Plan of my lectures

- Cooperation and conflict in evolution
  - Monday
    - Molecules to societies
    - Multicellularity
  - Sunday
    - Teaching of biology (10:30am)
      - NSF high school teacher internship in our lab
    - Sex & immortality of life (4:30pm)

Teaching Evolution and Biological Complexity

Using cooperation and conflict during evolutionary transitions in individuality

Plan of talk

- Darwinism and evolution
- Bad designs
- Multi-level selection
- Complexity
- Multicellularity
- NSF sponsored teacher intern program

DARWINISM

- In the theory with which we have to deal, Absolute Ignorance is the artificer; so that we may enunciate as the fundamental principle of the whole system, that, in order to make a perfect and beautiful machine, it is not requisite to know how to make it. This proposition will be found, on careful examination, to express, in condensed form, the essential purport of the Theory, and to express in a few words all Mr. Darwin's meaning; who, by a strange inversion of reasoning, seems to think Absolute Ignorance fully qualified to take the place of Absolute Wisdom in all the achievements of creative skill.

  --Robert Beverley MacKenzie, 1868

Explanation

- Teleological or theological
  - Things exist or have properties because purposeful agents (people, God) made them
- Mechanistic
  - Things have properties because of their parts
- Darwin: Population thinking
  - Darwin argued that if a population of organisms vary, and if some variants leave more offspring than others, and if parents tend to resemble their offspring, then the composition of the population will change over time so that the fittest variants gradually supplant the less fit.

Biology is a Science

- Science is
  - A particular way of understanding the world
  - A way of knowing
  - Science begins with observations and the formulation of hypotheses that can be tested and be rejected
- Distinguish science from religion
  - Science has no absolute truth but a method of proof
  - Religion claims absolute truth but no method of proof
- Science is NOT
  - A democratic or political process
    - We don’t vote on what is scientifically true, or what is science, there is a method for determining this.
  - Tells us what “is” not what “ought” to be
  - Amoral or anti-religion

Evolution IS

- IS science
- IS a fact and a theory
- IS testable
- IS variation, selection and inheritance
- IS common descent with modification
- IS change in gene frequency in a population over time
- IS an explanation for the appearance of design in living things (adaptation)
- IS an explanation for examples of “bad” design
- IS the intellectual framework for all of biology

Evolution IS NOT

- IS NOT a completely random process
- IS NOT change in an individual over time
- IS NOT an inevitable form of "progress"
- IS NOT proof that there is no purpose or meaning to life
- IS NOT proof that God does not exist
- IS NOT justification for immorality
  "is" does not imply "ought"

Biological Order

- Design
  - Good design
  - Bad design
- Species

BAD DESIGN

Evolution Explains Bad Design

- Evolution can't design from scratch: it can only modify what went before
- Sometimes this leads to "bad design"
- When we swallow, we risk choking because our breathing hole is in the way, and needs to be closed off.
- We inherited this bad design from an ancestral lungfish.

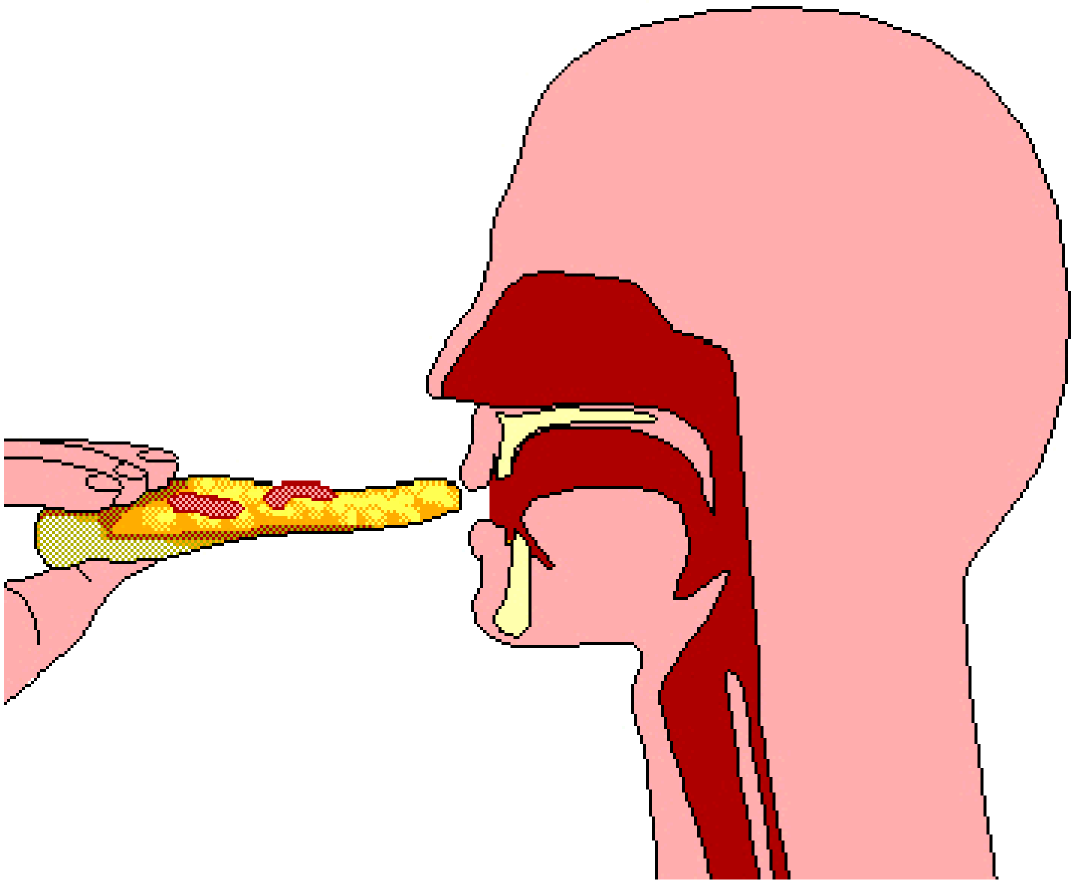
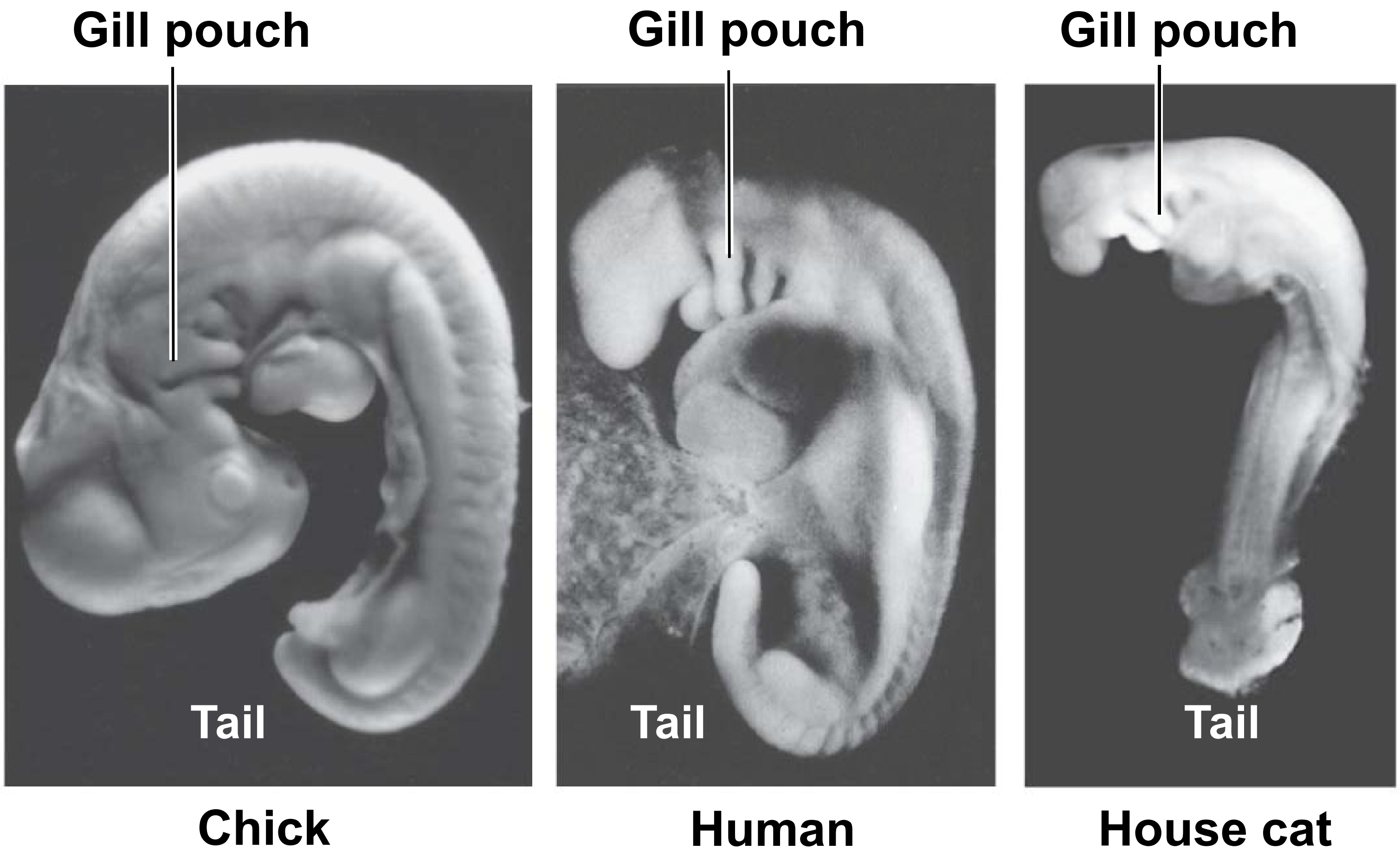
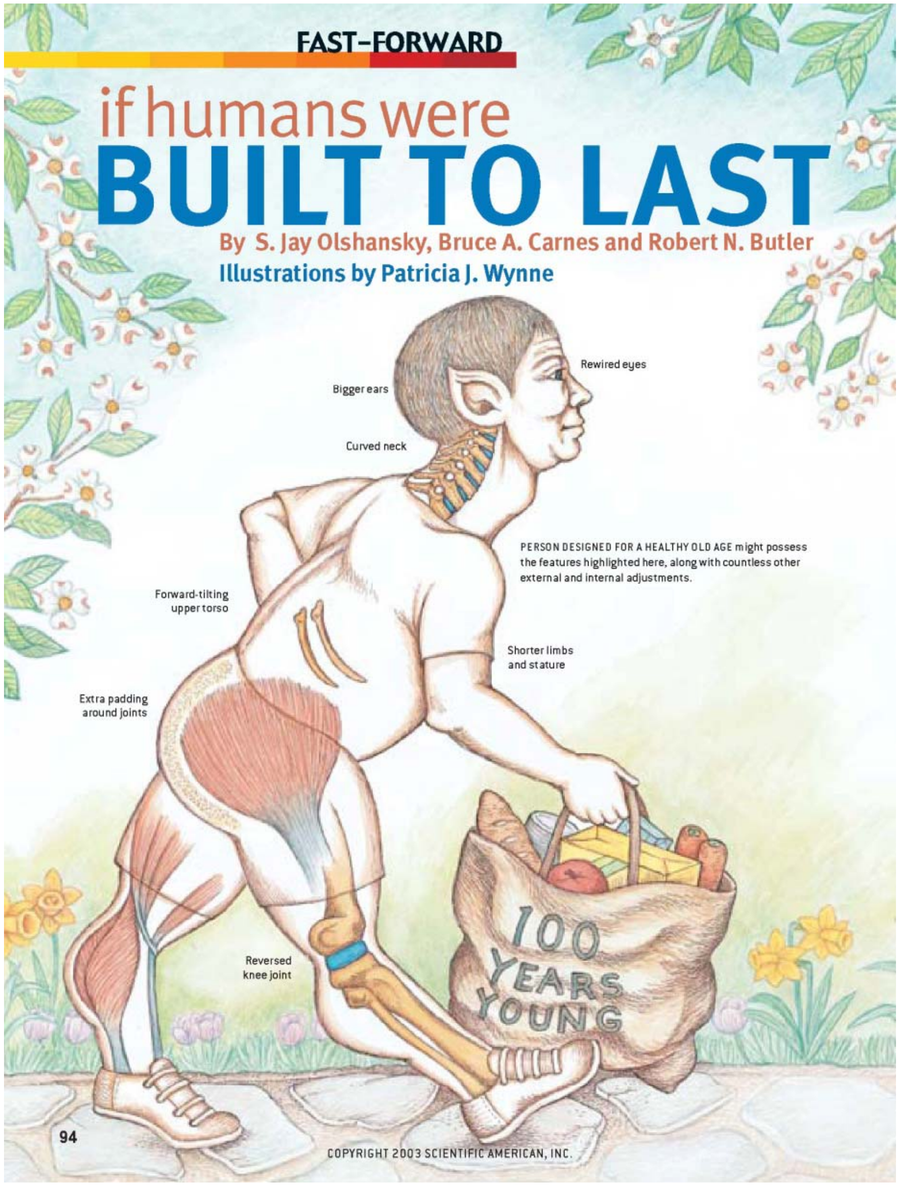


Figure 24-8


Gill pouch
Gill pouch
Gill pouch
Tail
Tail
Tail
Chick
Human
House cat

A Better Human Design



- Curved neck
- Forward-tilting upper torso
- Extra padding around joints
- Reversed knee joint
- In addition, countless other external and internal adjustments.
  - Rewired eyes
  - Bigger ears
  - Shorter limbs and stature

Credit: S. Jay Olshansky, Bruce A. Carnes and Robert N. Butler COPYRIGHT 2003 SCIENTIFIC AMERICAN, INC. Article originally appeared in March 2001 issue of Scientific American.

MULTI-LEVEL SELECTION

Levels of selection

- Levels of selection is outgrowth of three factors
  - abstract nature of the principle of natural selection
  - hierarchical organization of living world
  - altruism
    - and other traits which do not seem to benefit organisms

Abstract nature of Darwin’s conditions

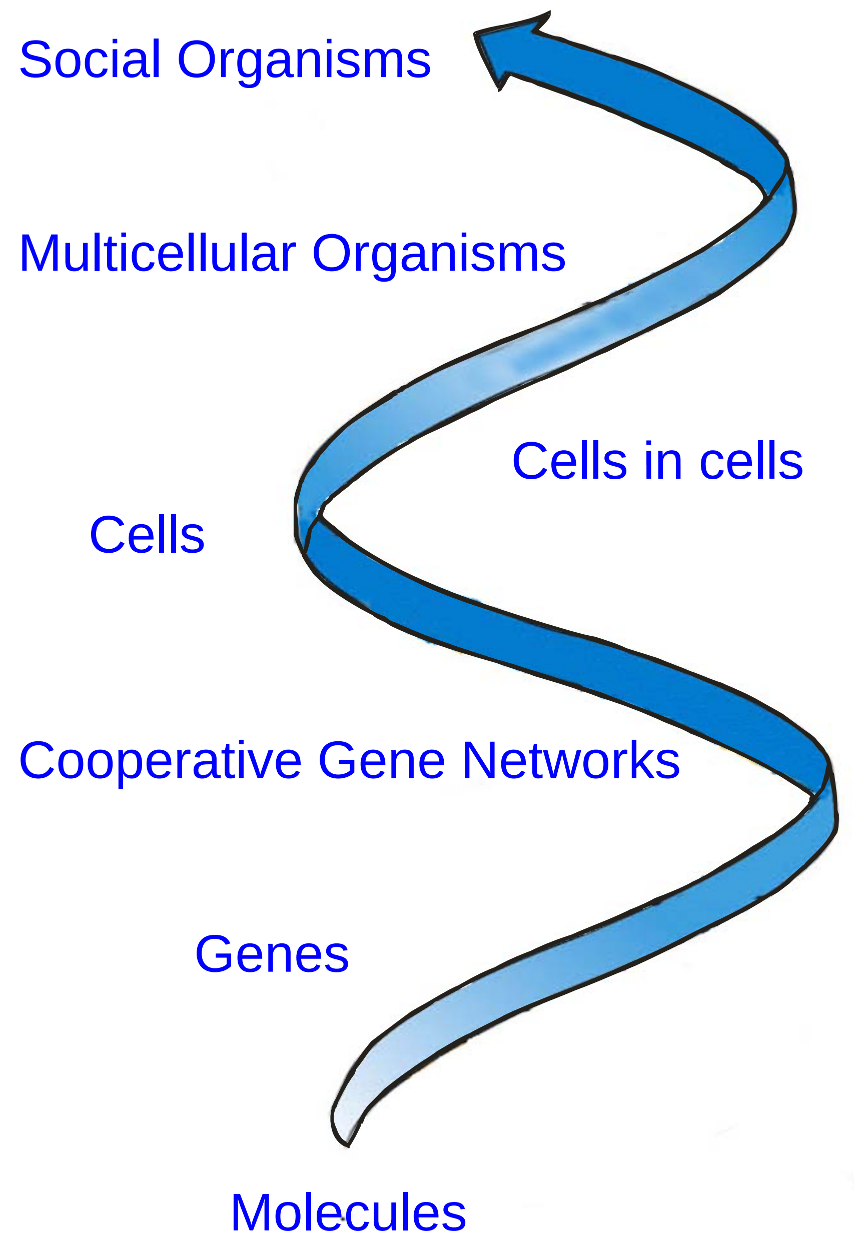
- Natural selection
  - Darwin argued that if a population of organisms vary, and if some variants leave more offspring than others, and if parents tend to resemble their offspring, then the composition of the population will change over time so that the fittest variants gradually supplant the less fit.
- Apply to other entities which vary and reproduce
  - It is easy to see that Darwin's reasoning applies not just to individual organisms. Any entities which vary, reproduce differentially as a result, and beget offspring that are similar to them, could in principle be subject to Darwinian evolution. The basic logic of natural selection is the same whatever the "entities" in question are.

Multi-level selection

- Darwin's postulates apply to other units in the hierarchy of life: genes, chromosomes, cells, organisms, kin groups, groups, …
- For just as organisms give rise to other organisms by reproduction, so cells give rise to other cells by cell division, genes give rise to other genes by DNA replication, colonies give rise to other colonies by fission (among other ways), species give rise to other species by speciation, and so-on.
- Thus the Darwinian concept of fitness, i.e. expected number of offspring, applies to entities of each of these types.
- So in principle, these entities could form populations that evolve by natural selection.

Life's hierarchical organization

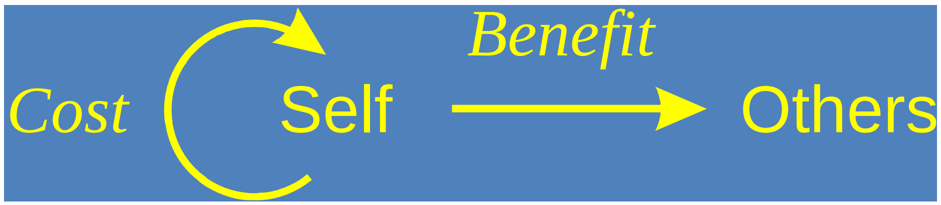
- Genes
- Gene networks
- Chromosomes
- Cells
- Cells inside other cells (eukaryotic cell)
- Multicellular organisms
- Societies of organisms
- Species



There is no progress in evolution, but the level of complexity can increase under certain conditions

Altruism and adaptation

- Adaptation
  - NS leads to adaptations - traits that enhance survival and reproductive success of organisms
  - Organisms also exhibit non-adaptive traits.
- Altruism
  - Selection at the level of the organism should disfavor altruism
  - Yet altruism is found throughout life.
  - Altruism evolves by selection at higher levels of organization
- Group selection
  - Groups containing a high proportion of altruists have a selective advantage over groups contain a preponderance of selfish types, even though within each group, selection favors selfishness (Darwin 1871).

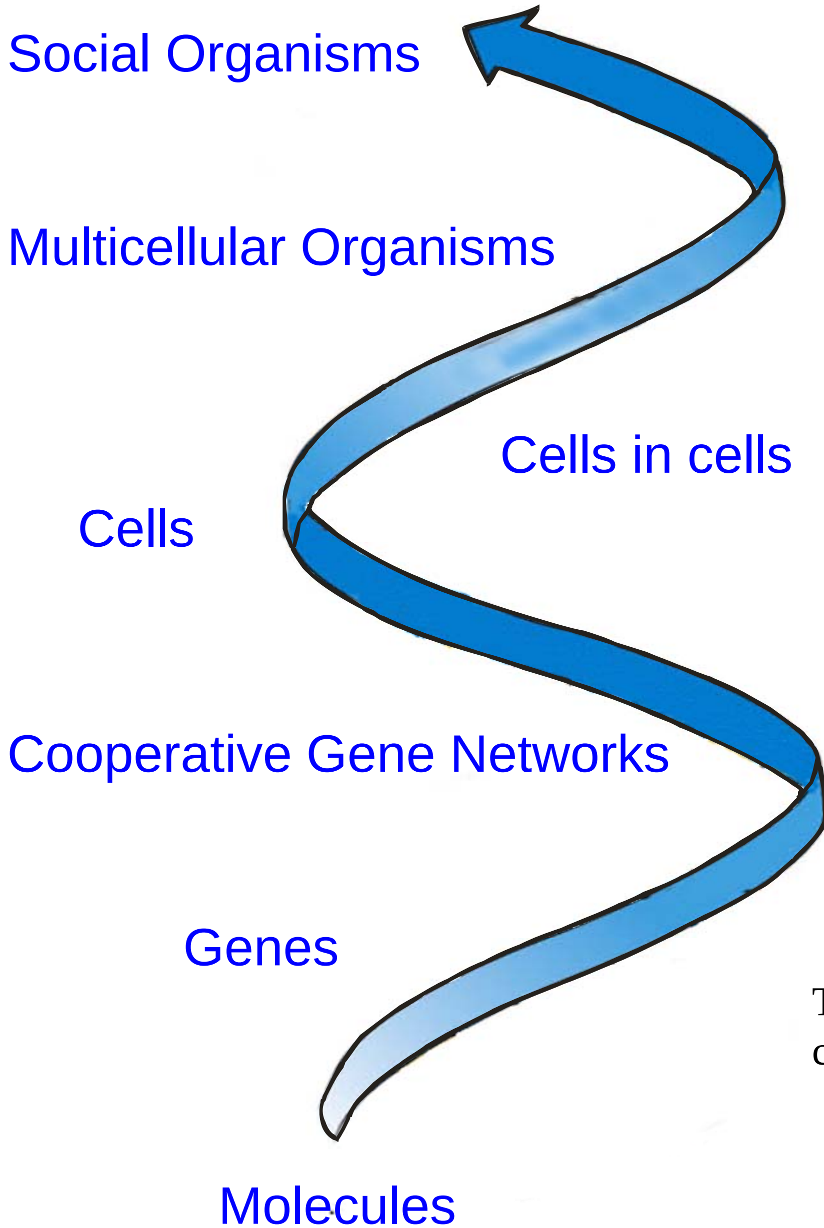


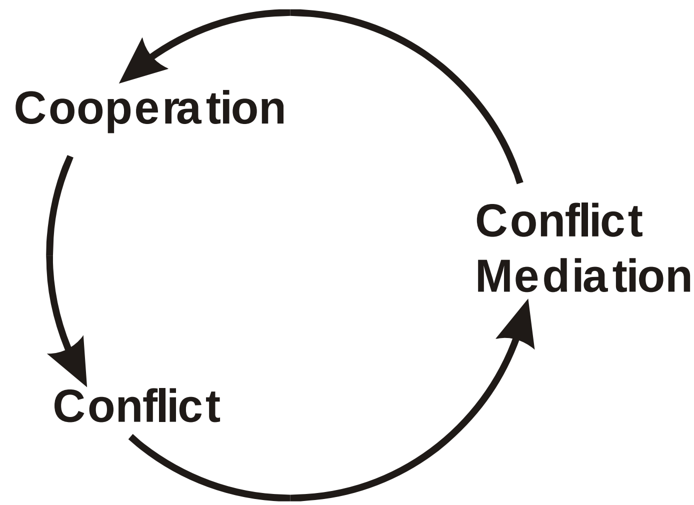
Cancer

- The case of altruism illustrates an important principle, namely that what is advantageous at one hierarchical level may be disadvantageous at another level, leading to a conflict of interest.
- Various features of modern organisms suggest the importance of such inter-level conflicts. Mammalian cancer is an example.
- Cancer involves a process of cellular selection, for cancerous cells increase in frequency relative to other cell lineages within the organism's body.
- So a maladaptive feature of individual organisms is explained by selection at a lower hierarchical level, in the case the cellular level.

COMPLEXITY

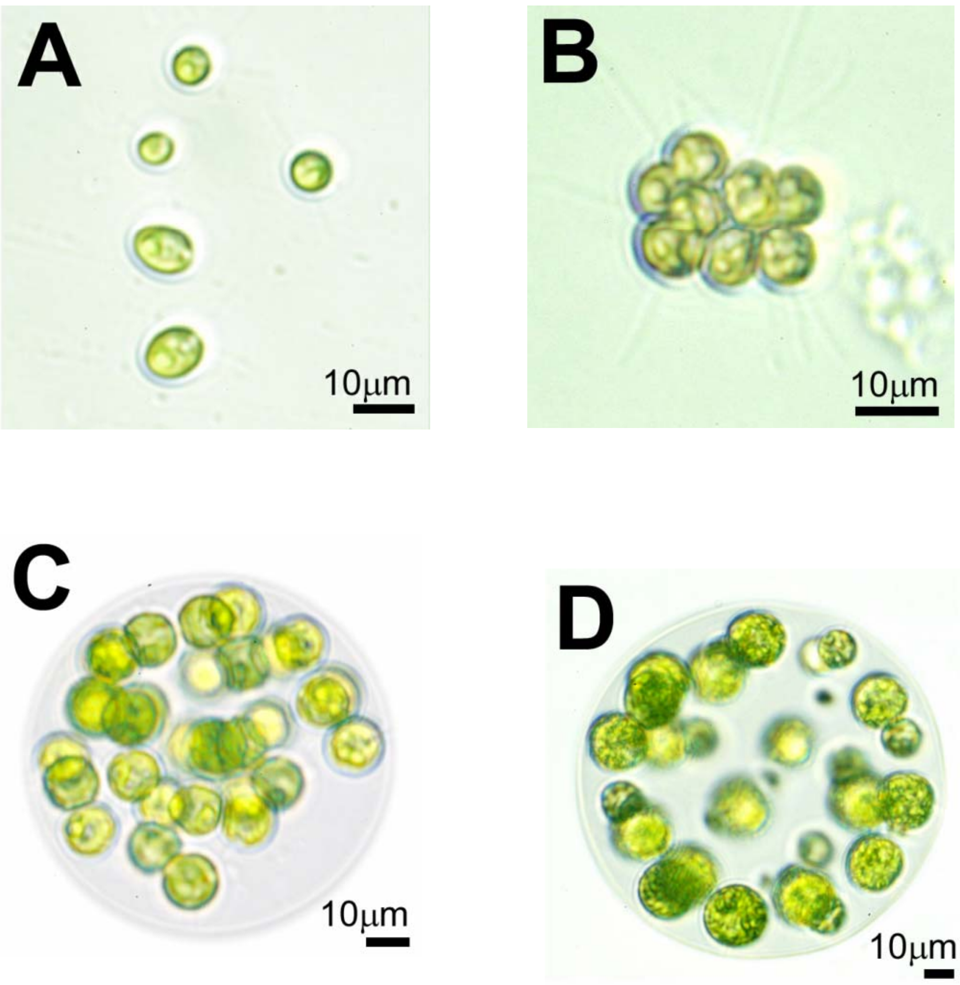
Cooperation drives complexity

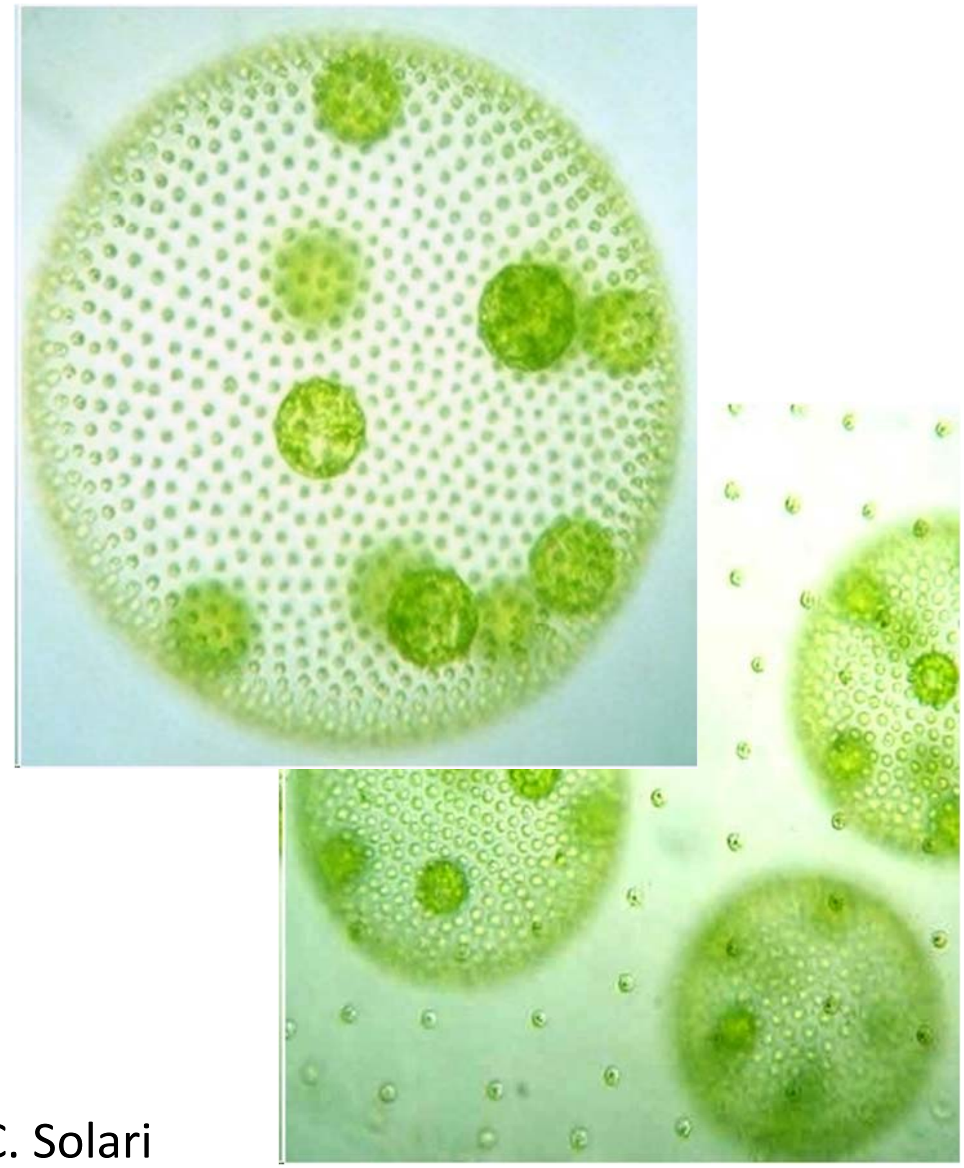




There is no progress in evolution, but the level of complexity can increase under certain conditions

Volvocine green algae as a model system for the study of complexity





Picture credit: C. Solari

What about “intelligent design”?

- Intelligent design: adaptations and life created by an “intelligent designer”
- What about all the examples of bad design?
  - Pigs toes, human tail and gill slits, 97% of human genome is junk…
- Religious teaching in state schools is restricted by the Constitution.
- Intelligent design is creationism masquerading as science in order to be taught in schools.
- It is not science, as the US District Court has ruled in Kitzmiller vs. Dover
- Irreducible complexity

http://coop.www.uscourts.gov/pamd/kitzmiller_342.pdf

So called “irreducible complexity”

- Intelligent design’s alleged scientific centerpiece.
- Certain biological structures appear to require multiple components to come together simultaneously, implying no selection until all of them are in place.
- This combination is too unlikely to come together by chance and they are produced by an “intelligent designer” according to intelligent design.

Answer to irreducible complexity

- Intermediate stages were, in fact, selected for.
- Sometimes we have good evidence for them, sometimes not.
- Much of the science of evolutionary biology is devoted to this problem
- These intermediate and earlier stages, which were useful for something else, were co-opted to produce a new, more complex structure, sometimes with a different function.
  - Example of *regA* gene in origin of multicellularity in *Volvox*

Darwin already answered this

- The Origin of Species, Chapter 6 “Difficulties of the theory” and see the section “Organs of extreme perfection and complication”
- “To suppose that the eye with all its inimitable contrivances for adjusting the focus to different distances, for admitting different amounts of light, and for the correction of spherical and chromatic aberration, could have been formed by natural selection, seems, I freely confess, absurd in the highest degree…”

What Darwin said next

- When it was first said that the sun stood still and the world turned round, the common sense of mankind declared the doctrine false; but the old saying of Vox populi, vox Dei ["the voice of the people = the voice of God "], as every philosopher knows, cannot be trusted in science.
- Reason tells me, that if numerous gradations from a simple and imperfect eye to one complex and perfect can be shown to exist, each grade being useful to its possessor, as is certain the case; if further, the eye ever varies and the variations be inherited, as is likewise certainly the case; and if such variations should be useful to any animal under changing conditions of life, then the difficulty of believing that a perfect and complex eye could be formed by natural selection, should not be considered as subversive of the theory.

What Darwin said after that

- Darwin then went on to discuss intermediate eye forms found in nature
  - light sensitive cells
  - depression that gives an indication of direction without being so precise as a lens
- Even more intermediate forms have been studied since

EVOLUTIONARY TRANSITION UNICELLULAR TO MULTICELLULAR

Multicellularity is a complex trait

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

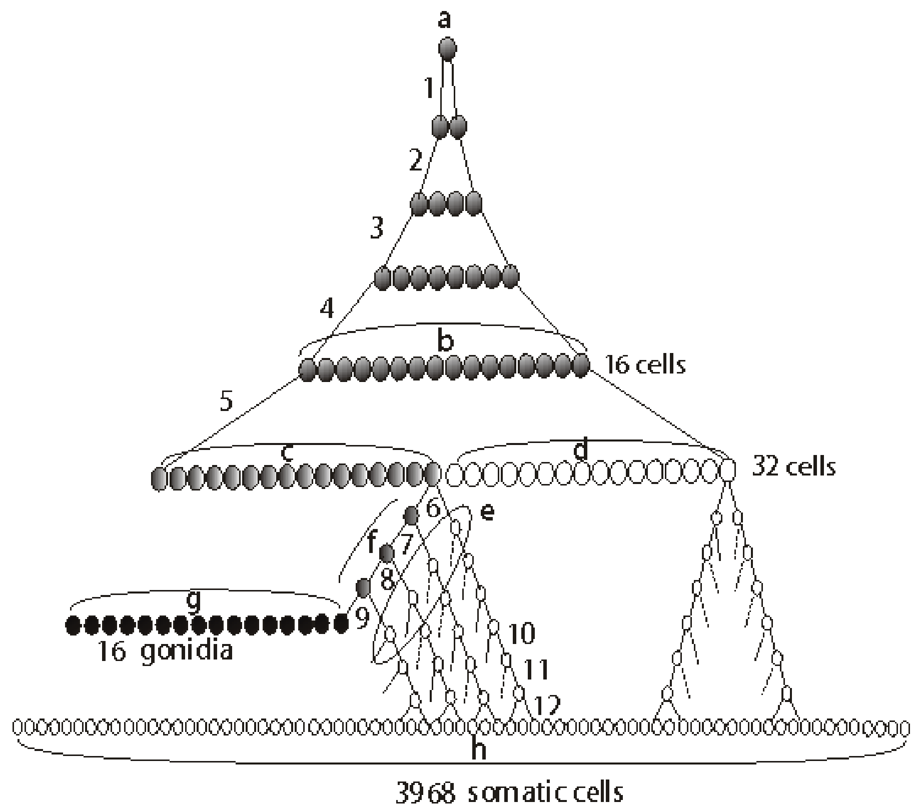
- Multi-level selection
  - Group formation (why? how?)
  - Groups increase in size
  - Cells within groups cooperate and specialize
  - Conflict mediation so cheating is less likely
  - Group becomes indivisible and hence an individual

- Kirk's 12 developmental steps
  - 1. Incomplete cytokinesis
  - 2. Partial inversion of the embryo
  - 3. Rotation of the basal bodies
  - 4. Establishment of organismal polarity
  - 5. Transformation of cell walls in to ECM
  - 6. Genetic modulation of cell number
  - 7. Complete inversion of the embryo
  - 8. Increased volume of ECM
  - 9. Partial germ/soma division of labor
  - 10. Complete germ/soma division of labor
  - 11. Asymmetric division
  - 12. Bifurcated cell division program

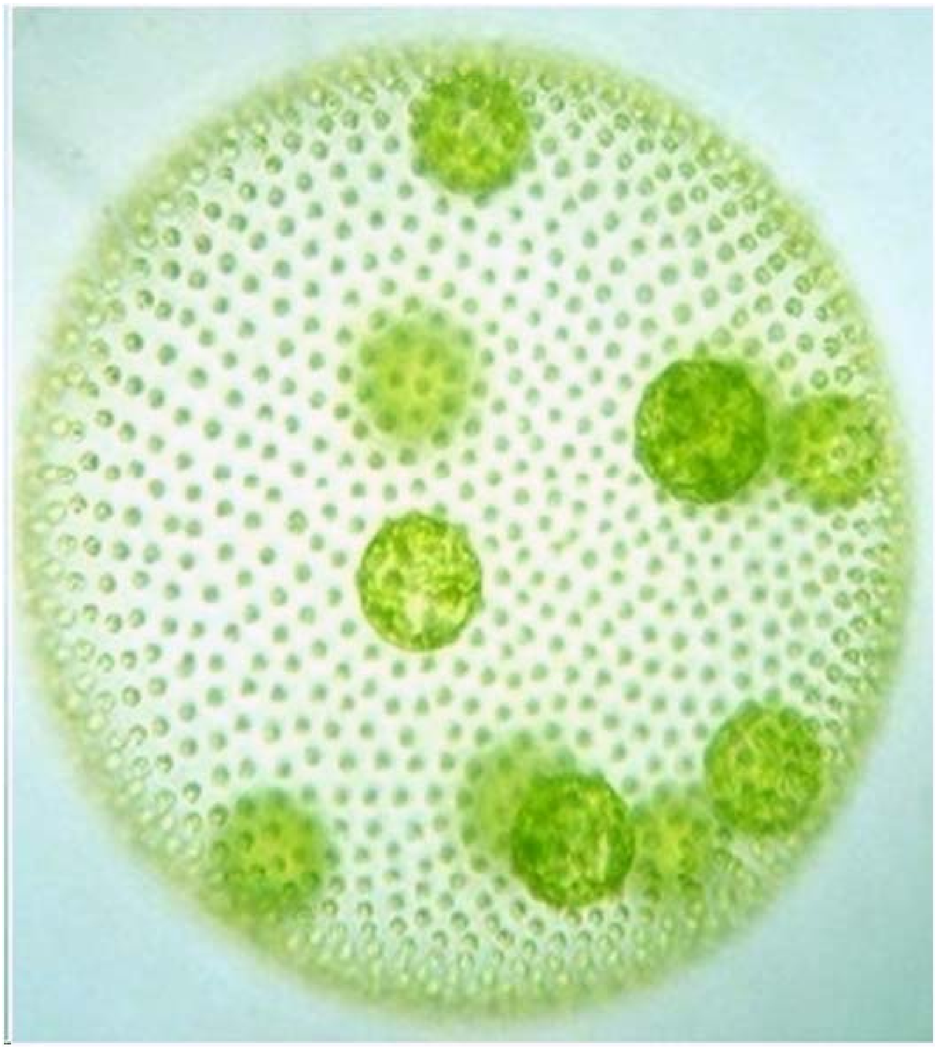
STEPS
MULTI-LEVEL SELECTION

Group formation

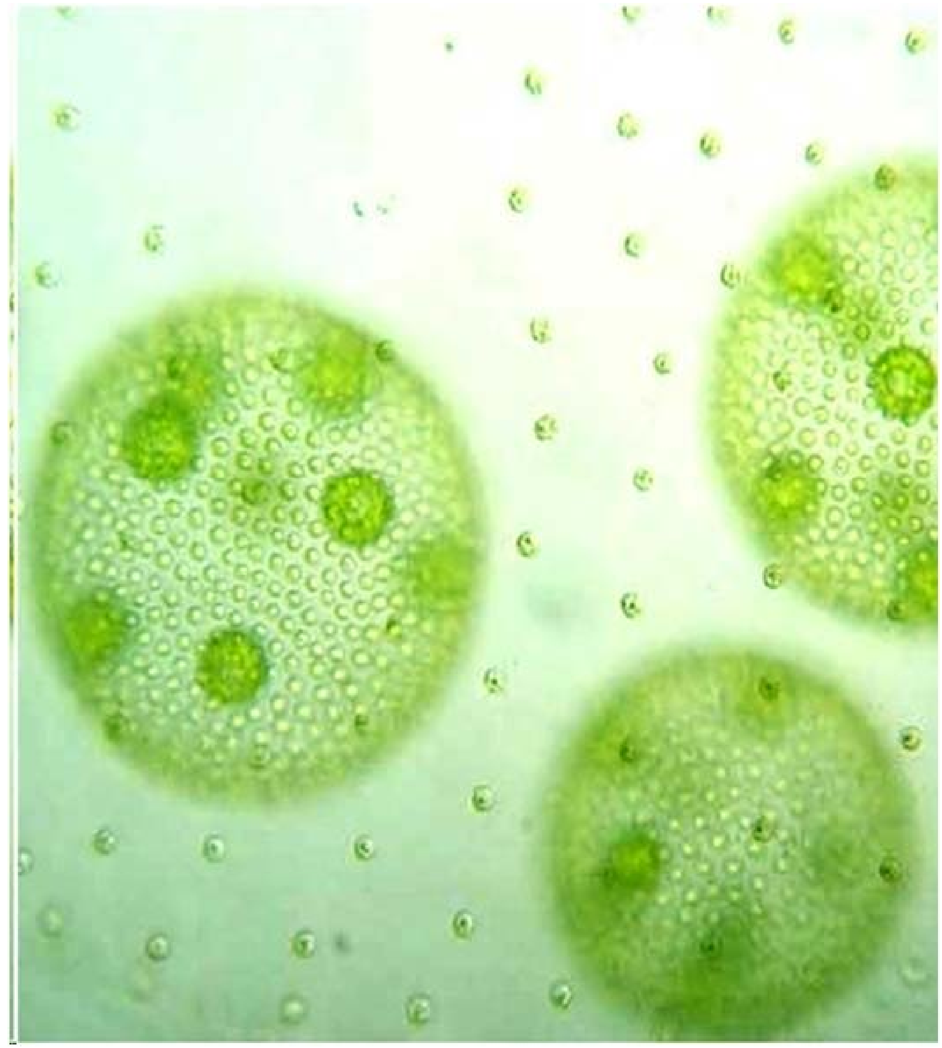
- How?
  - Daughter cells fail to separate
- Why?
  - Homeostasis in the group
  - Predation



Reproductive altruism in *Volvox*

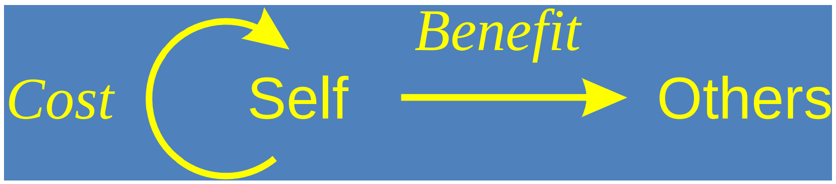


Juvenile



Mother with babies inside

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
- Originates from trade-offs

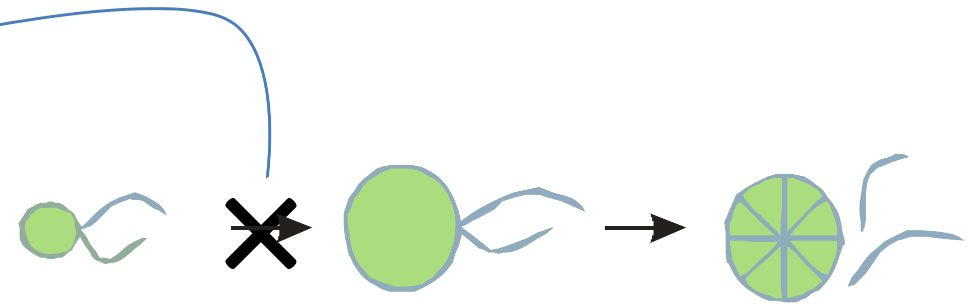
Altruism trades fitness between levels

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

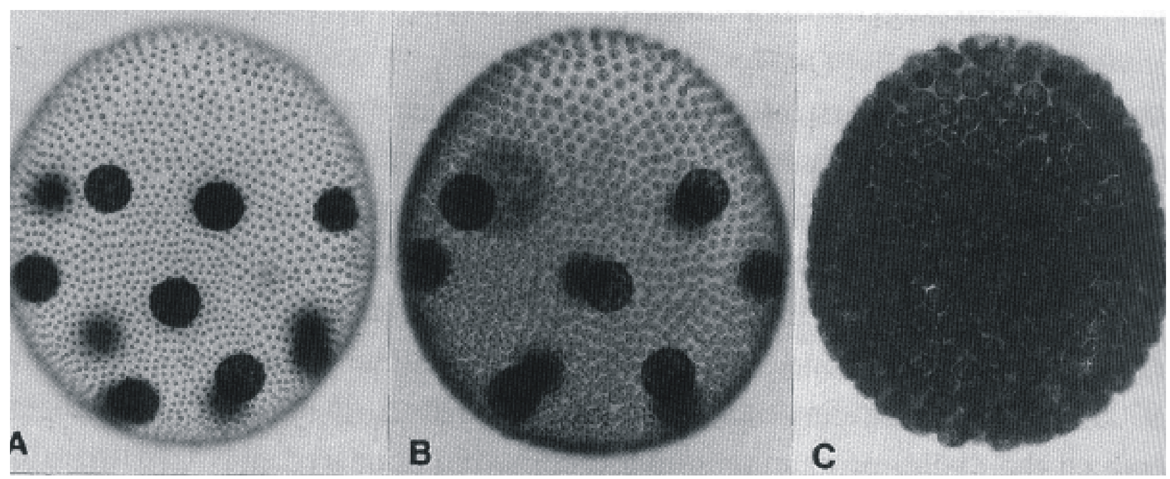
- Cooperation creates conflict which must be mediated
- Conflict mediation enhances cooperation and evolvability

Altruism & cheating in *Volvox*

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



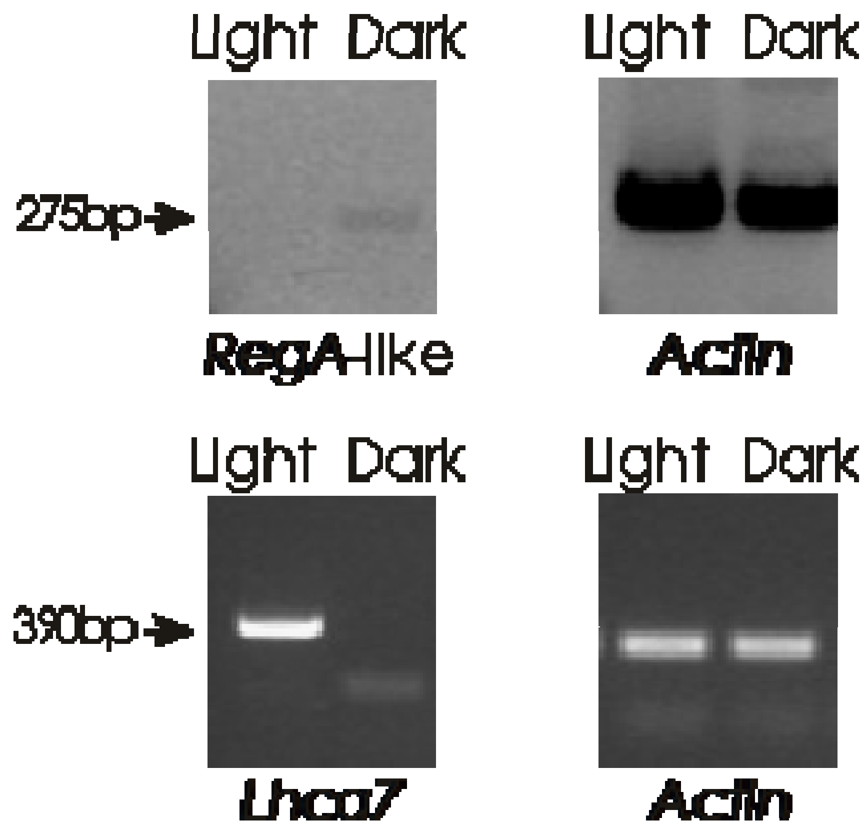
- Origin of *regA*?
  - Can the evolutionary origin of *regA* be traced back to the unicellular ancestors of this group?
  - If so, what was its role?



Kirk, D. 1998

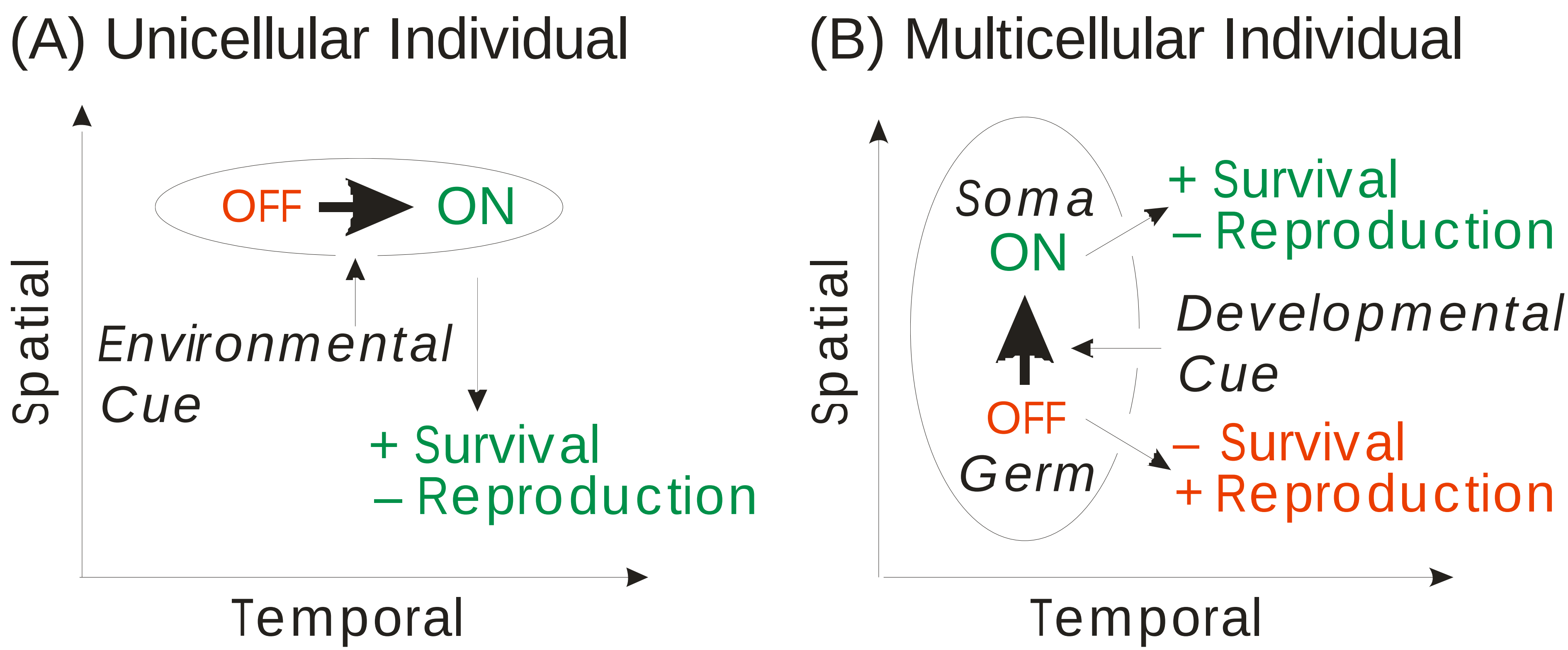
In what environments should reproduction be suppressed?

- 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



Credits: A. Nedelcu

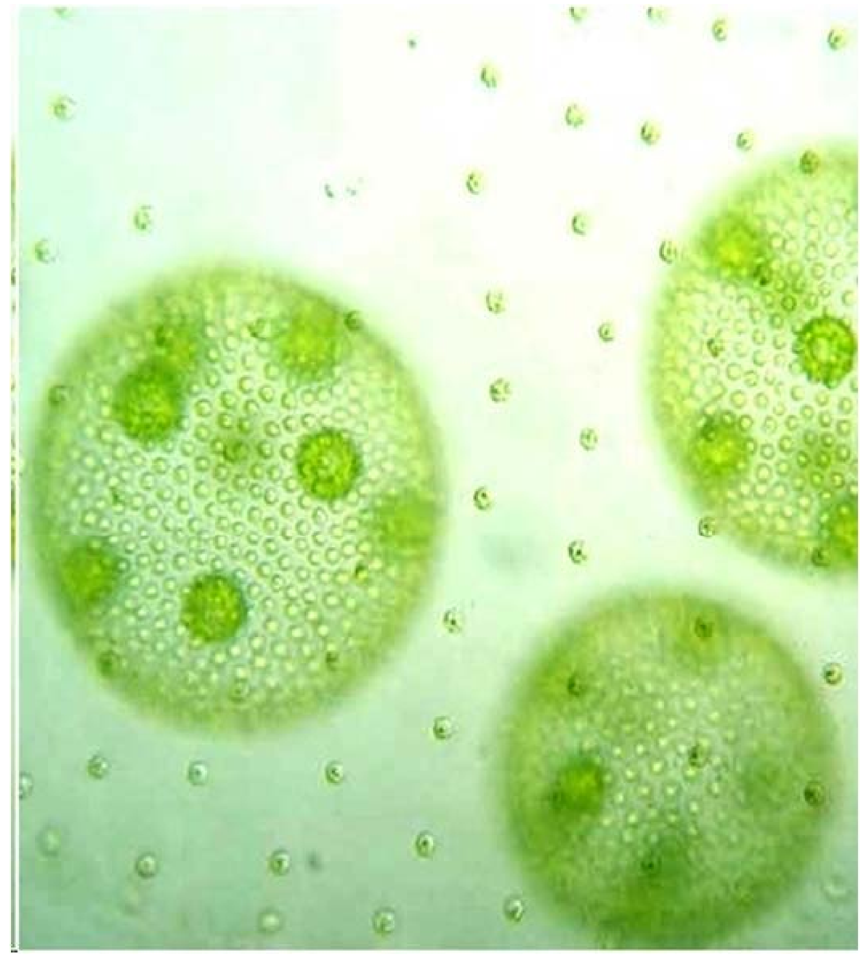
Hypothesis: Altruistic gene originates via co-option of life history gene



"Spatial" means within a cell group

How? and why?

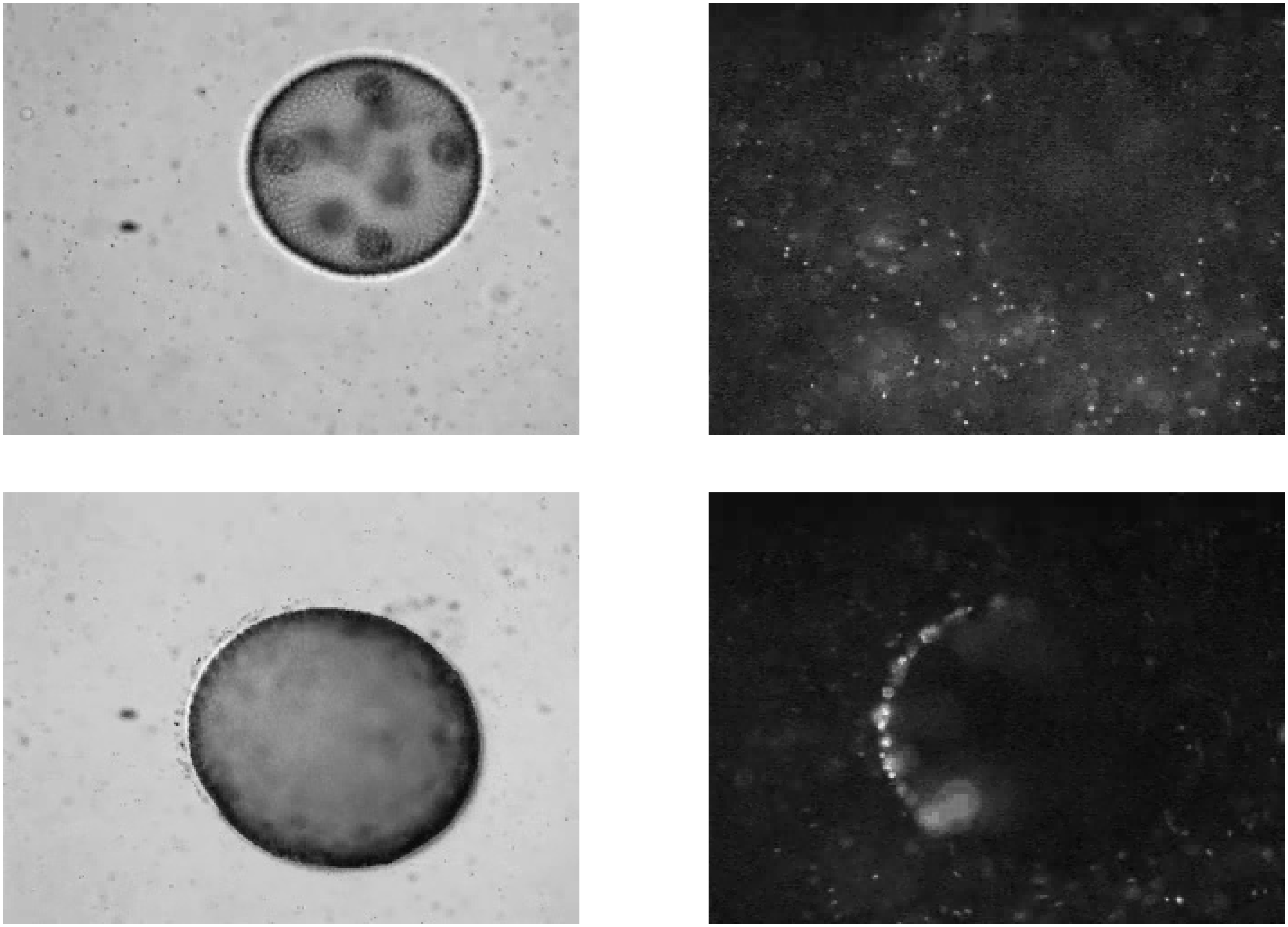
- How can a gene for reproductive altruism arise?
  - Co-option of life history gene
- Why does reproductive altruism evolve?
  - Only in the larger species
  - Kinship



Flagella-driven flows & transport

V. carteri

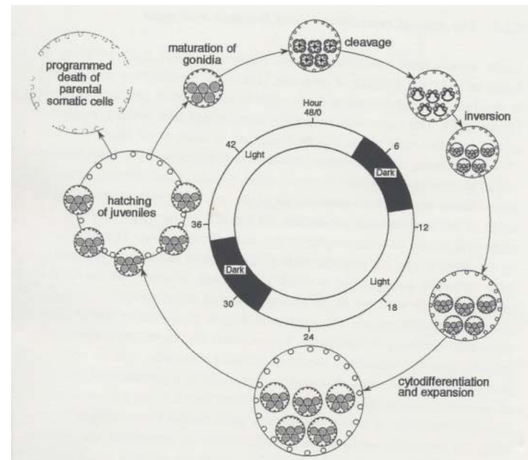
V. rousseletii



Credits: C. Solari, J. Kessler, R. Goldstein

Motility *Volvox*

- Upward swimming speed
- Sinking speed (mass)
- During development
  - 2 hours after hatching
  - 14 hours after hatching
- Conclusion: cost of reproduction increases with size during development



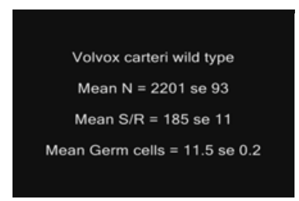


Figure Credit. D. Kirk

Research Credits:
C. Solari, J. Kessler

How does a group become an individual?

- General Points
  - Kinship important, not sufficient
    - Conflict mediation enhances cooperation
  - Fitness Reorganization
  - Altruism and cell specialization trade fitness from lower to higher level
  - Conflict Mediation
- How?
  - Life history genes in uni-cells co-opted for reproductive altruism in group
  - Early integration via covariance effect
- Why?
  - Trade-off between reproduction and survival
  - Trade-off becomes convex with increasing size
  - Increasing cost of reproduction selects for specialization and soma

STEPS
DEVELOPMENT

A twelve-step program for evolving multicellularity and a division of labor

David L. Kirk

Summary

The volvocine algae provide an unrivalled opportunity to explore details of an evolutionary pathway leading from a unicellular ancestor to multicellular organisms with a division of labor between different cell types. Members of this monophyletic group of green flagellates range in complexity from unicellular *Chlamydomonas* through a series of extant organisms of intermediate size and complexity to *Volvox*, a genus of spherical organisms that have thousands of cells and a germ–soma division of labor. It is estimated that these organisms all shared a common ancestor about 50 ± 20 MYA. Here we outline twelve important ways in which the developmental repertoire of an ancestral unicell similar to modern *C. reinhardtii* was modified to produce first a small colonial organism like *Gonium* that was capable of swimming directionally, then a sequence of larger organisms (such as *Pandorina*, *Eudorina* and *Pleodorina*) in which there was an increasing tendency to differentiate two cell types, and eventually *Volvox carteri* with its complete germ–soma division of labor. *BioEssays* 27:299–310, 2005.

Introduction

The evolution of multicellular eukaryotes was one of the most-profound developmental transitions in the history of life. Although most of the individual organisms living on Earth today are still unicellular, if all multicellular eukaryotes suddenly vanished from Earth, our planet would appear as barren as Mars.

The origin of multicellular organisms with a division of labor is also one of the most interesting and complex problems in the field of evolution of development, because it presumably involved—at a minimum—a transition from cellular autonomy to cellular cooperation, the invention of novel morphogenetic mechanisms, and the elaboration of novel spatial patterns of differential gene expression.

Such a transition from unicellularity to multicellularity occurred not just once, of course, but repeatedly.[1,2] It is now widely accepted that—except for animals and fungi[3,4]—the major lineages of large, multicellular "crown" eukaryotes (namely, plants, animals, fungi, red algae and brown algae) had independent origins, being derived from different unicellular ancestors more than 1,000 million years ago (MYA).[5,6] Moreover, multicellularity evolved independently in two different groups of cellular slime molds, in diatoms, in ciliates and in several other minor eukaryotic groups, as well as in several groups of prokaryotes.[1,2] However, the Guinness record for the most-repetitive invention of multicellularity goes to the green algae in the class Chlorophyceae. Most chlorophyceans are unicellular, but multicellular forms are found in 9 of the 11 chlorophycean orders, and it appears that multicellularity has arisen independently in each of those orders at least once, and sometimes more than once.[7] One of the best-known and most-studied examples of chlorophycean multicellularity occurs in *Volvox*, a spherical green alga with a division of labor between somatic and germline cells (Fig. 1).

The volvocine algae as a model system for studying the evolution of multicellularity

Volvox and its closest relatives ("the volvocine algae") provide a particularly promising model system for exploring the details of an evolutionary pathway leading from a unicellular ancestor to multicellular organisms with a division of labor.

Recency

Molecular–phylogenetic studies indicate that, whereas multicellularity evolved in the various eukaryotic crown-groups more than 1,000 MYA, it evolved much more recently in the volvocine algae (Fig. 2A): it has been estimated that multicellular *Volvox carteri* and unicellular *Chlamydomonas reinhardtii* shared a common ancestor as recently as 50 ± 20 MYA.[2,8] Thus, the winds of time have had only about 1/20th as long to obscure details of the pathway leading from

Department of Biology, Washington University, Campus box 1229, St. Louis, MO 63130, USA.
E-mail: kirk@biology.wustl.edu
DOI 10.1002/bies.20197
Published online in Wiley InterScience (www.interscience.wiley.com).

Abbreviations: AP, anterior-to-posterior; BAC, bacterial artificial chromosome; BBs, basal bodies; ECM, extracellular matrix; HRGP, hydroxyproline-rich glycoprotein; ISG, inversion specific (or initial-scaffold) glycoprotein; MYA, million years ago; *n*, the number of divisions that occur in one round of multiple fission in a volvocine alga; VSP-3, vegetative serine/proline-rich protein-3.

Kirk's 12 Steps to multicellularity

- 1. Incomplete cytokinesis
- 2. Partial inversion of the embryo
- 3. Rotation of the basal bodies
- 4. Establishment of organismal polarity
- 5. Transformation of cell walls in to ECM
- 6. Genetic modulation of cell number
- 7. Complete inversion of the embryo
- 8. Increased volume of ECM
- 9. Partial germ/soma division of labor
- 10. Complete germ/soma division of labor
- 11. Asymmetric division
- 12. Bifurcated cell division program

EVOLUTION OF COMPLEXITY IN THE VOLVOCINE ALGAE: TRANSITIONS IN INDIVIDUALITY THROUGH DARWIN'S EYE

Matthew D. Herron[1,2] and Richard E. Michod[1]

[1]Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721

[2]E-mail: mherron@email.arizona.edu

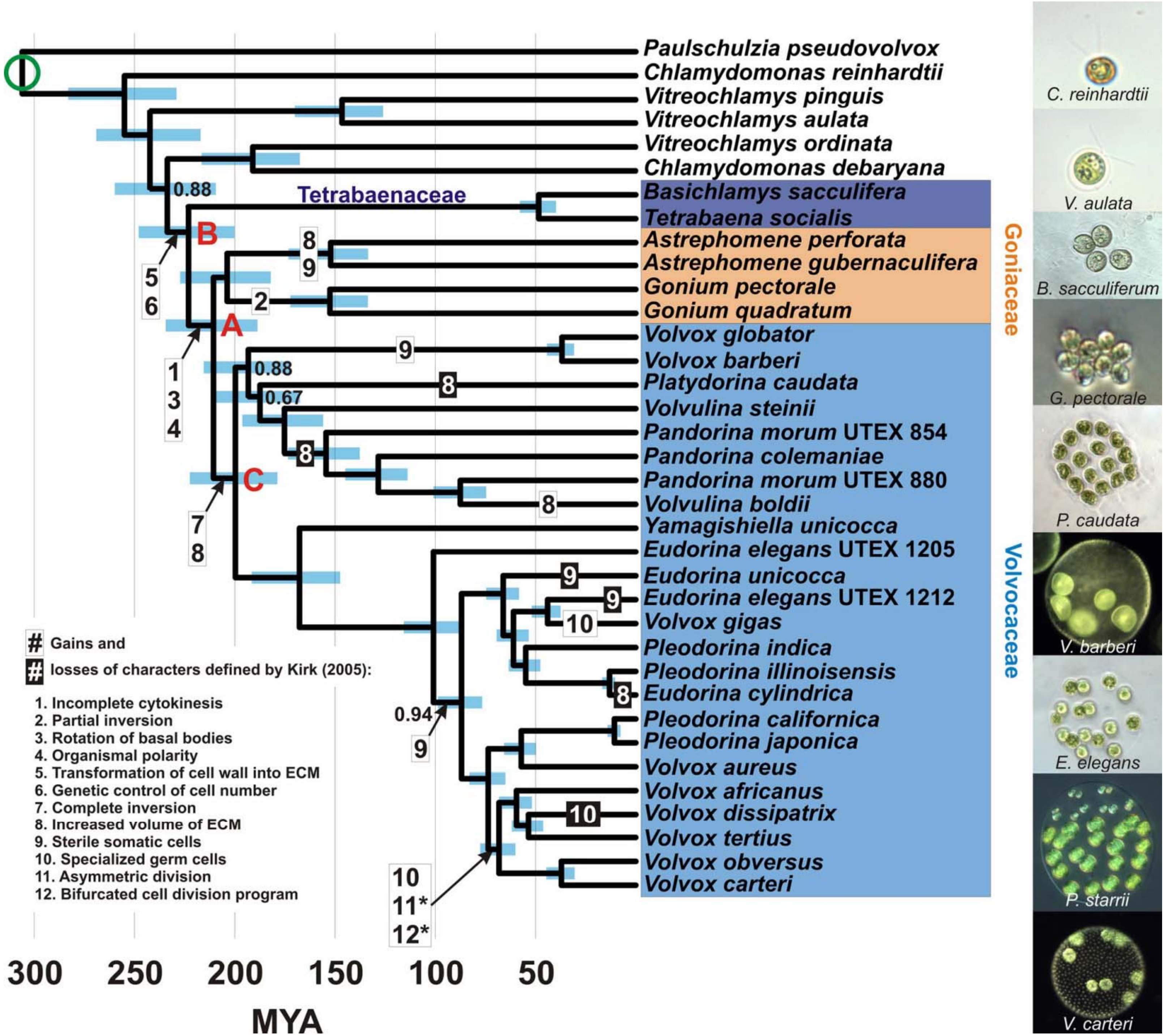
Received September 14, 2007
Accepted November 5, 2007

The transition from unicellular to differentiated multicellular organisms constitutes an increase in the level complexity, because previously existing individuals are combined to form a new, higher-level individual. The volvocine algae represent a unique opportunity to study this transition because they diverged relatively recently from unicellular relatives and because extant species display a range of intermediate grades between unicellular and multicellular, with functional specialization of cells. Following the approach Darwin used to understand "organs of extreme perfection" such as the vertebrate eye, this jump in complexity can be reduced to a series of small steps that cumulatively describe a gradual transition between the two levels. We use phylogenetic reconstructions of ancestral character states to trace the evolution of steps involved in this transition in volvocine algae. The history of these characters includes several well-supported instances of multiple origins and reversals. The inferred changes can be understood as components of cooperation–conflict–conflict mediation cycles as predicted by multilevel selection theory. One such cycle may have taken place early in volvocine evolution, leading to the highly integrated colonies seen in extant volvocine algae. A second cycle, in which the defection of somatic cells must be prevented, may still be in progress.

KEY WORDS: *Chlamydomonas*, *Gonium*, multicellularity, multilevel selection, *Pleodorina*, Volvocaceae, *Volvox*

The four billion or so years during which life has existed on Earth have seen some millions of speciation events and innumerable instances of evolutionary change within populations. In contrast, only a few dozen examples are known in which such changes have led to the reorganization of the very units of adaptation and evolution. These reorganizations, in which groups of previously existing evolutionary individuals form a new kind of individual, include the transitions from groups of replicating molecules to prokaryotic cells, from associations of prokaryotic cells to eukaryotic cells, from groups of cells to multicellular organisms, and from individual organisms to societies. Collectively, these transitions have been called changes in the level of complexity (Maynard Smith 1988), transitions in the units of fitness (Michod and Roze 1999), and evolutionary transitions in individuality (ETIs; Buss 1987; Maynard Smith and Szathmáry 1995; Michod 1996, 1997; Michod and Roze 1997).

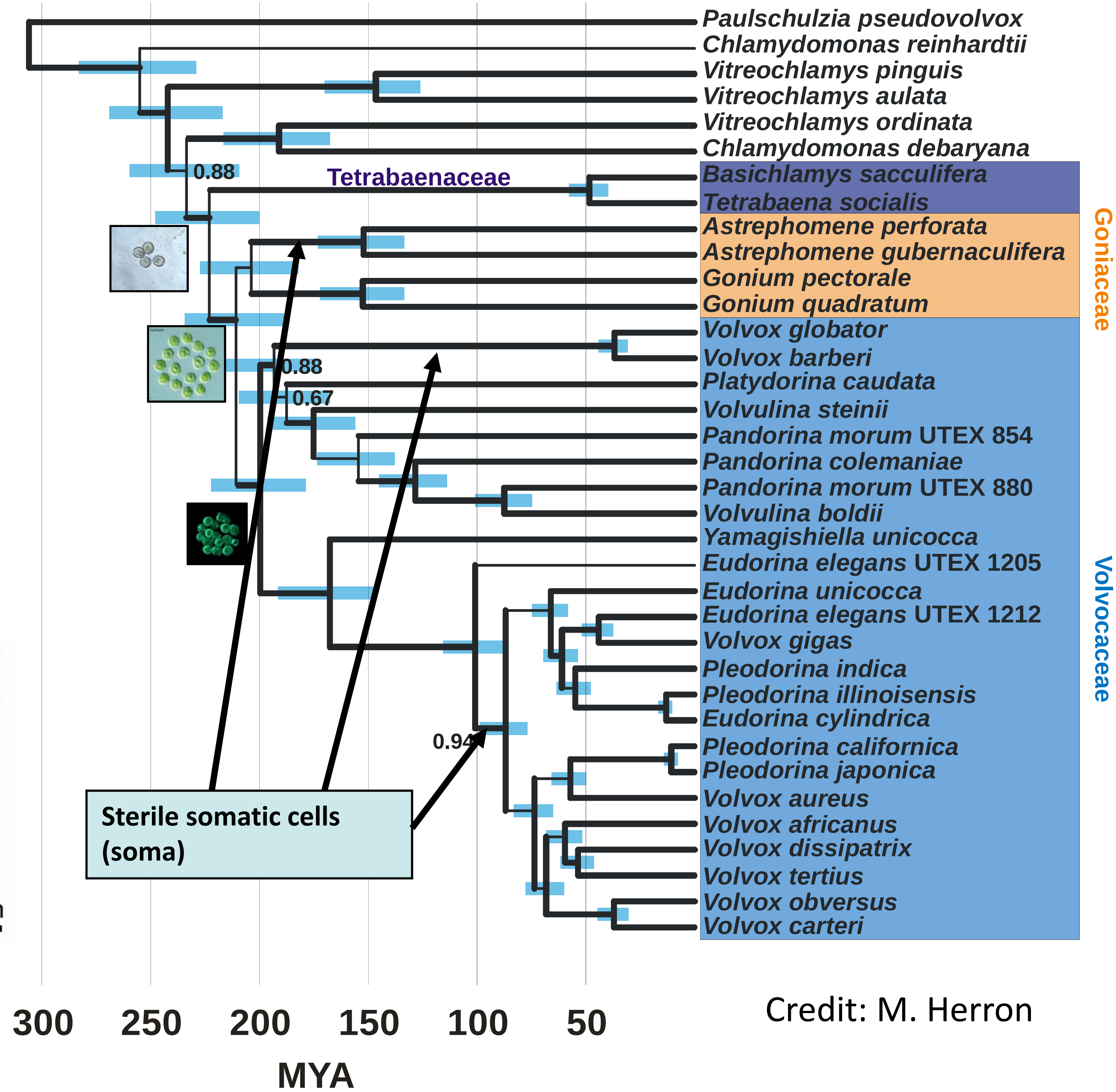
One of the best-studied ETIs is that from unicellular organisms to differentiated multicellular organisms in the volvocine green algae (Chlorophyta) (Kirk 1998, 2005; Solari 2005; Nedelcu and Michod 2006; Solari et al. 2006a). The volvocine algae are biflagellated, photosynthetic, facultatively sexual, haploid eukaryotes, comprising both unicellular species (*Chlamydomonas* and *Vitreochlamys*), and colonial forms with widely varying colony sizes, colony structures, and degrees of cellular specialization (see Fig. 4). Except in discussions of individuality, we will refer to any species with more than one cell as "colonial" (see Kirk 1998 pp. 115–116 for a discussion of terminology). Among the colonial forms, organization can be as simple as clumps of four *Chlamydomonas*-like cells that fail to separate after cytokinesis (*Basichlamys*, *Tetrabaena*). Colonial forms comprising 8–32 undifferentiated cells can be organized as flat or slightly curved sheets in a single layer (*Gonium*), as spheroidal colonies

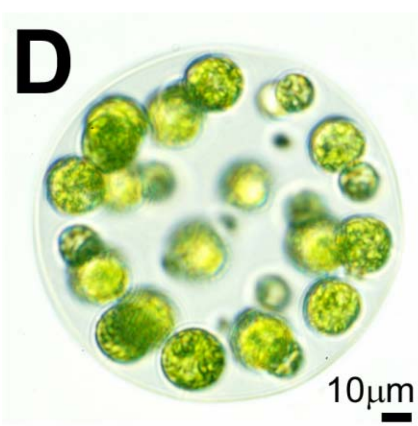


Credit: M. Herron

Gains and

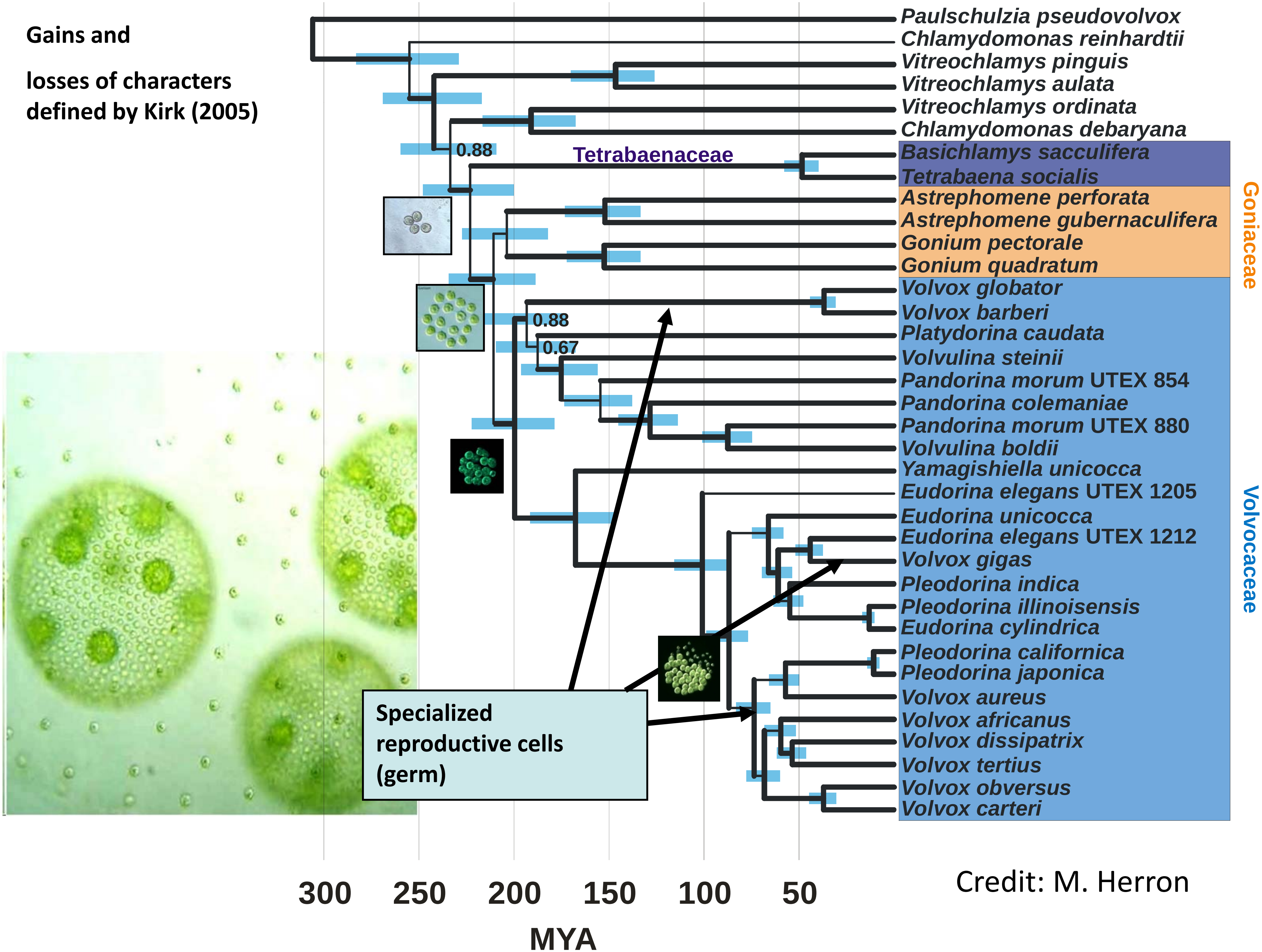
losses of characters defined by Kirk (2005)



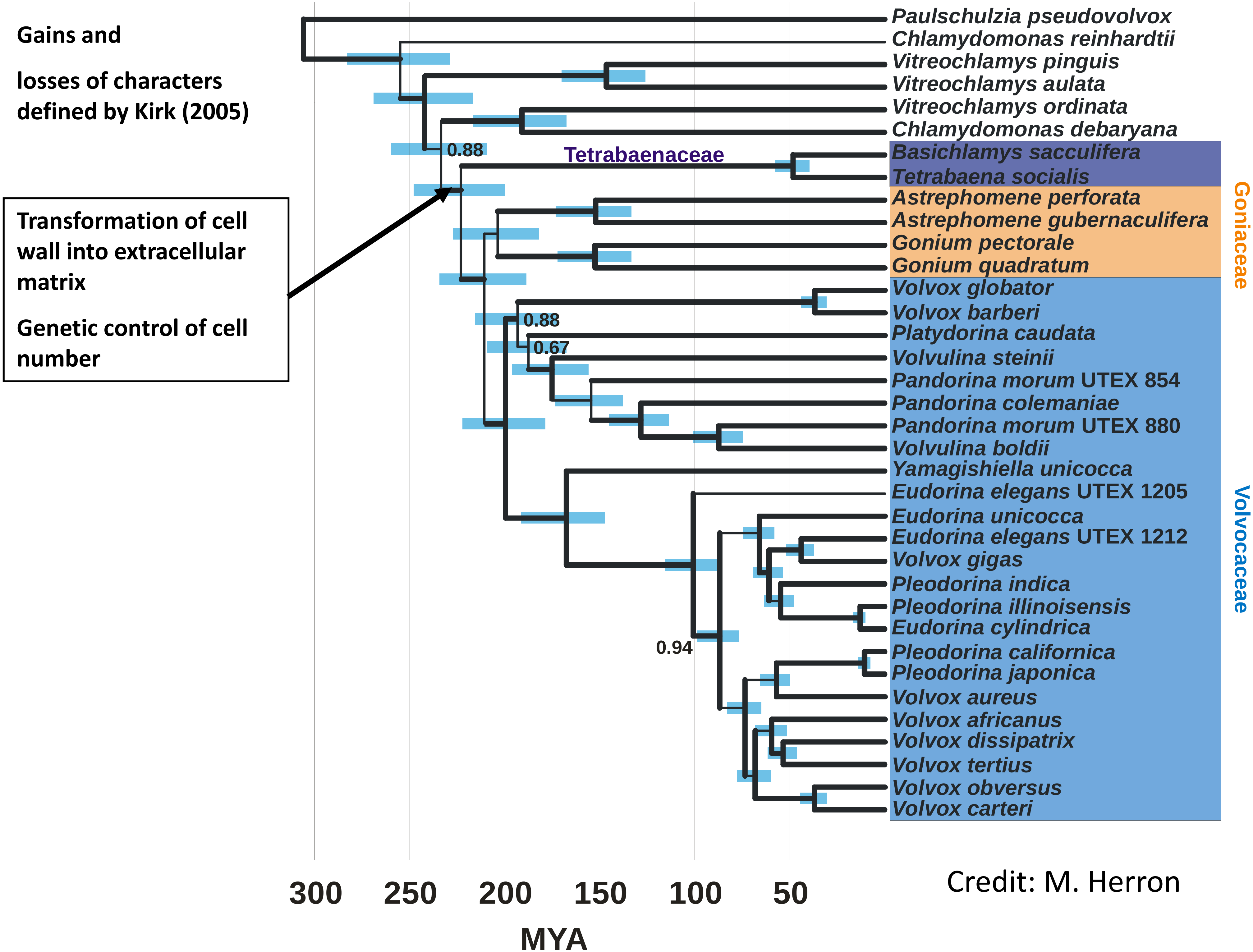


Gains and

losses of characters defined by Kirk (2005)



Credit: M. Herron

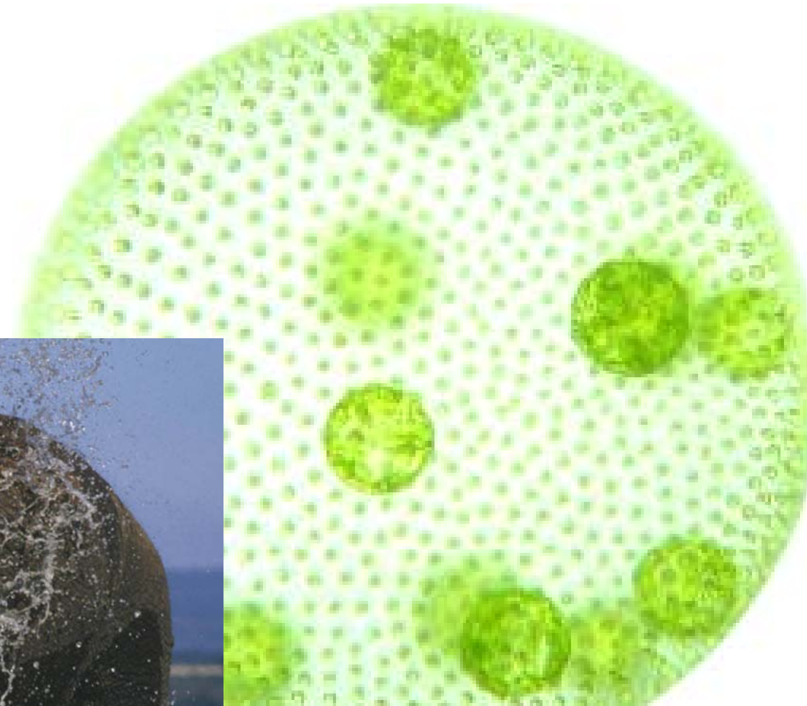

Gains and
losses of characters
defined by Kirk (2005)
Transformation of cell wall into extracellular matrix
Genetic control of cell number
Paulschulzia pseudovolvox
Chlamydomonas reinhardtii
Vitreochlamys pinguis
Vitreochlamys aulata
Vitreochlamys ordinata
Chlamydomonas debaryana
0.88
Tetrabaenaceae
Basichlamys sacculifera
Tetrabaena socialis
Astrephomene perforata
Astrephomene gubernaculifera
Gonium pectorale
Gonium quadratum
Goniaceae
Volvox globator
Volvox barberi
0.88
Platydorina caudata
0.67
Volvulina steinii
Pandorina morum UTEX 854
Pandorina colemaniae
Pandorina morum UTEX 880
Volvulina boldii
Yamagishiella unicocca
Eudorina elegans UTEX 1205
Eudorina unicocca
Eudorina elegans UTEX 1212
Volvox gigas
Pleodorina indica
Pleodorina illinoisensis
Eudorina cylindrica
0.94
Pleodorina californica
Pleodorina japonica
Volvox aureus
Volvox africanus
Volvox dissipatrix
Volvox tertius
Volvox obversus
Volvox carteri
Volvocaceae
300
250
200
150
100
50
MYA
Credit: M. Herron

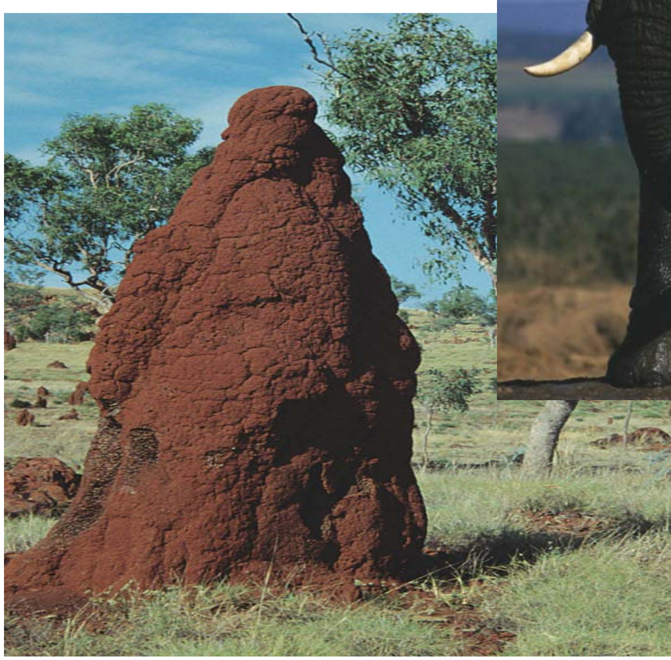
Sum up multicellularity ETI

- “Strange inversion of logic” to explain a jump in the level of complexity
- Steps from unicellular to multicellular
  - Multi-level selection
  - Development

TEACHER INTERN PROGRAM

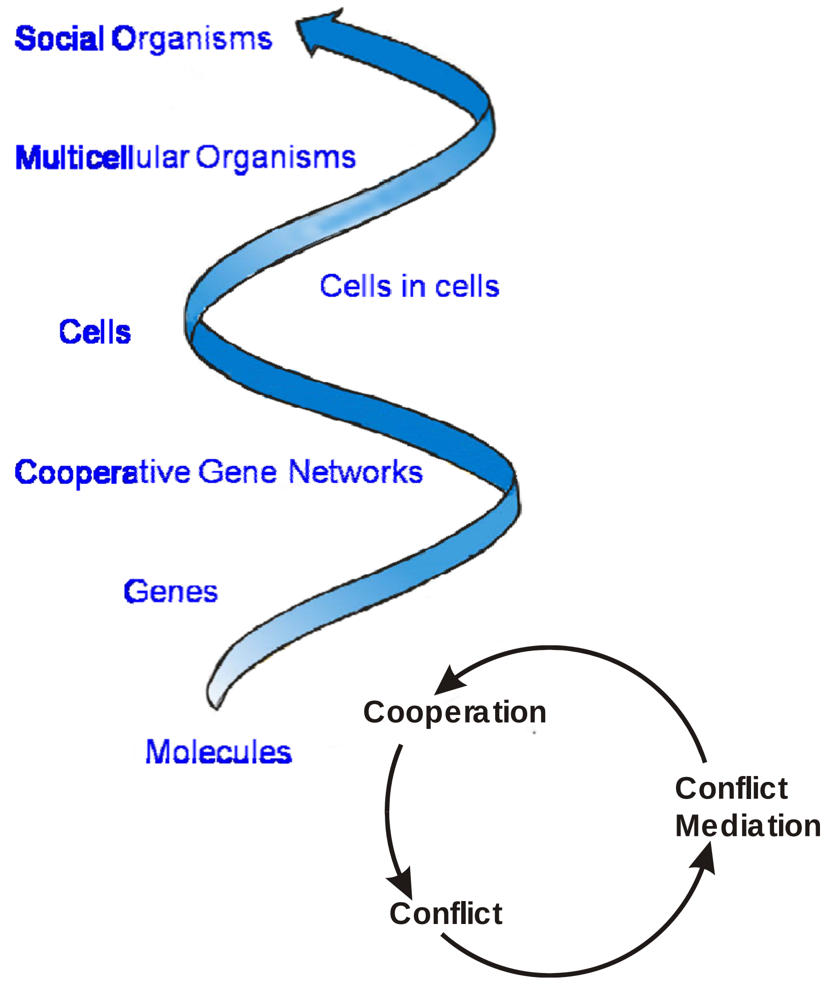
Societies of the world



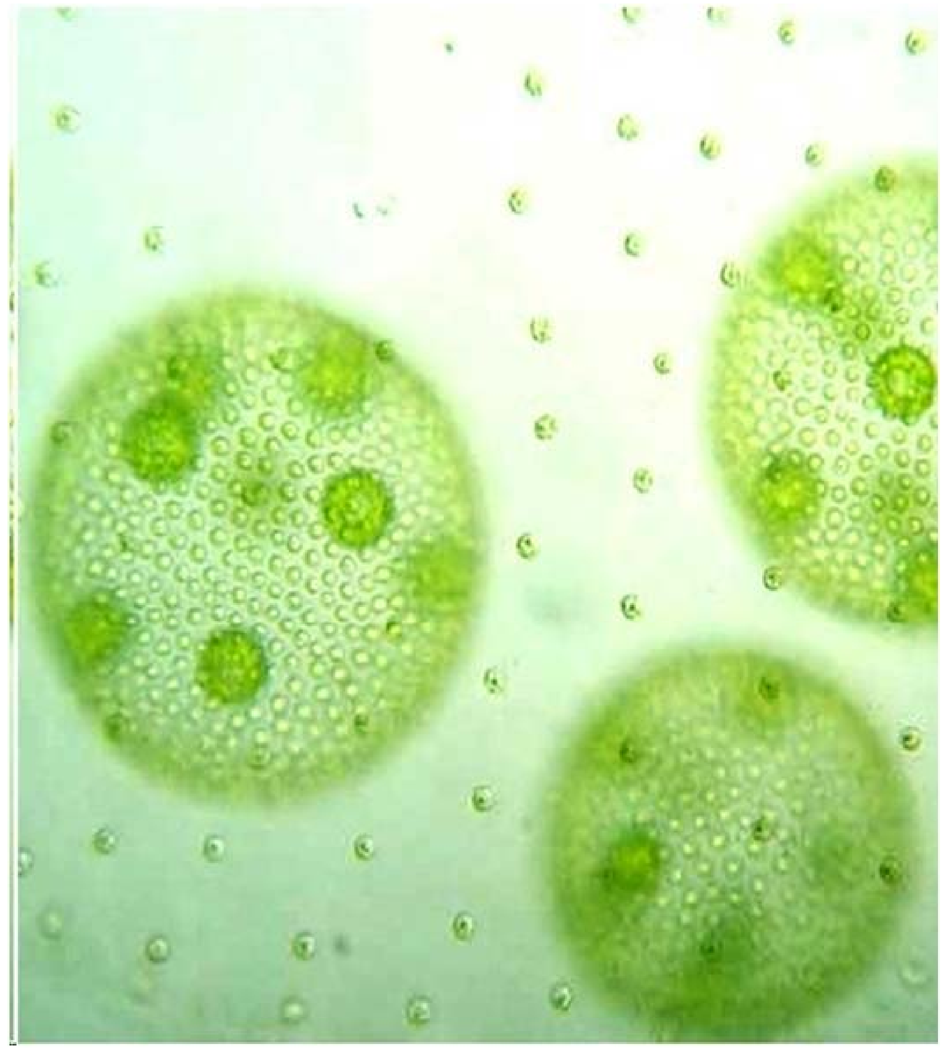

Cooperation, conflict, mediation

- A society is a group of cooperating individuals
- The individuals can be genes, cells, organisms
- Cooperation benefits the group, costs the individual
- Cheating benefits the individual, costs the group
- The temptation to cheat may be mediated
- The group may become a new individual



NSF research grant

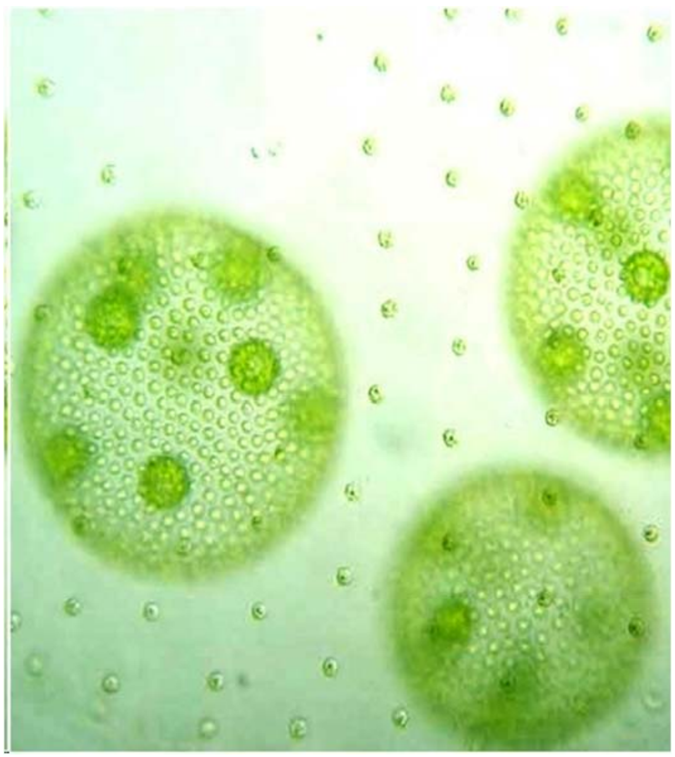
- Broader Impacts
- Teaching biological complexity
- Children are social creatures
- Volvocine green algae as model system for studying complexity
- High school teacher internship program in our lab
- Evaluation pre- & post-
- First of three years



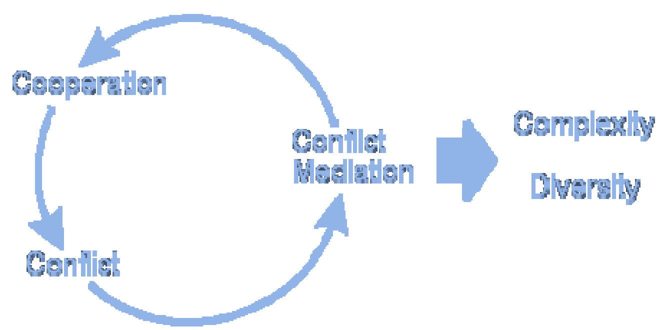
THE UNIVERSITY OF ARIZONA.

U of A internships in complexity for high school biology teachers

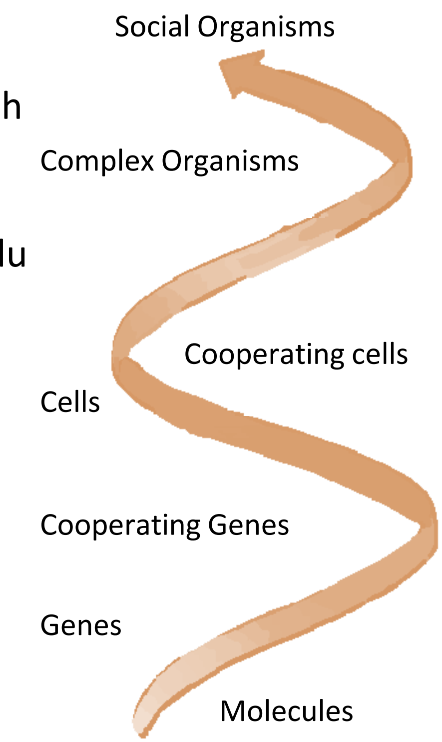
- Get paid to be involved in research at the U of A and to develop a teaching module on the evolution of biological complexity for use in your classroom
  - Understand how simple groups of cells evolve into complex organisms
  - Use the green alga, *Volvox*, to address the "intelligent design" controversy
  - Learn and apply cooperation/conflict theories from social biology
  - Explain to students how diseases like cancer are like cheaters in social groups



- In the lab of Dr. Michod at the UA
- Stipend $4,000; 6 weeks during summer with possibility of renewal next summer
- For more information call Elaine Mattes at 520-621-7509 or emattes@email.arizona.edu



http://eebweb.arizona.edu/michod/
click on "teacher interns"



Prisoner's dilemma game

- *C*=cooperate, *D*=defect
- T > R > P > S
- Cooperation
  - c = cost
  - b = benefit
- No matter what your partner does it pays to defect
- Defection does not maximize individual or population fitness
- Tragedy of the commons

	C	*D*
C	R	S
D	T	P

	C	*D*
C	1-c+b	1-c
D	1+b	1

Puccini's tragedy in *Tosca*

- Heroine: Tosca
- Her lover Cavaradossi is condemned to death by the police chief Scarpia
- Scarpia offers Tosca a deal—sleep with me and I will put blanks in the guns of the firing squad and Cavaradossi will live

Lesson plans

- Lesson plan
- Prisoner's dilemma as a model of cooperation
- Module cooperation conflict
- Cooperation and increasing complexity
- Complexity of life
- Evolution of multicellularity
- Slime mold lab
- Social insects lab

Credits: Kevin Steeves, Josh Farr

SUM UP

Sum up

- Complexity should be taught explicitly
- Evolutionary transitions in individuality
- Cooperation and conflict
- Students are social beings
- Common set of concepts that apply throughout their life and their studies
  – Many cross-curricular connections
- Help take the negative “edge” off of Darwinism