Many roads lead to Rome: plasticity and convergence as illustrated by the Dictyostelid amoebae

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Workshop "*Flags, Landscapes, Signalling*"
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Broad themes

1. Microorganisms vary a lot, and often their phenotypes appear uncorrelated with the local environment. (“Everything is everywhere”).

1. Explanations can be special (for one species, one strain, one set of conditions) or general.

3. An explanation may be sufficient but not necessary.

4. Group traits can originate both via self-organisation (based on preadaptation) and natural selection (based on new genes).

VN, Ruiz-Trillo and Kirk (2018), “Protists and multiple routes to the evolution of multicellularity”

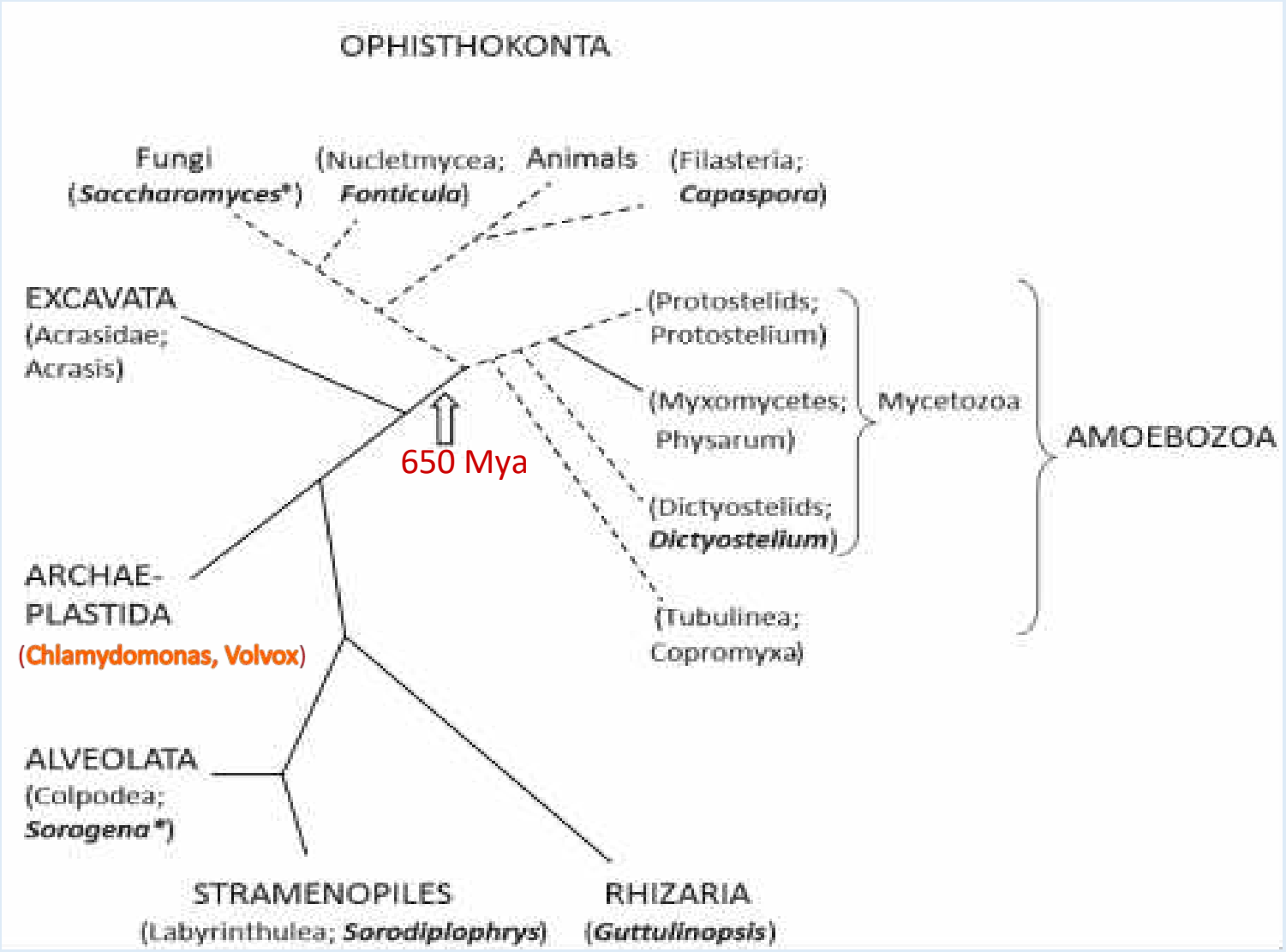
Focus of interest

Facultatively multicellular organisms

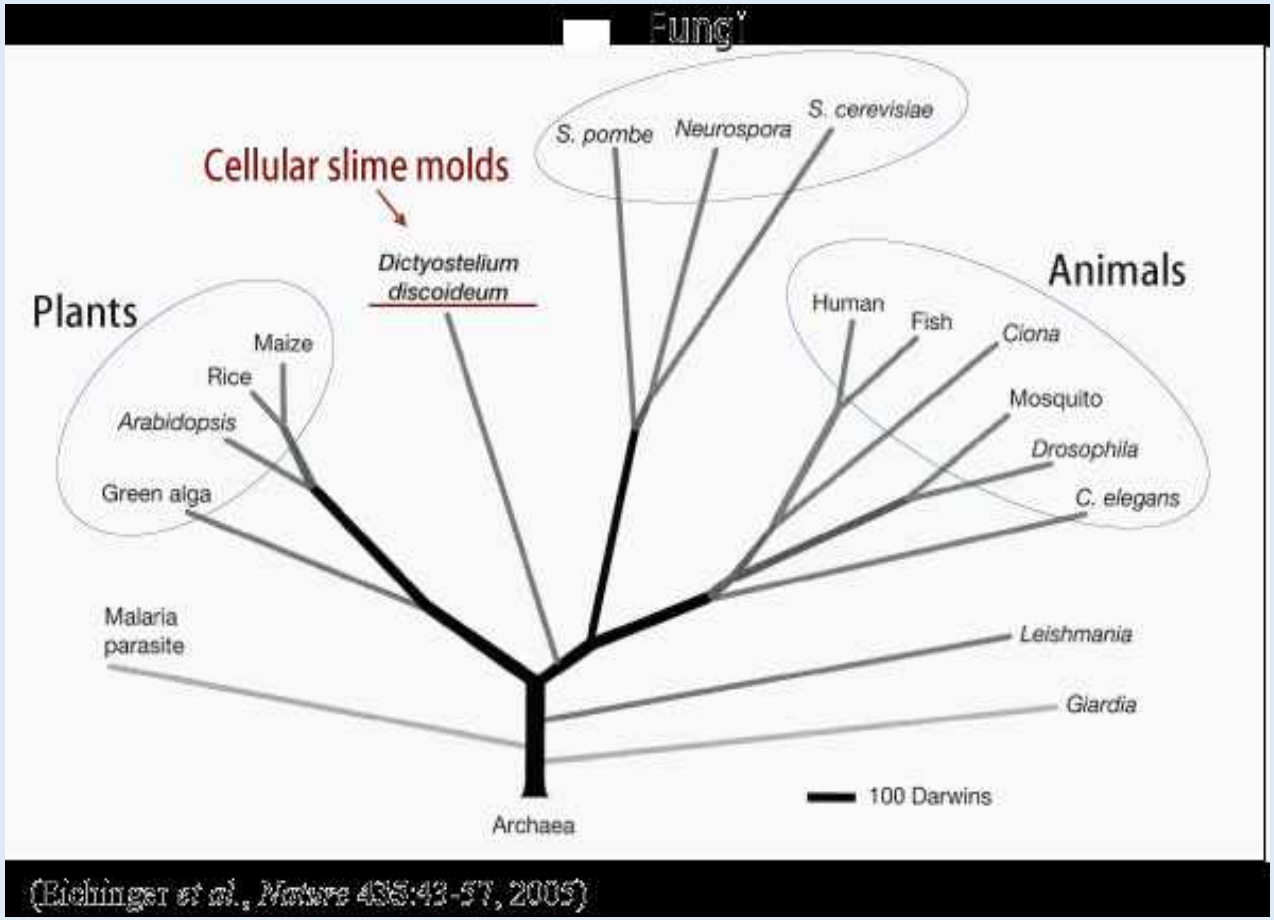
Multicellular amoebae = Social amoebae

Cellular slime moulds
(*Dictyostelium discoideum* and *Dictyostelium giganteum*)

Aggregative multicellularity :
Ubiquitous across eukaryote phylogeny



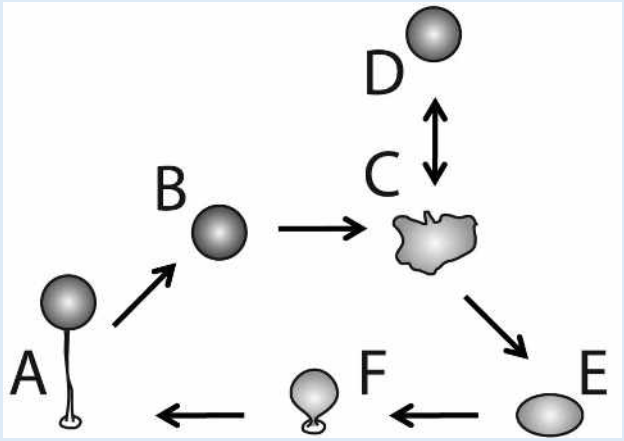
Based on Burki , F. (2014). The eukaryotic tree of life from a global phylogenomic perspective. *Cold Spring Harbor Perspectives in Biology* , 6 , a016147



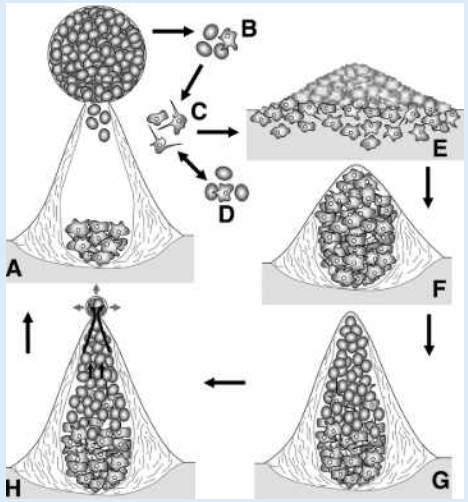
(Eichinger *et al.*, *Nature* 435:43-57, 2005)

Similarities

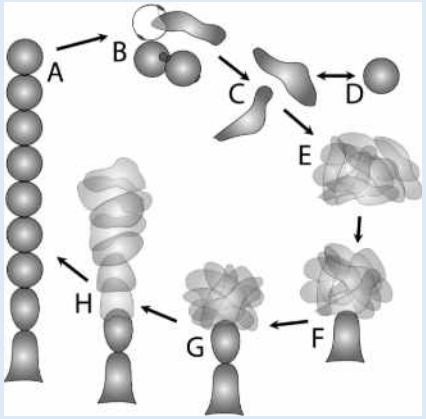
Very similar aggregative life cycles
(starvation-driven)



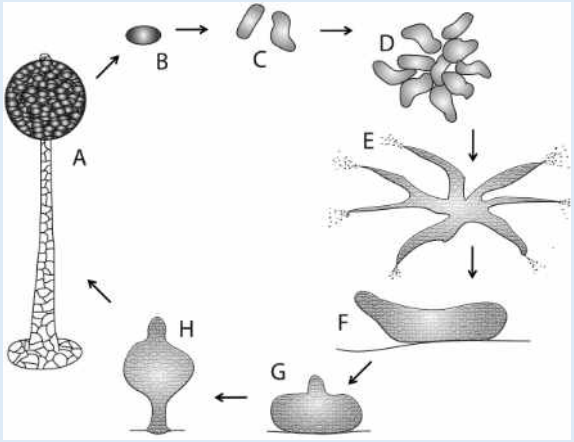
Protostelium (Amoebozoa)



Fonticula (Opisthokonta)



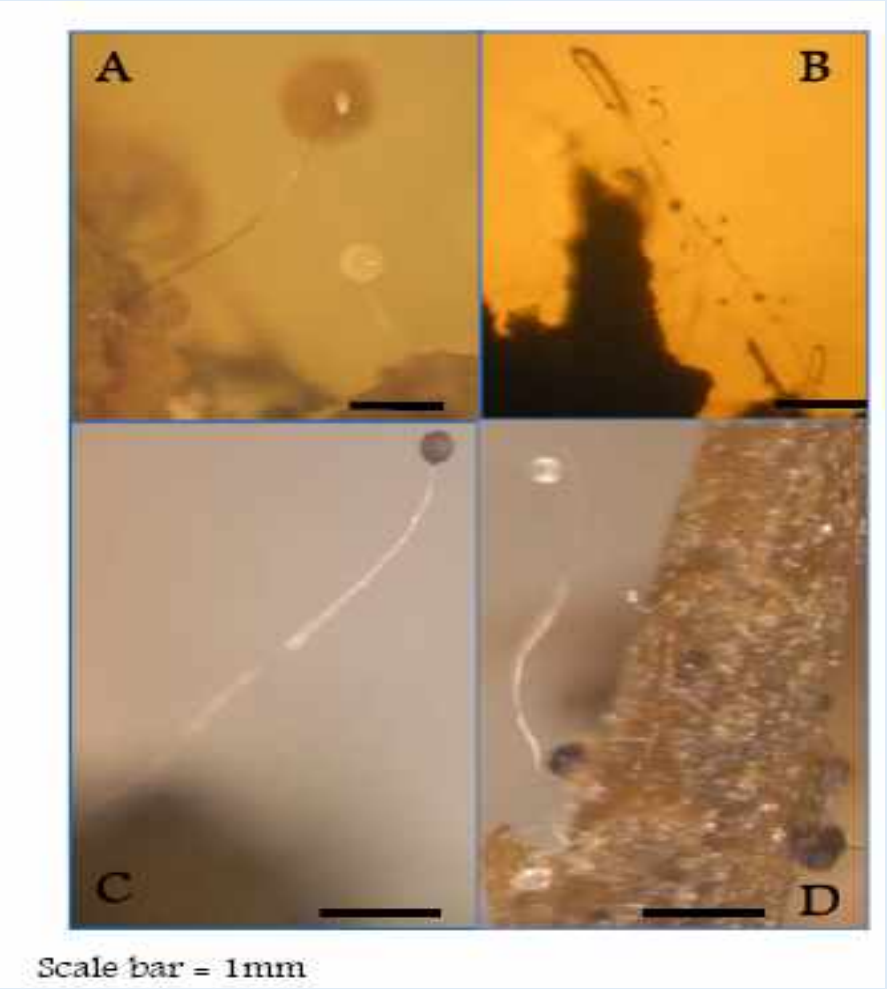
Acrasis (Excavata)

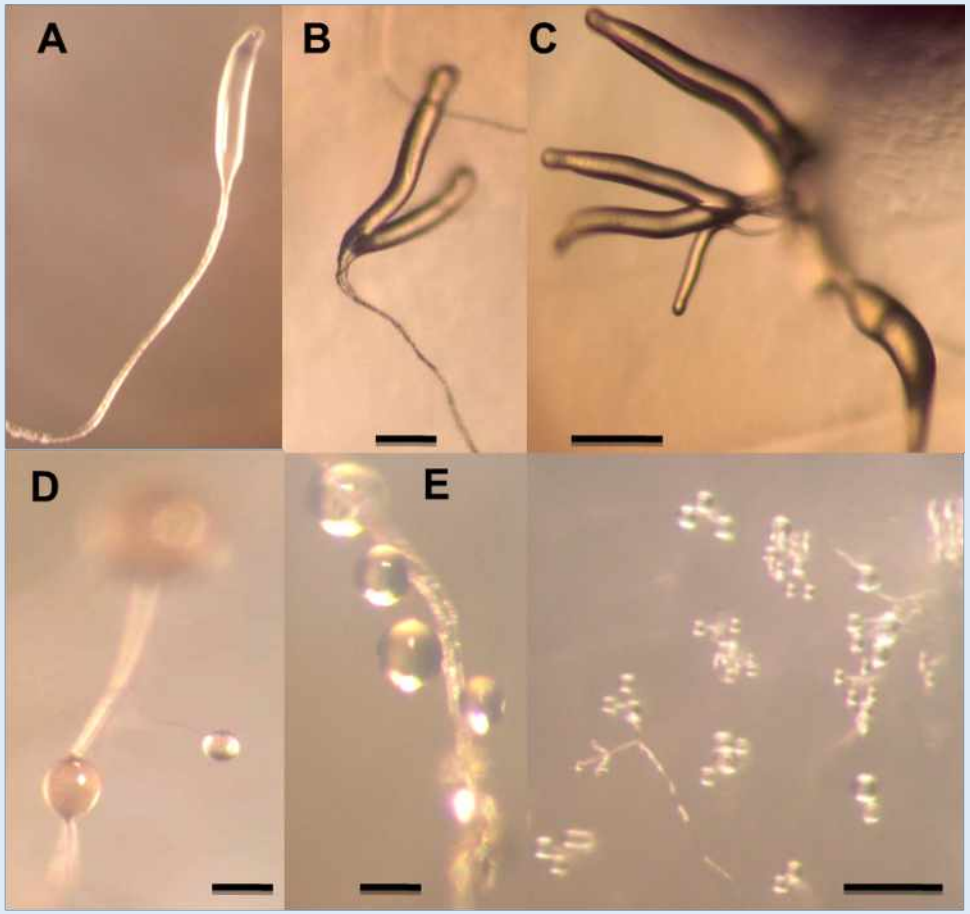


Dictyostelium (Amoebozoa)

Brown, 2010, PhD thesis, University of Arkansas

Cellular slime moulds in the wild

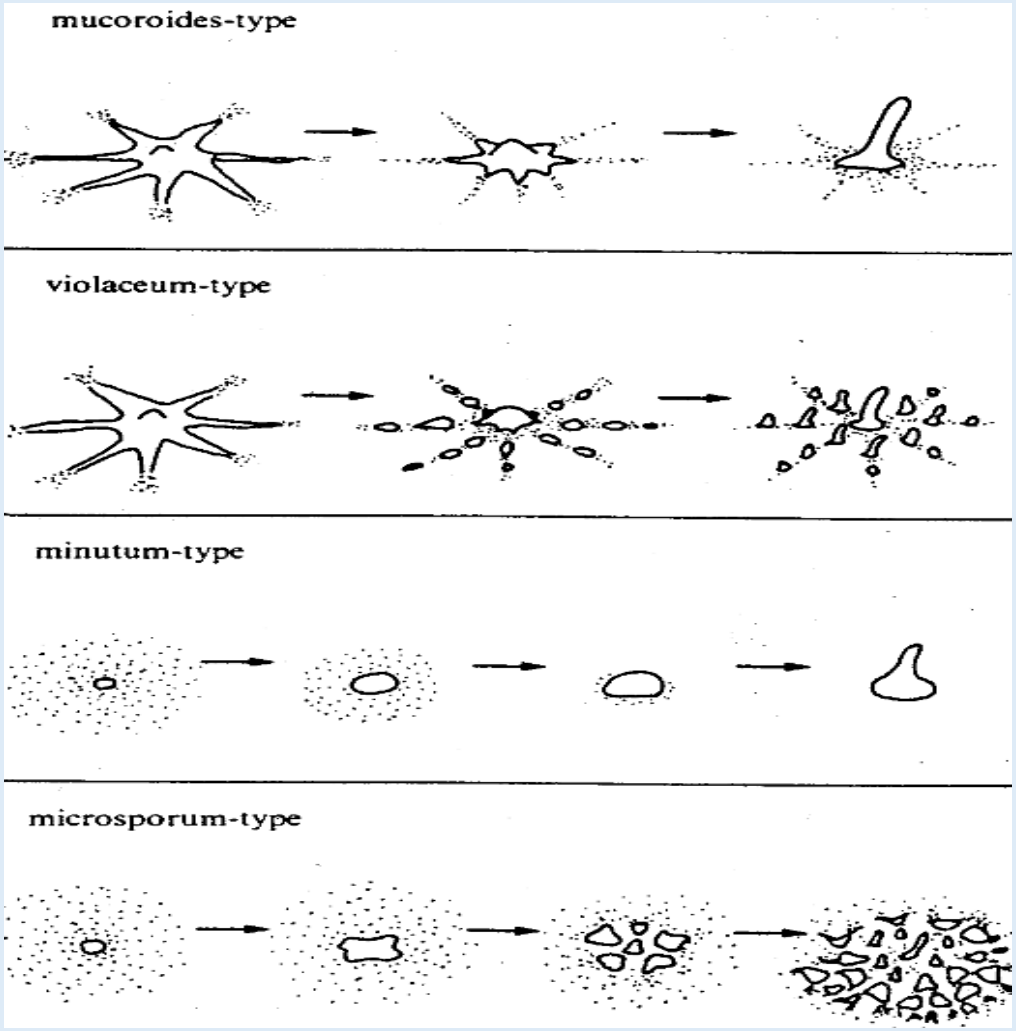




Sathe et al. 2010

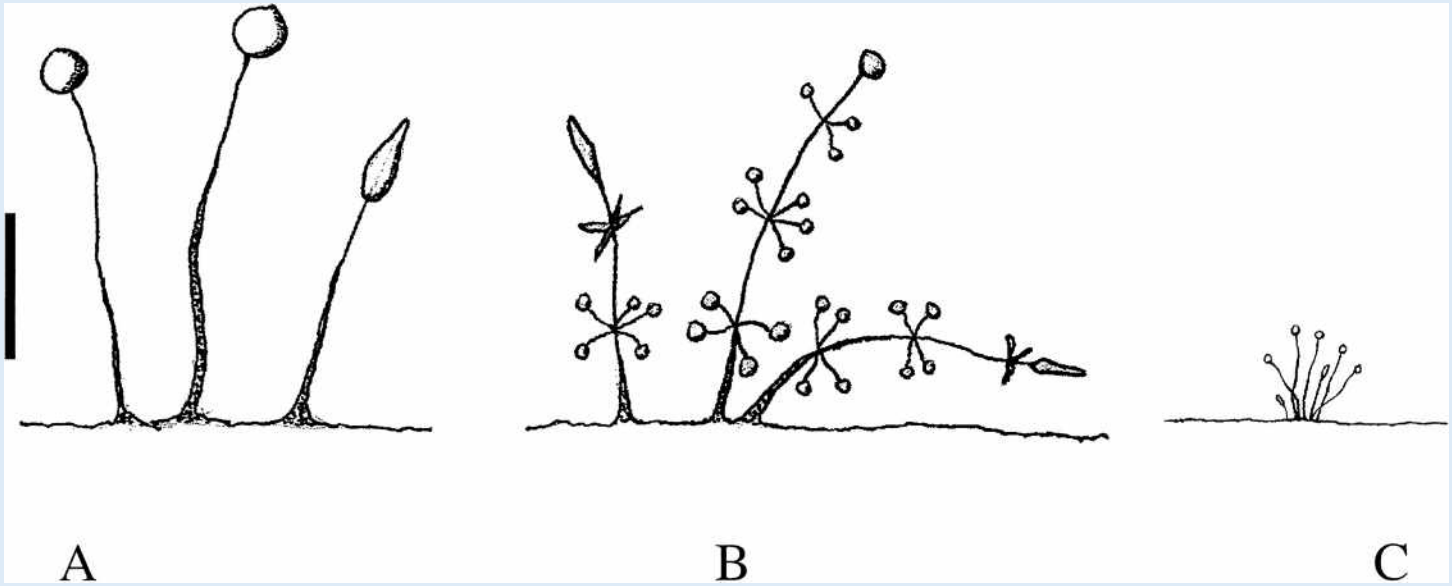
Differences

CSM aggregation: diversity



(Hagiwara, 1989 and earlier)

Facultative morphologies



Dictyostelium*
(cellular stalk)

Polysphondylium
(cellular stalk + branching)

Acytostelium*
(acellular stalk)

Swanson; http://faculty.scf.edu/swansoa/aboutme.htm

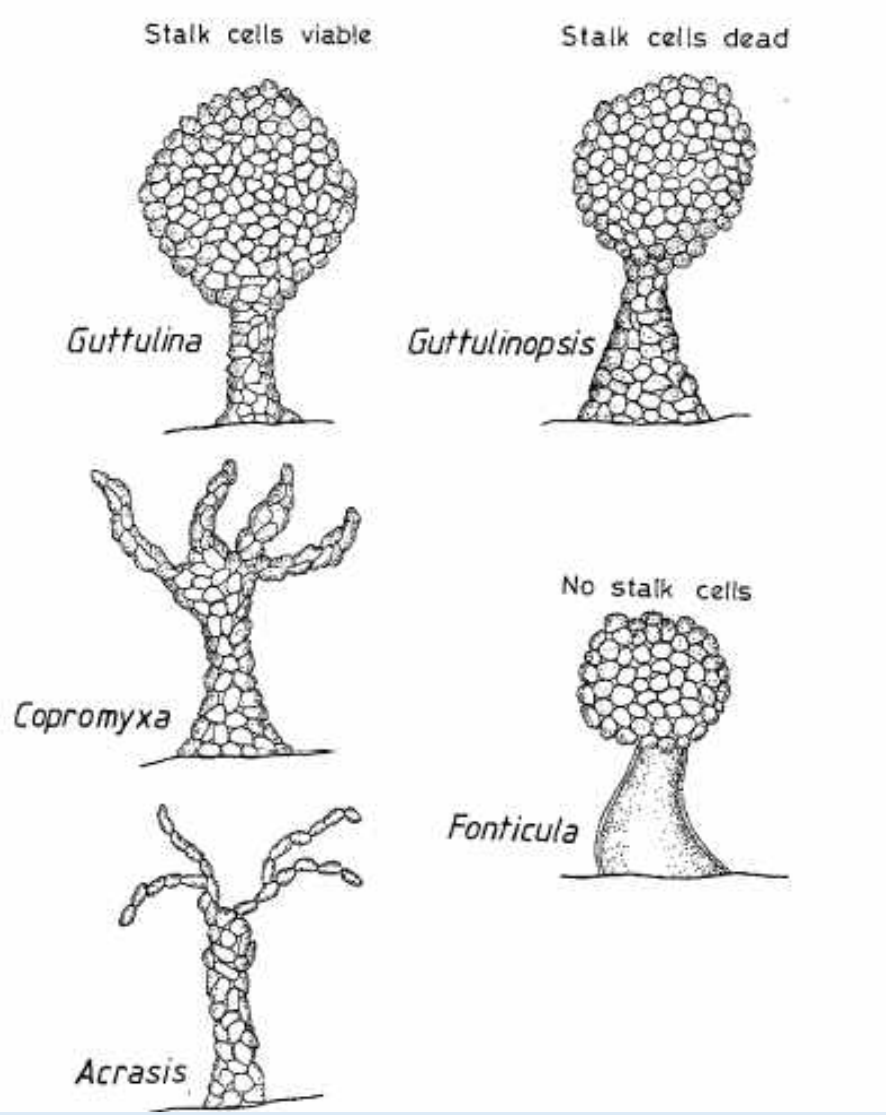
(Polyphyletic distribution; * *D. lacteum*: like A when many cells, like C when few cells)

Sorocarpic amoebae: diversity in fruiting bodies

Excavata

Amoebozoa

Excavata

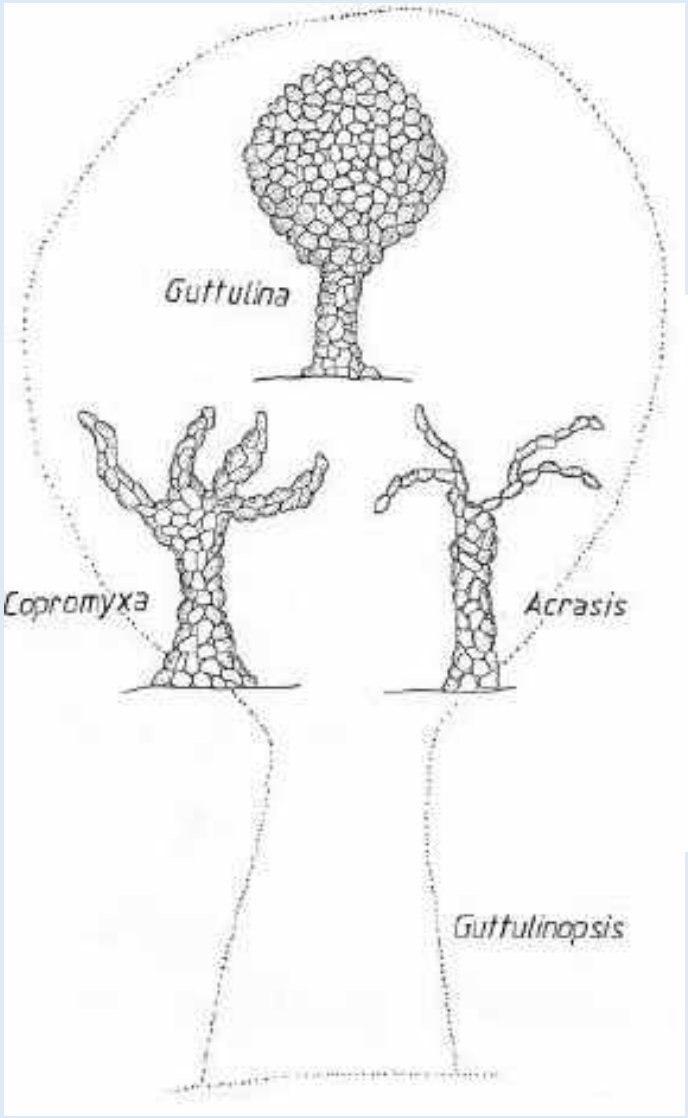


Rhizaria

Ophisthokonta

(Bonner, 1967)

Size and complexity



	Average number of spores
One cell type	
Guttulina	~ 200
Acrasis	~ 200
Copromyxa	~ 2000
Two cell types	
Guttulinopsis	~ 24,000

Bonner J Biosci 2003

Slime mould aggregation – 1

Continuum model

Local conc. of cells

$$\frac{\partial a}{\partial t} = \nabla \cdot (D_a \nabla a - D_c \nabla \rho),$$

Local conc. of attractant

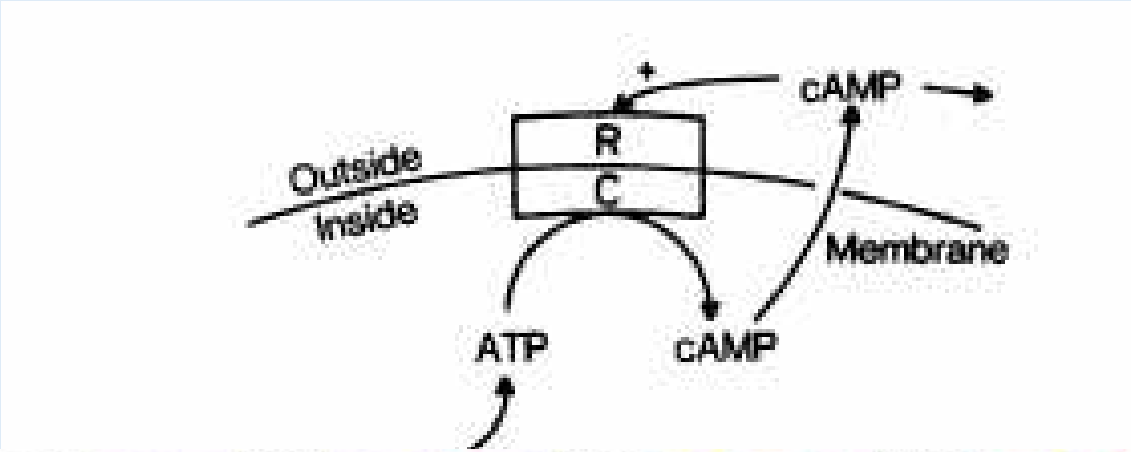
$$\frac{\partial \rho}{\partial t} = \nabla \cdot (D_\rho \nabla \rho) + f(\rho, a) - k(\rho, a)$$

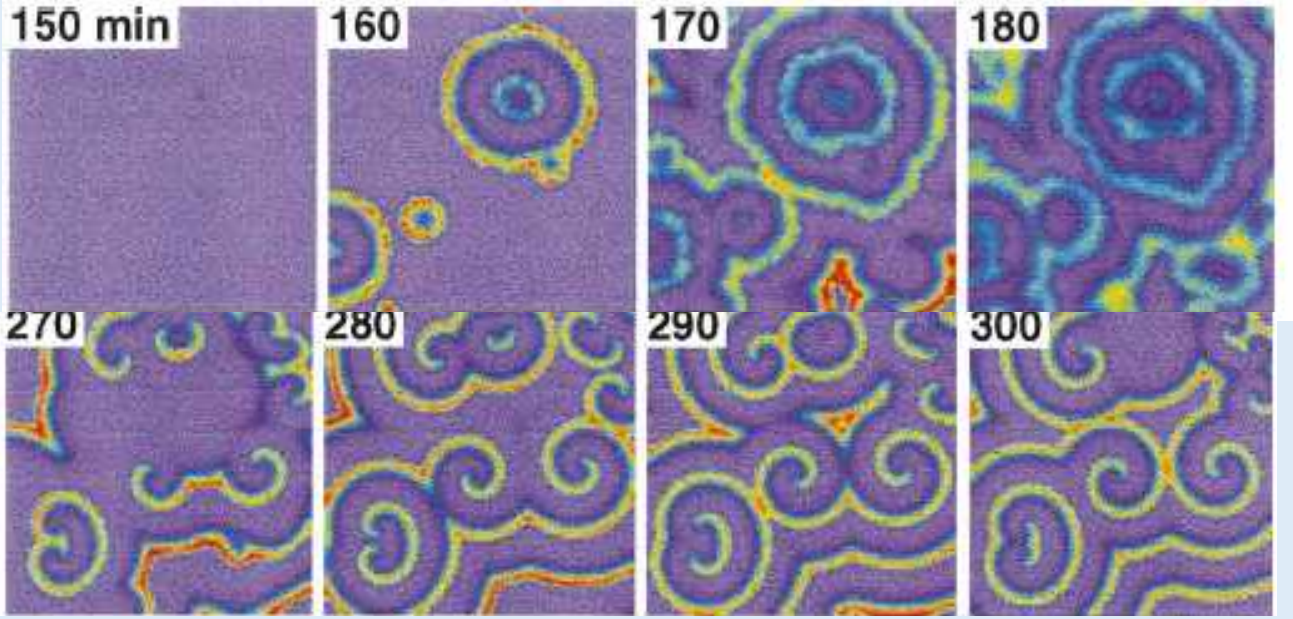
Keller and Segel (1970). J. theor. Biol. 26: 399-405

Nanjundiah (1973) J theor biol 42: 63-105

Slime mould aggregation - 2

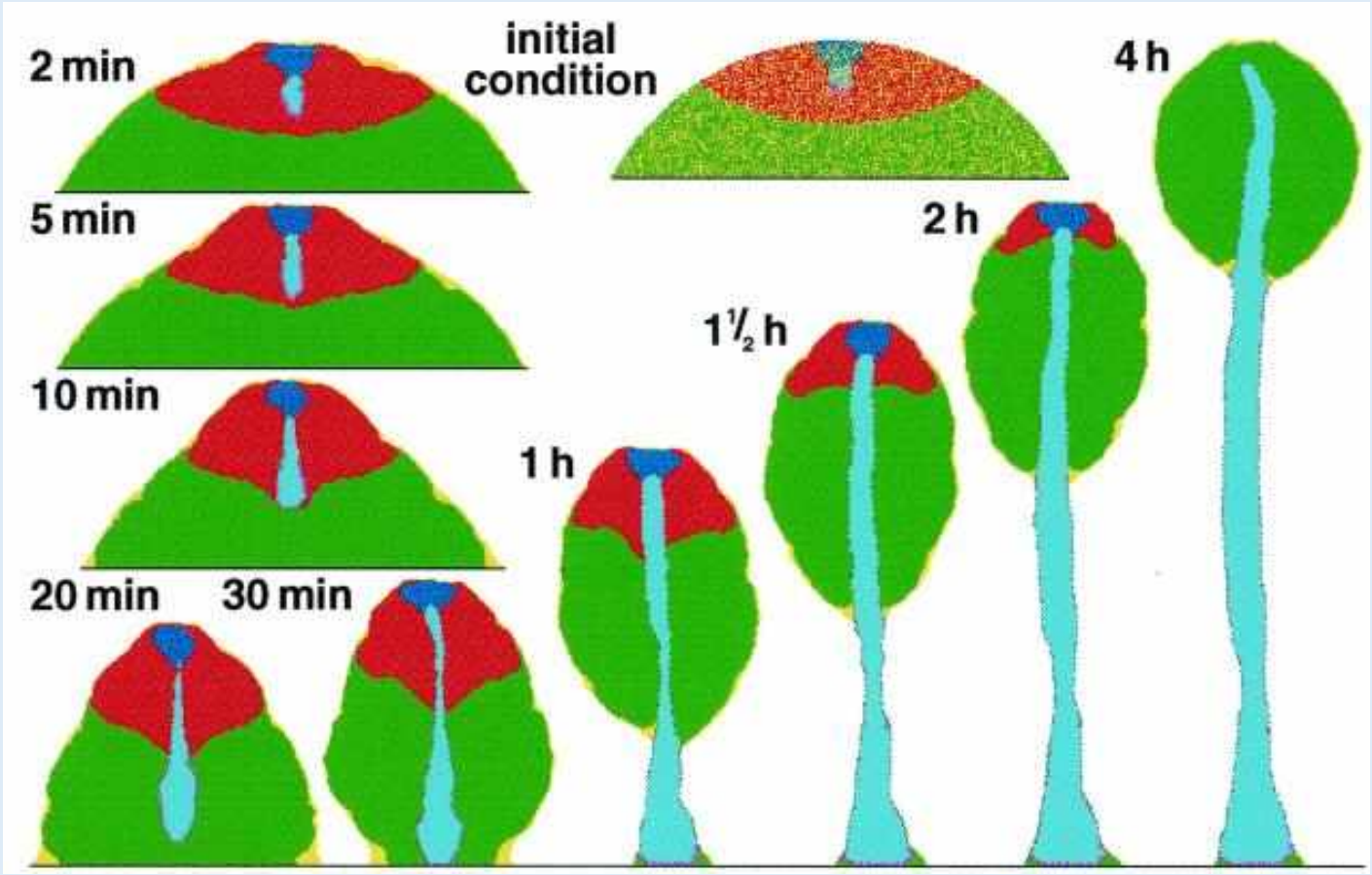
Discrete model





Halloy et al. Biophysical Chemistry 72 (1998) 9–19

Model for fruiting by self-organisation



Uses heterogeneity; Marée and Hogeweg, PNAS (2001) 98(7): 3879-3883;
See life cycle movie in https://www.youtube.com/watch?v=GyAQepksJLU

Dictyostelium discoideum: extracellular soluble PDE

STRAIN	ORIGIN	DEVELOPMENTAL PHENOTYPE	EXTRACELLULAR PHOSPHODIESTERASE ACTIVITY
NC4	Decomposing forest leaf (Raper 1984)	Wild-type	Plates: peaks during aggregation; Suspension: peaks before starvation, much lower at aggregation phase
V-12, sub-clones M1, M2	Forest leaf litter (Raper 1984)	Wild-type	Plates: negligible during aggregation; Suspension: peaks before starvation, much lower at aggregation phase
Ax2	Spontaneous axenic mutant, isolated from NC4 in two steps	Normal (superficially, wild-type)	Suspension: peaks before starvation, much lower at aggregation phase
ga86, ga88	Independently derived UV-induced mutants of V-12	Normal, but very large aggregation territories	Suspension: enzyme activity barely detectable at all times

VN (2019) Exp Zool (Mol Dev Evol) 1–10.

Polyclonal social groups in nature

17 independent isolates of *D.giganteum and D. purpureum* from animal dung and undisturbed forest soil

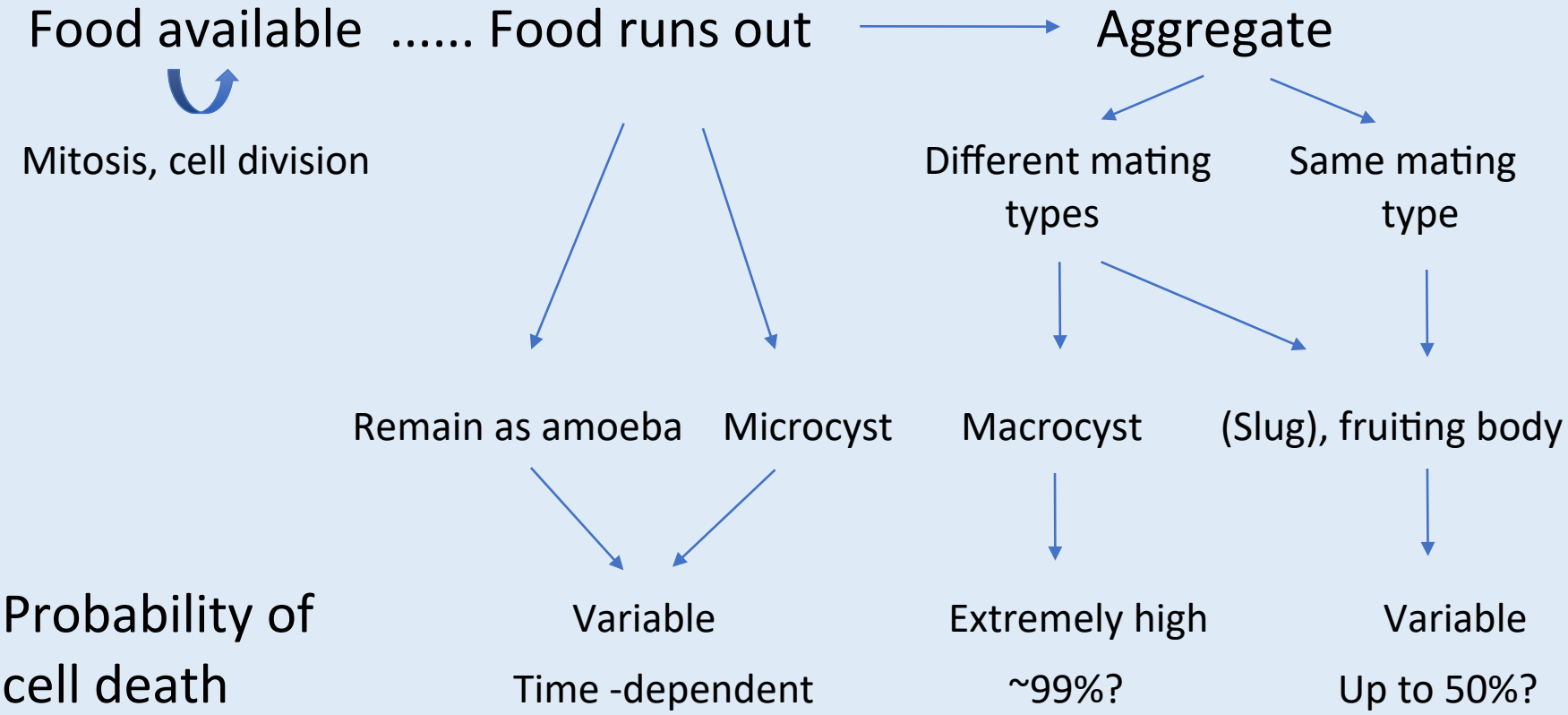
'Wild-type' phenotypes

15 multiclonal, 2 clonal

Number of clones found in multiclonal group **3-9**

The developmental basis of social traits

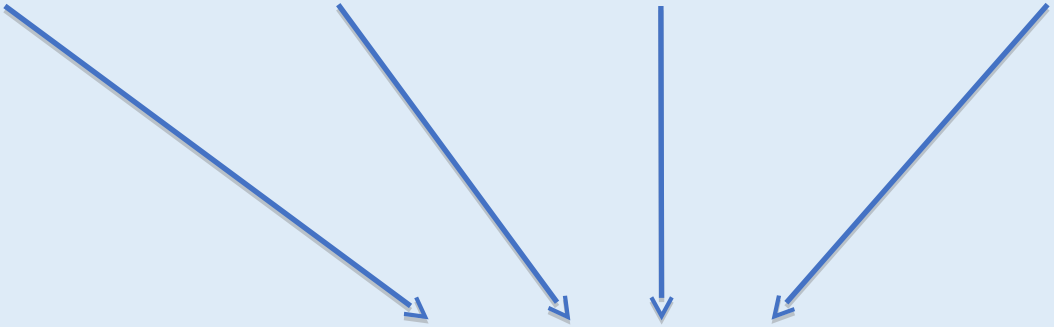
Developmental decisions and consequences



Decisions facultative, 'tactical' rather than 'strategic'

Pre-aggregation functional differences

Genotype Nutrition Calcium Cell cycle phase

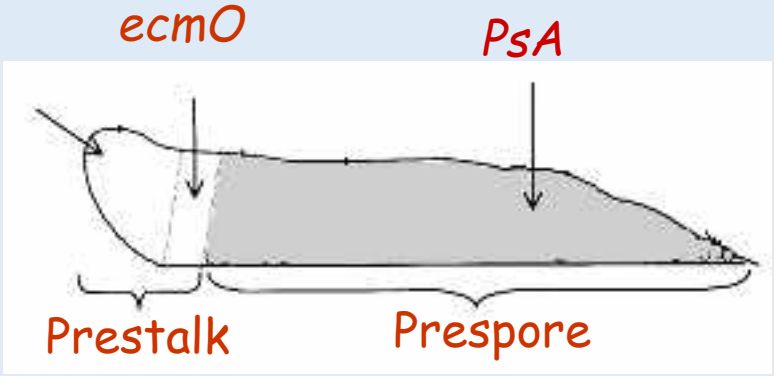


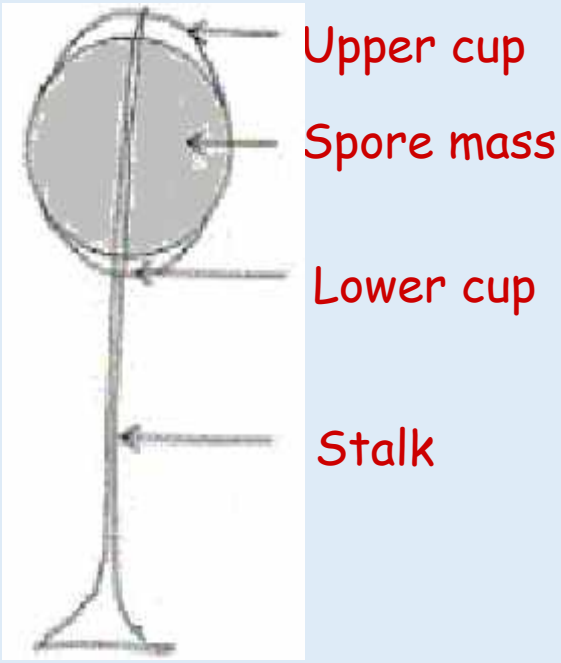
Phenotypic heterogeneity

before multicellular phase

***Relative* bias: there is no such thing as a "cheater" per se**

Spatial patterns of gene expression correlate with cell types

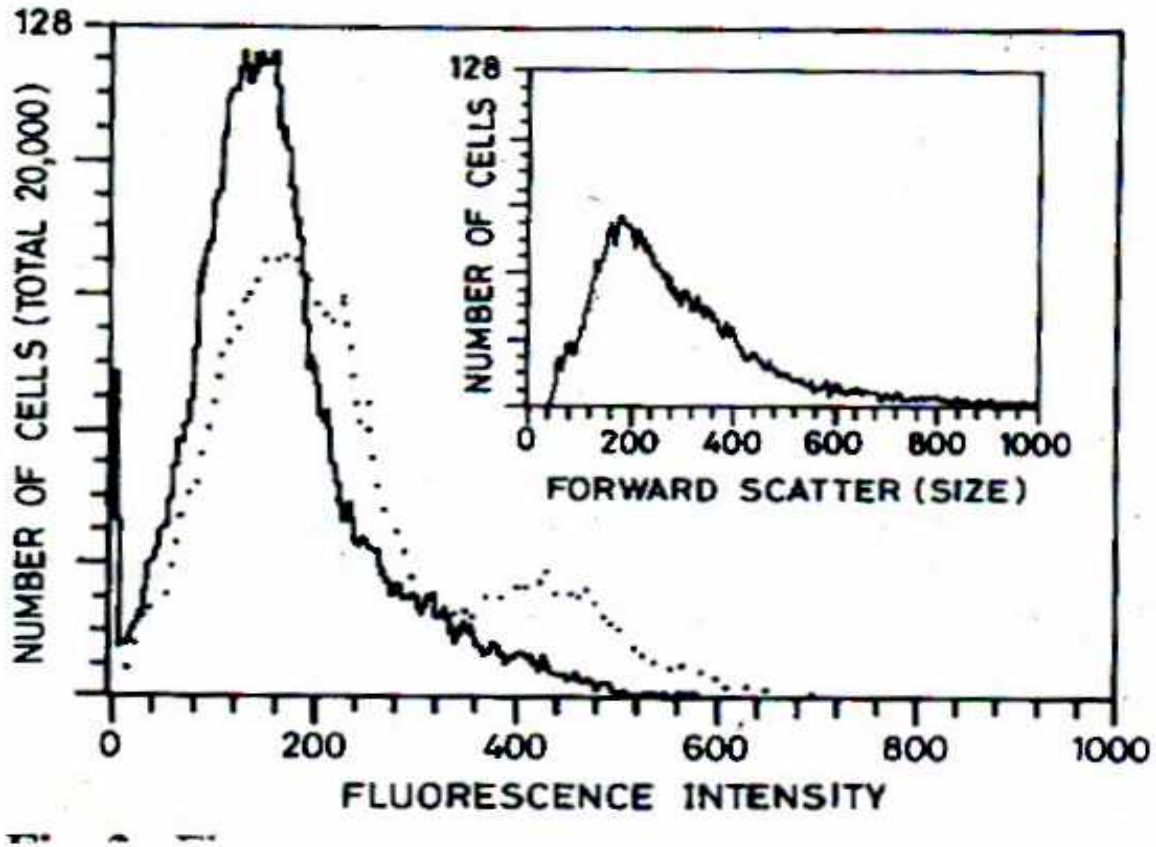




Amoeba → Spore ("germ line")

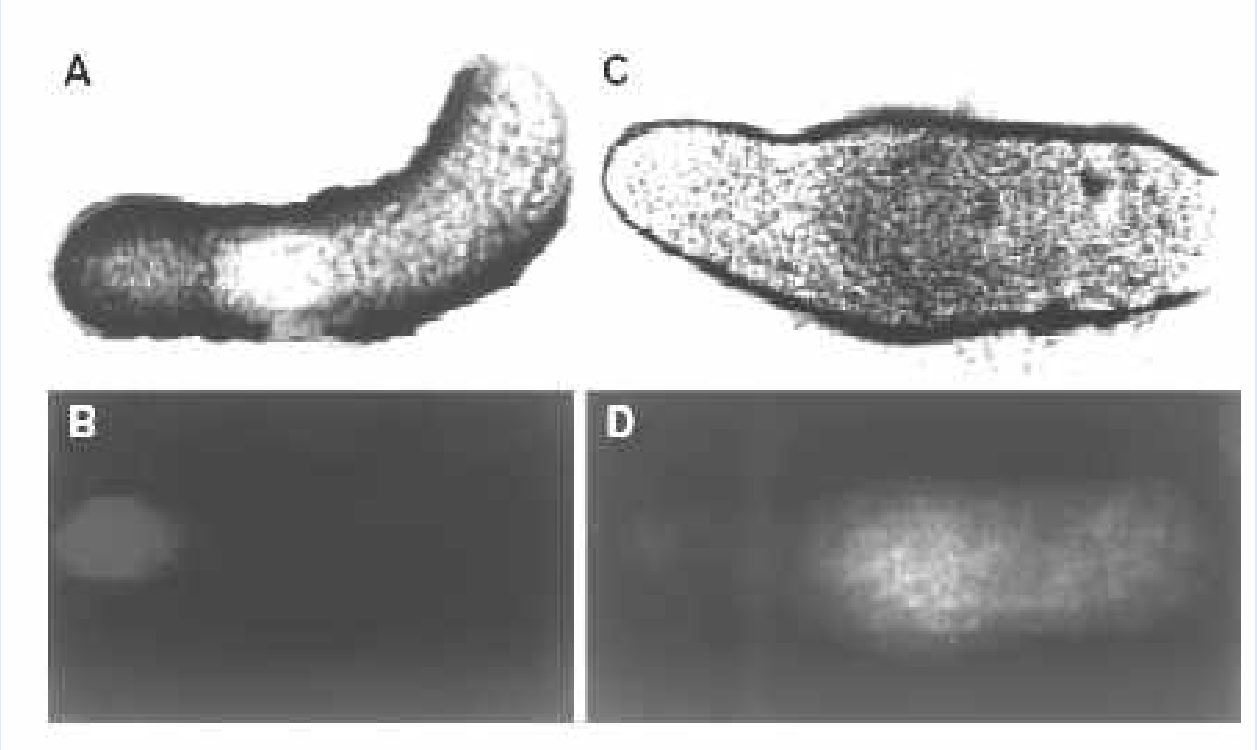
Amoeba → Stalk ("soma")

Spontaneous arising heterogeneity (Ca^{++})



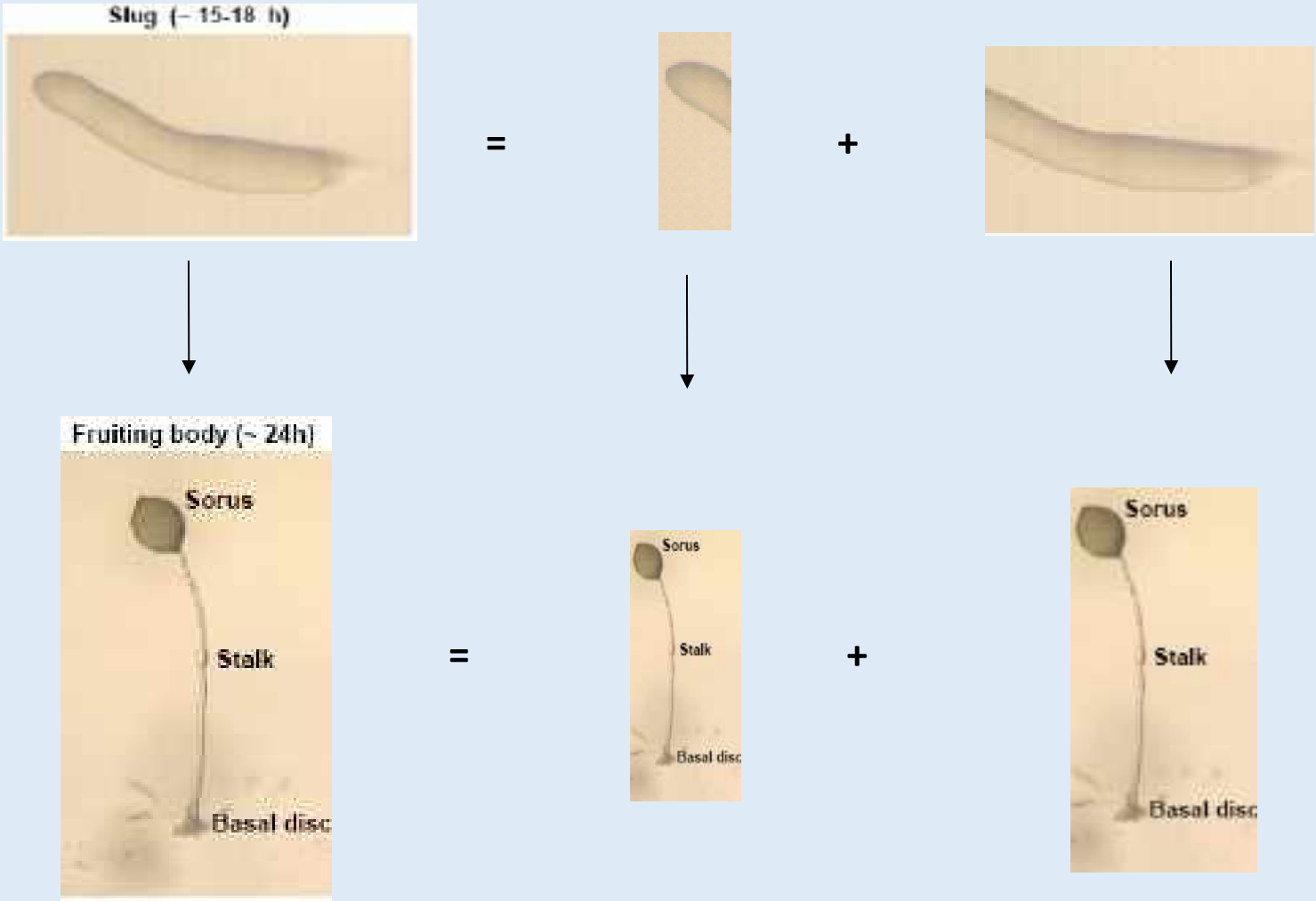
D. discoideum; Saran et al. (1994)

‘High’ and ‘Low’ calcium lead to different fates



Azhar et al. (2001) Int. J. Dev. Biol. 45: 405-414

Post-aggregation interactions (*Dictyostelium discoideum*)

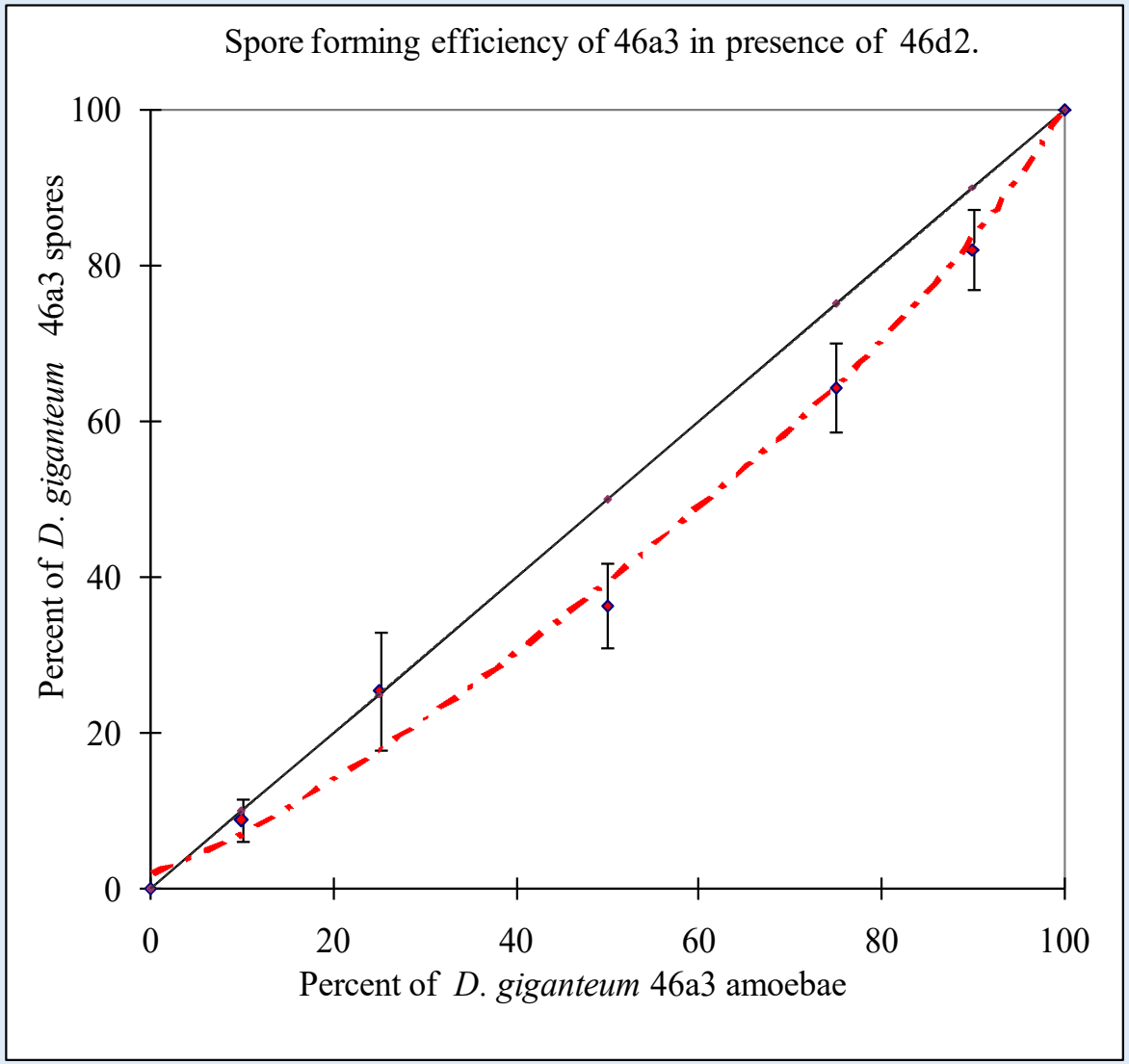


Raper, J. Elisha Mitchell Soc. 1940

The importance of interactions

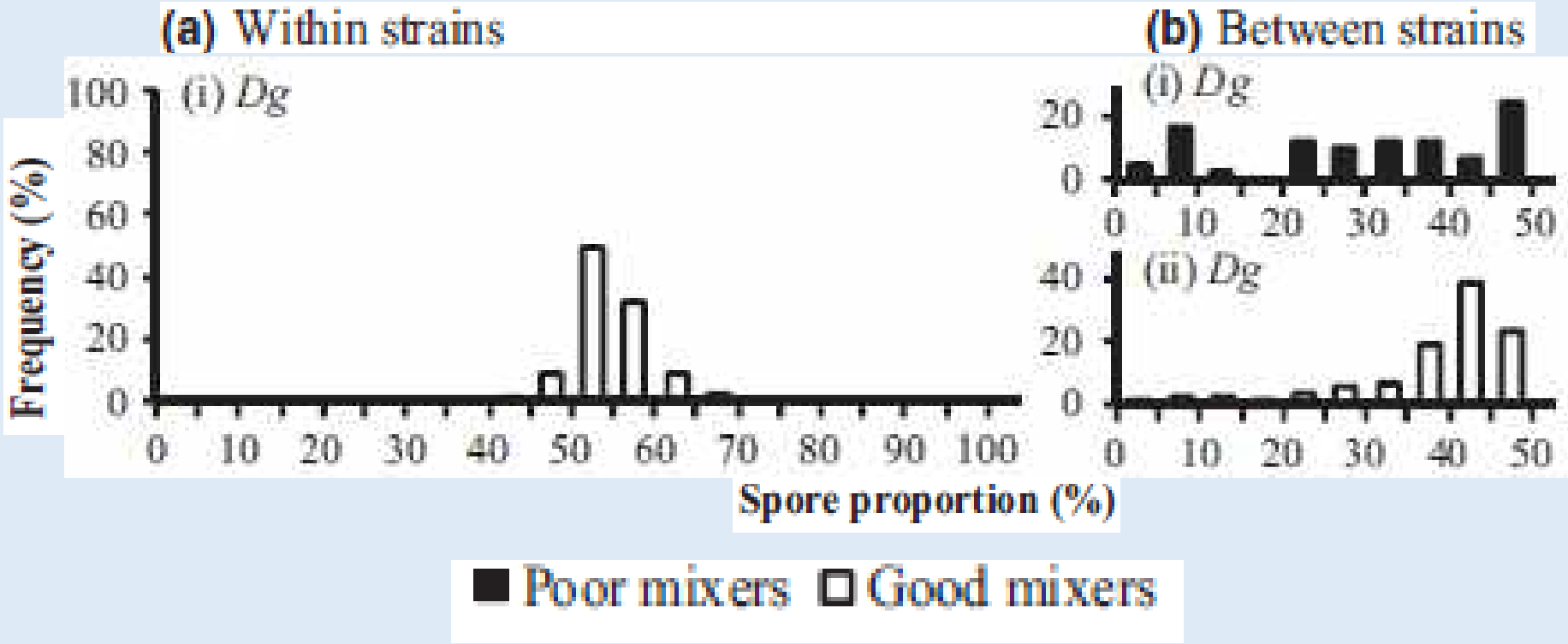
Functional difference between co-occuring strains

(*D. giganteum*)



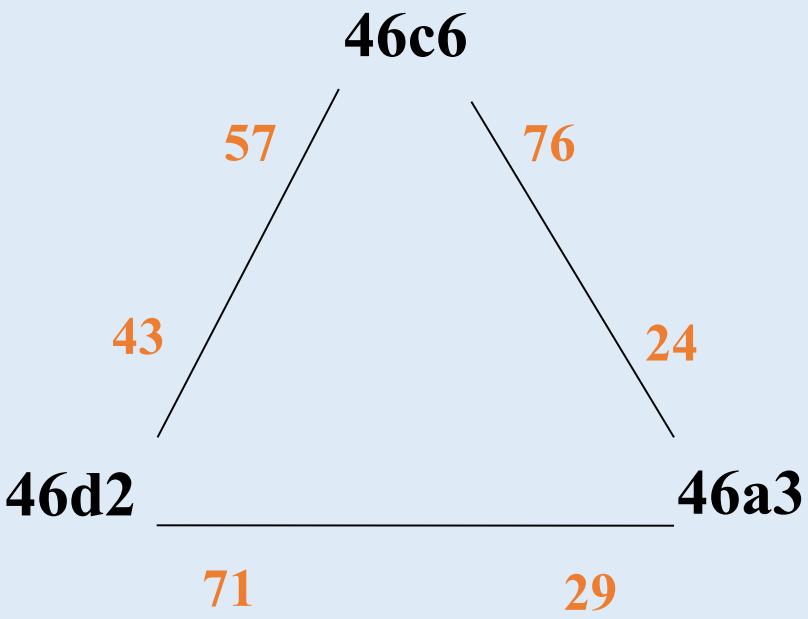
Sathe and VN, 2009

Self/Non-self discrimination: “Guilds” in nature



Sathe et al. J Evol Biol. 2013

More strains ➔ Lower reproductive skew



46c6 : 46d2 : 46a3 = 35.5 : 33.4 : 31.1

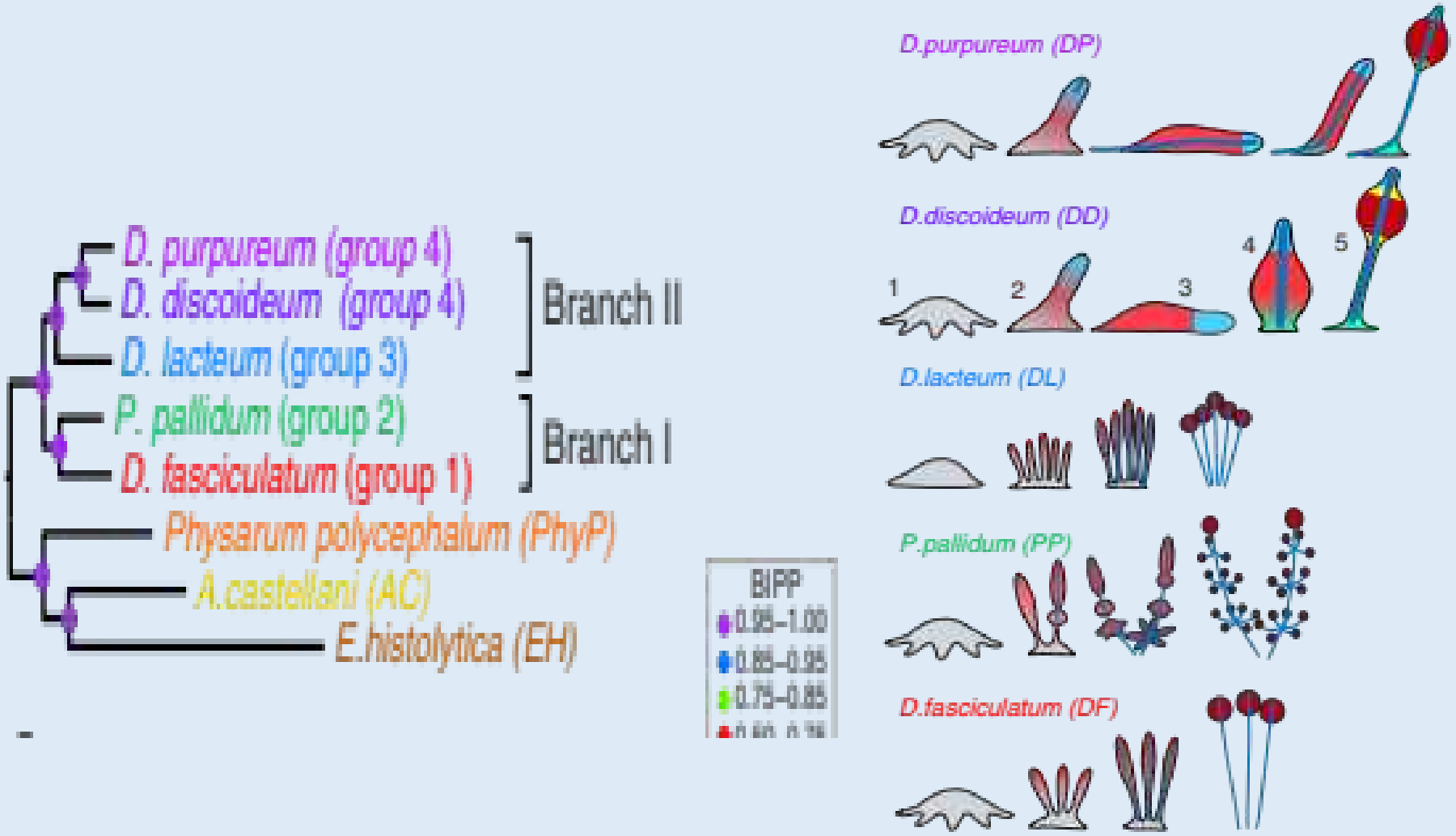
Cooperative interactions and development in nature

Filosa (1956):
Four different clones from naturally occurring fruiting body of *Dictyostelium mucoroides;* 1 normal and 3 unable to aggregate by themselves.

Buss (1982):
Two strains of *D. mucoroides* in close proximity; one forms no stalk and develops normally only in combination with other.

Ellison and Buss (1983): Isolate of *D. mucoroides* develops normally only in association with fungus *Mucor hiemalis*.

Genotype and Phenotype



Glöckner et al. Nature Comm. 2016

Lack of specificity with regard to 'developmentally essential' or 'multicellularity' genes

385 DEGs (absence → no development; growth unaffected):
80% in unicellular relatives
72% in non-Amoebozoan species
37 not shared by all four CSMs

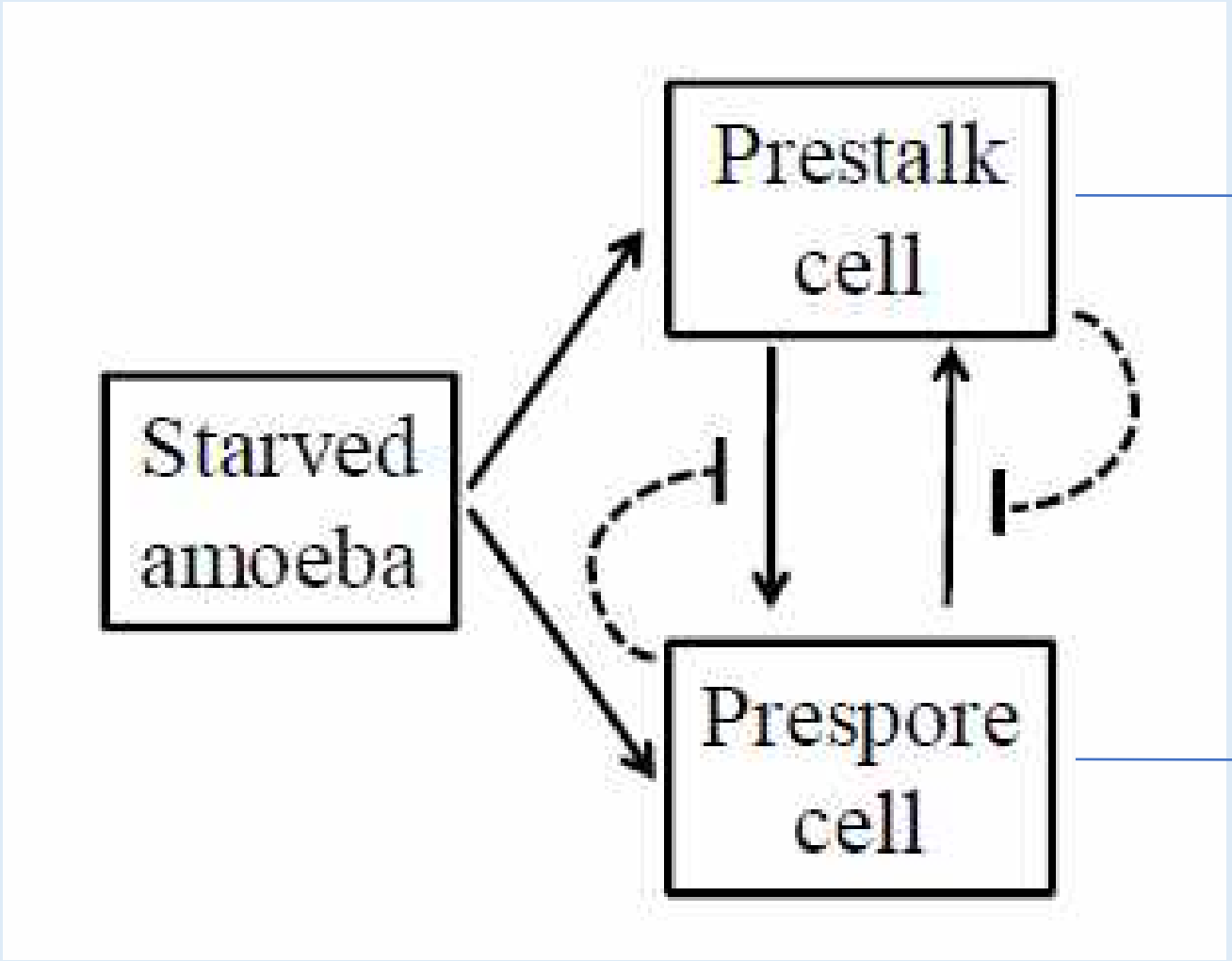
186 MGs (upregulated 3x, manipulation→ aberrant development):
33 lack orthologue in at least one of other three CSMs
20 lack orthologue in all three
50% of ~2400 3x upregulated genes in all species lack orthologue in any of remaining three

Homologues in other species of *D. discoideum*

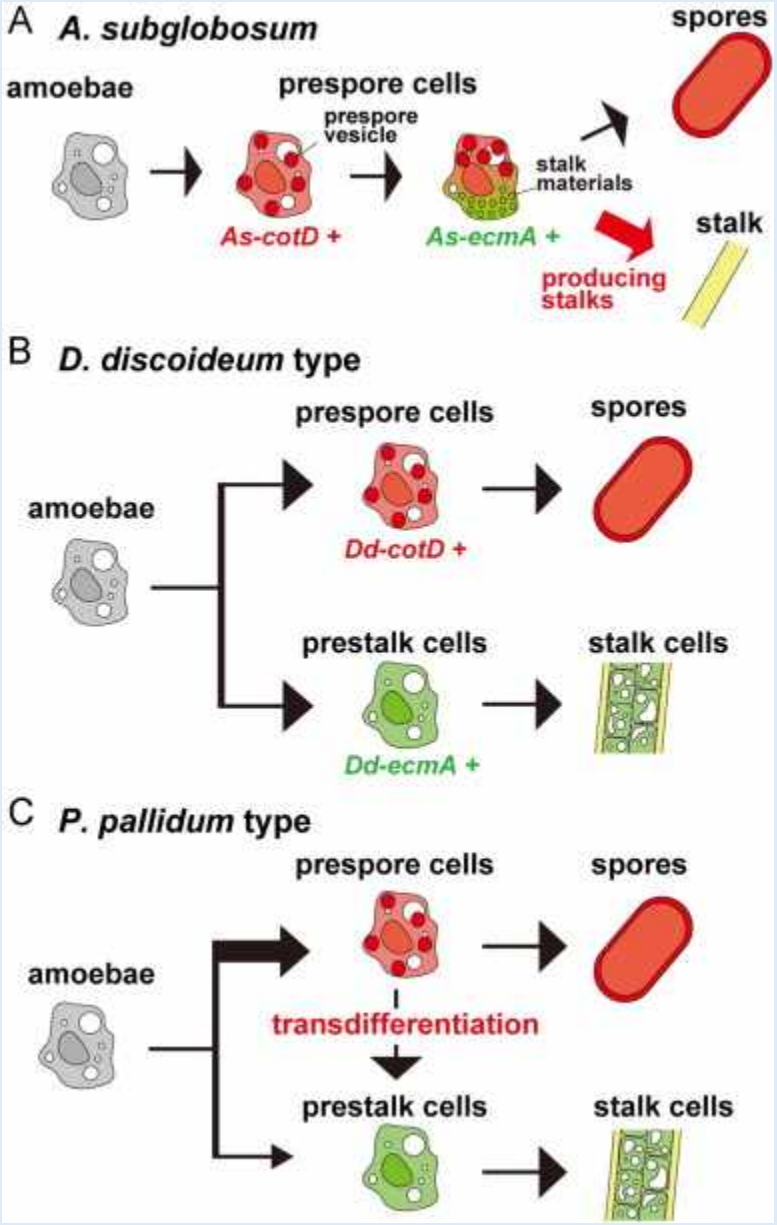
Schilde et al. 2016, Gloeckner et al. 2016

Conceptual scheme

Differentiation and proportioning: Conceptual scheme



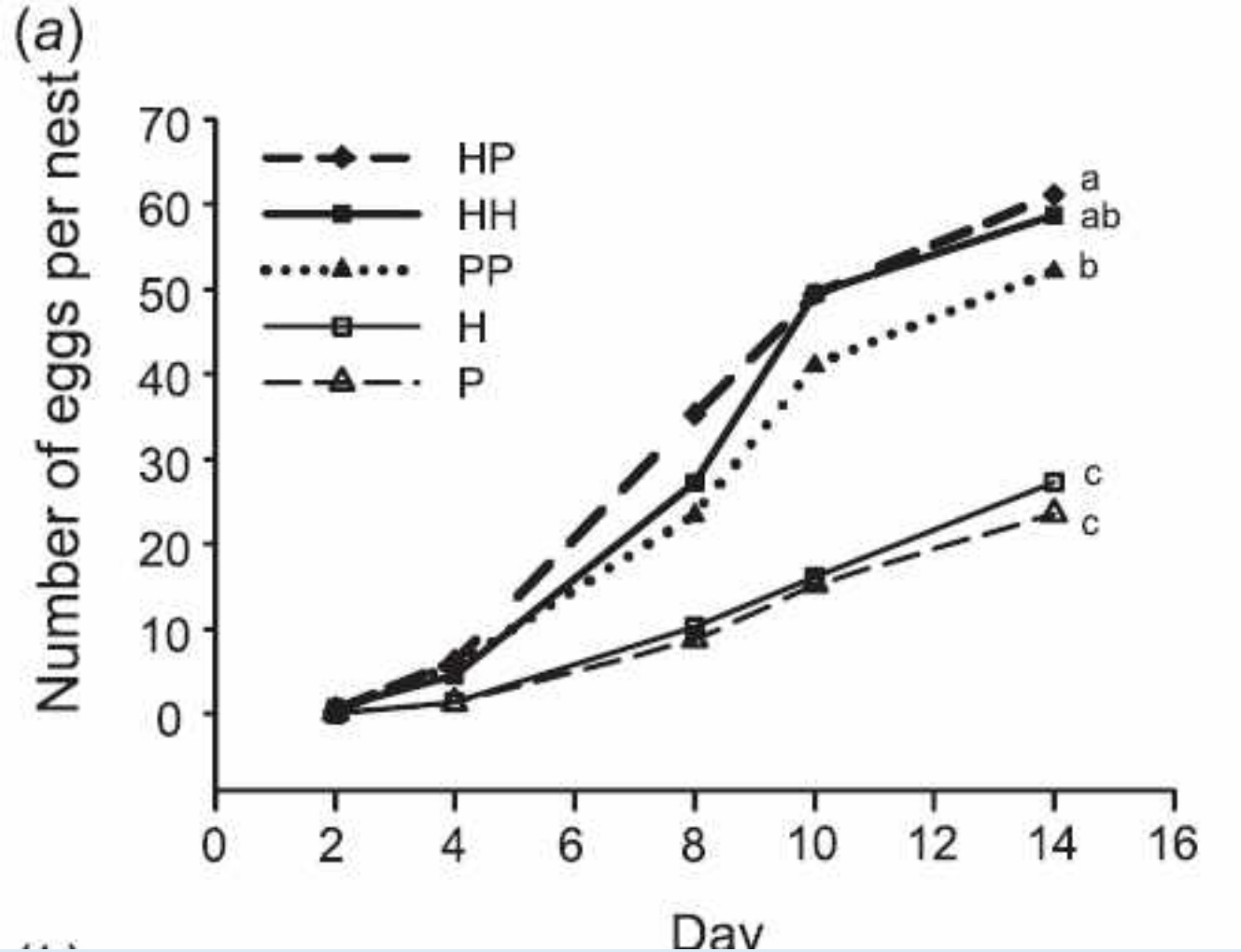
Temporal differentiation → Spatial differentiation



Mohri et al. Dev Biol (2013) 375 (2): 202-209

Productivity of solitary (H) and cooperative (Q) queens

(Harvester ant *Pogonomyrmex californicus*)

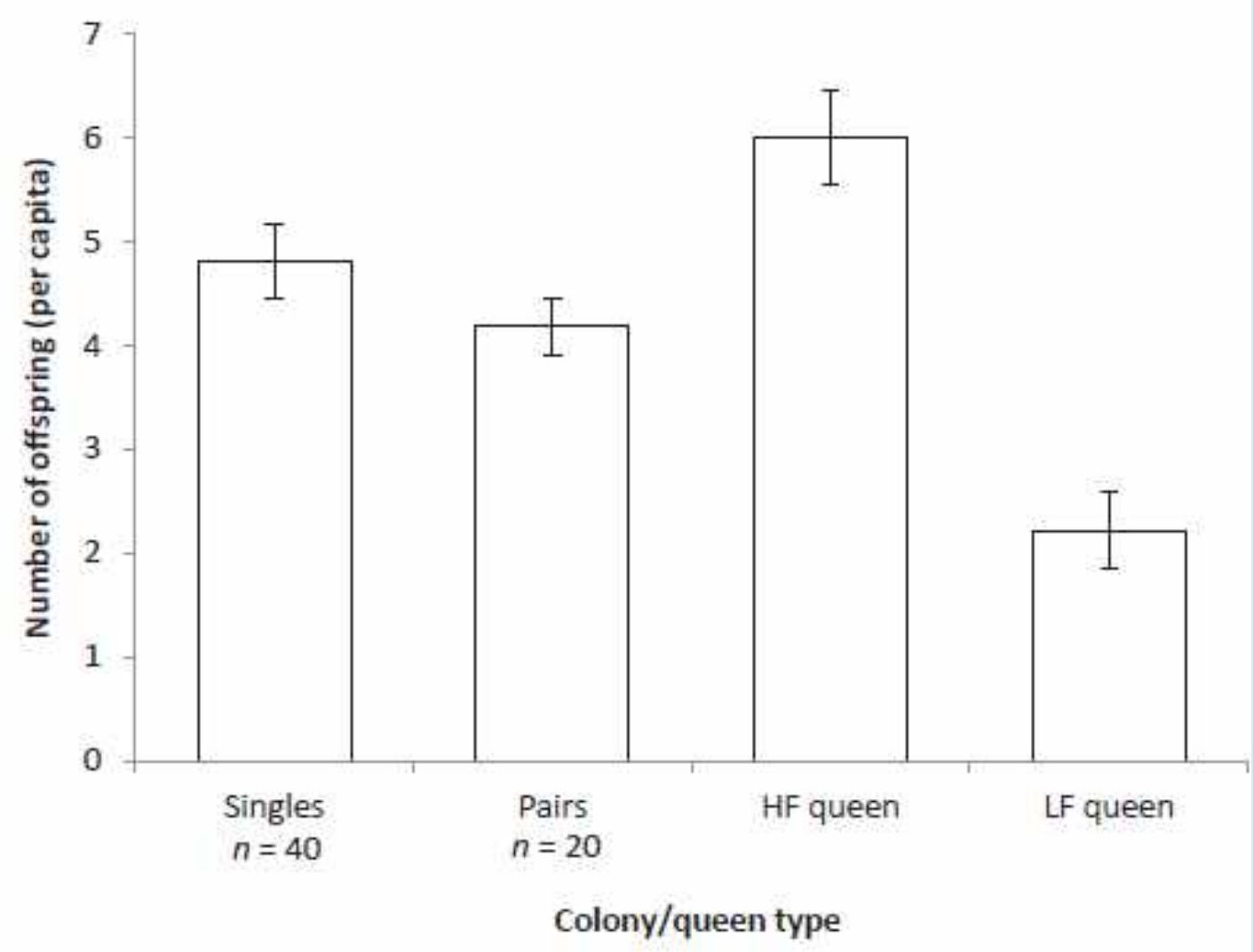


Productivity depends on social dynamics only;

Clark and Fewell, Behavioral Ecology (2014), 25(1), 117–123.

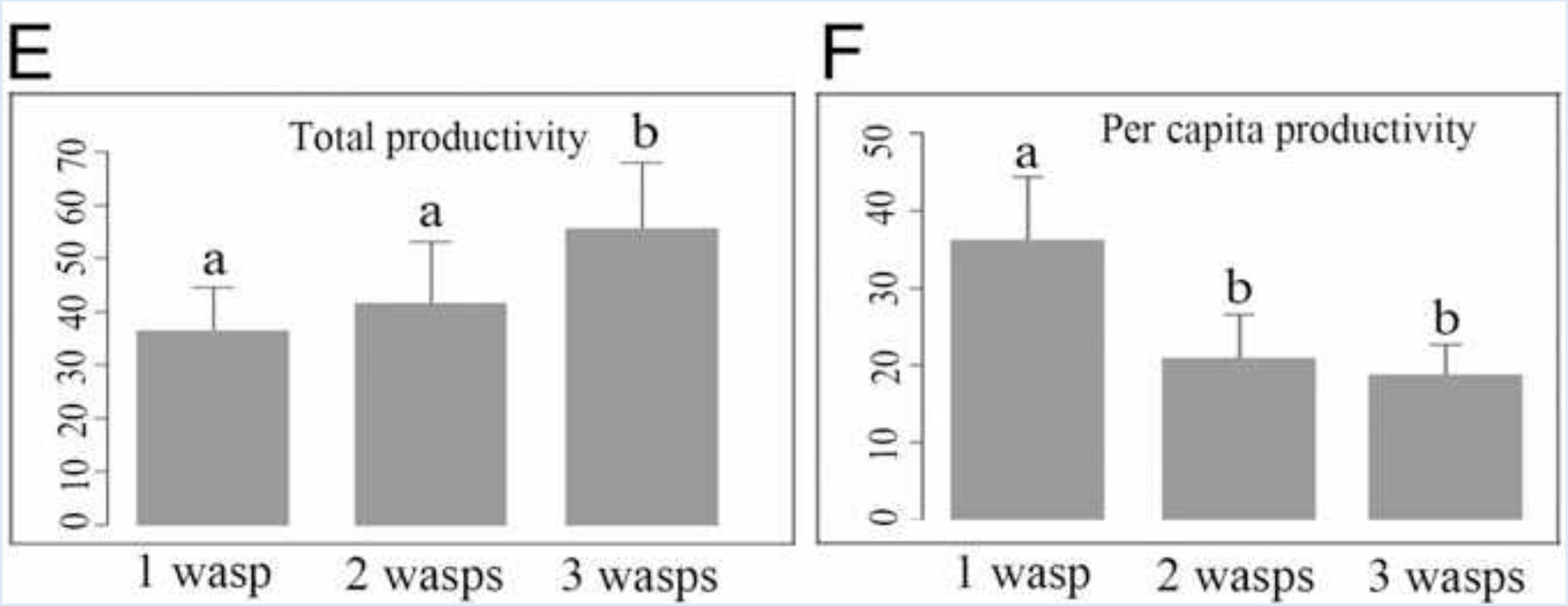
Spontaneous emergence of reproductive division of labour

(Forced joining of "solitary" females in *Pogonomyrmex barbatus*)



Helms Cahan and Gardner-Morse (2013) Journal of Zoology 291: 12–22

Productivity with size of founding colony size
(*Ropalidia marginata*)



2 wasps suff. for repr divn of labour; 3 for non-repr.

Total nest productivity goes up only with latter

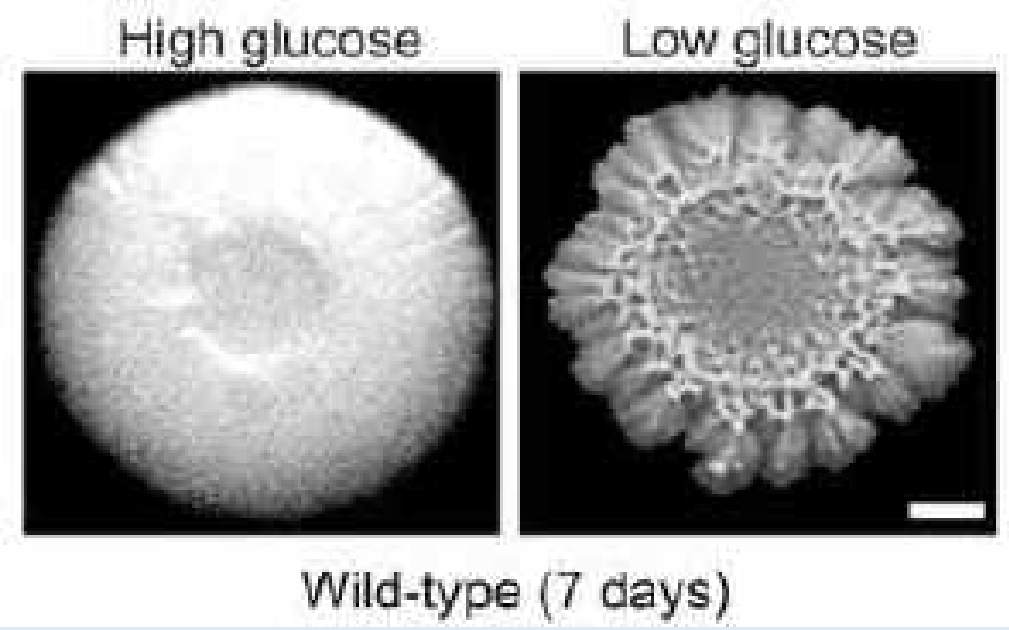
Brahma et al. (2018) PNAS 115(4): 756-761

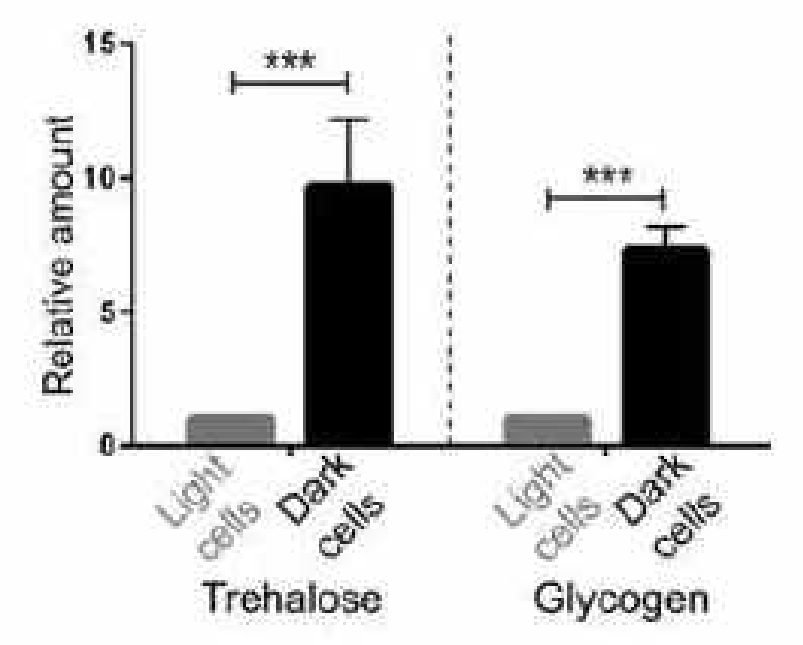
What sorts of cues
might inform one individual
of another individual's internal state?

Growth involves cell-environment communication anyway.

Therefore released by-products
of metabolism, correlated with the particular state,
are good candidates

Spontaneous division of labour in yeast cells





Varahan et al. (2019) eLife 8:e46735.

How might multicellularity have evolved?

Spontaneous self-organisation and division of labour based on phenotypic heterogeneity and inter-individual interactions

followed by

Stabilisation due to subsequent genetic change