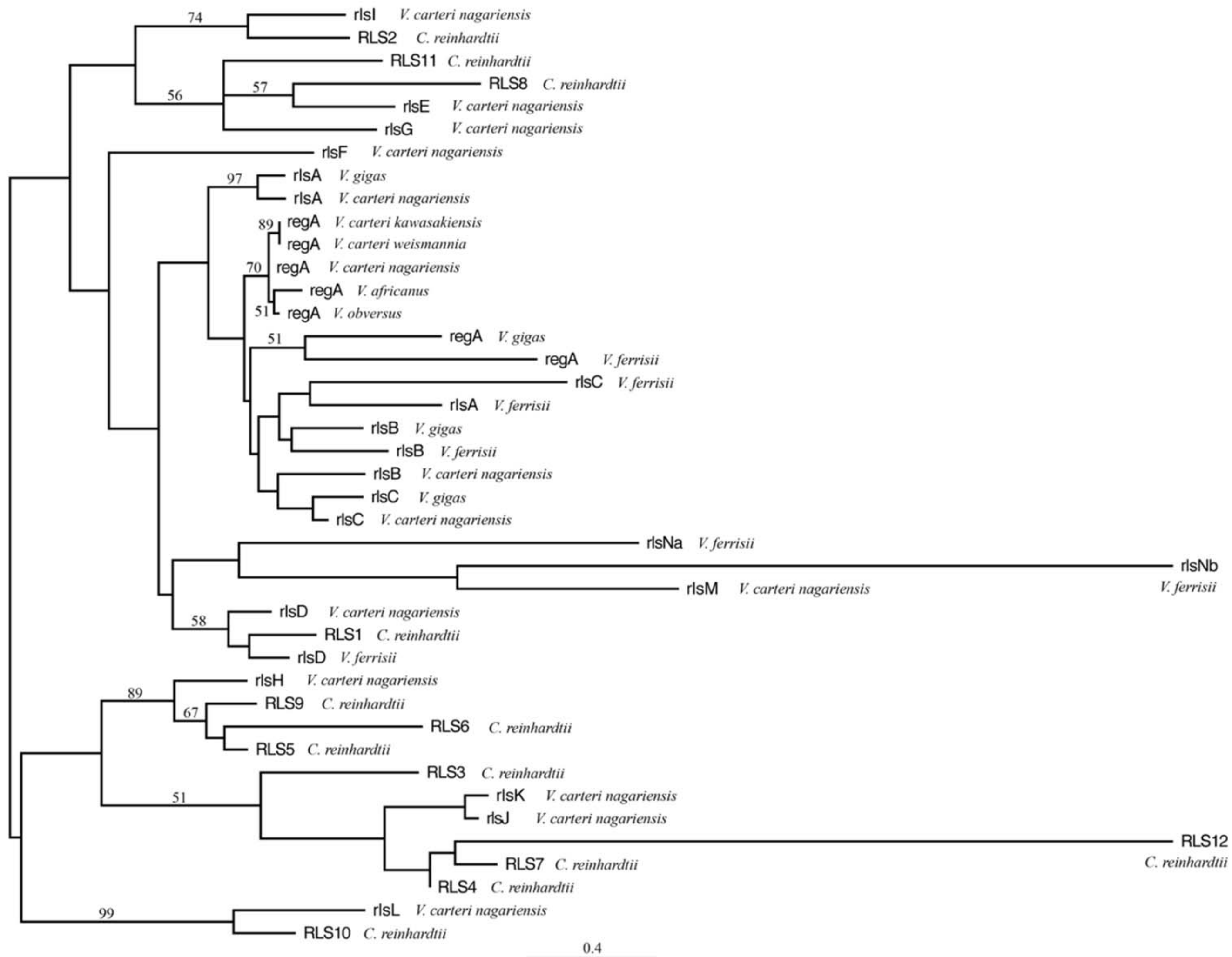
•Credit: P. Ferris

•Credit: P. Ferris



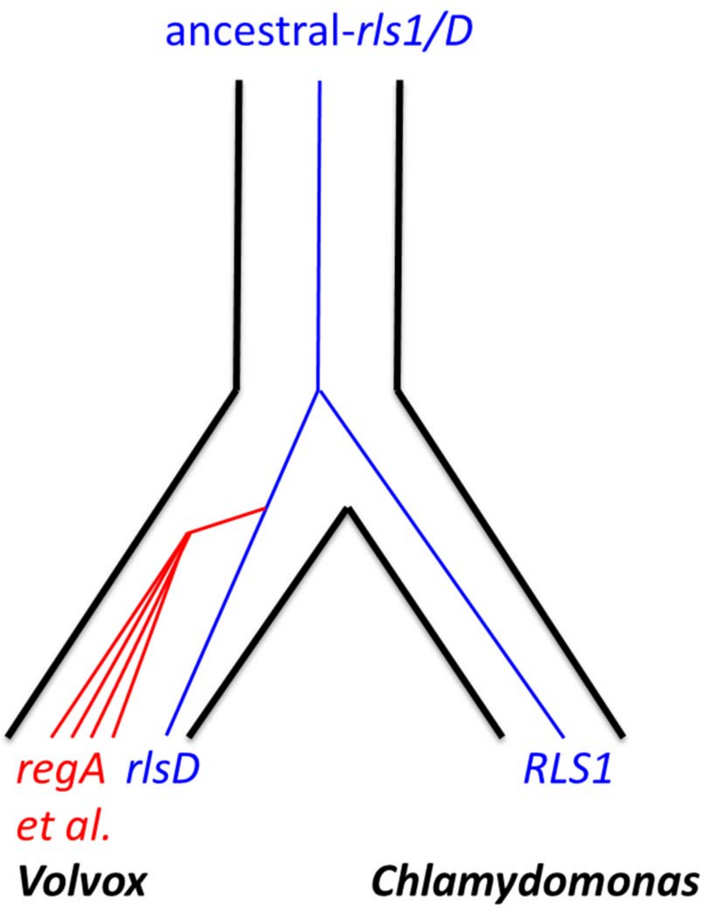
Tree from Nozaki, et al, (6)

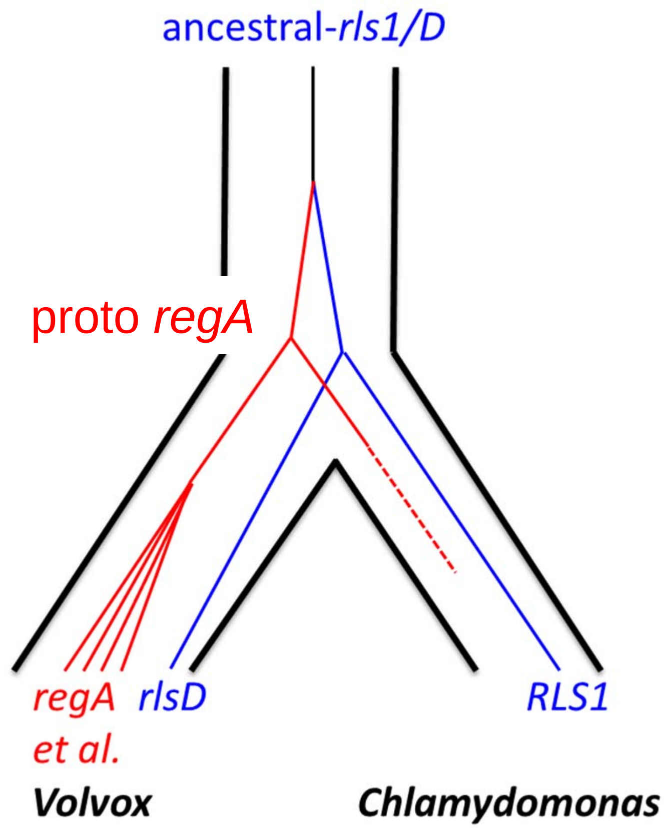
regA-family gene tree



•Credit: Duncan et al., E. Hanschen, P. Ferris

regA evolution





Duncan, et al., 2007

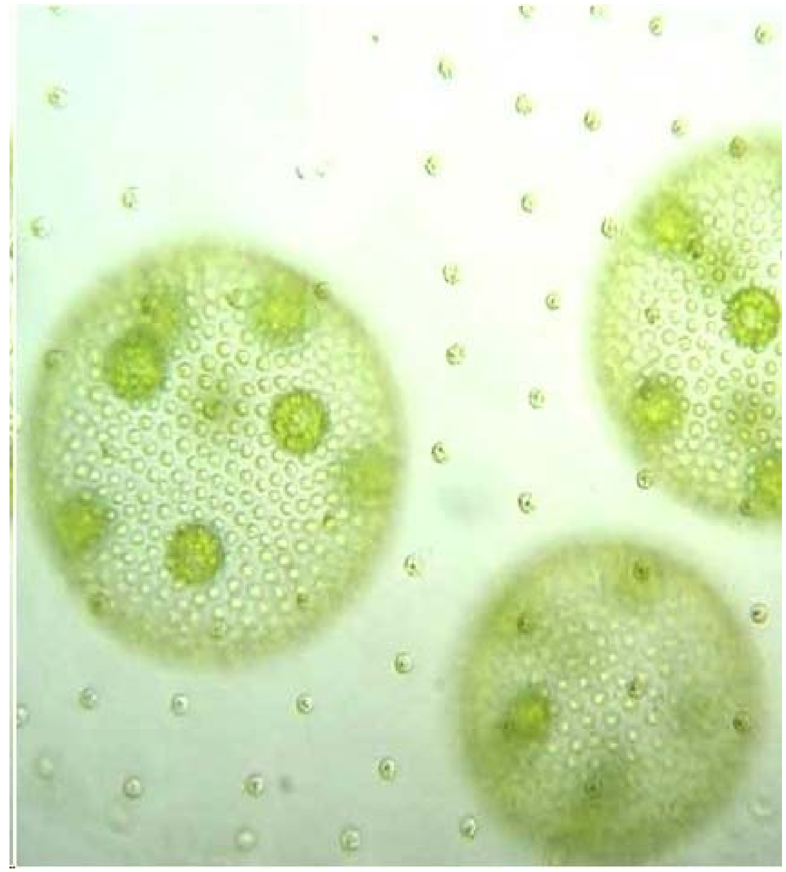
Conclusions

- Alternate views
  - *regA* gene family repeatedly co-opted for soma, but serves some other purpose in species without soma but with *regA*
  - *regA* gene family originally evolved to produce soma, but this is lost in species without soma but with *regA*
- Either way, soma, reproductive altruism, and individuality are evolutionarily labile traits

Time: half way?

Cooperation: How? and why?

- How can a gene for reproductive altruism arise?
  - Co-option of life history gene
- Why does reproductive altruism evolve?
  - Kin selection
  - Only in the larger species
  - Costs of larger size

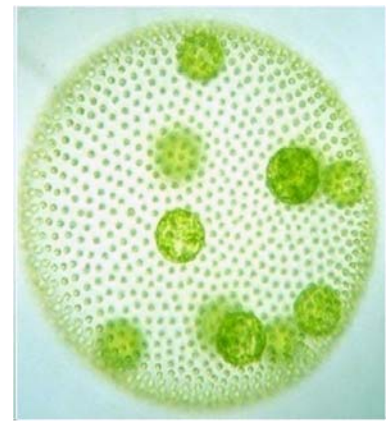


Life History Evolution

COST OF REPRODUCTION

Cost of reproduction to motility

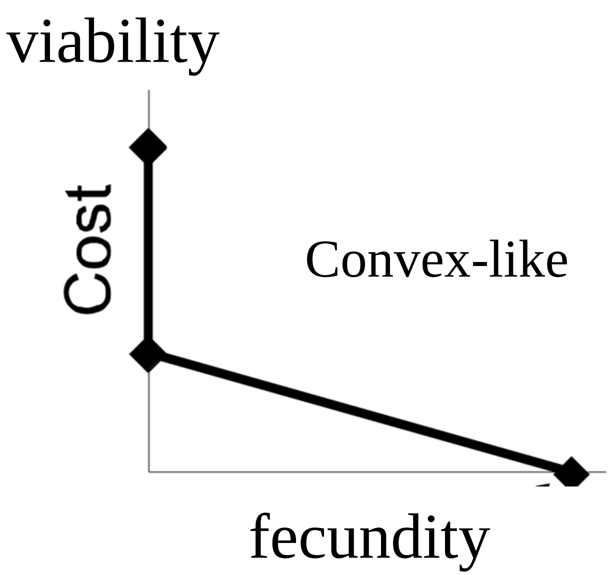
- Motility = survival
- No growth by cell division after birth
- Hydrodynamic drag
- Flagellation constraint
- Cost of reproduction increases with body size

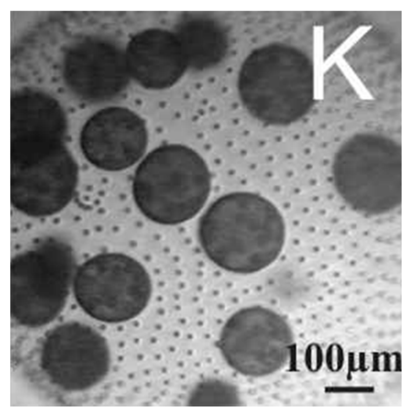


Initial cost of reproduction to flagellar force in *V. carteri* mutants

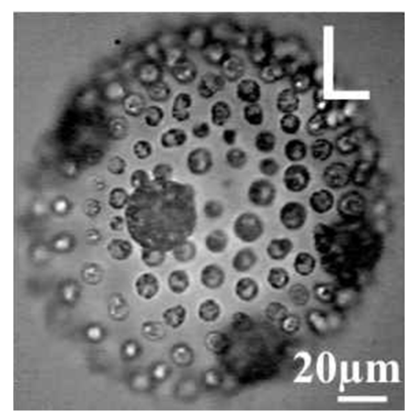
Forms	PIC	Colony	N	Change	*f* (dynes)
wt	K	G/S	2202		8.0×10^{-8}
regA^{-}	L	G/GS	239	235S→GS	4.9×10^{-8}

Credit: C. Solari





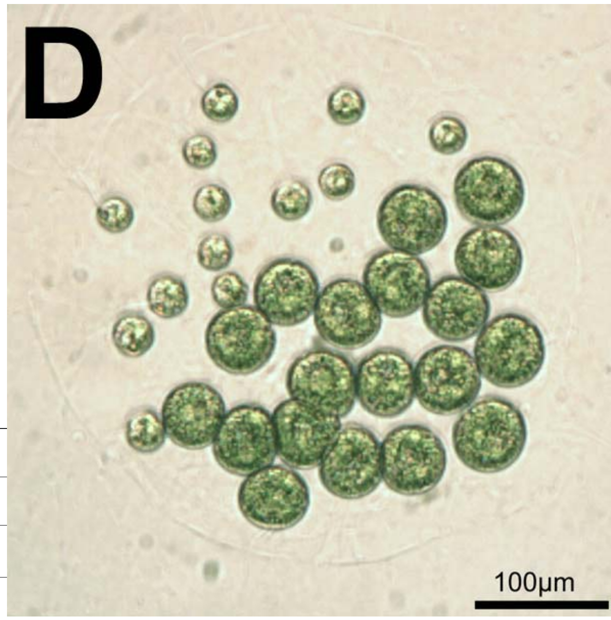
wild type



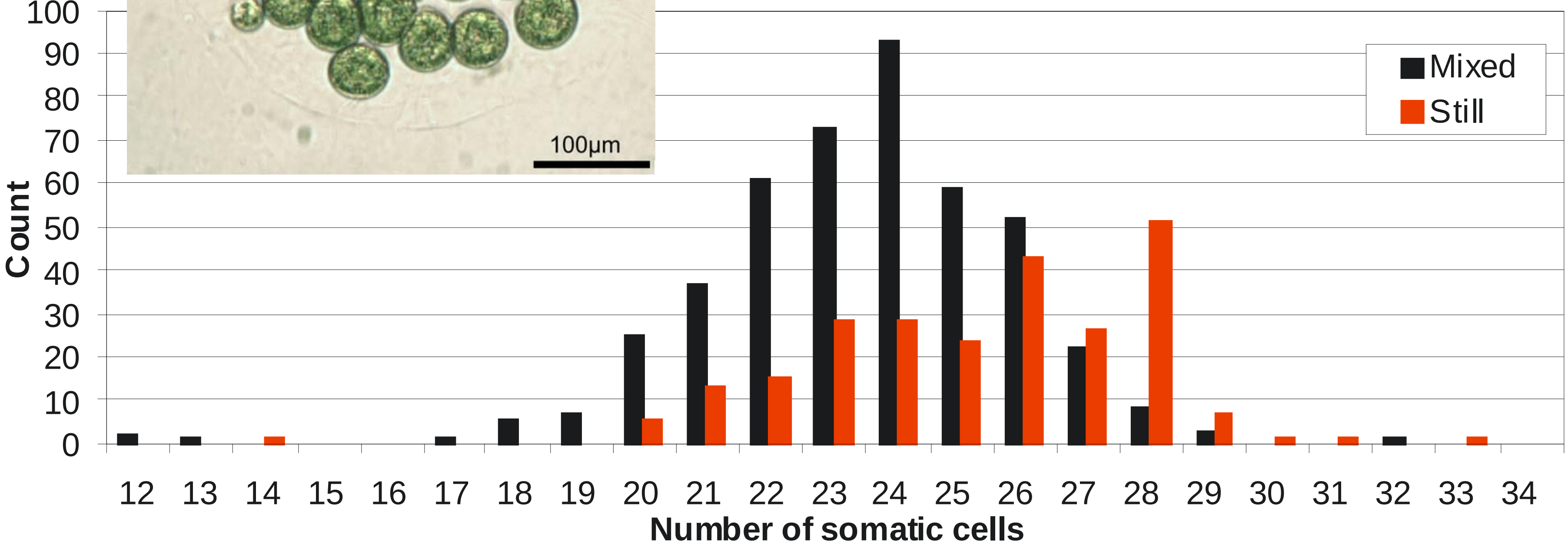
regA-

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 transitions in individuality

GROUP LIVING

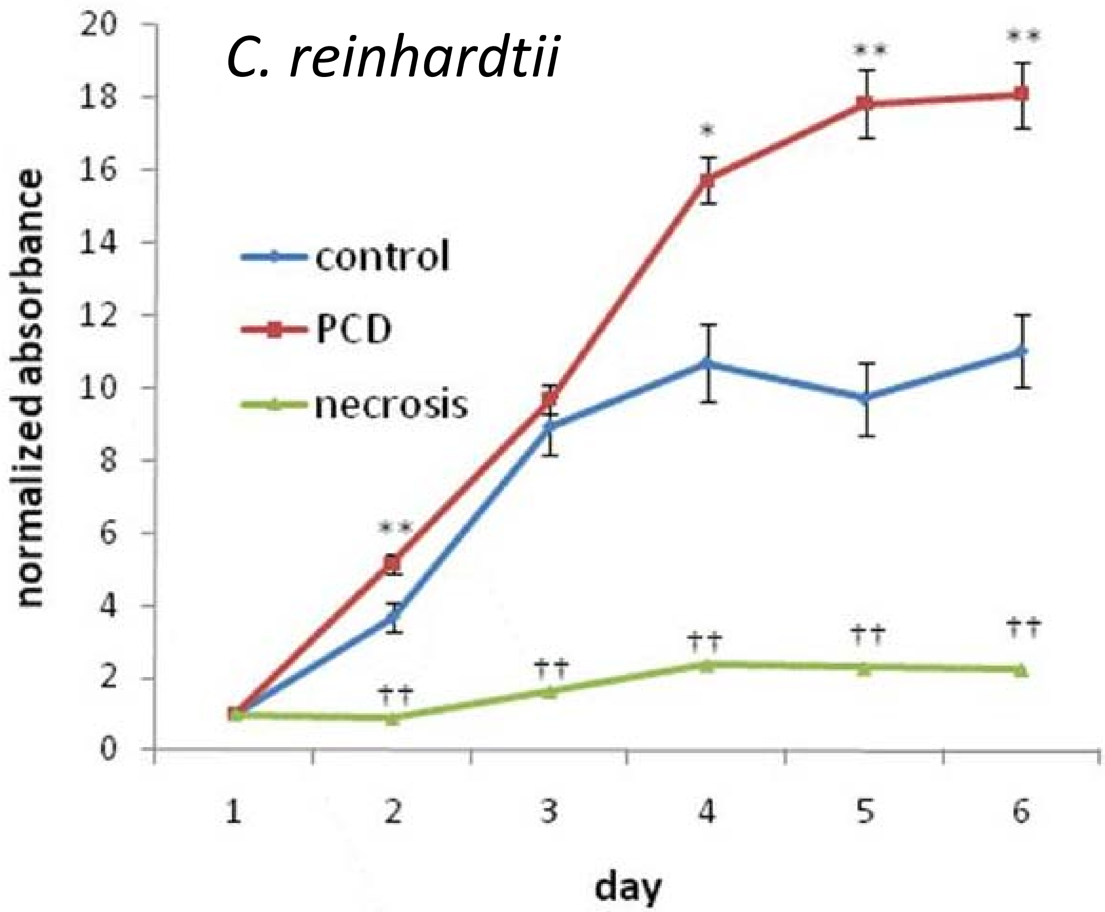
Death

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

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

- Necrosis is a barrier to group living

How an organism dies affects it neighbor's fitness

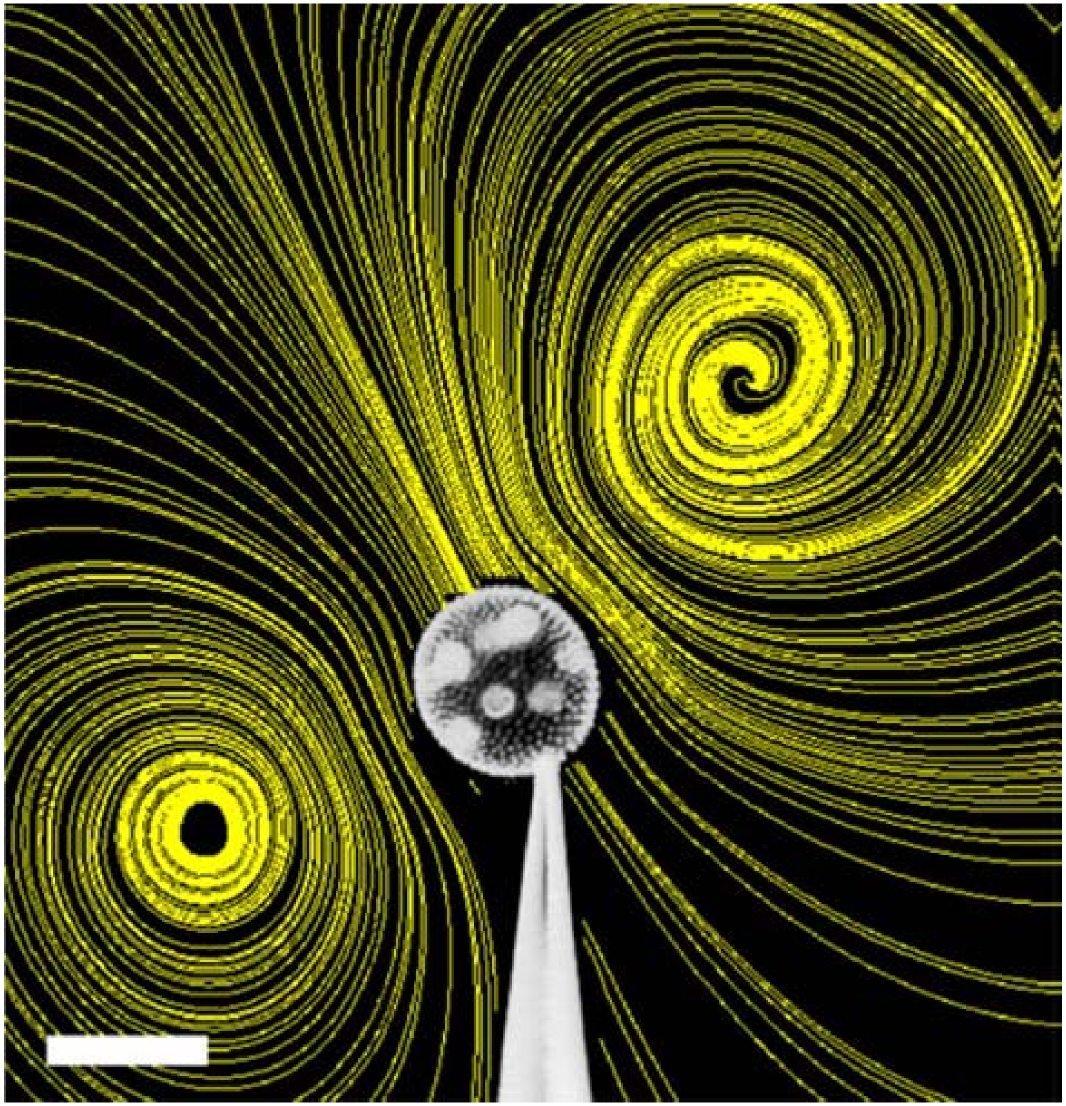


Durand, P. A. Rashidi, & R. E. Michod. 2011. *Am Nat.* 177, 224-232.

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.



•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.

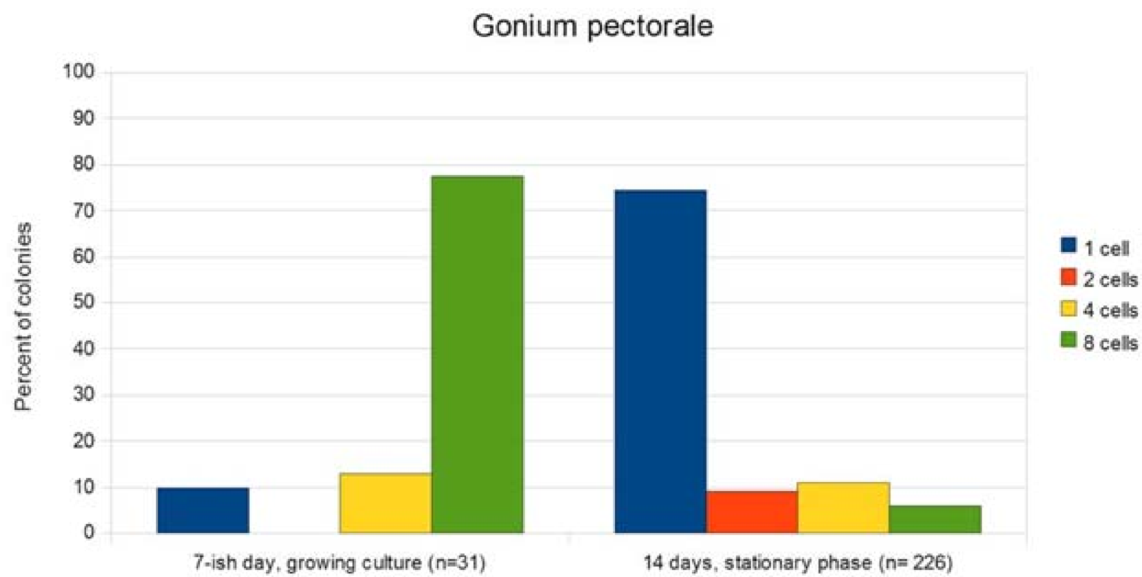
Evolutionary transitions

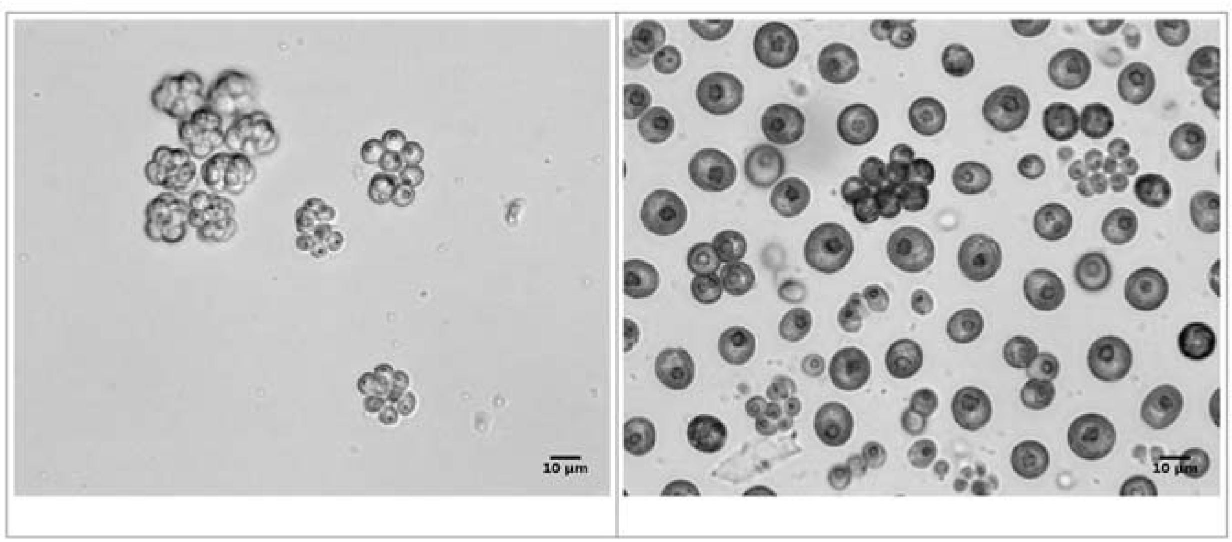
INDIVIDUALITY

Individuality concepts

- Indivisibility
- Distinctness
- Homogeneity
- Physiological unity
- Integration of components
- A stable level of selection and adaptation
  - conflict mediation
  - specialization of members at fitness components of group

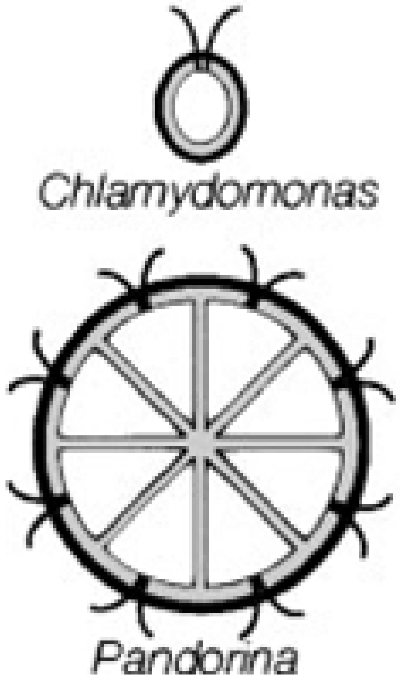
Low Individuality

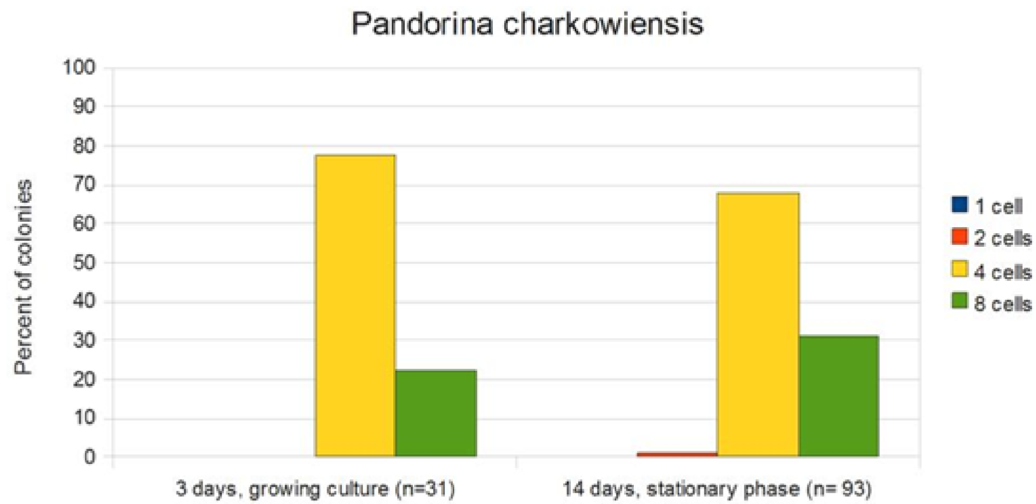


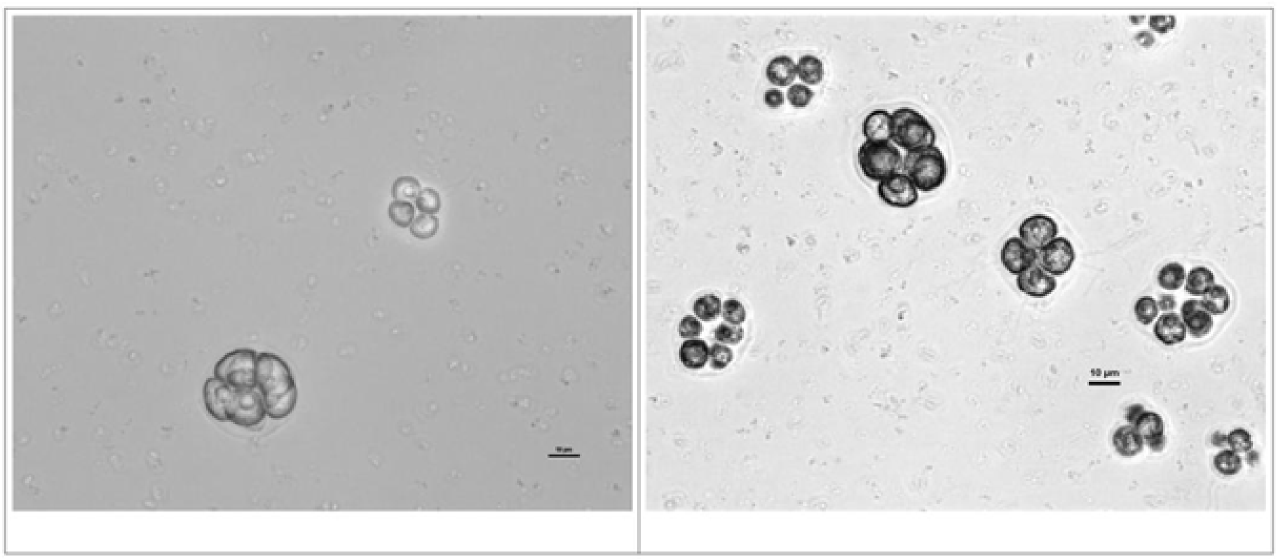


Credit: D. Shelton

High Individuality





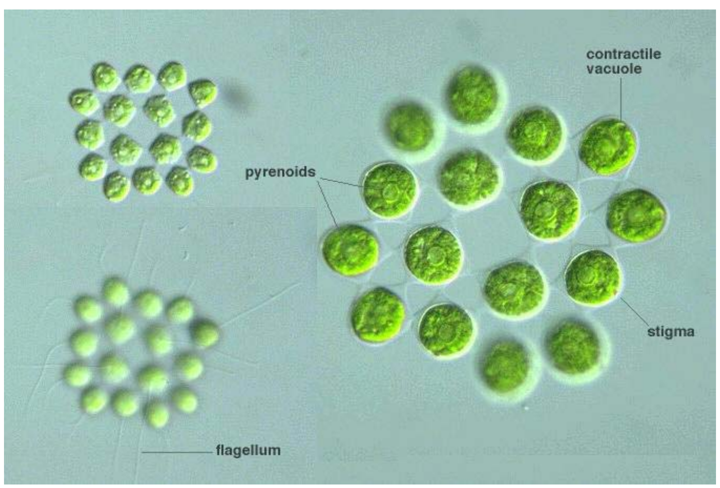


Credit: D. Shelton

Is *Gonium* an Individual?

For

- Functional integration
- Level of selection
- Focus of interest



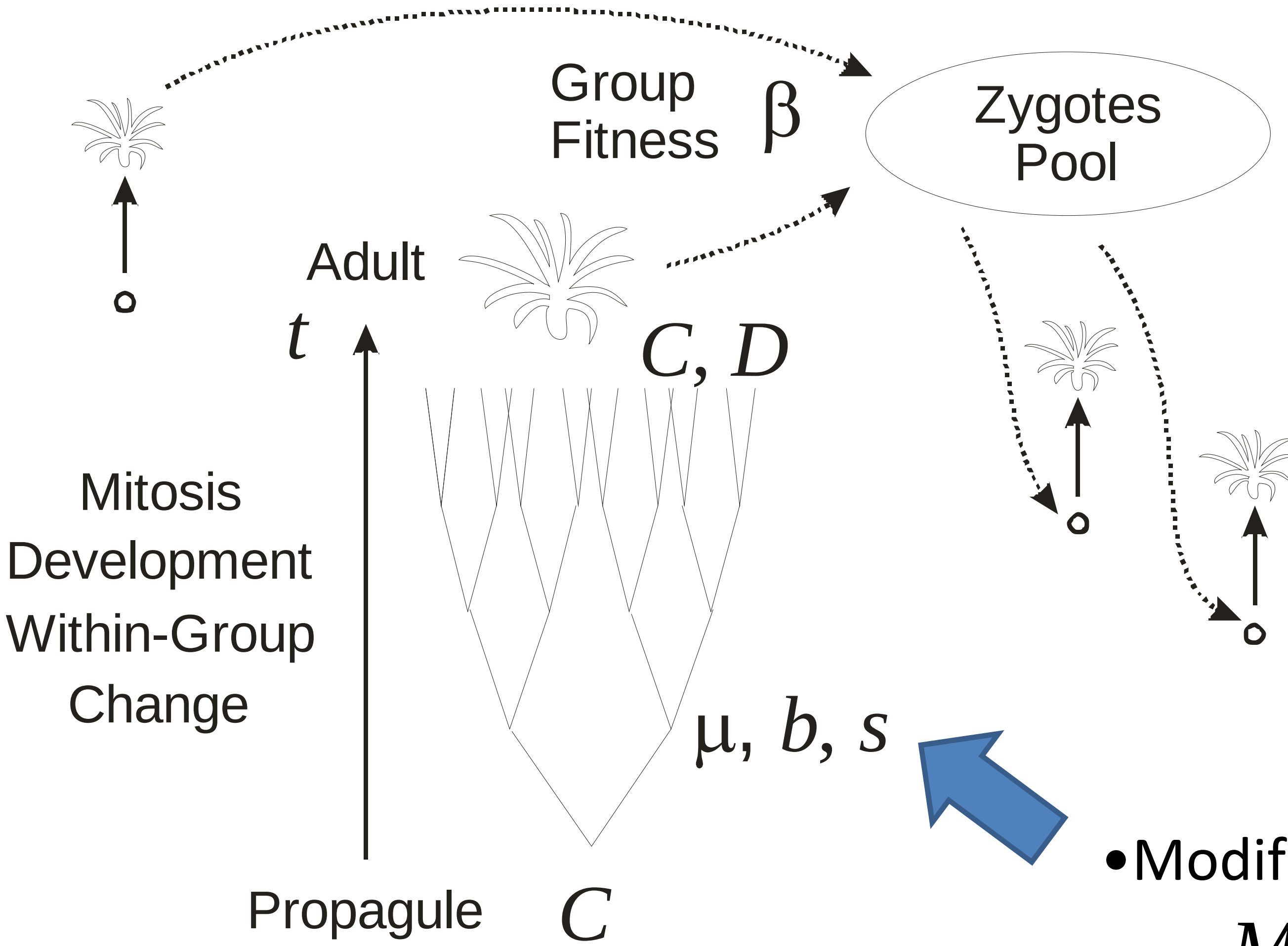
Against

- Group fitness not decoupled from cell fitness
- Group fitness is average of cell fitness
- *Gonium* is at step 2 of Okasha’s 3-step
- Group state is plastic response to environmental conditions

Evolutionary transitions in individuality

MODELS

Model of Development



- Modifier Locus

M/m

Population Genetics
Two-locus Modifier Equations

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

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

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

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

Linkage Disequilibrum

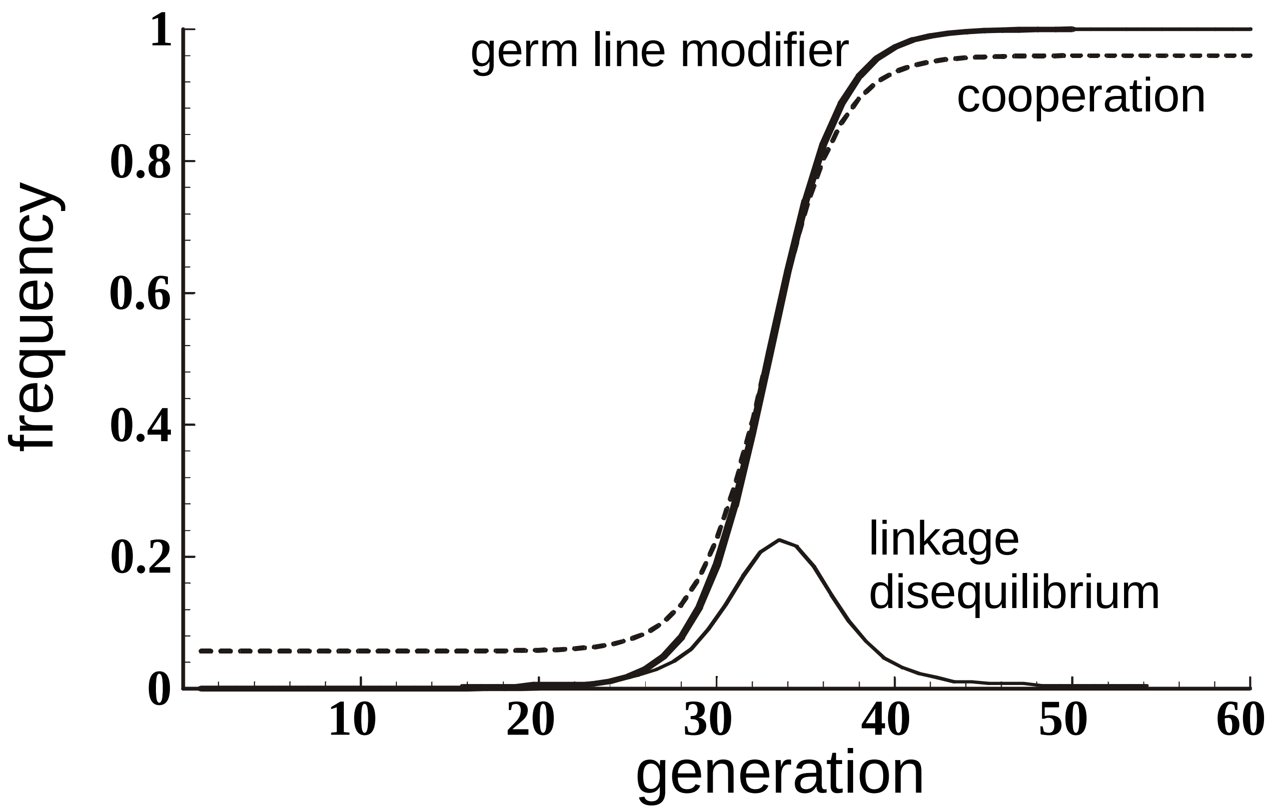
$$G = x_1 x_4 - x_2 x_3$$

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

Evolutionary Equilibria (*G*=0)

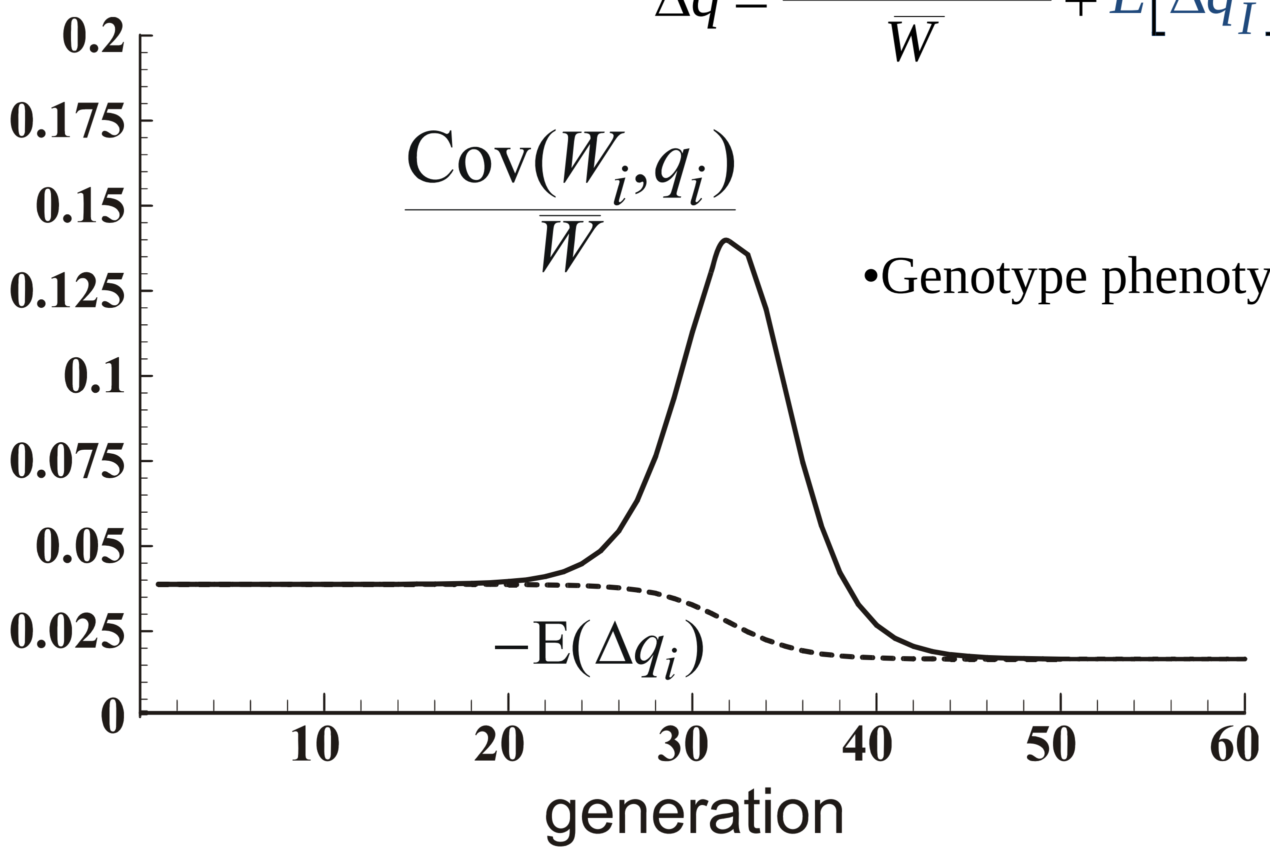
Eq.	Alleles		Description	Interpretation
1	*D*	*m*	no cooperation; no modifier	*Single cells*, no organism
2	*D*	*M*	no cooperation; modifier fixed	Not of biological interest, never stable
3	*C*,*D*	*m*	polymorphic for cooperation and defection; no modifier	*Group of cooperating cells*: no higher level 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

Level of Altruism Increases During Evolutionary Transition



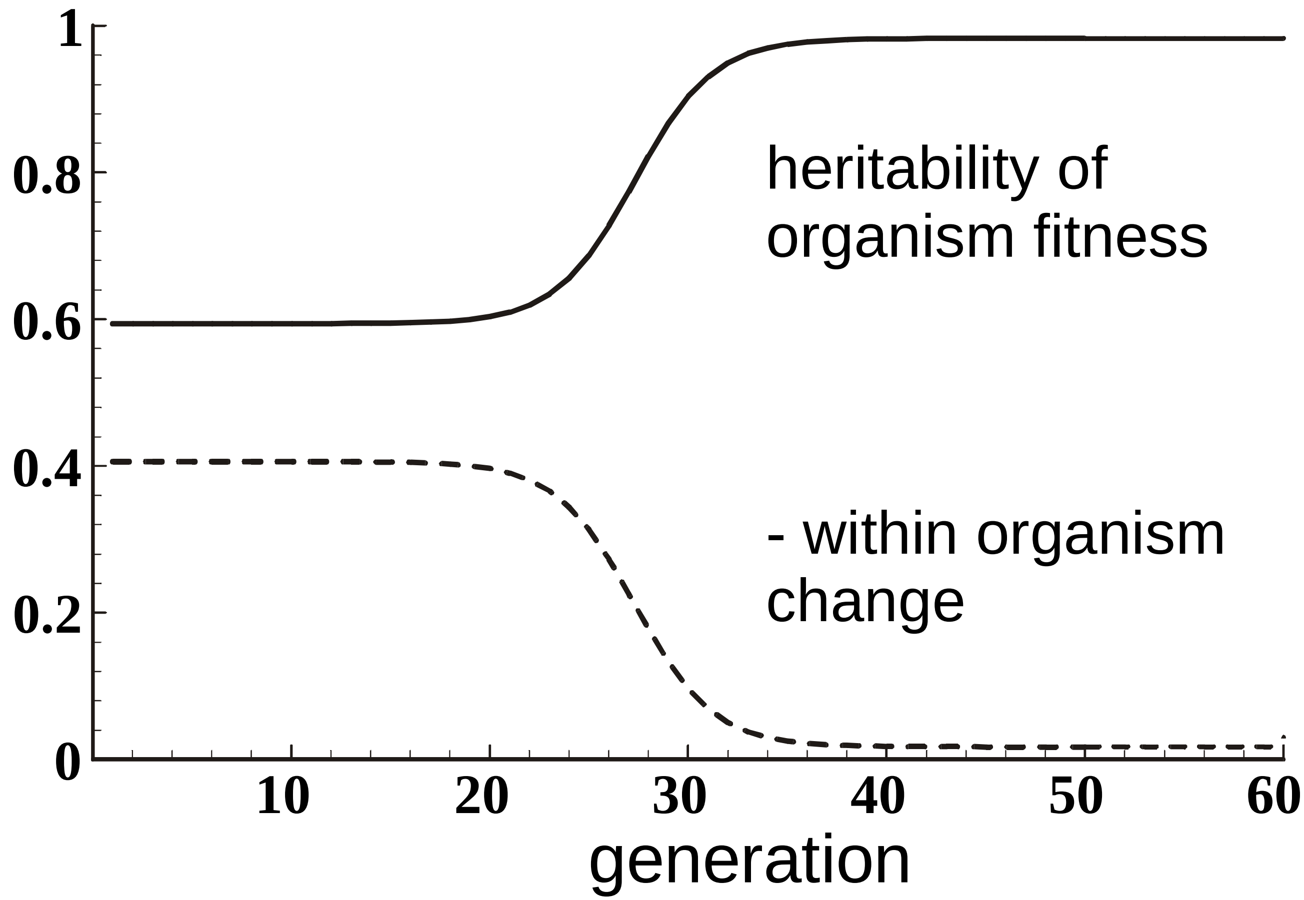
Group Fitness Covariance

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



- Genotype phenotype map

Heritability of Fitness Increases During Evolutionary Transition



CONCLUSIONS

Reorganization of fitness during evolutionary transitions

Fitness Components	Viability (vegetative/somatic functions). Fecundity (reproductive functions).
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. 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 and why does a group become an individual?

- General Points
  - Kinship and/or coloniality
    - Important, not sufficient
    - Individuality arises in only the larger species
  - Altruism and cell specialization trade fitness from lower to higher level
  - Conflict mediation
  - Fitness reorganization
  - Individuality is an evolutionarily labile trait in this group
- How?
  - Life history genes in uni-cells co-opted for reproductive altruism in group
- Why?
  - Trade-off between reproduction and survival
  - Trade-off becomes convex with increasing size
  - Increasing cost of reproduction selects for specialization and soma

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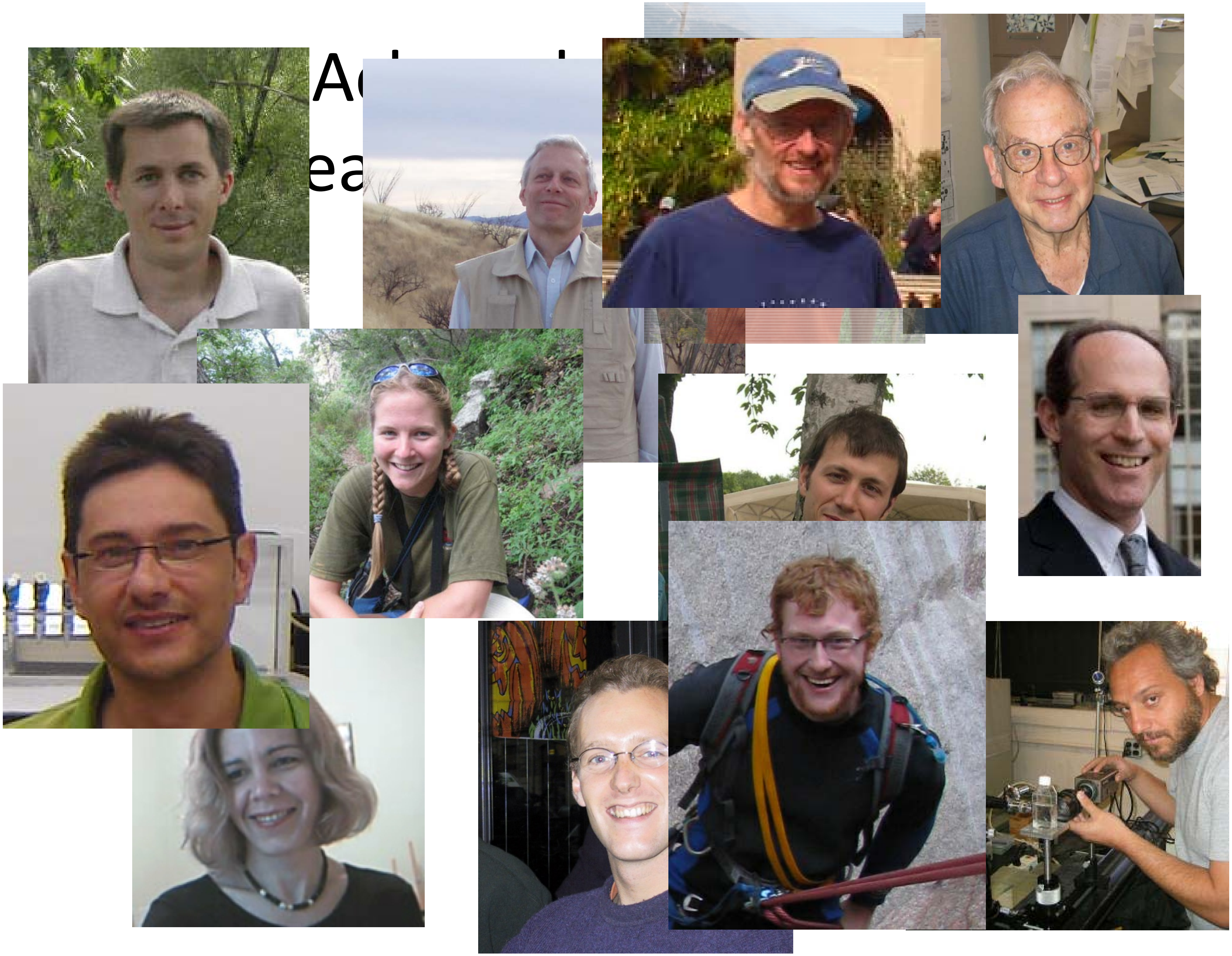

The End