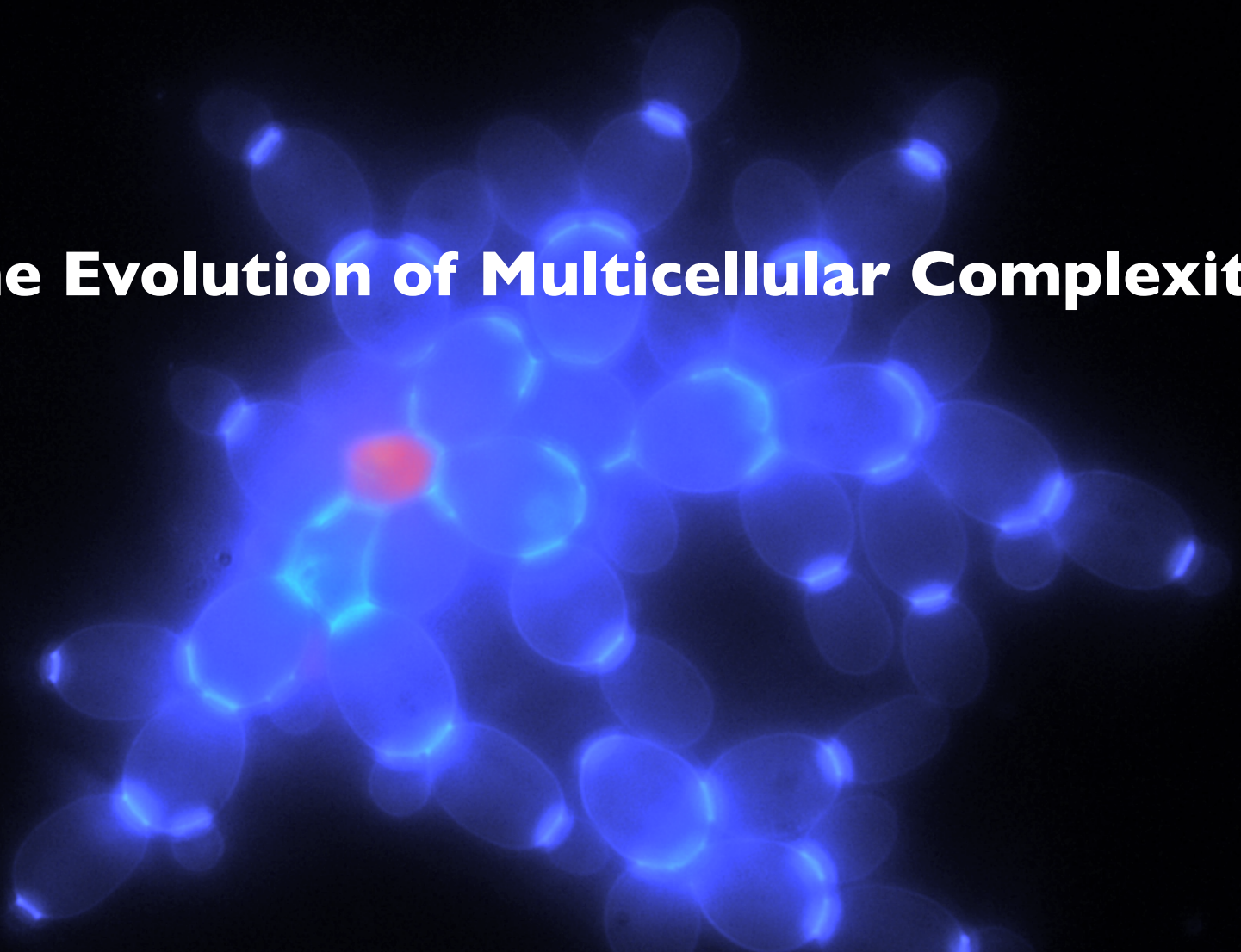


# The Evolution of Multicellular Complexity



Michael Travisano

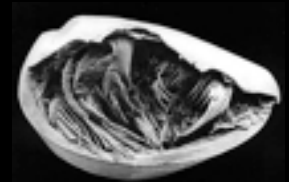
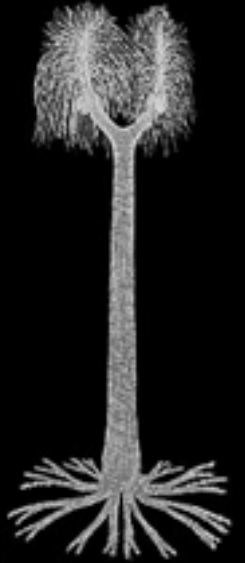
University of Minnesota

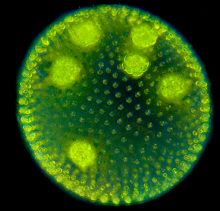


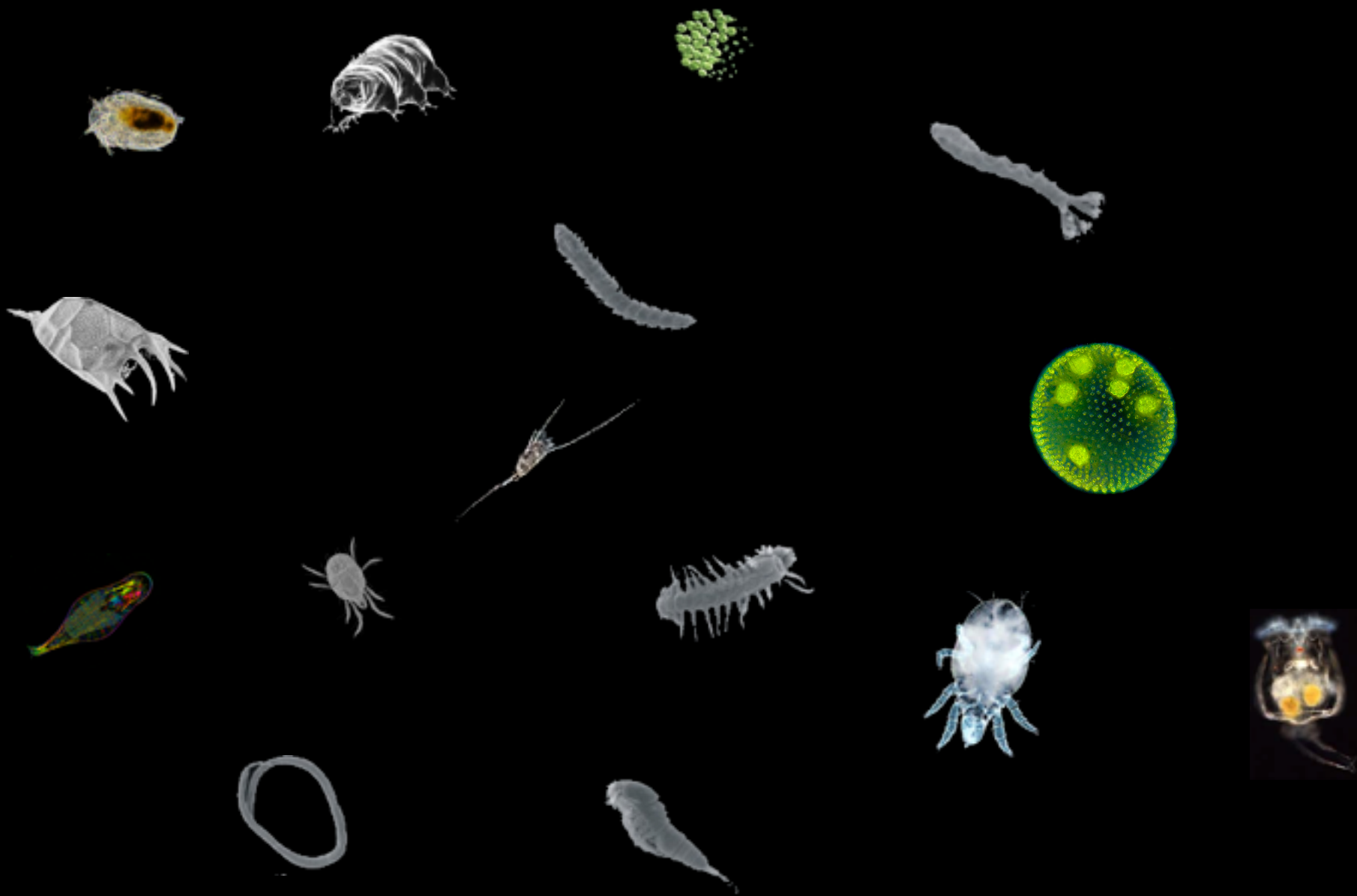




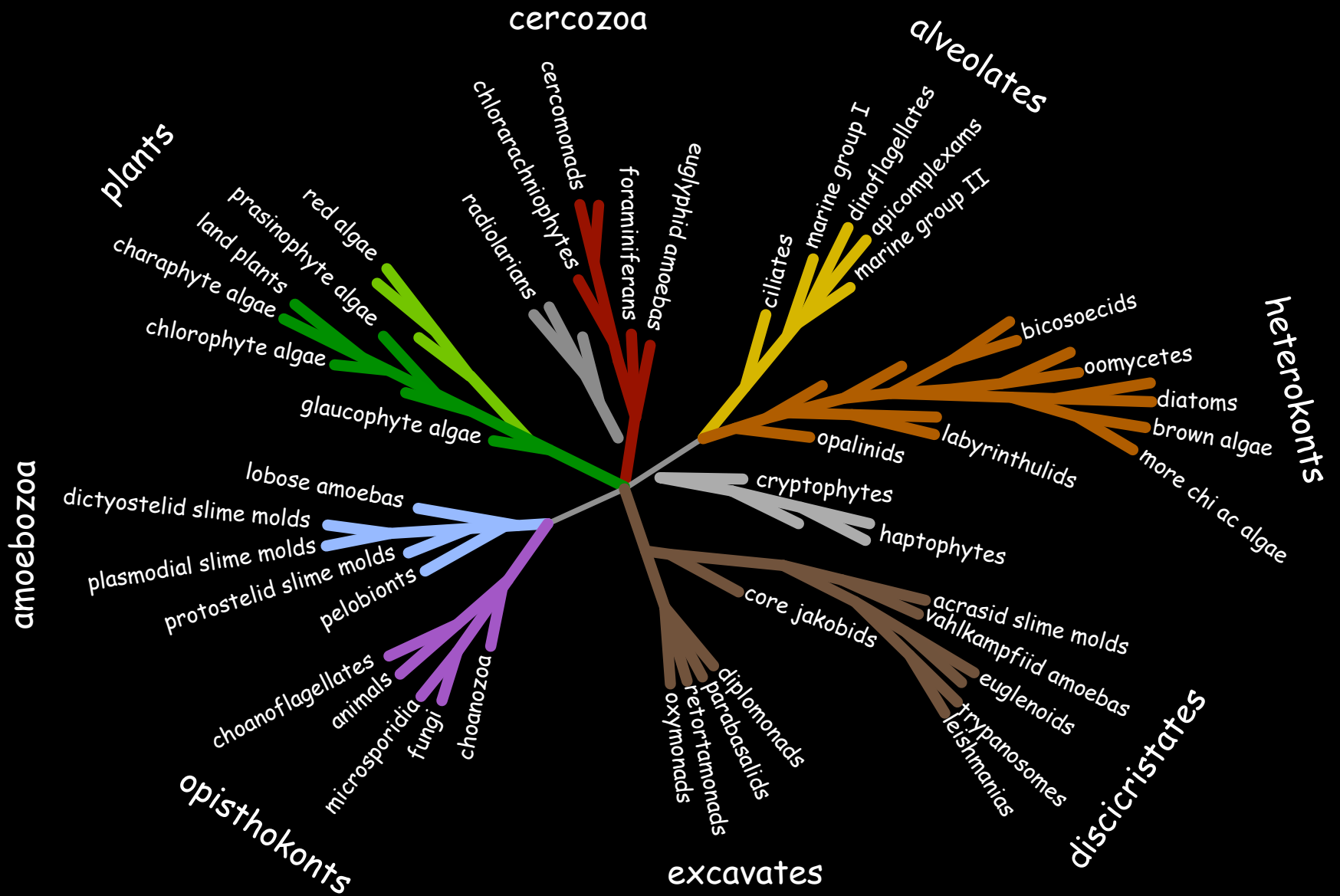








# Eukaryotic Tree of Life





# Eukaryotic Tree of Life



Lineages with at least one multicellular species

Baldauf 2003, King 2004  
Grosberg & Strathmann 2007



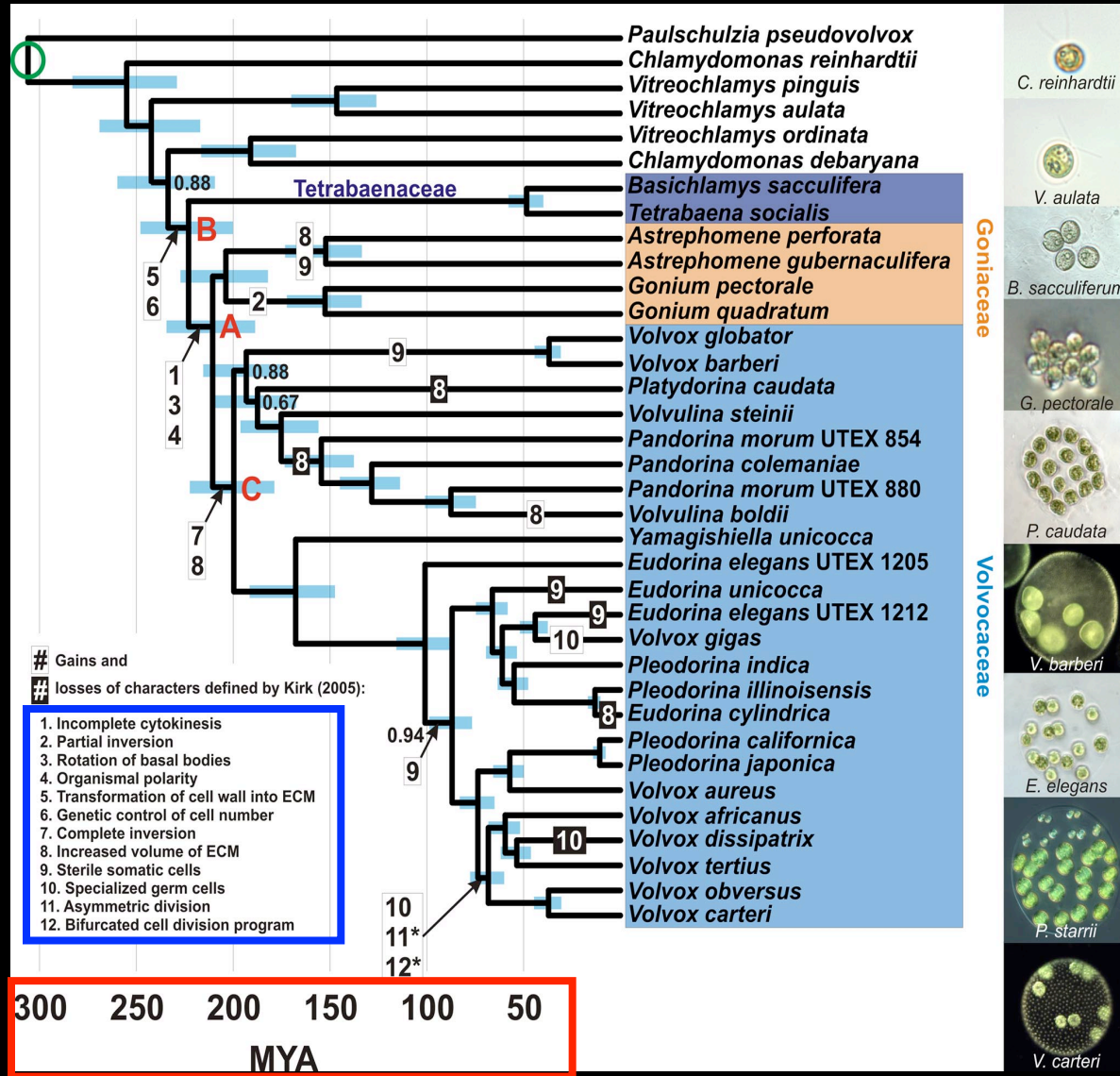
There were at least 25 transitions to multicellularity



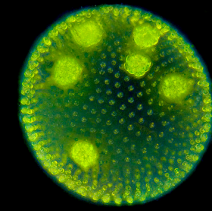
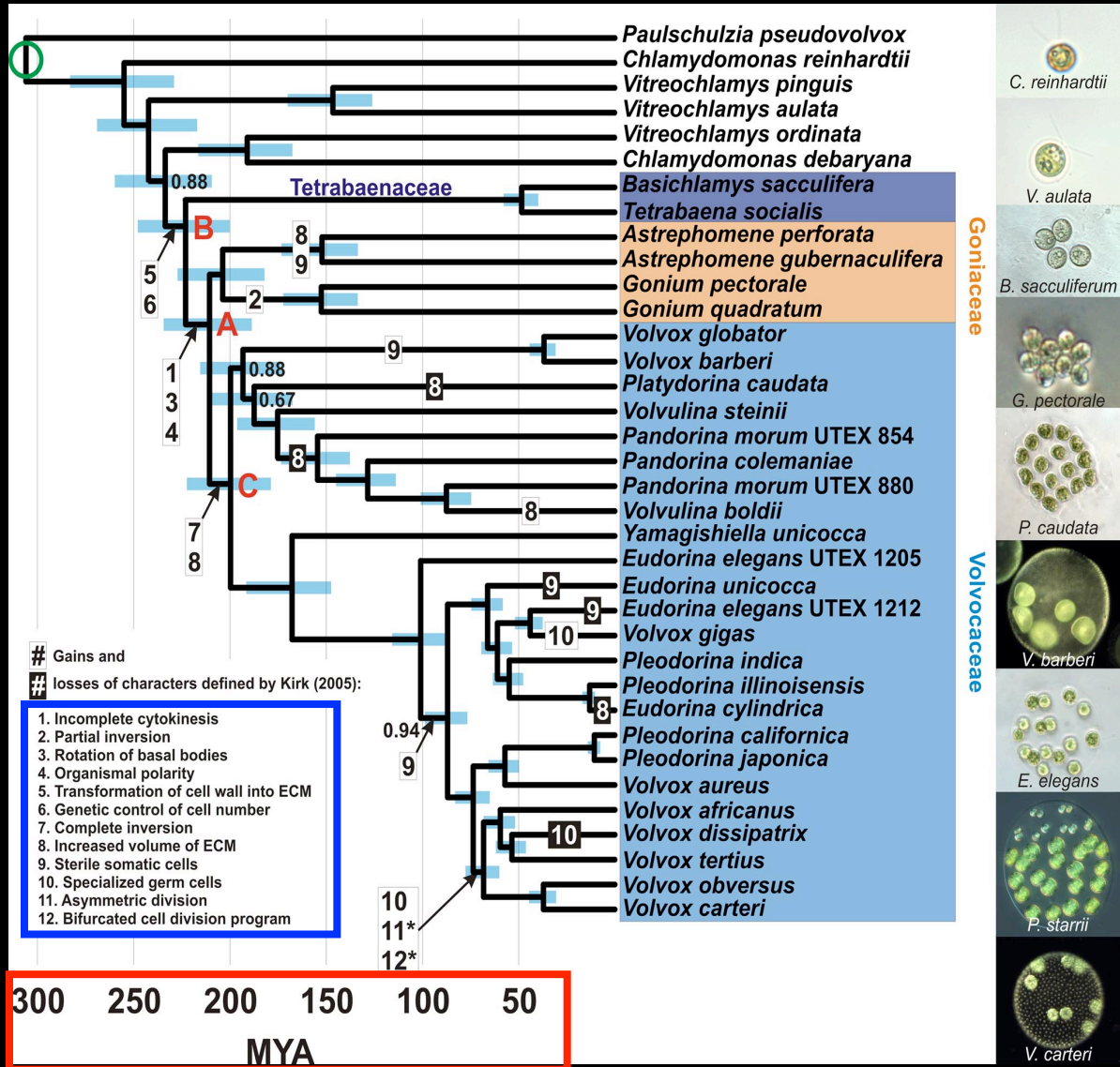
There were at least 25  
transitions to  
multicellularity

Why?

If multicellularity is a key innovation,  
then wouldn't selection had lead to an ecological selective sweep?



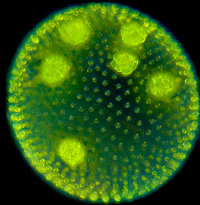
Herron et al 2009



Herron et al 2009

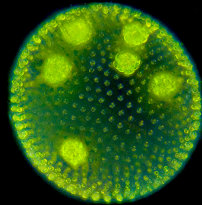


# I. Multiple origins of multicellularity





# 1. Multiple origins of multicellularity



# 2. An ongoing process?





# Evolution by Natural Selection

# Evolution by Natural Selection

I. Individuals within populations are variable.

## Evolution by Natural Selection

1. Individuals within populations are variable.
2. The variation among individuals is, at least in part, heritable from parents to offspring.

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## Evolution by Natural Selection

1. Individuals within populations are variable.
2. The variation among individuals is, at least in part, heritable from parents to offspring.
3. Some individuals are more successful at surviving and reproducing than others.
4. The survival and reproduction of individuals is tied to the variation among individuals. The individuals with the most favorable variations are naturally selected.

The theory of natural selection does not  
predict increases in complexity

It predicts that fitness will increase in the short-term

# The theory of natural selection does not predict increases in complexity

It predicts that fitness will increase in the short-term



cyanobacteria  
little change in  
3,500 million years



crinoids  
little change in  
450 million years



horsetails  
little change in  
375 million years

## YET SOME LINEAGES HAVE BECOME MORE COMPLEX





**YET SOME LINEAGES HAVE BECOME MORE COMPLEX**

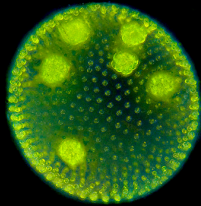


**IS COMPLEXITY ADAPTIVE?**

# Questions about multicellularity



1. Why were there multiple origins?



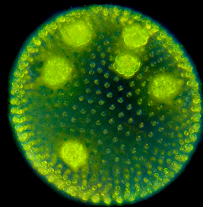
2. Why is it ongoing process?



# Questions about multicellularity



1. Why were there multiple origins?



2. Why is it ongoing process?

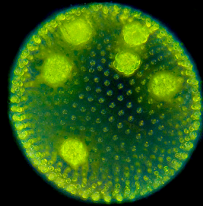


3. How? Not directly predicted by Natural Selection.

# Questions about multicellularity



1. Why were there multiple origins?



2. Why is it ongoing process?



3. How? Not directly predicted by Natural Selection.

# NATURAL ENGINEERING

# NATURAL ENGINEERING

## Dynamics of adaptation and diversification: A 10,000-generation experiment with bacterial populations

(experimental evolution/macroevolution/natural selection/cell size/*Escherichia coli*)

RICHARD E. LENSKI AND MICHAEL TRAVISANO\*

*Proc. Natl. Acad. Sci. USA*  
Vol. 91, pp. 6808–6814, July 1994

## Experimental Tests of the Roles of Adaptation, Chance, and History in Evolution

Michael Travisano, Judith A. Mongold, Albert F. Bennett,  
Richard E. Lenski\* *SCIENCE* • VOL. 267 • 6 JANUARY 1995

## Adaptive radiation in a heterogeneous environment

Paul B. Rainey & Michael Travisano

*NATURE* | VOL 394 | 2 JULY 1998

## Hybrid Speciation in Experimental Populations of Yeast

Duncan Greig,<sup>1,2</sup> Edward J. Louis,<sup>3</sup> Rhona H. Borts,<sup>3</sup>  
Michael Travisano<sup>2\*</sup>

PROCEEDINGS  
OF  
THE ROYAL  
SOCIETY



THE ROYAL SOCIETY *biology letters*

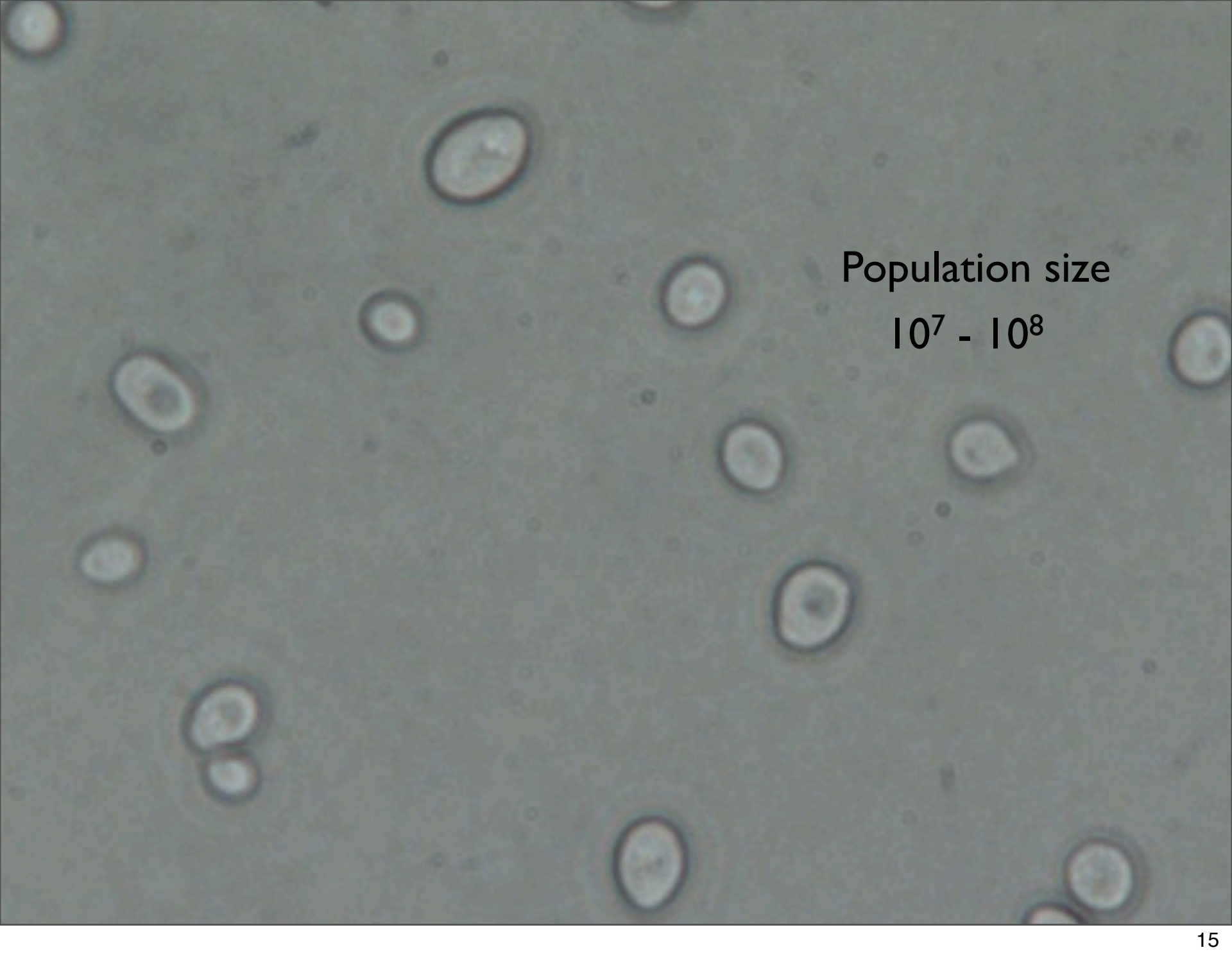
## The Prisoner's Dilemma and polymorphism in yeast *SUC* genes

Duncan Greig\* and Michael Travisano © 2003 The Royal Society

*Proc. R. Soc. B* (2009) 276, 2065–2070  
doi:10.1098/rspb.2008.1827  
Published online 4 March 2009

## Spatial structure leads to ecological breakdown and loss of diversity

Gerda Saxer<sup>1,2,3,\*</sup>, Michael Doebeli<sup>1,4</sup> and Michael Travisano<sup>2,5</sup>

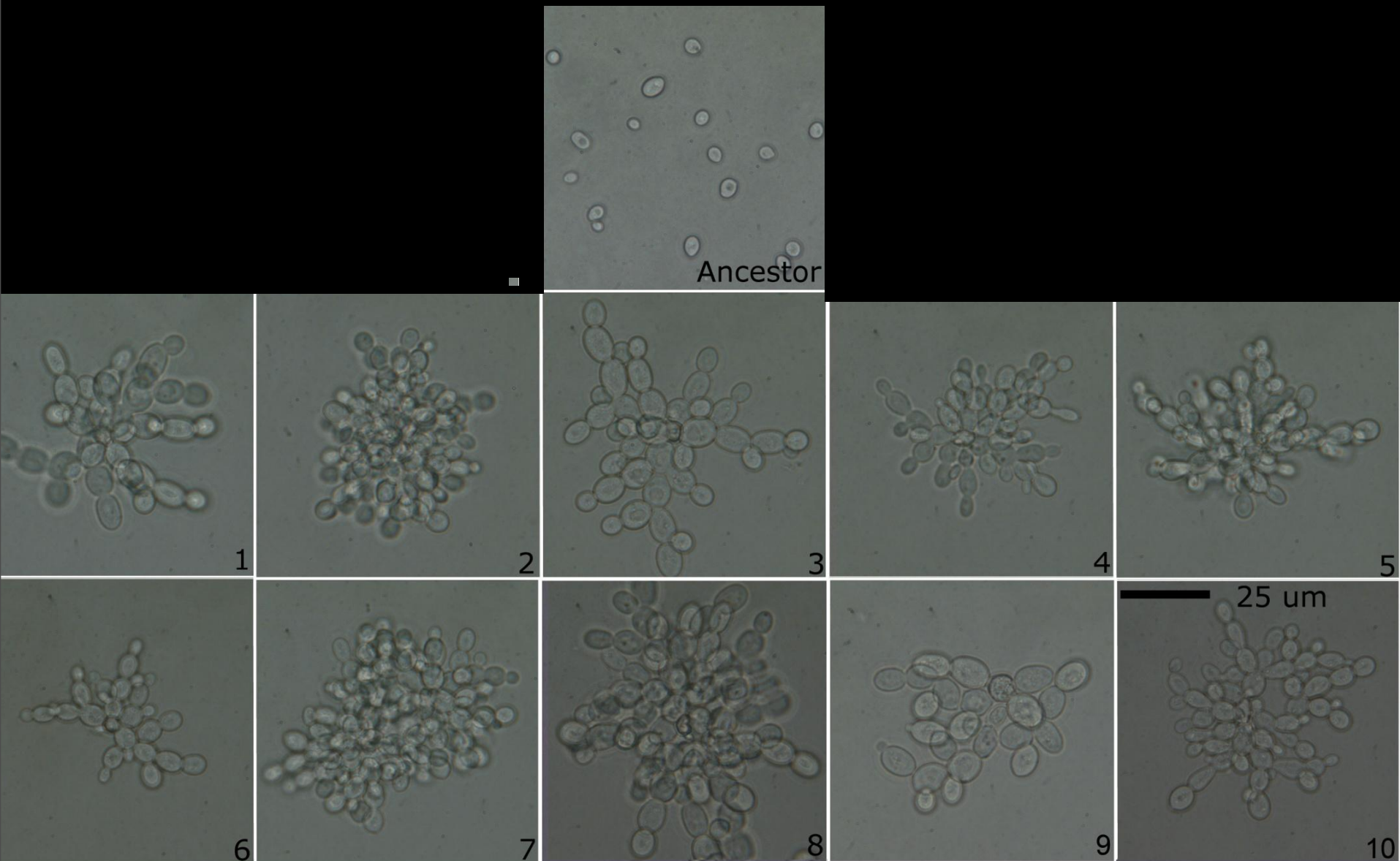


Population size  
 $10^7 - 10^8$

# Experimental evolution of multicellularity

William C. Ratcliff<sup>a,1</sup>, R. Ford Denison<sup>a</sup>, Mark Borrello<sup>a</sup>, and Michael Travisano<sup>a,b</sup>

[www.pnas.org/cgi/doi/10.1073/pnas.1115323109](http://www.pnas.org/cgi/doi/10.1073/pnas.1115323109) 2012

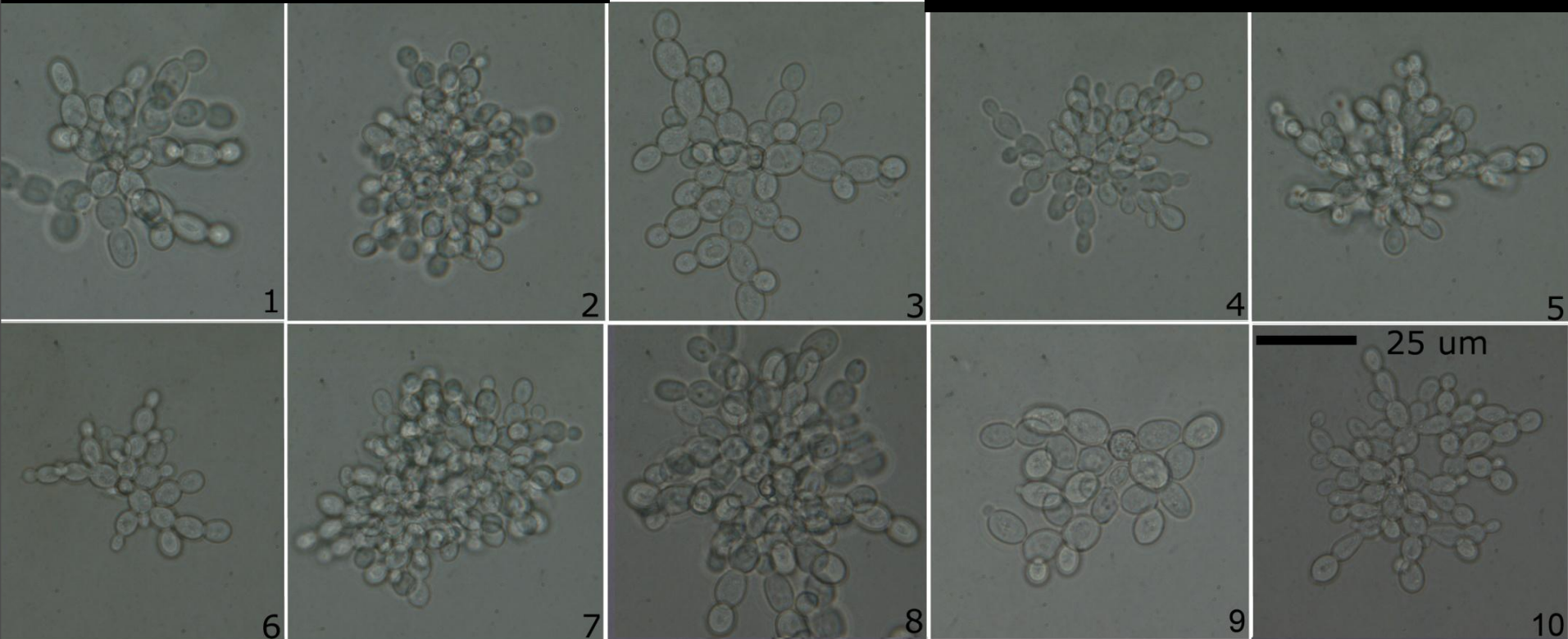
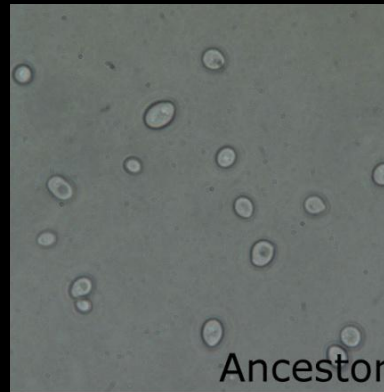




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[www.pnas.org/cgi/doi/10.1073/pnas.1115323109](http://www.pnas.org/cgi/doi/10.1073/pnas.1115323109) 2012

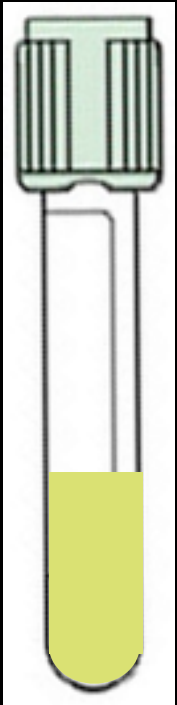






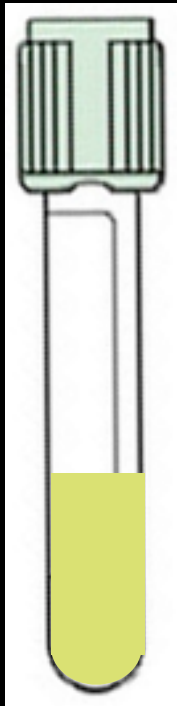


# selection scheme



24 hour, shaking  
incubation

# selection scheme

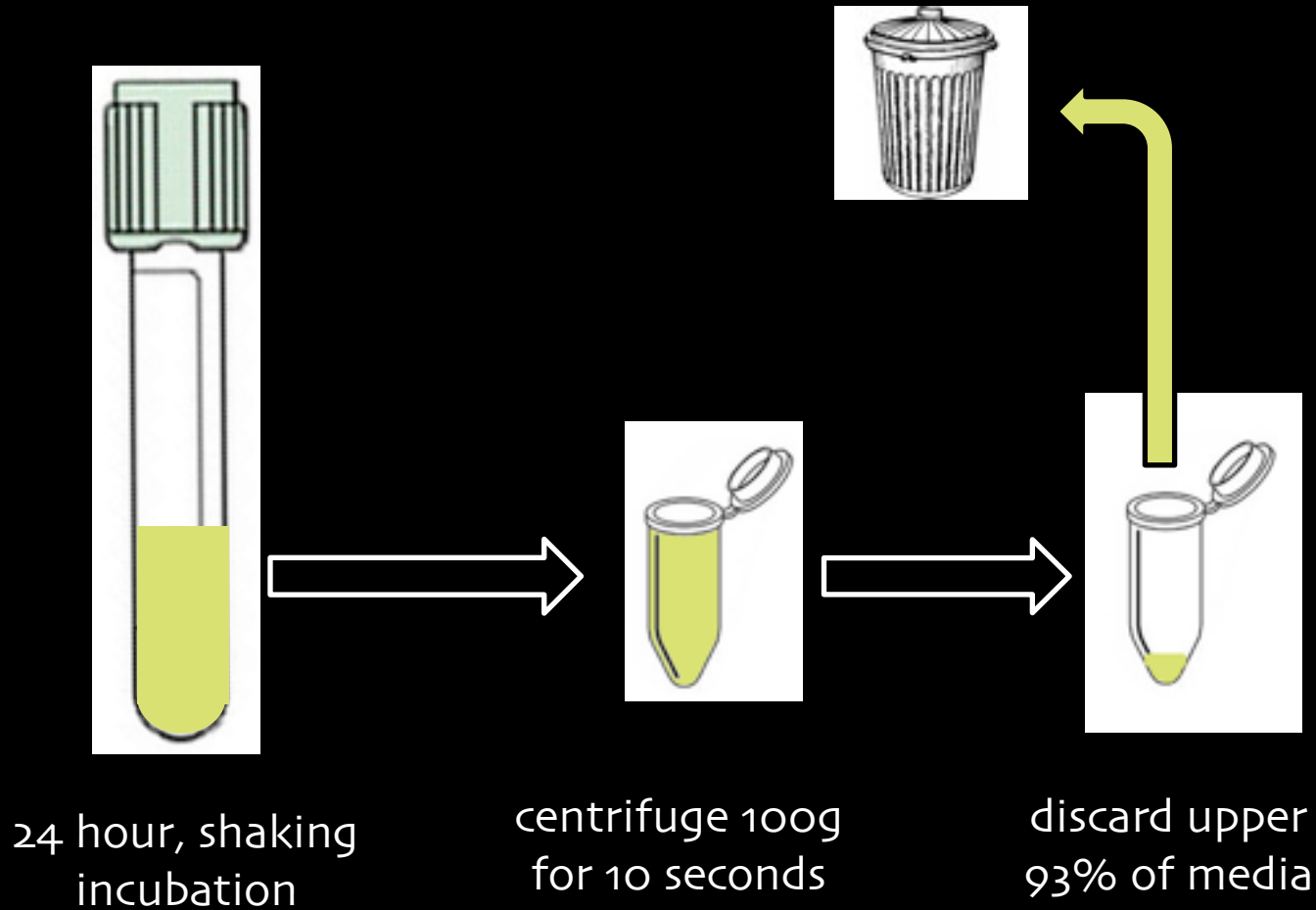


24 hour, shaking  
incubation

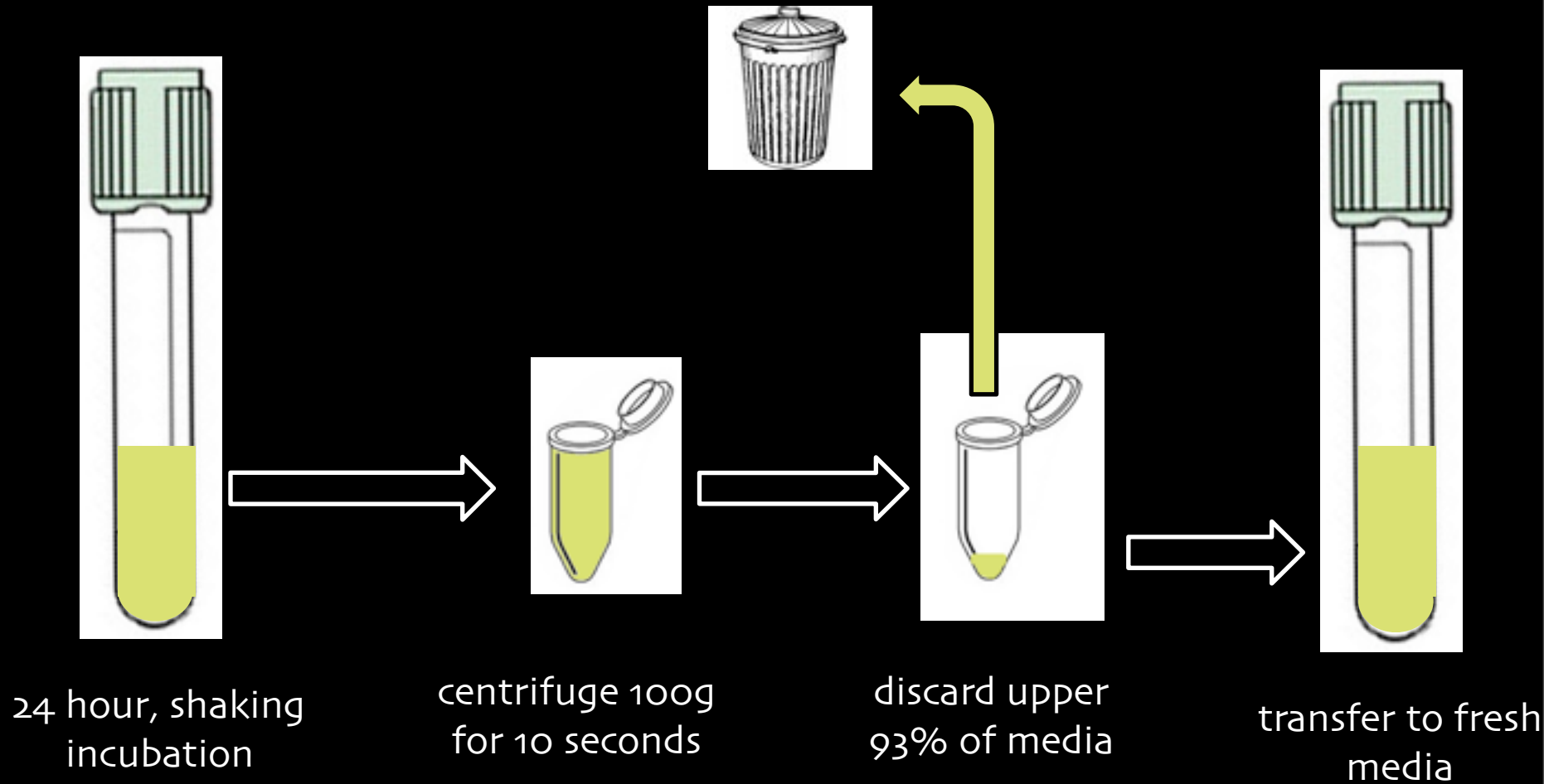


centrifuge 100g  
for 10 seconds

# selection scheme



# selection scheme





# evolution of rapid settling

time series of a single replicate

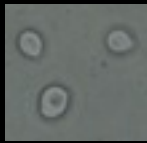


multicellularity is a simple solution to selection  
for larger size

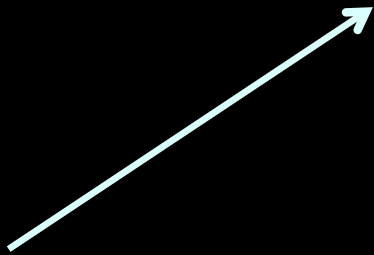


Unicellular ancestor

# multicellularity is a simple solution to selection for larger size

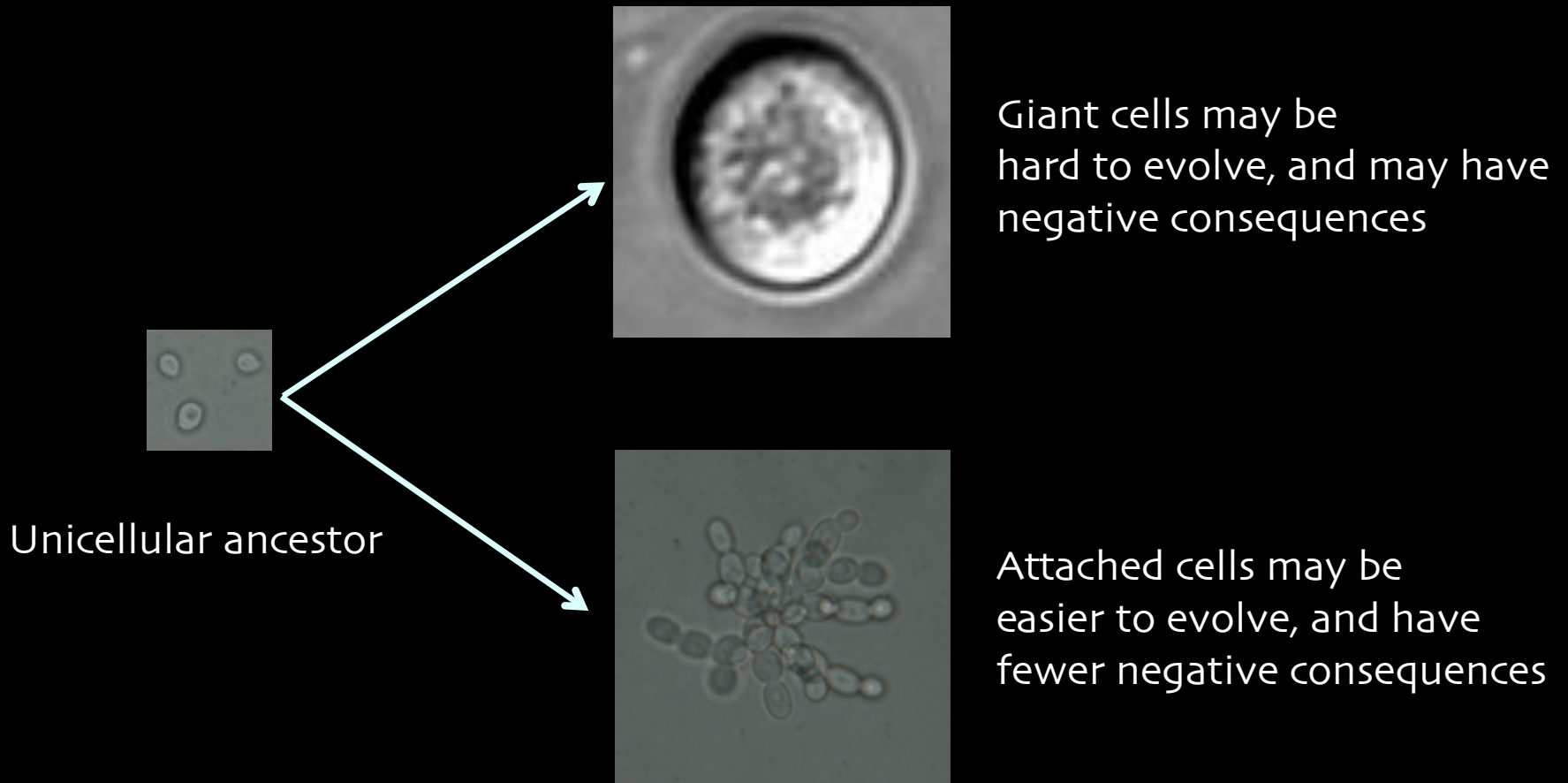


Unicellular ancestor



Giant cells may be hard to evolve, and may have negative consequences

# multicellularity is a simple solution to selection for larger size



# Two routes to faster settling

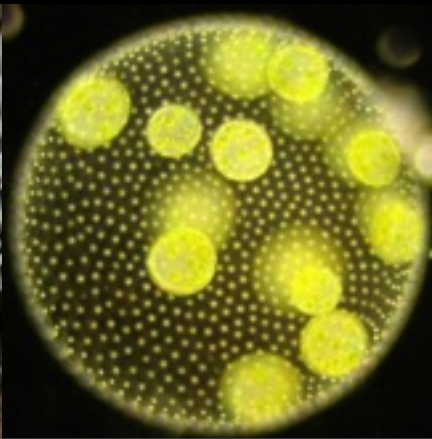
unicellular

normal size cell



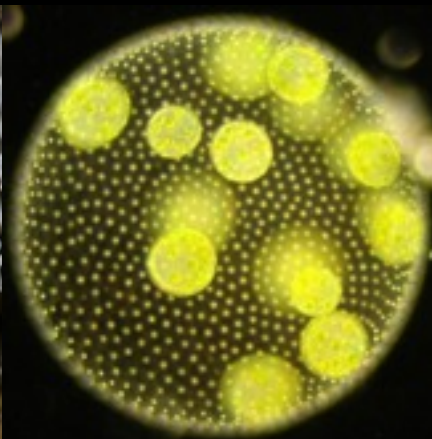
large-celled genotype

# Characteristics of multicellularity



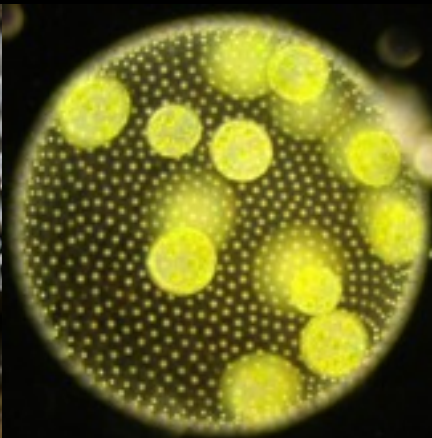
# Characteristics of multicellularity

- Physical adhesion between cells



# Characteristics of multicellularity

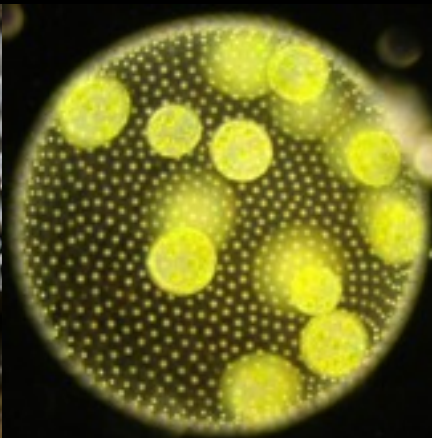
- Physical adhesion between cells
- Multicellular life-history





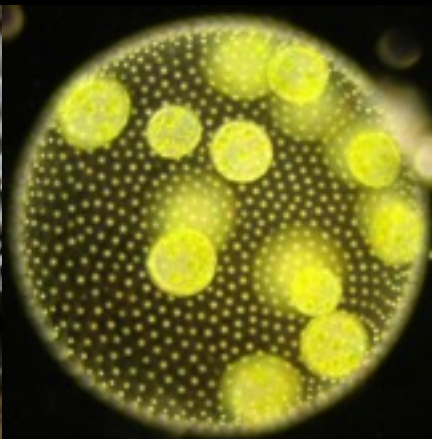
# Characteristics of multicellularity

- Physical adhesion between cells
- Multicellular life-history
  - reproduction



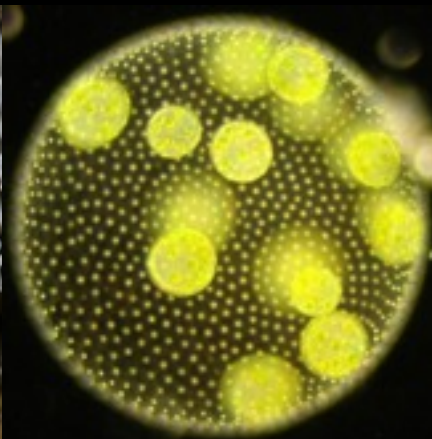
# Characteristics of multicellularity

- Physical adhesion between cells
- Multicellular life-history
  - reproduction
  - juvenile and adult stages



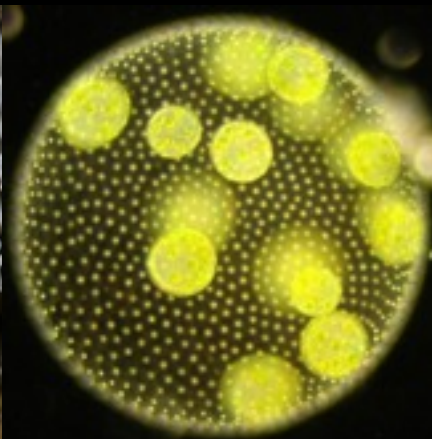
# Characteristics of multicellularity

- Physical adhesion between cells
- Multicellular life-history
  - reproduction
  - juvenile and adult stages
- Life history responds to selection



# Characteristics of multicellularity

- Physical adhesion between cells
- Multicellular life-history
  - reproduction
  - juvenile and adult stages
- Life history responds to selection
- Division of labor among cells

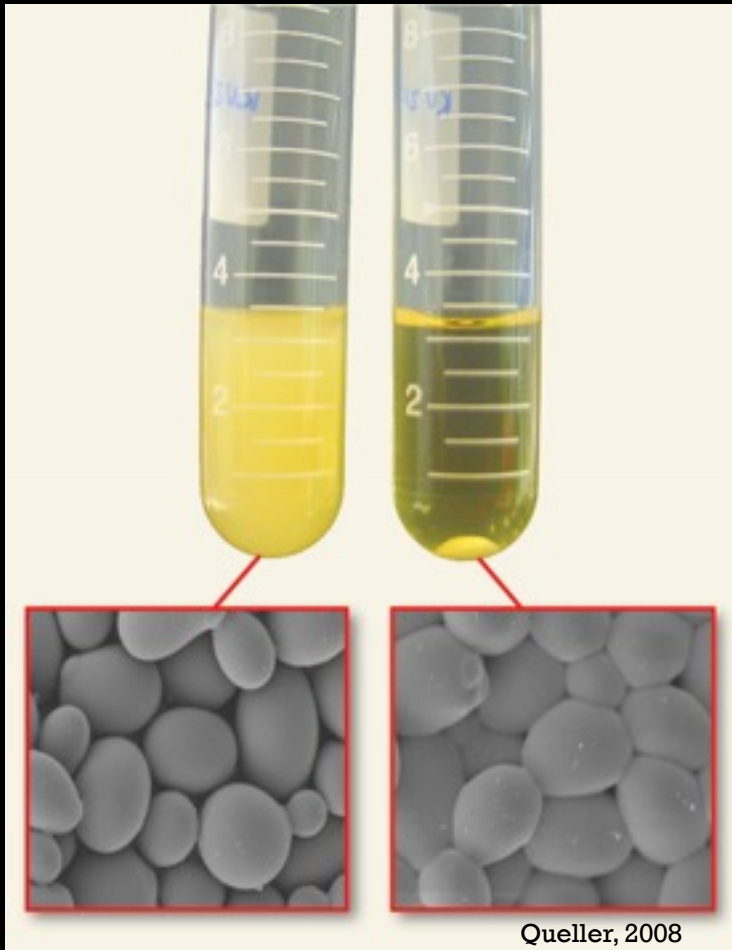


# Modes for Evolution of Multicellularity

coming together

staying together

# Modes for Evolution of Multicellularity



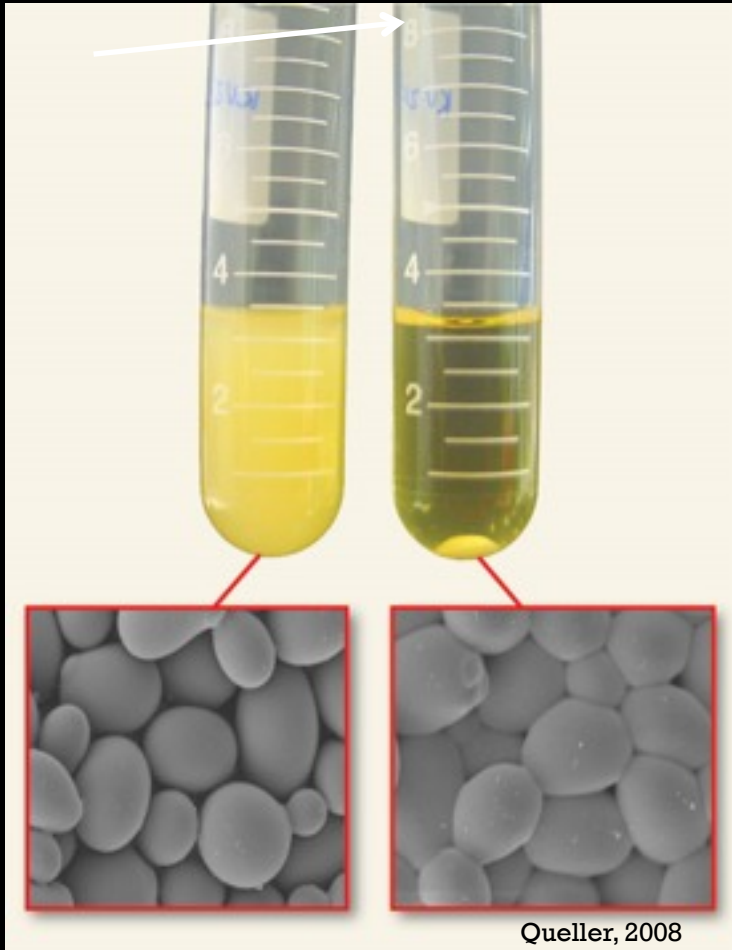
unicellular  
wild type

coming together

floc +

staying together

# Modes for Evolution of Multicellularity

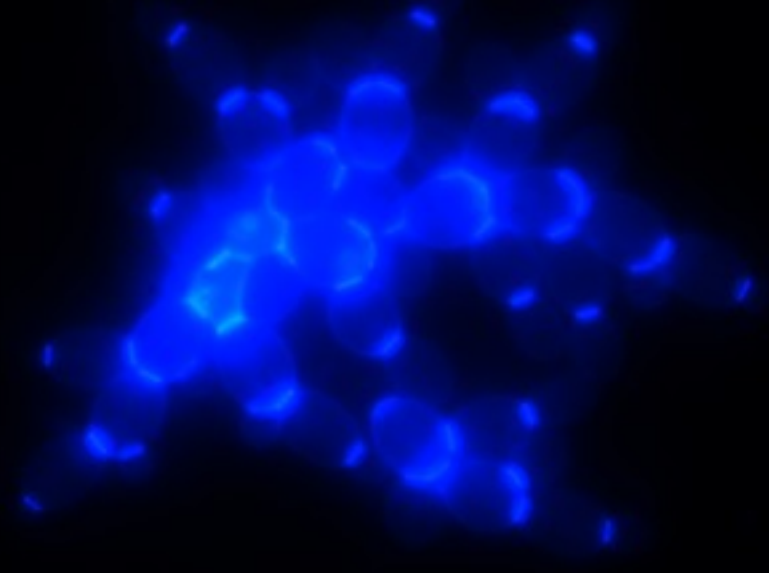


Queller, 2008

unicellular  
wild type

floc +

coming together

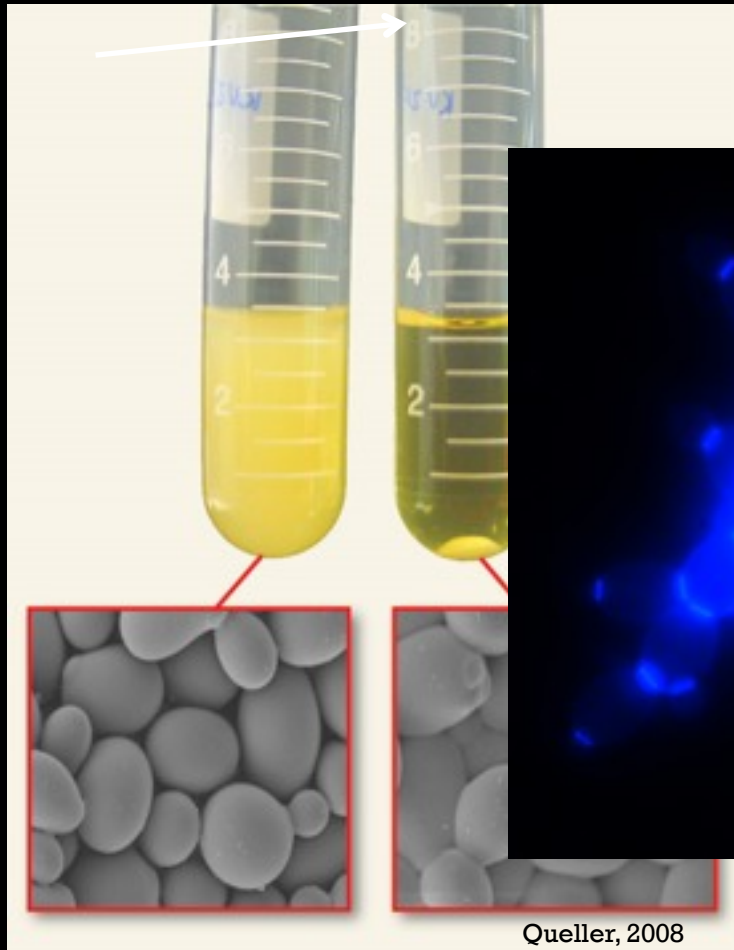


snowflake phenotype cluster

Ratcliff, Denison, Borrello, & Travisano. 2012

staying together

# Modes for Evolution of Multicellularity



unicellular  
wild type

coming together

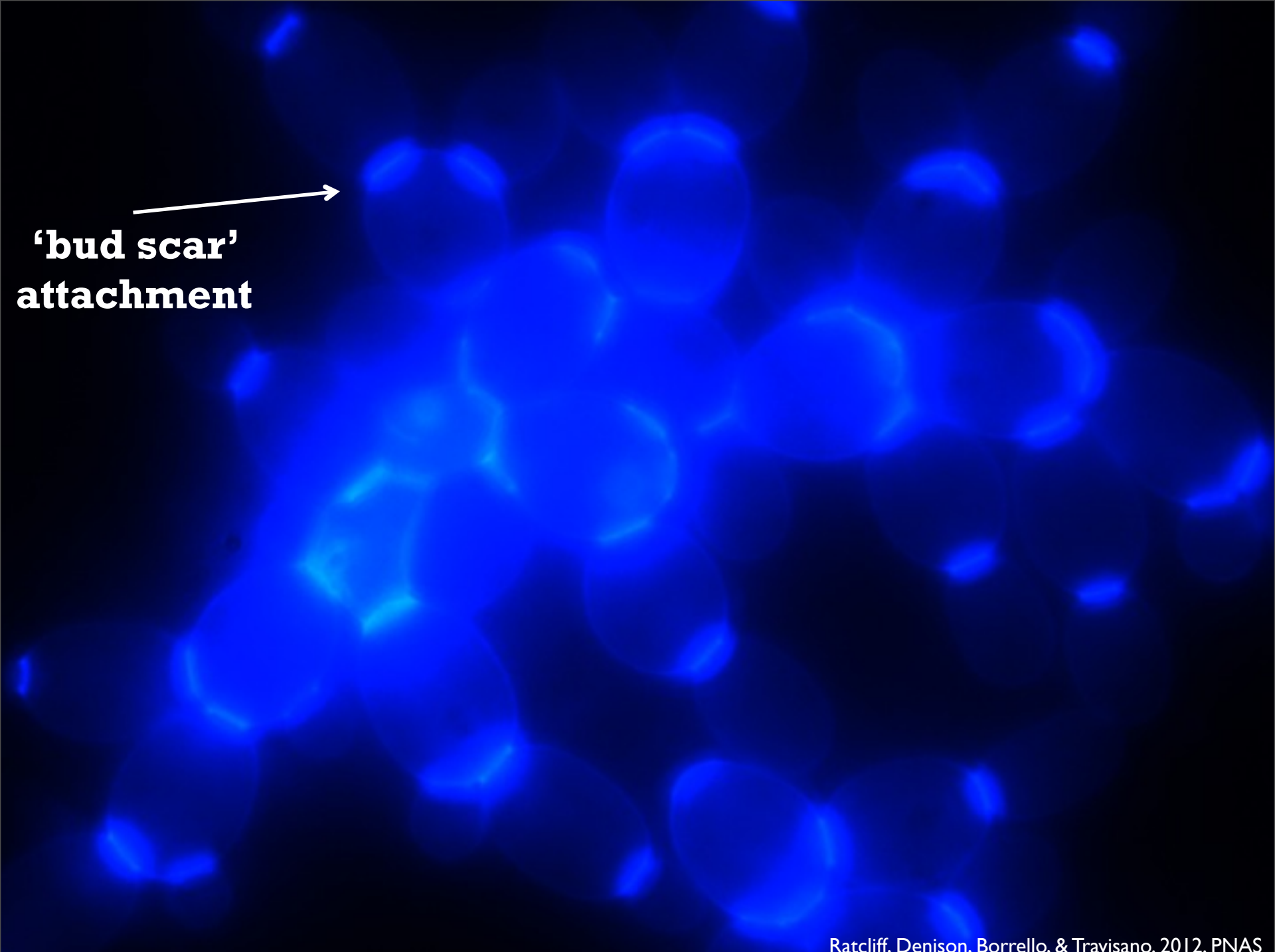
floc +

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Ratcliff, Denison, Borrello, & Travisano. 2012

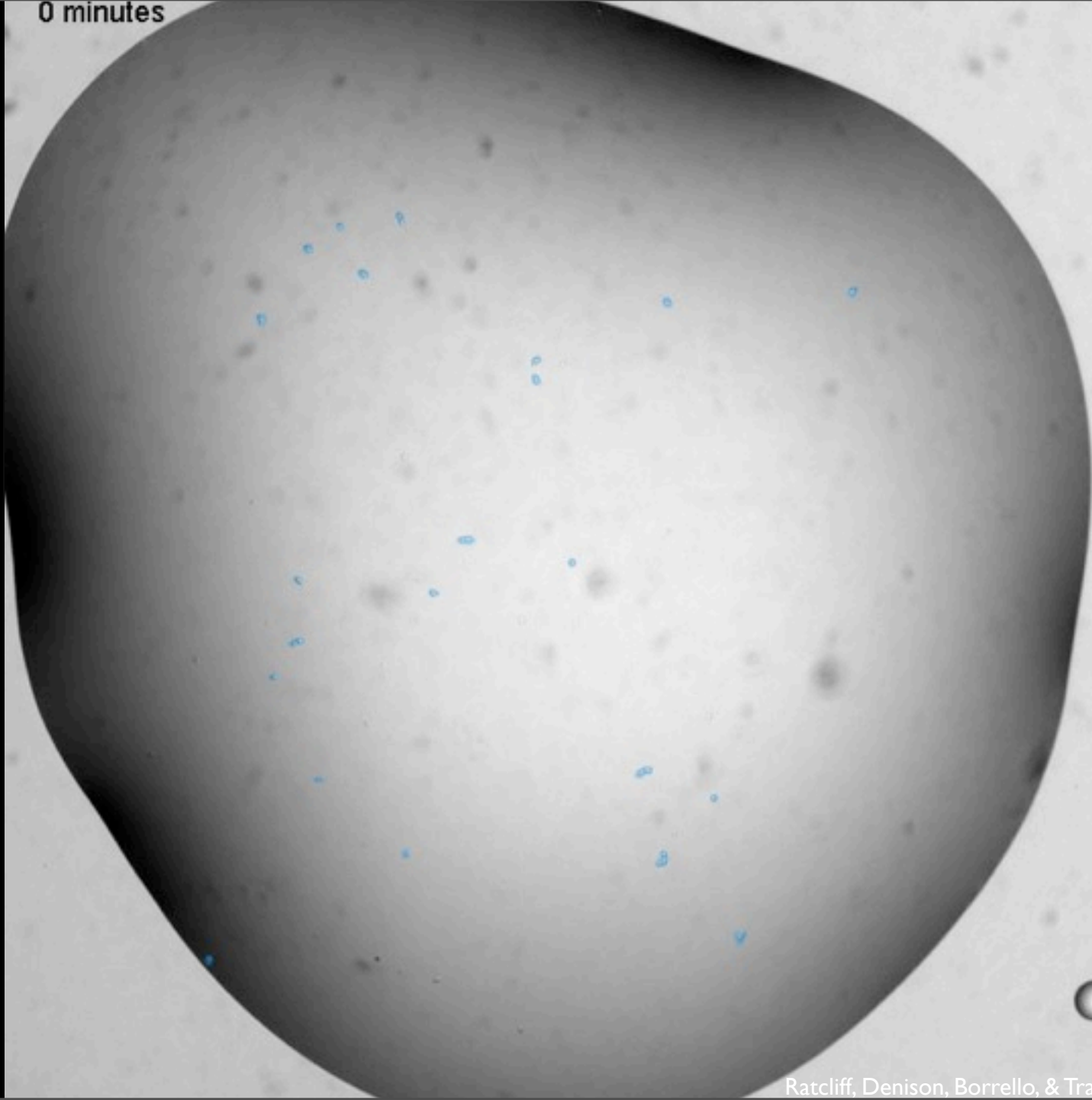
staying together





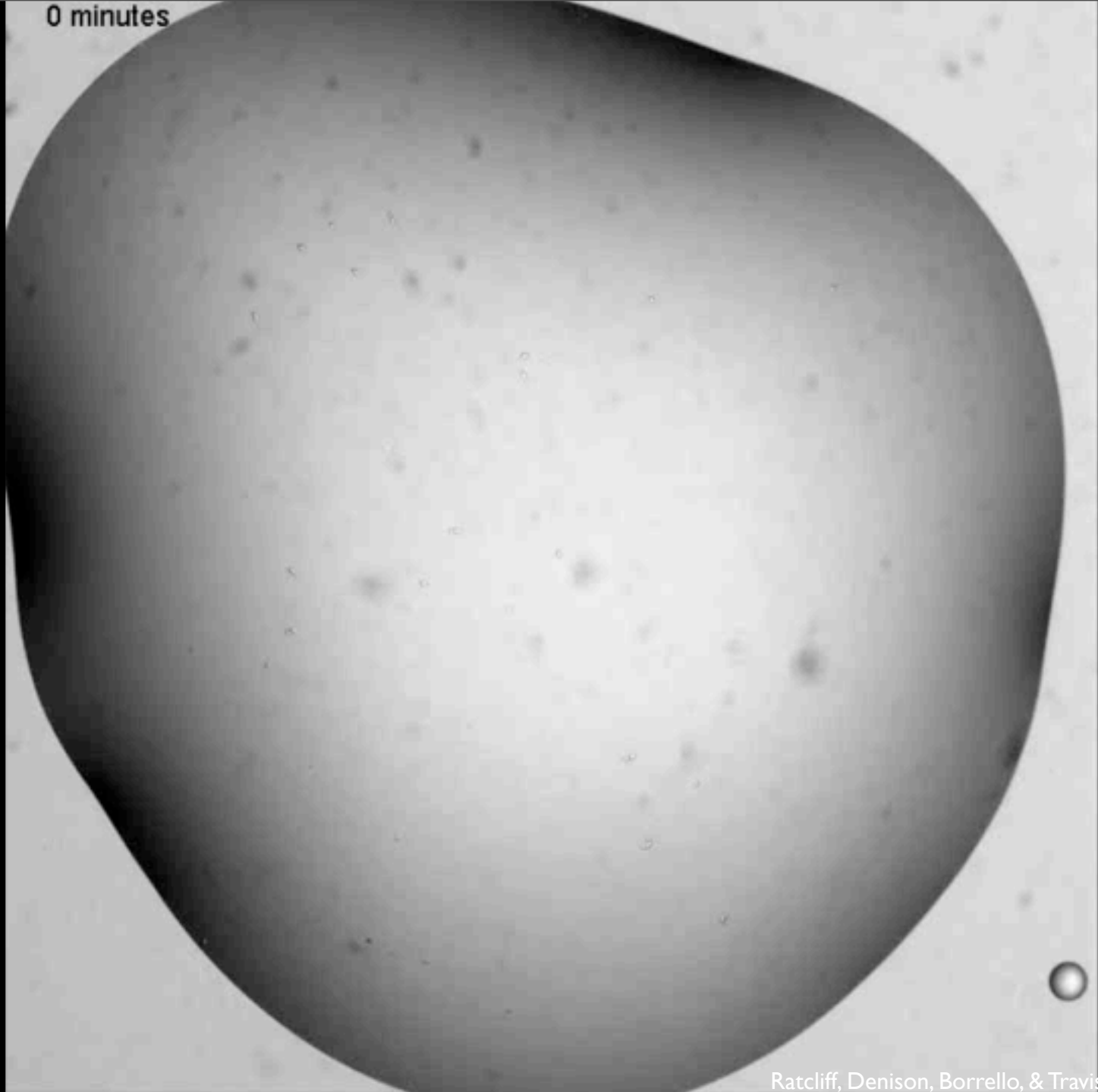
**'bud scar'  
attachment**

0 minutes



single cells regenerate clusters

0 minutes

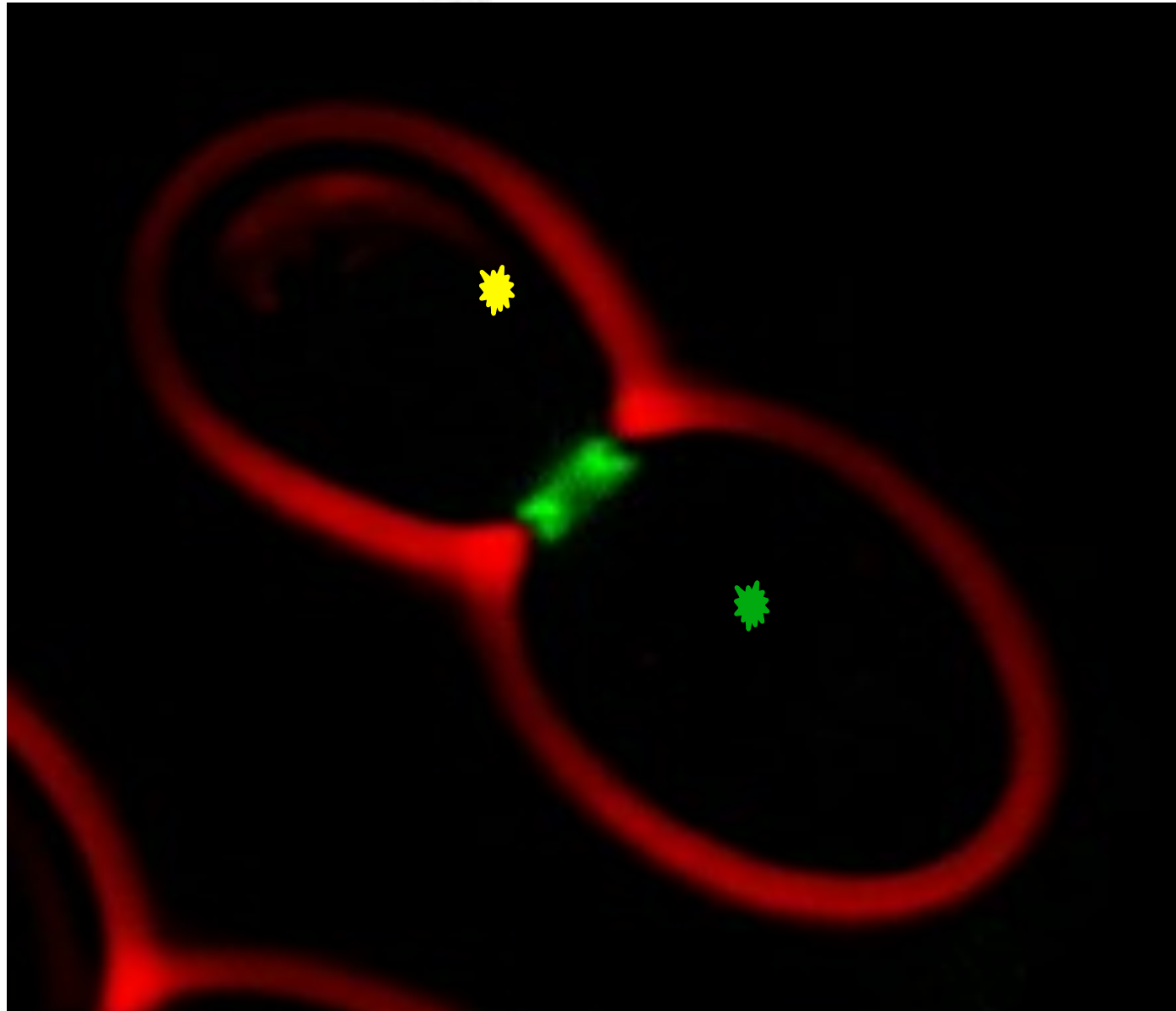


# Molecular Mechanism

ACE2 TF activity  
impaired but  
where?

Fluorescent micrograph of  
*Saccharomyces cerevisiae*  
Green: Septum  
Red: Cell outline

Spitfire ch, Philippsen Lab,  
Biozentrum Basel (2006)

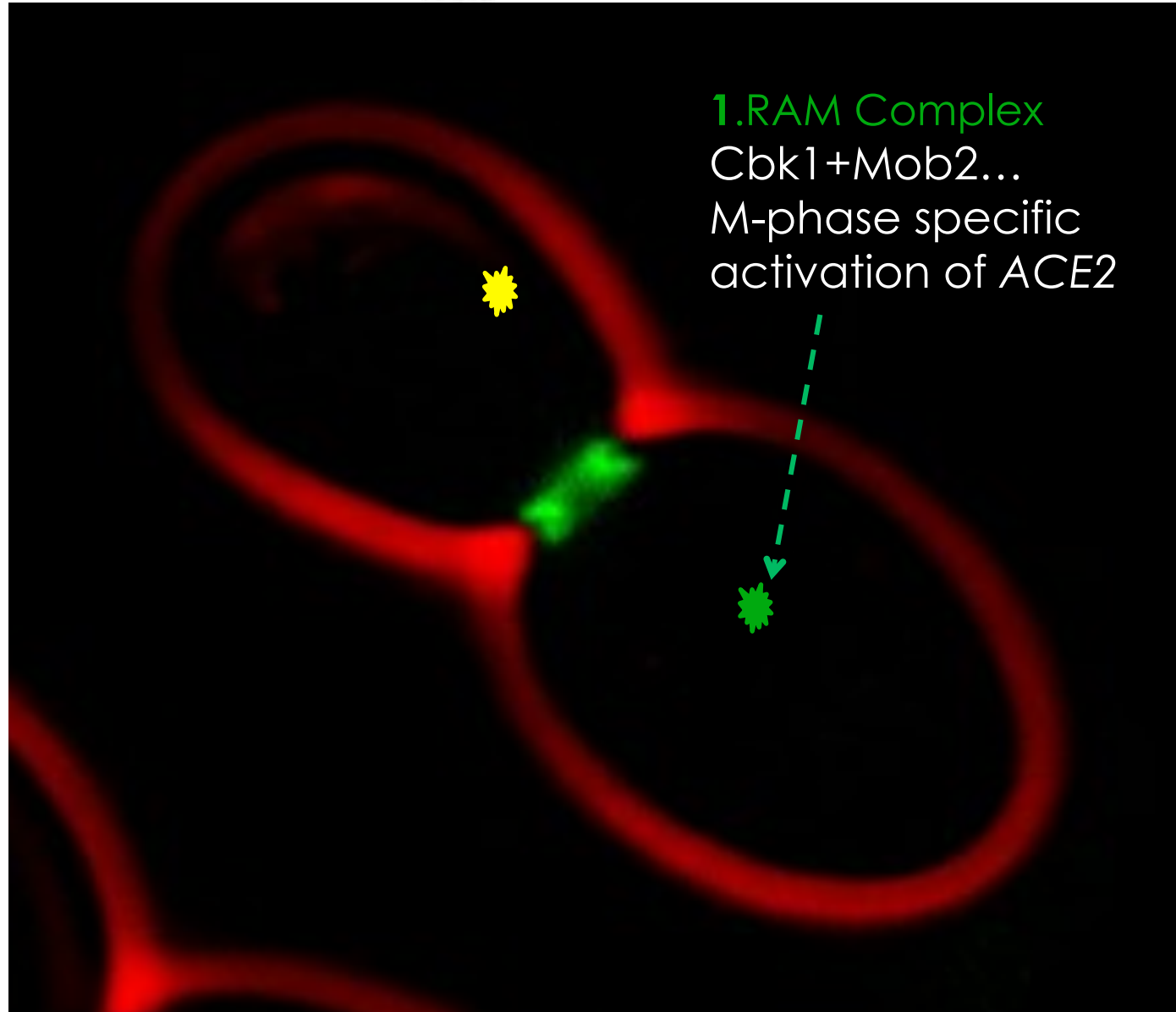


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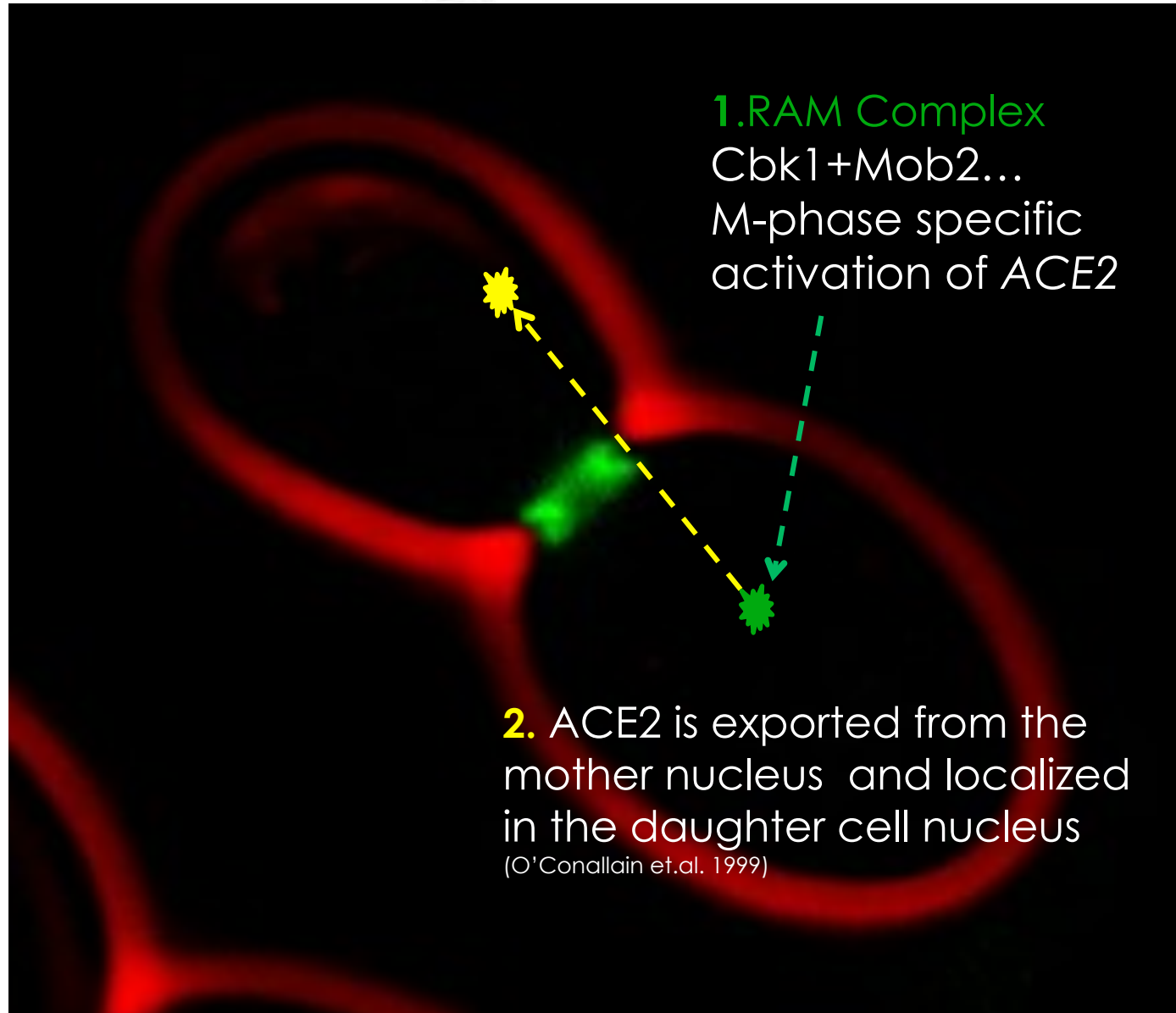


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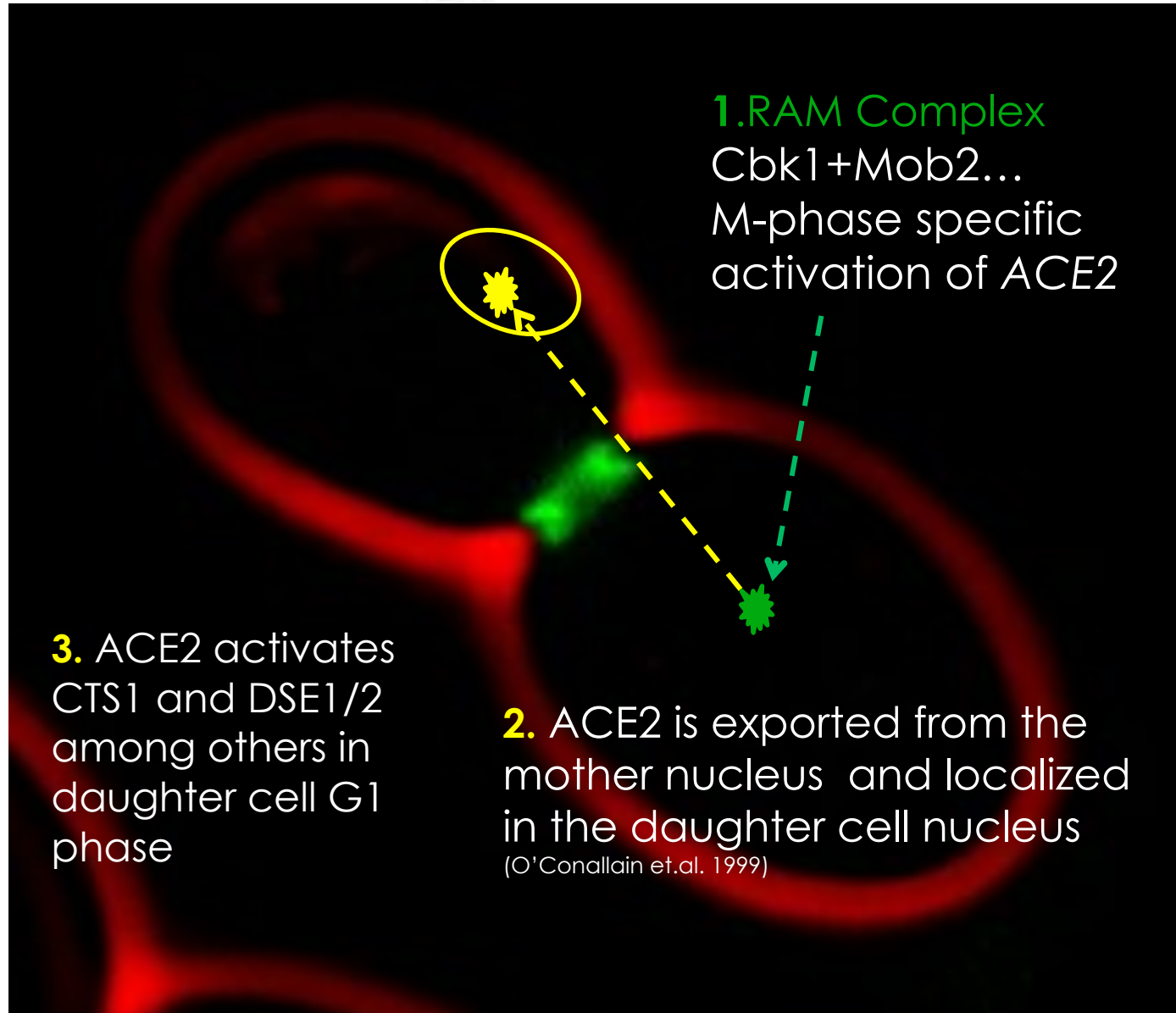


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Spitfire ch, Philippsen Lab,  
Biozentrum Basel (2006)





# Molecular Mechanism

ACE2 TF activity impaired but where?

Fluorescent micrograph of *Saccharomyces cerevisiae*  
Green: Septum  
Red: Cell outline

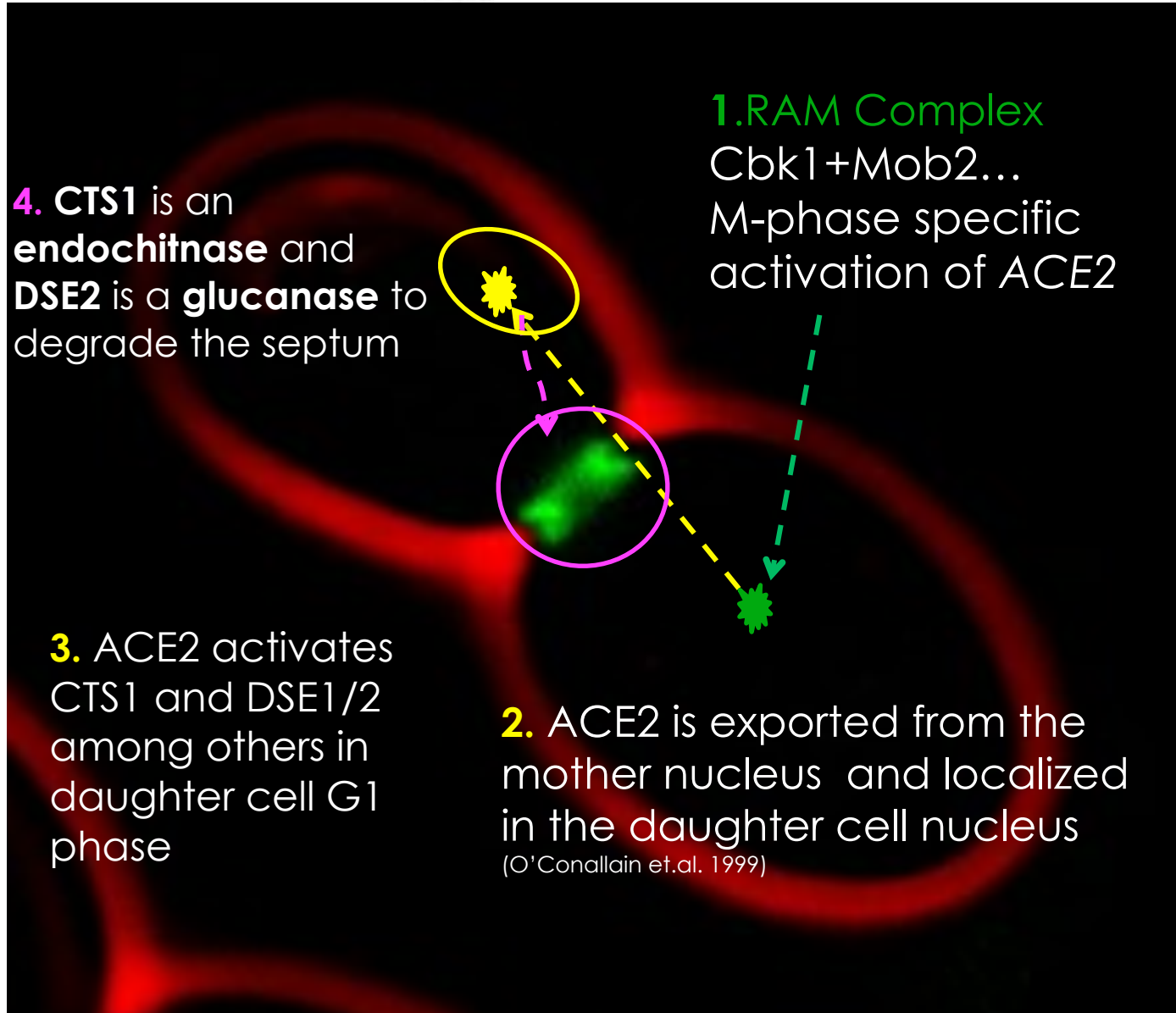
Spitfire ch, Philippsen Lab,  
Biozentrum Basel (2006)

4. **CTS1** is an **endochitinase** and **DSE2** is a **glucanase** to degrade the septum

3. ACE2 activates **CTS1** and **DSE1/2** among others in daughter cell G1 phase

1. **RAM Complex**  
Cbk1+Mob2...  
M-phase specific activation of ACE2

2. ACE2 is exported from the mother nucleus and localized in the daughter cell nucleus  
(O'Conallain et.al. 1999)

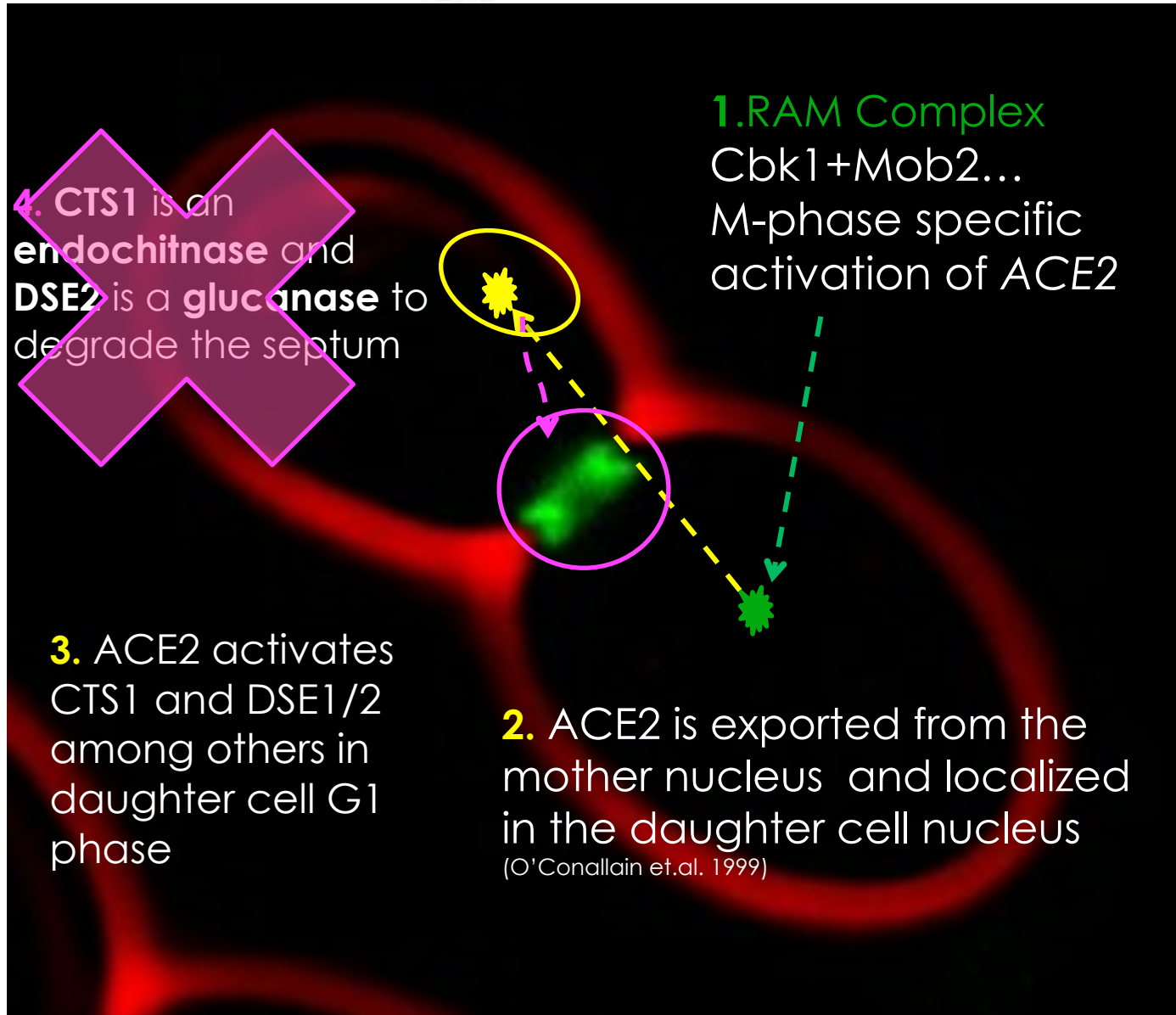


# Molecular Mechanism

ACE2 TF activity impaired but where?

Fluorescent micrograph of *Saccharomyces cerevisiae*  
Green: Septum  
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Spitfire ch, Philippsen Lab,  
Biozentrum Basel (2006)



Are snowflake yeast multicellular?

# Are snowflake yeast multicellular?

- physical adhesion between cells

# Are snowflake yeast multicellular?

- physical adhesion between cells
- multicellular life-history

# Are snowflake yeast multicellular?

- physical adhesion between cells
- multicellular life-history
  - Reproduction



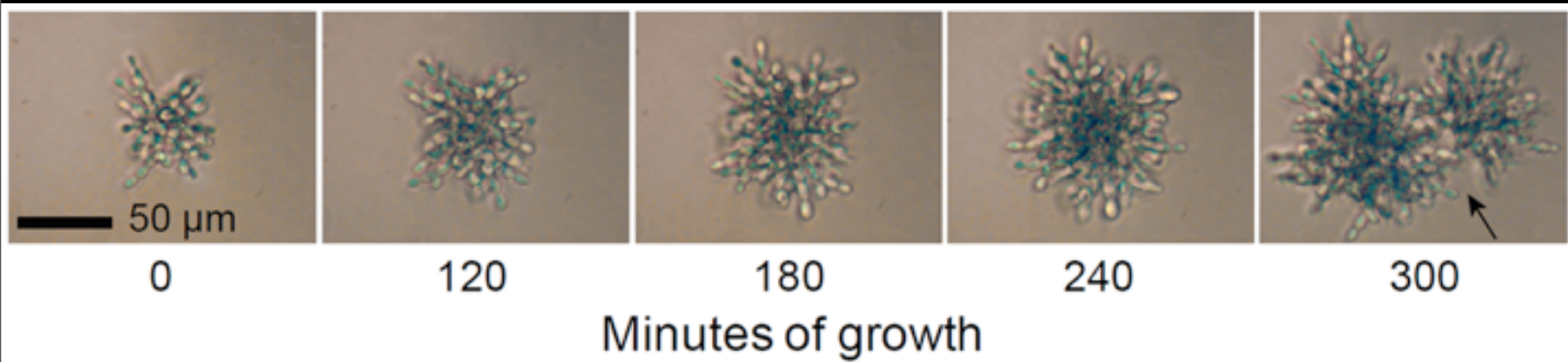




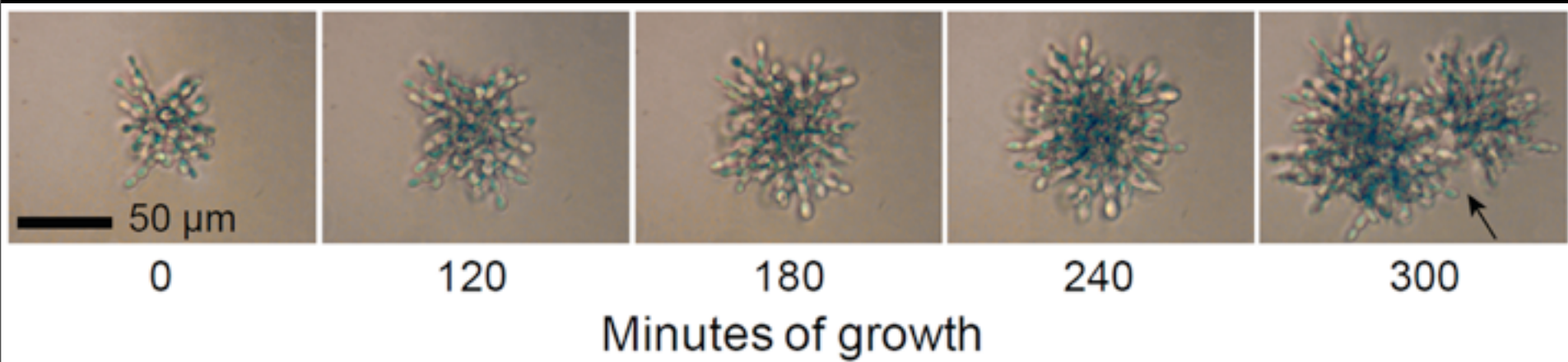




# Offspring are functionally juvenile



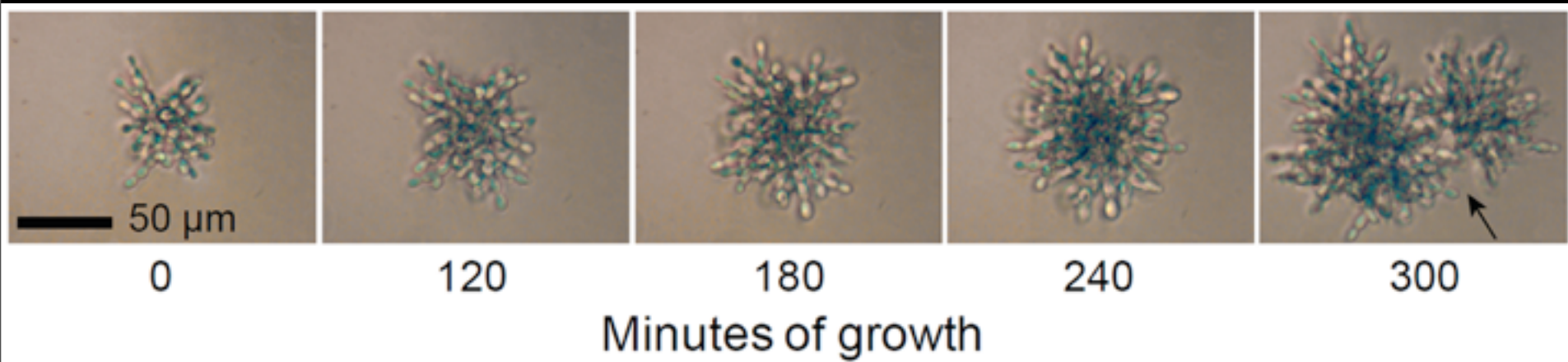
# Offspring are functionally juvenile



maturation

reproduction

# Offspring are functionally juvenile

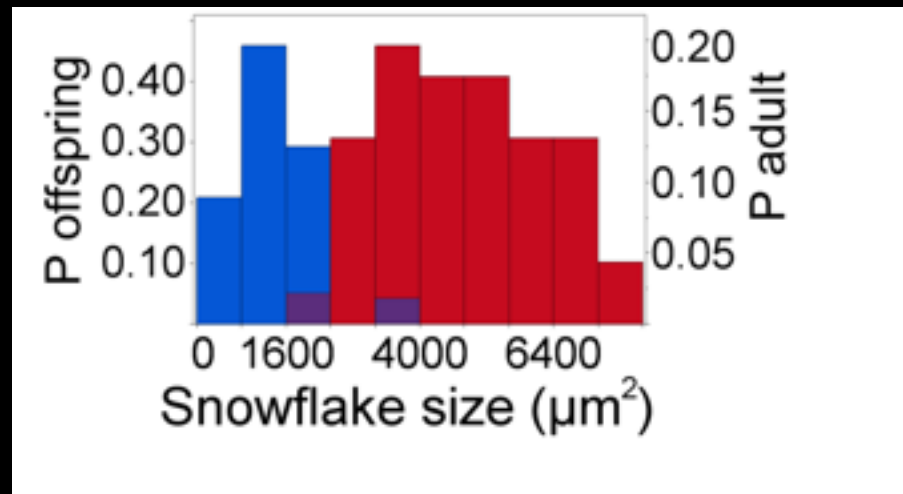


maturation

reproduction

parental size at  
reproduction

offspring size



# Are snowflake yeast multicellular?

- physical adhesion between cells
- multicellular life-history
  - Reproduction
  - juvenile and adult stages

# Are snowflake yeast multicellular?

- physical adhesion between cells
- multicellular life-history
  - Reproduction
  - juvenile and adult stages
- Life history responds to selection

# Are snowflake yeast multicellular?

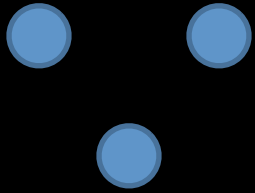
- physical adhesion between cells
- multicellular life-history
  - Reproduction
  - juvenile and adult stages
- Life history responds to selection

“Major transitions [i.e. multicellularity] are major stages in the evolution of complexity that involve a change in the level of organization, and hence the level of selection.”

Maynard Smith and Szathmary, 1995



# evolutionary theory

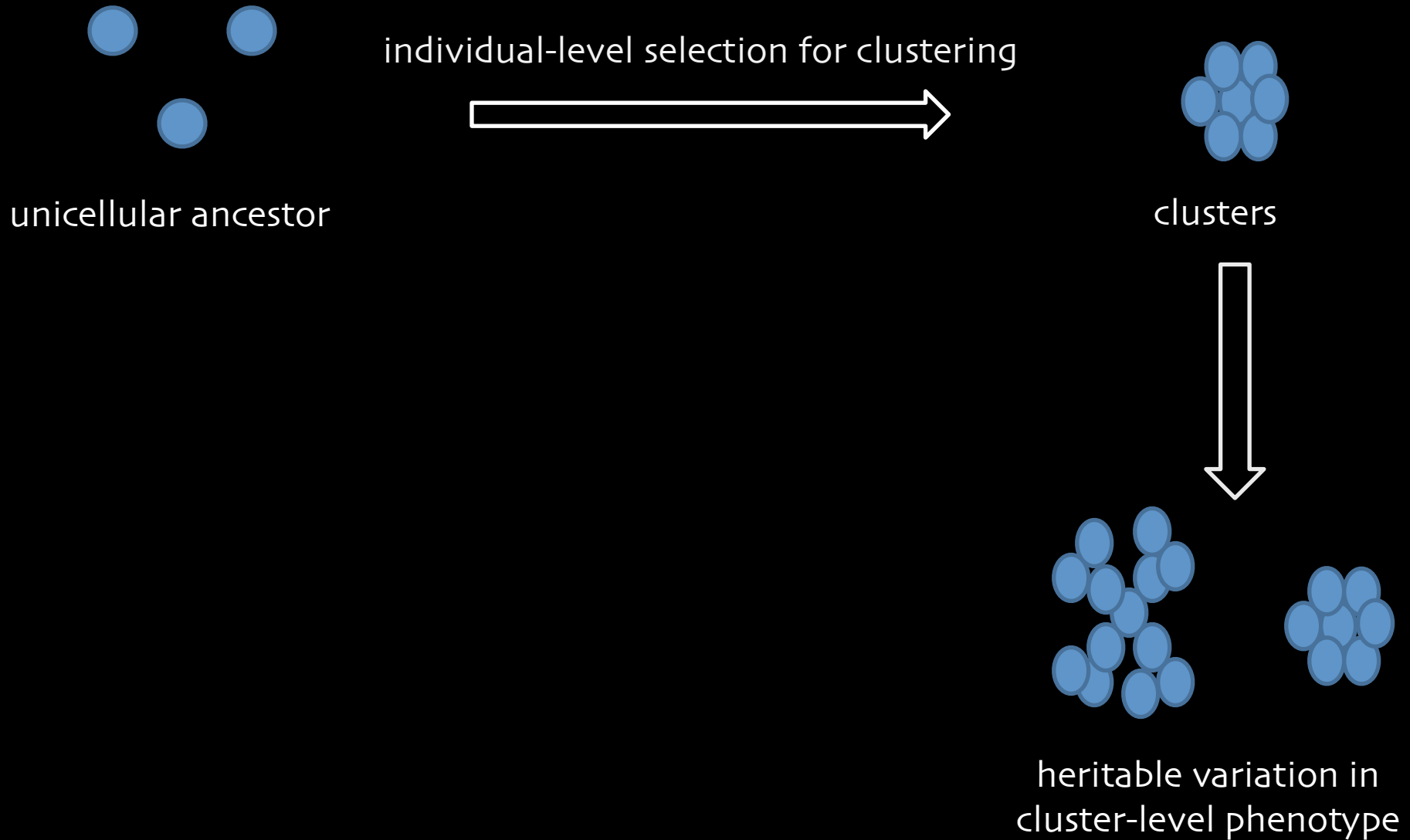


unicellular ancestor

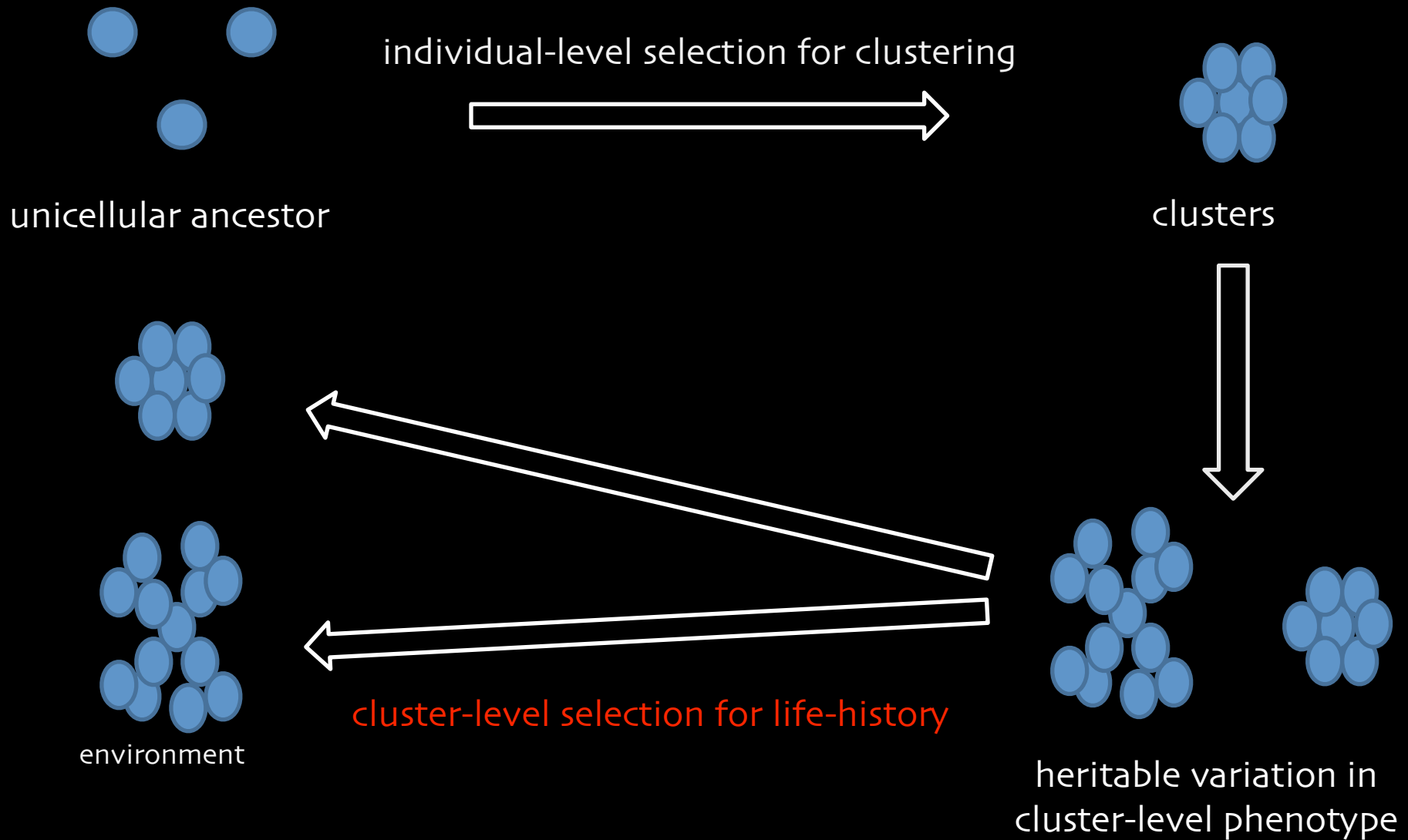
# evolutionary theory



# evolutionary theory



# evolutionary theory



# our experiments

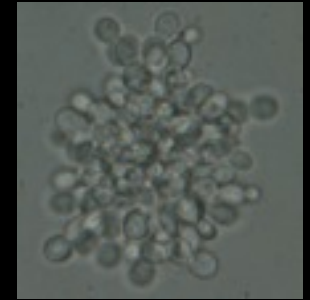


unicellular ancestor

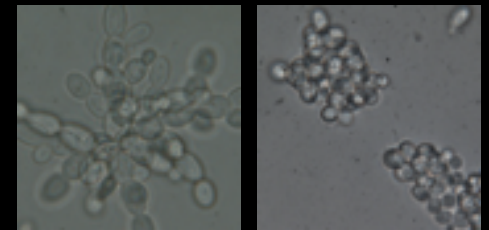
individual-level selection for clustering



rapid settling

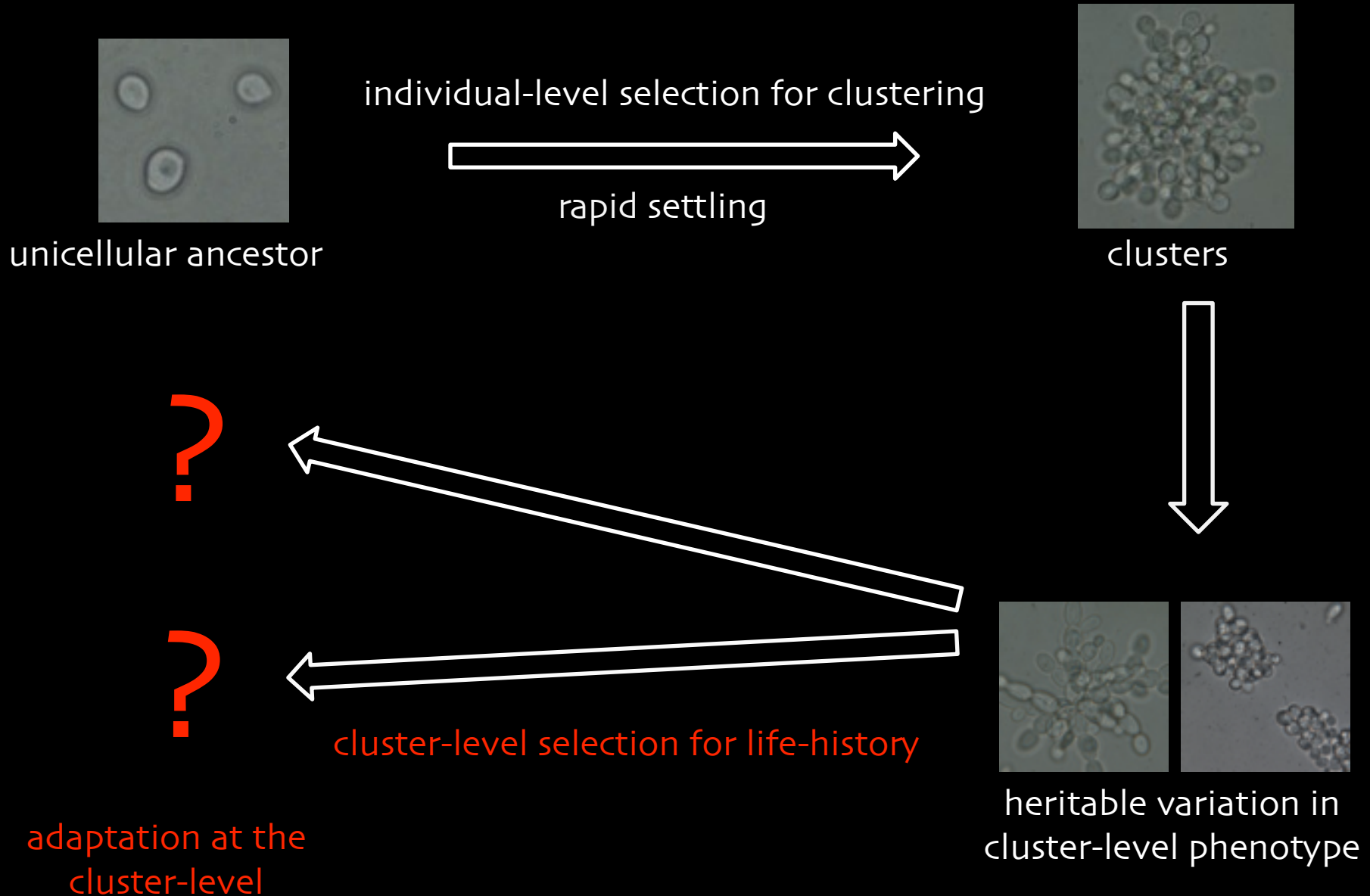


clusters



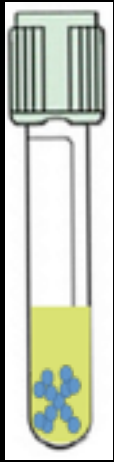
heritable variation in cluster-level phenotype

# our experiments



# divergent selection on settling rate

starting population



selection



5 minutes settling

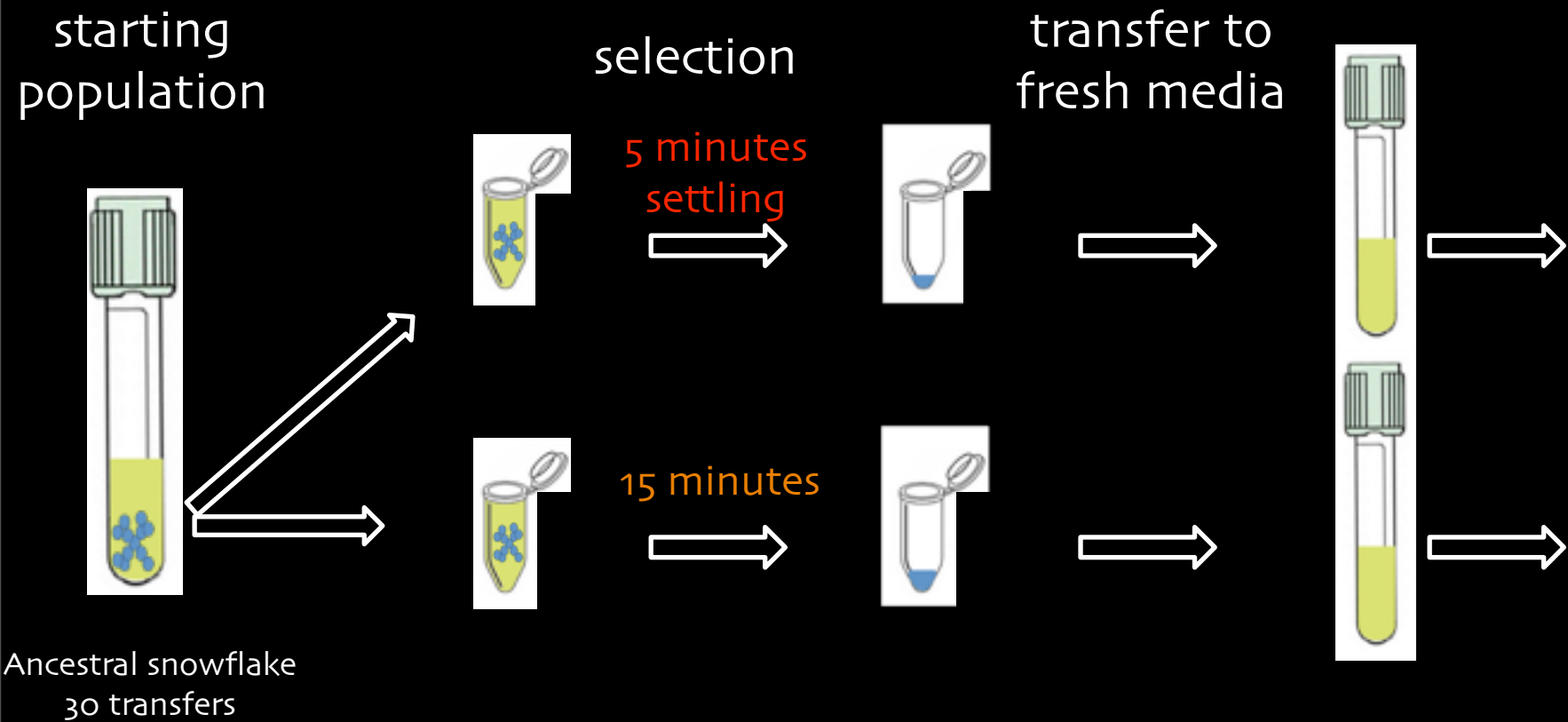


transfer to fresh media



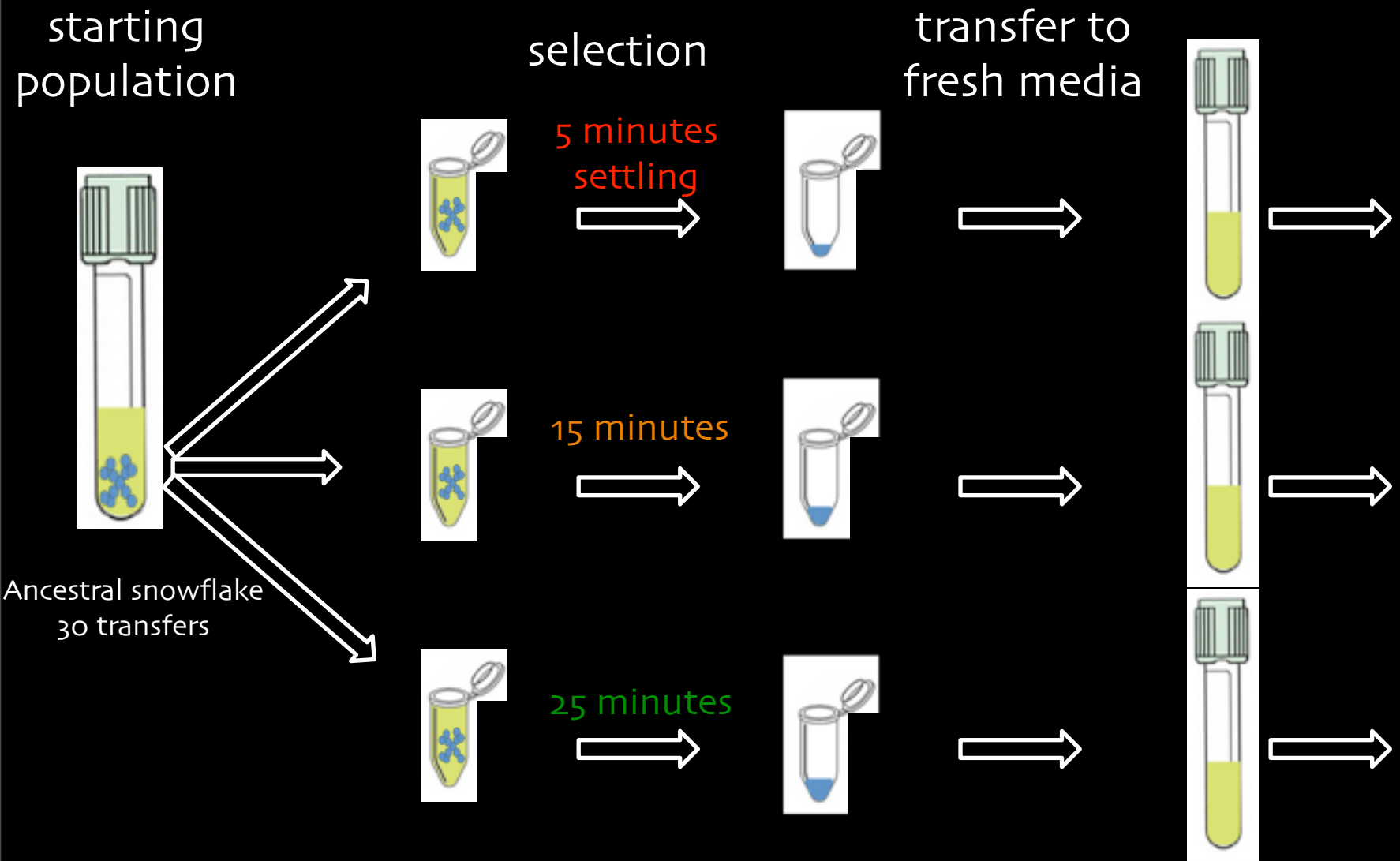
Ancestral snowflake  
30 transfers

# divergent selection on settling rate

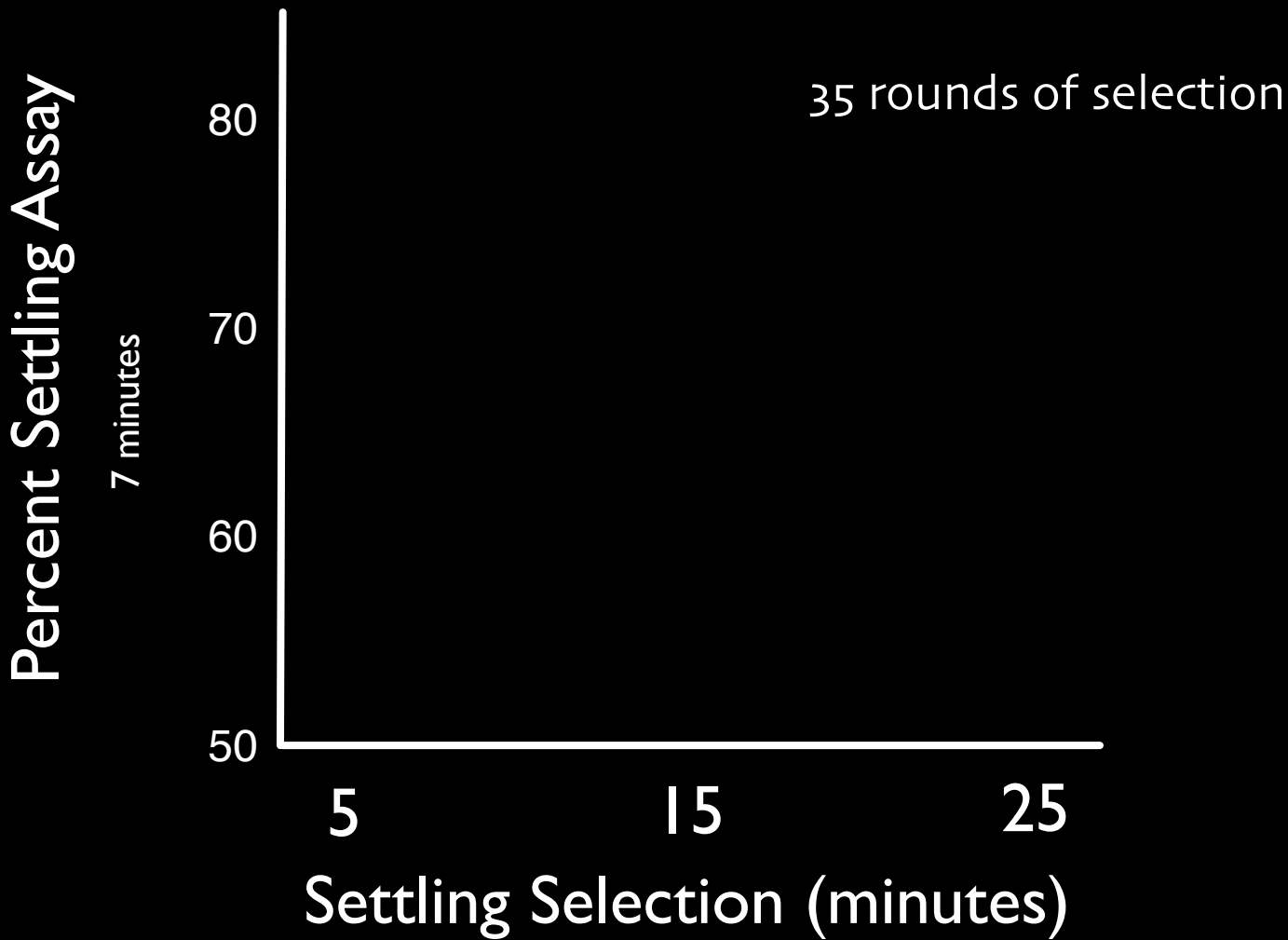




# divergent selection on settling rate



# Strong response to selection



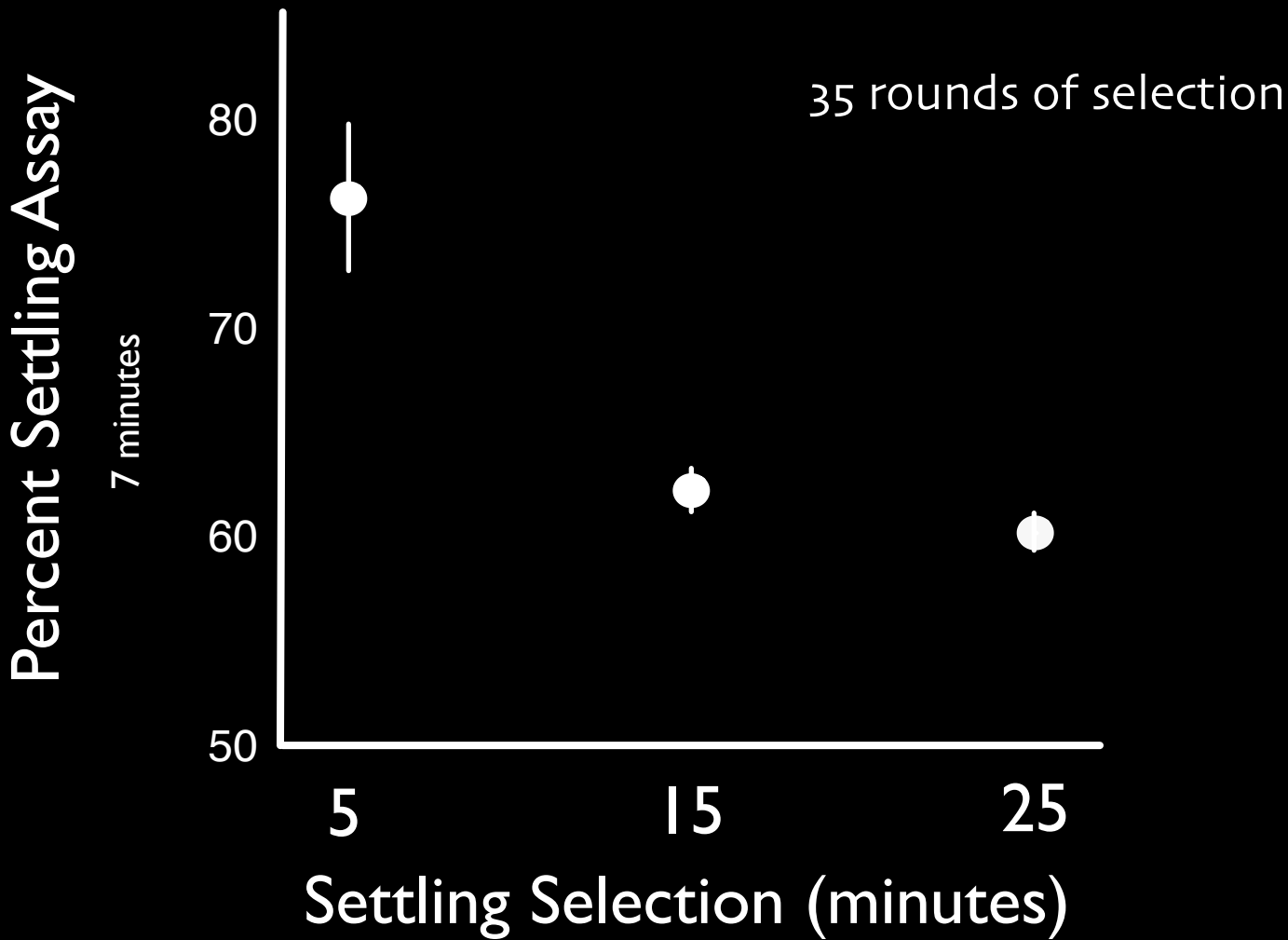
strength of selection  
for rapid settling

strong

moderate

weak

# Strong response to selection



strength of selection  
for rapid settling

strong

moderate

weak

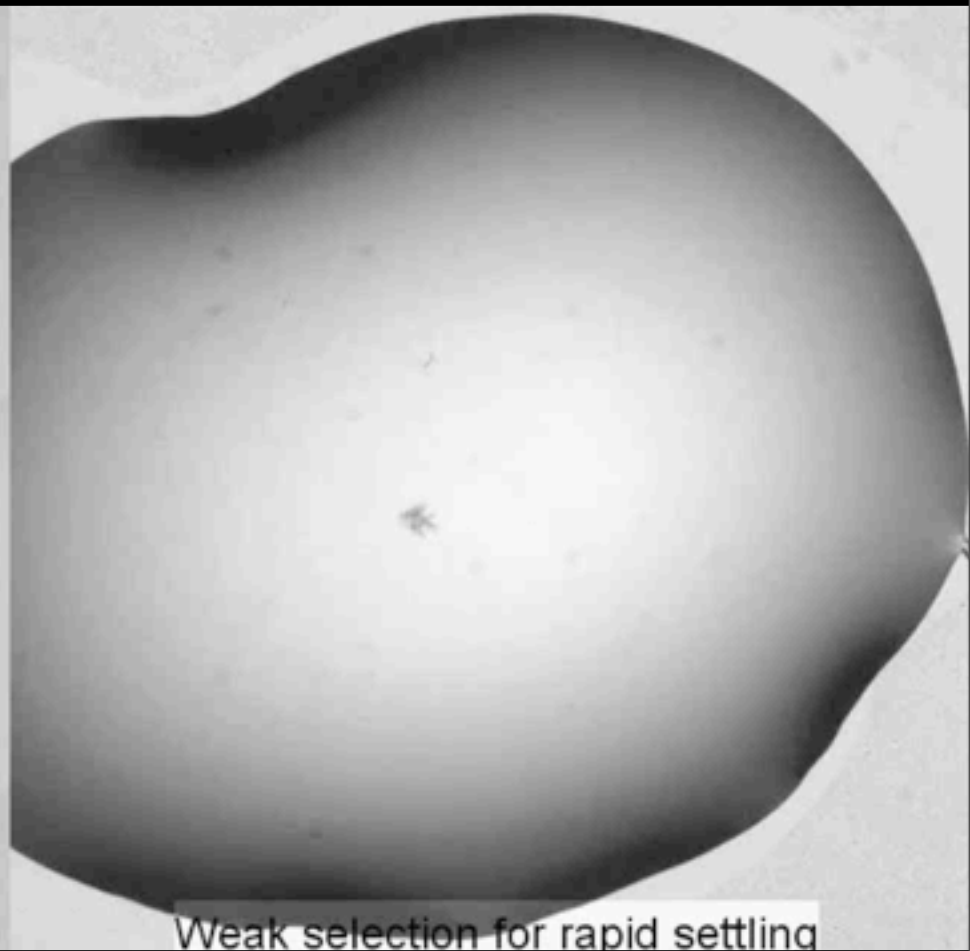
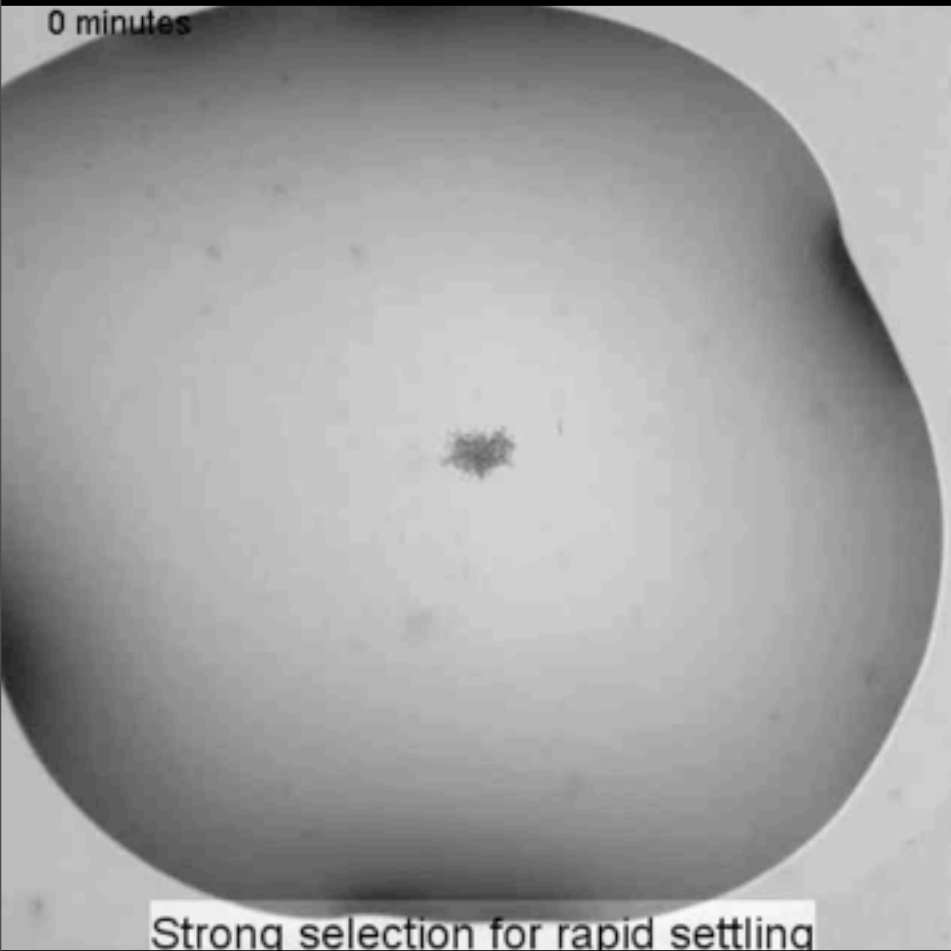
this was due to the evolution of larger clusters

Duration of settling in  
evolution experiment

5 minutes

25 minutes

this was due to the evolution of larger clusters

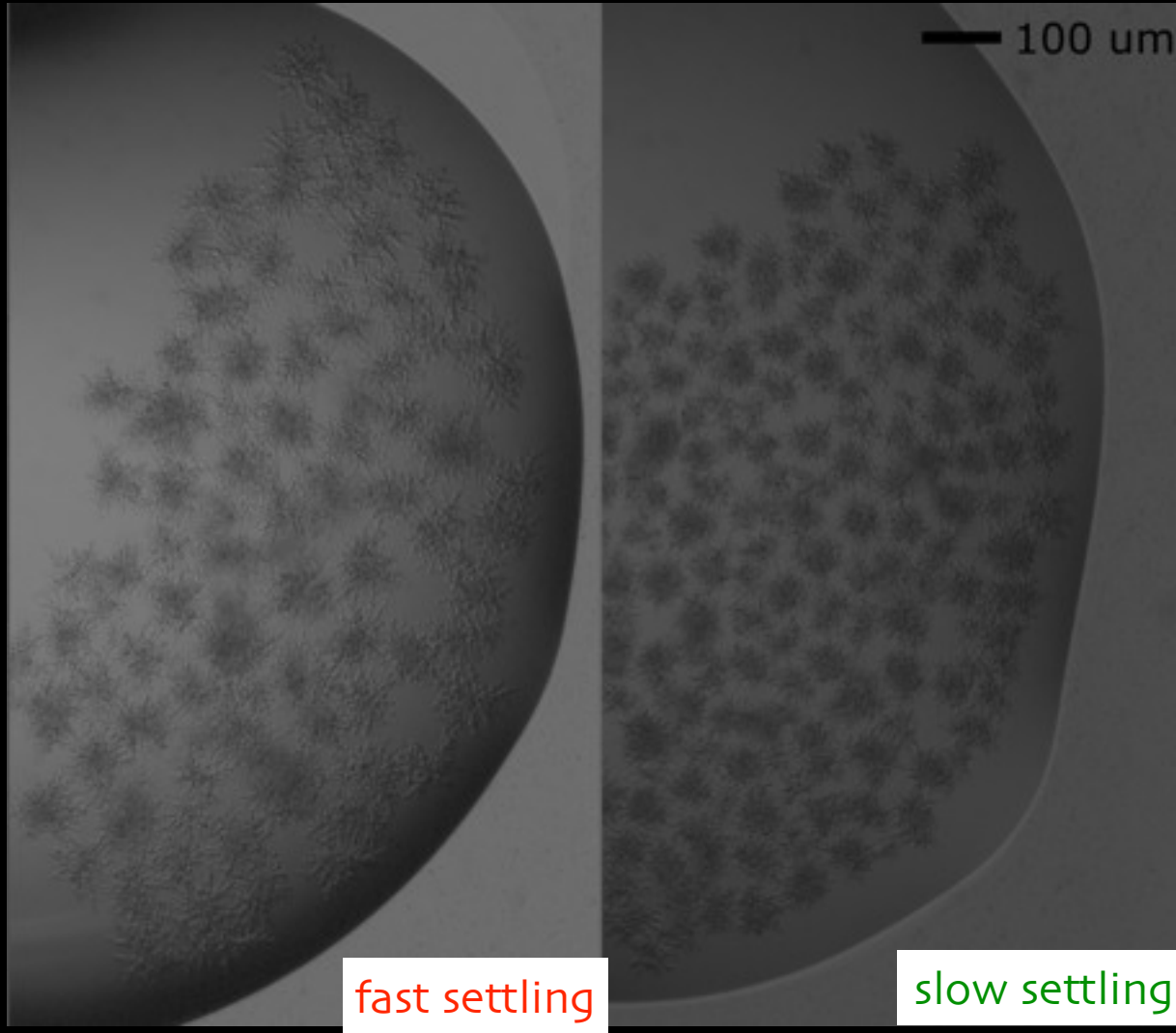


Duration of settling in evolution experiment

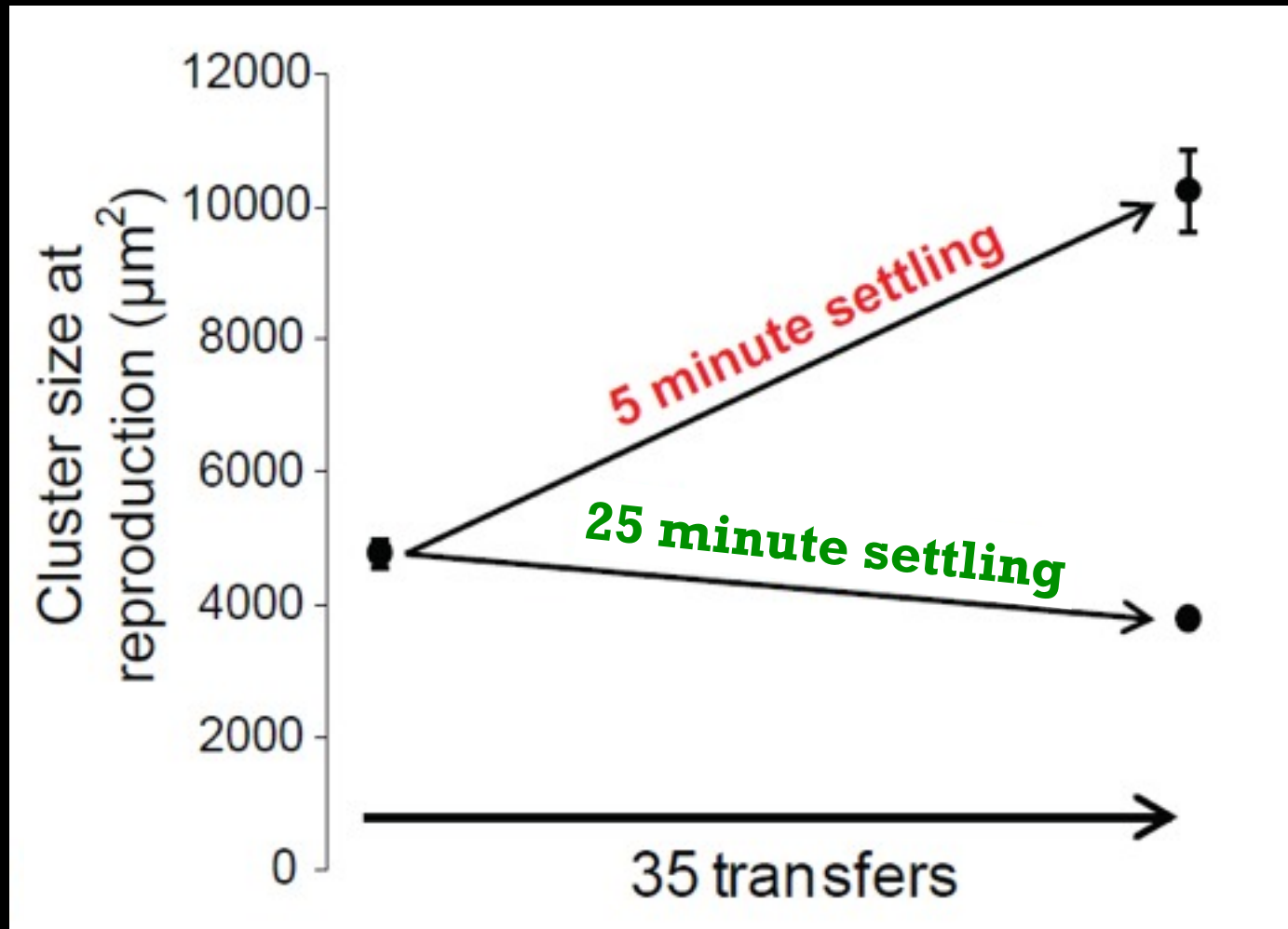
5 minutes

25 minutes

# 7 generations of growth from a single cluster



# The multicellular life-history responded to selection



# characteristics of multicellularity

- physical adhesion between cells
- multicellular life-history
  - propagule production
  - juvenile and adult stages
- this life history responds to selection



# characteristics of multicellularity

- physical adhesion between cells
- multicellular life-history
  - propagule production
  - juvenile and adult stages
- this life history responds to selection
- division of labor among cells



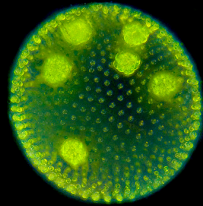
# Evolution of programmed cell death in snowflake yeast



# Questions about multicellularity



1. Why were there multiple origins?



2. Why is it ongoing process?



3. How? Not directly predicted by Natural Selection.

'the metazoan brain trust'

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