Lakatos Award Lecture

Individuals and Groups in Evolutionary Biology

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Individuals versus Groups in Evolutionary Biology

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Themes of the talk

- hierarchy in the biological world

- individual versus group interests

- conflict versus cooperation

- 'levels of selection' in evolution

Social evolution theory

- natural selection in 'social settings'

- evolution of social behaviour

- conceptual problems

- requires careful philosophical scrutiny

Puzzle of altruism

- how can 'altruistic' behaviour evolve?

- surely natural selection should disfavour altruism?

- yet quite common in nature

Vampire bats

- need regular blood

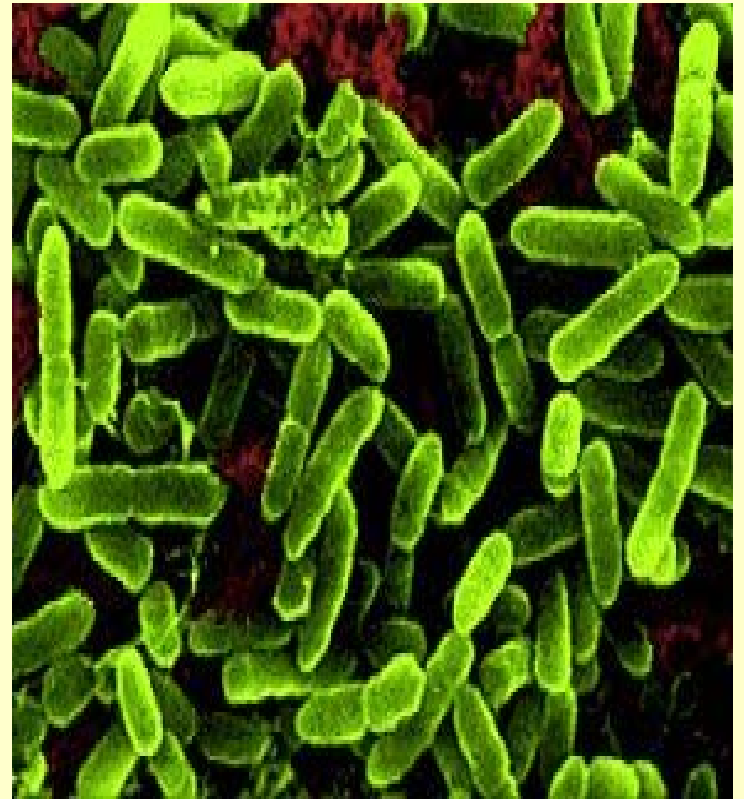- regurgitate blood to feed others

- appears altruistic

Honey-bees

- sterile workers help queen reproduce

- extreme of altruism

- similar in many social insect species

Bacteria

- *Pseudomonas aeruginosa*

- produce siderophores

- a public good

Darwin on the 'noble savage'

"he who was ready to sacrifice his life… rather than betray his comrades… would often leave no offspring to inherit his noble nature"
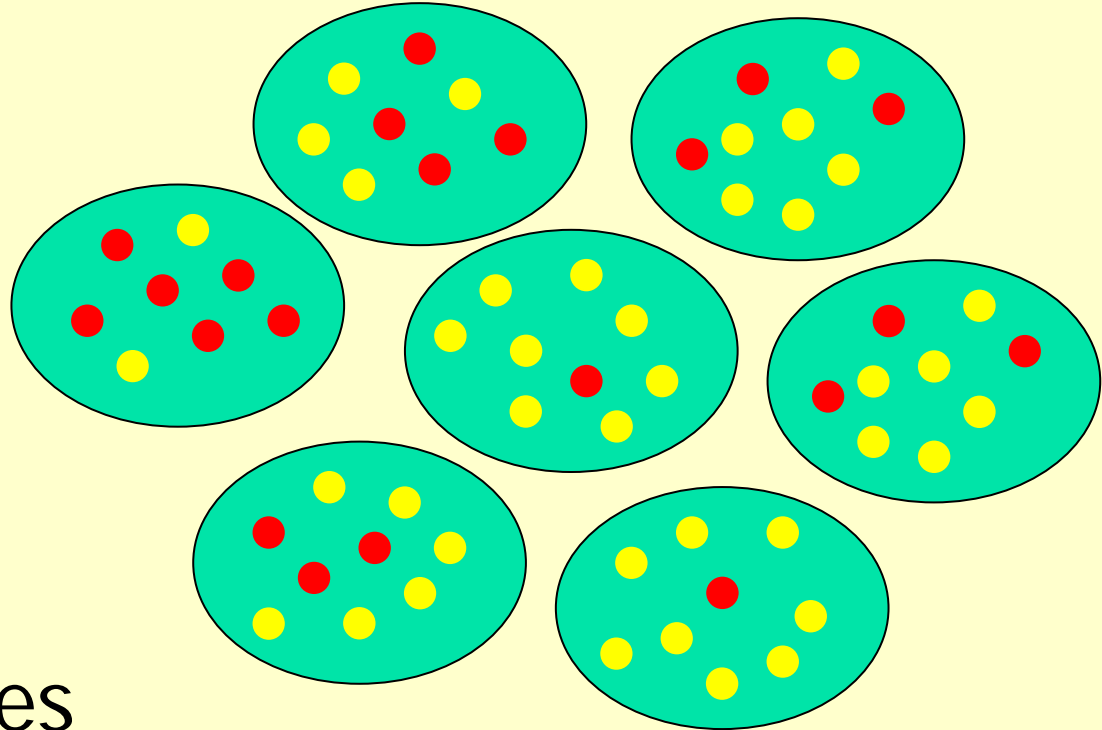
Darwin on 'group selection'

"however... a tribe including many members who were always ready to sacrifice themselves for the common good... would be victorious over most other tribes... **and this would be natural selection**"

The Descent of Man (1879)

Individual and group selection

- selfish types (yellow)
- altruistic types (red)

Levels of selection question

- level of the biological hierarchy at which natural selection acts?

- question stems from:
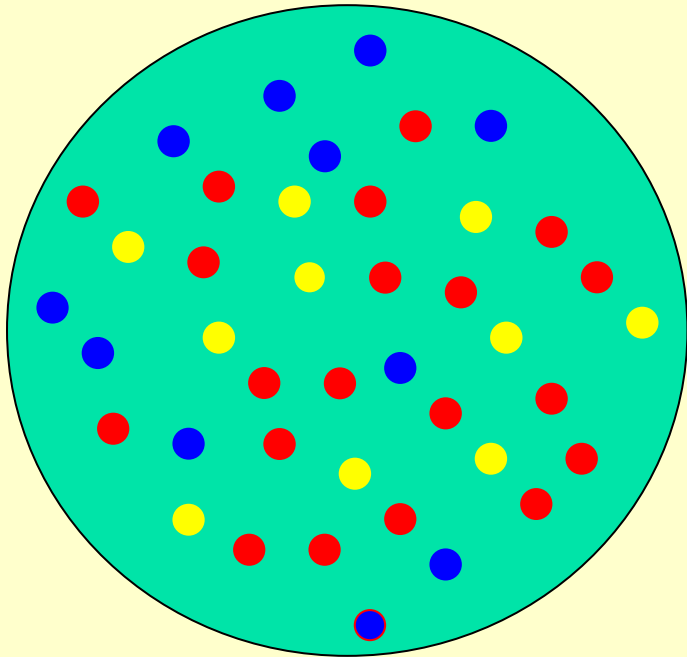 (a) hierarchical organization
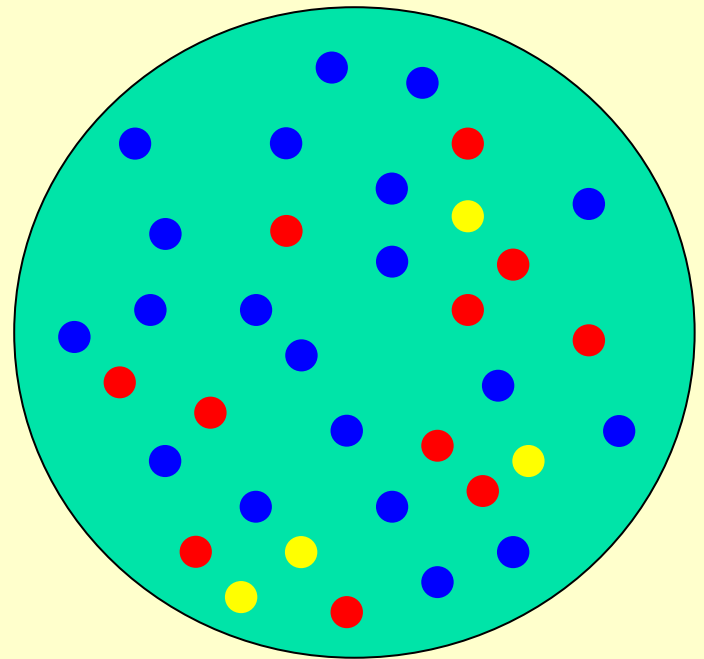 (b) *abstractness* of Darwinian logic

Darwinian logic

- suppose a population exhibits:

  (i) variation
  (ii) fitness differences
  (iii) heritability

- then the population will evolve

An evolving population

Pre-Selection   Post-Selection

Hierarchical organization

gene
chromosome
cell
tissue
organ
multi-celled organism
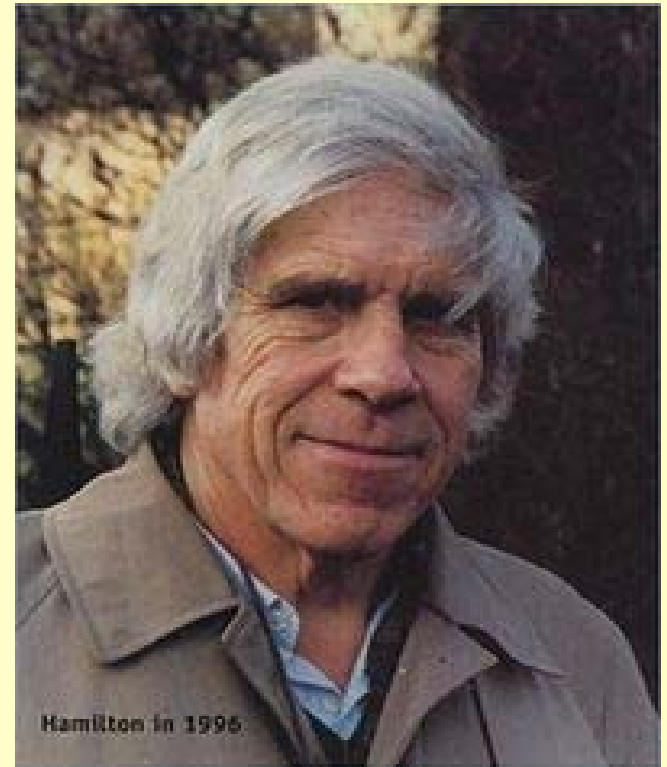colony/group
species
ecosystem

Consensus in 1960s and 1970s

- group selection a minor factor

- altruism explicable in other ways
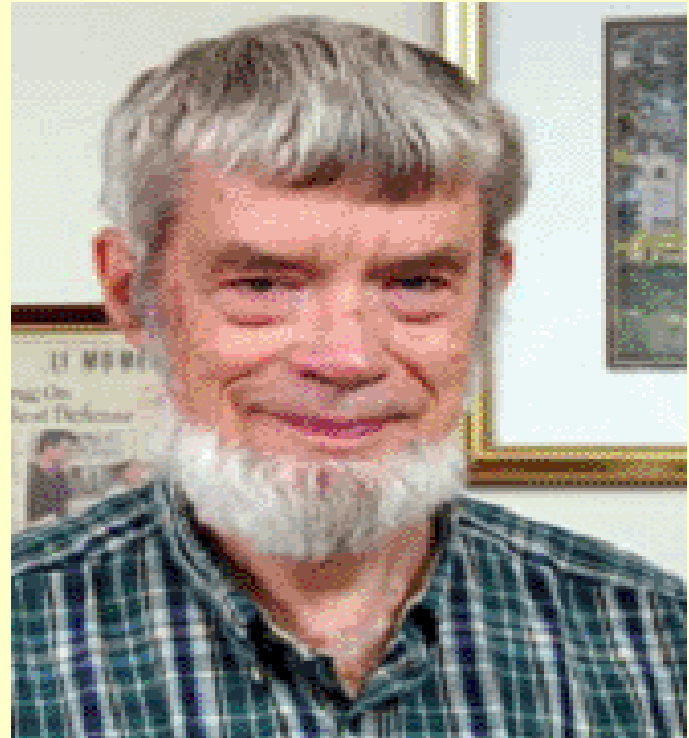
- "individual selection all that matters in practice"

Source of the consensus

- W.D. Hamilton

- 'kin selection' theory

- 'gene's eye' view of evolution

Hamilton in 1996

Source of the consensus

- G.C. Williams

- *Adaptation and Natural Selection* (1966)

- 'good of the group' fallacy

'Good of the group' fallacy

- assuming that individual selection will produce group-beneficial outcomes

- illegitimate appeal to 'group advantage'

- e.g. K. Lorenz on ritual fights

Rise of 'multi-level selection'

- a re-assessment of the old consensus

- selection at multiple hierarchical levels

- motivation partly empirical,
  partly conceptual

Motivation

- not all social behaviour is kin-directed

- opposition between 'gene's eye view' and group selection is mistaken

- 'individuals' are themselves groups of cooperating units

Evolutionary transitions in individuality

- free-living individuals coalesce

- groups become new individuals

- increase in hierarchical complexity

- involves multi-level selection

Examples of transitions

- single replicators → networks
- genes → chromosomes
- prokaryotic cells → eukaryotic cells
- single-celled → multi-celled organisms
- solitary organisms → colonies
- tribes → human societies (??)

Volvocine colonies
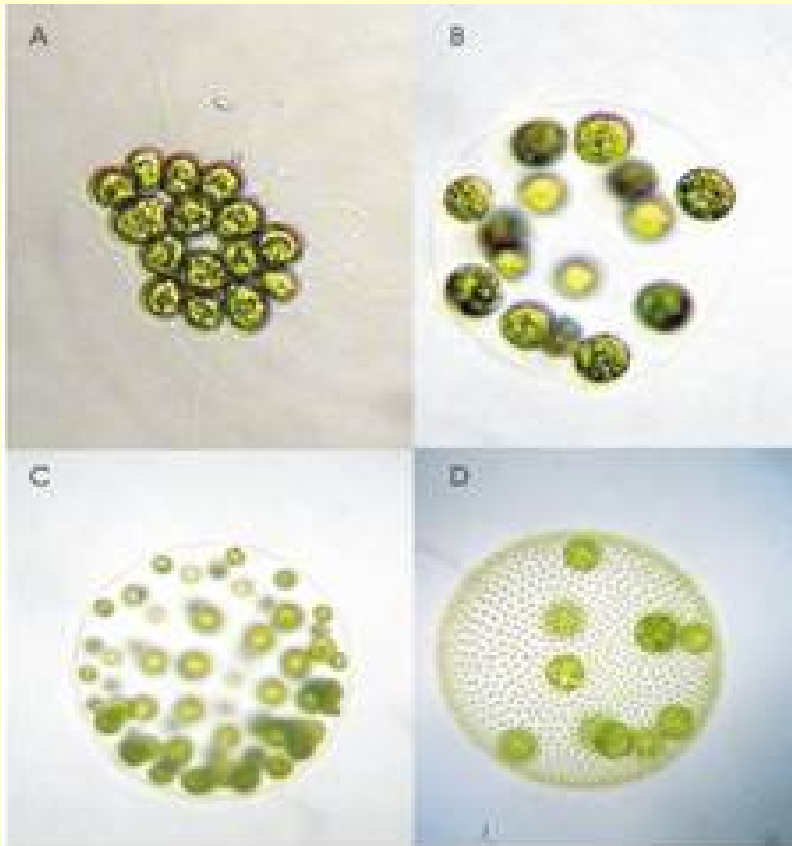
A – *Gonium pectorale*

B – *Eudorina pectorale*

C – *Pleodorina californica*

D – *Volvox carteri*

George Price

- a new formalism for analyzing multi-level selection
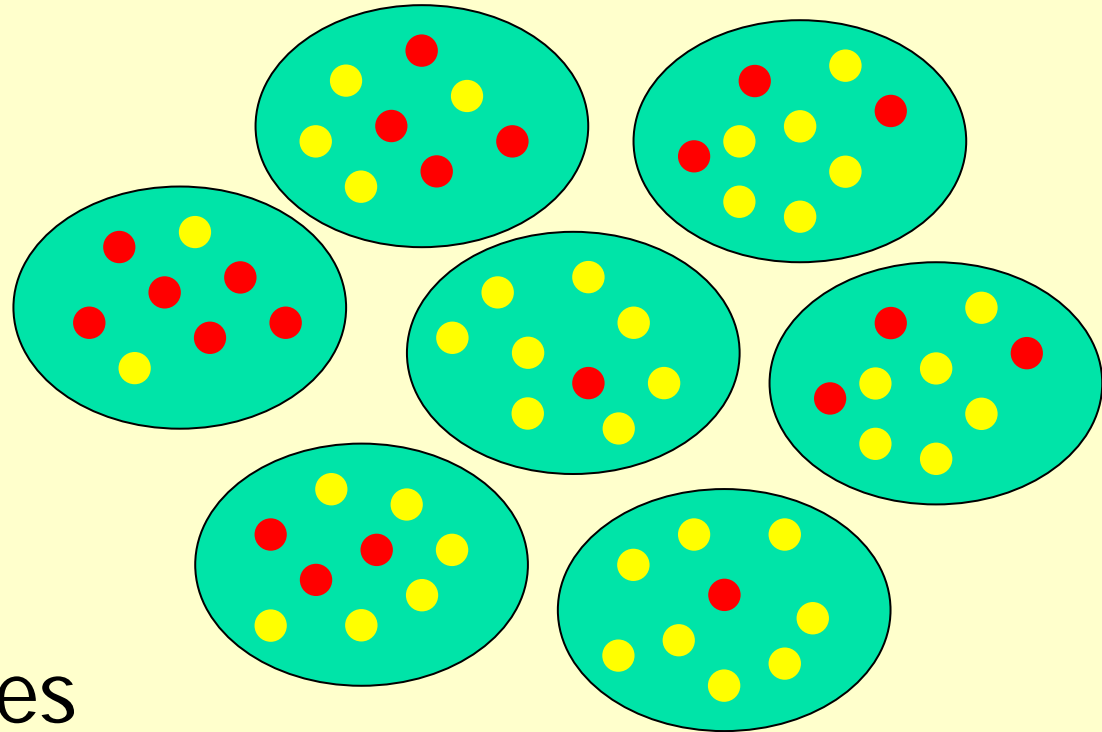
- **Price's equation**

Price's equation

- shows how strength of selection at each level can be compared

- selection as *character-fitness covariance*

- total evolutionary change depends on magnitude of covariance at each level

Individual and group selection

● - selfish types

● - altruistic types

Price's equation

total evolutionary change =

group selection component

Cov (group fitness, group character)

+

individual selection component

Av. [cov (ind. fitness, ind. character)]

Philosophical issues

- causality, reduction, emergence

- realism versus conventionalism

- links to political philosophy

Causality

- Darwinian explanations are causal

- 'selection for' a causal notion

- characters that causally affect fitness vs.
  ones that merely correlate with it

Causality at multiple levels

- cause / correlation distinction

- a character – fitness correlation at level x, may be a side-effect of selection at level x-1
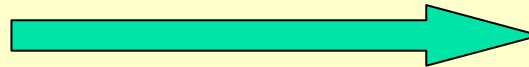
- a 'cross-level byproduct'

Cross-level byproducts

group character .... group fitness

|

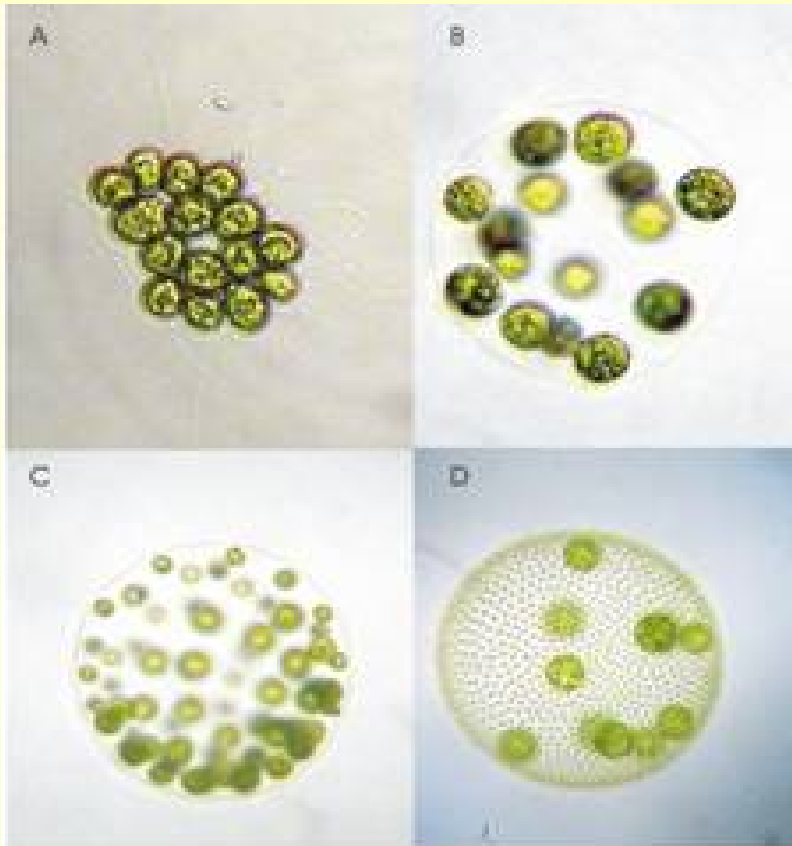lower-level characters → lower-level fitnesses

Examples

- selection on a non-social trait, in a multi-group population

- 'species selection' concept in macroevolution (cf. S.J. Gould)

- *Volvox* again

Volvocine colonies

A – *Gonium pectorale*

B – *Eudorina pectorale*

C – *Pleodorina californica*

D – *Volvox carteri*

Key issue

- what is required for a character-fitness covariance, at a given level, to be due to causal processes at that level?

- "autonomy" from lower-level processes

- one suggestion: emergent properties
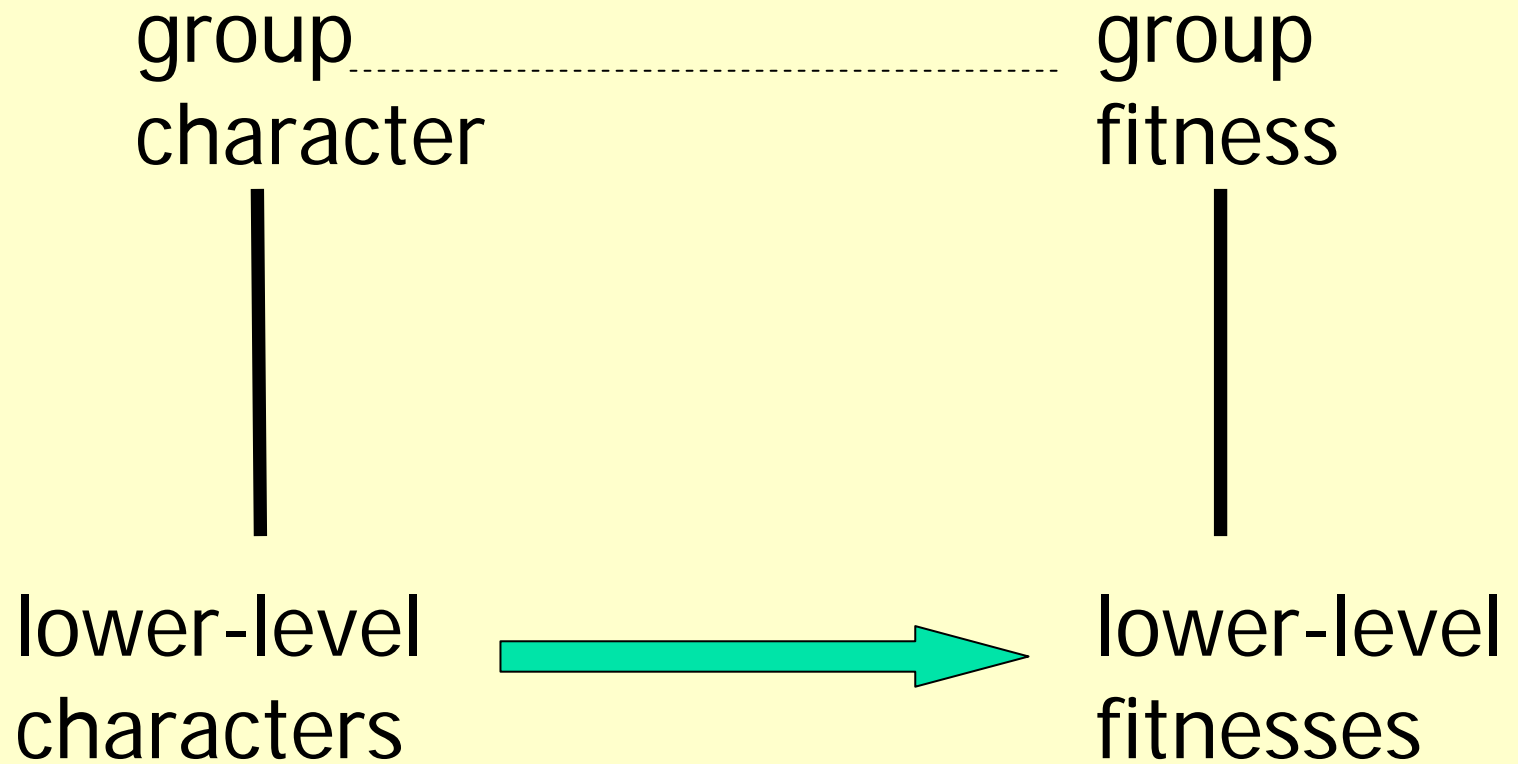- another: it's never possible

'Supervenience' argument

- group character, and group fitness, *always* supervene on individual characters and fitness

- so causation is always lower-level ??
- 'autonomous' higher-level selection impossible ??

'Causation from below'

group character $\cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots$ group fitness

lower-level characters $\longrightarrow$ lower-level fitnesses

Emergent properties

- group characters may be 'emergent' with respect to lower level

- emergent versus aggregate

- insect colony versus mammal group

Honey-bee colony versus baboon troop

However...

- a distinction:

(i) lower-level *selection* doing causal work

(ii) some lower-level processes *or other* doing causal work

- (i) is what matters
- so 'emergent properties' irrelevant

Individual vs. group interests

- potentially in conflict

- action of self-interested agents may not maximise collective welfare

- a central theme in political philosophy, and in social evolution
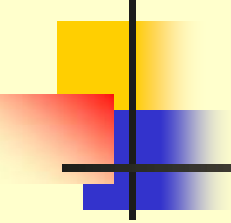
How can they be reconciled?

- such reconciliation has happened repeatedly in evolution

- 'evolutionary transitions in individuality'

- require that interests be aligned

Ways of aligning individual and group interests

- (i) clonality / relatedness
  (ii) division-of-labour
  (iii) policing of selfish behaviour
  (iv) randomization

- all have echoes in political philosophy

Rawls / Harsanyi veil-of-ignorance

- 'original position'

- you have to decide on society's allocation of resources, without knowing which individual you'll be

- equal chance of being any individual

Veil-of-ignorance

- Rawls: 'maximin' solution

- Harsanyi: utilitarian solution

- both implausible
- but underlying point is right
- veil aligns individual and group interests

Genes and genomes

- genes in an organism usually work for the 'good' of it
- roughly, to maximise its gametic output

- in sexual species, only half the genes are passed into each gamete

- creates potential for conflict

Meiosis
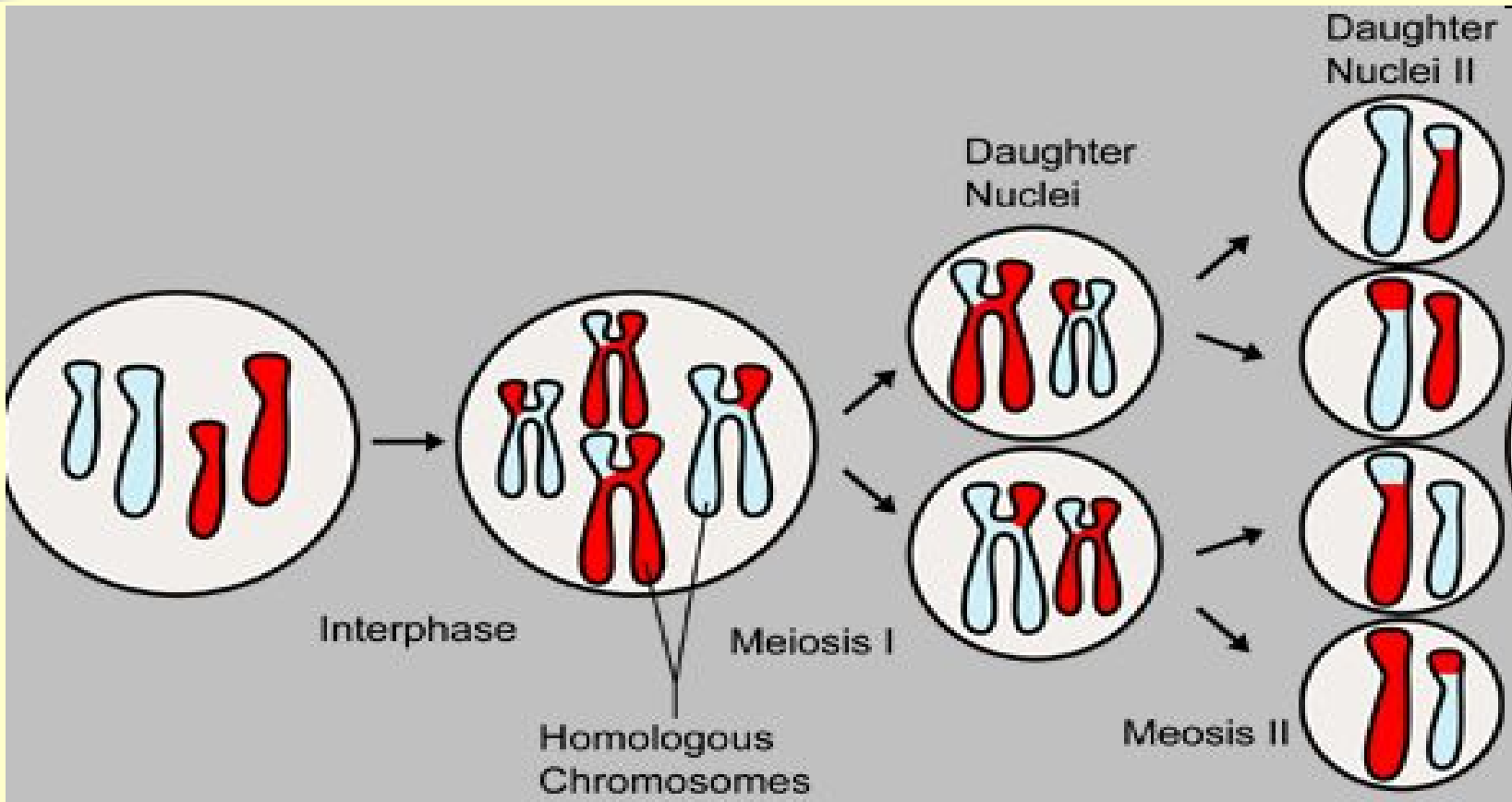
What aligns interests of gene and whole genome?

- randomization!

- each chromosome has an equal (50%) chance of transmission

- so a gene can't do better, than work for the collective good

What does this show?

- Rawls/Harsanyi thought experiment is actually put into practice by evolution

- confirms their general idea

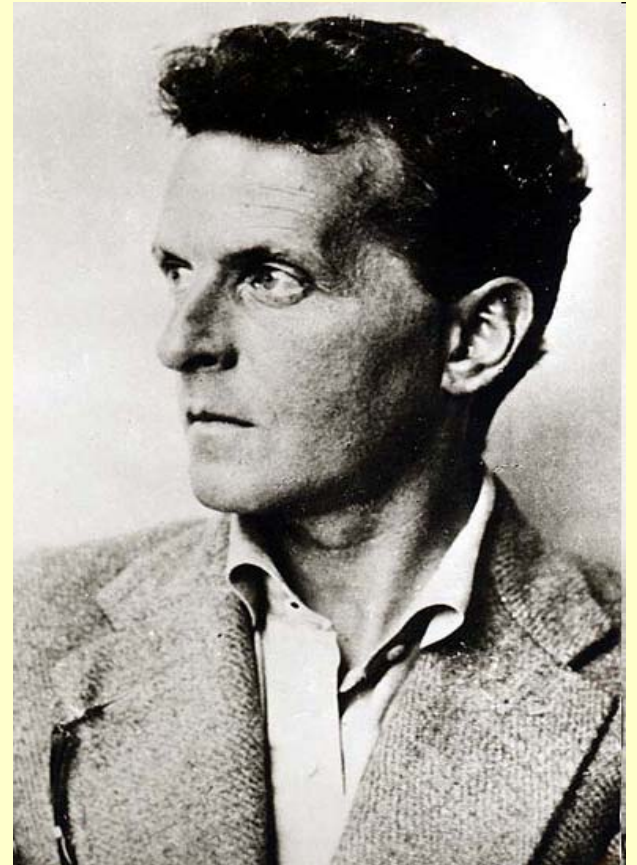- what become of Rawls' and Harsanyi's 'solutions', in the light of evolution?

Conclusion

- social evolution theory requires philosophical scrutiny

- and offers new insights

- Darwinism and philosophy

Ludwig Wittgenstein

"Darwin's theory has no more relevance for philosophy than any hypothesis in natural science"
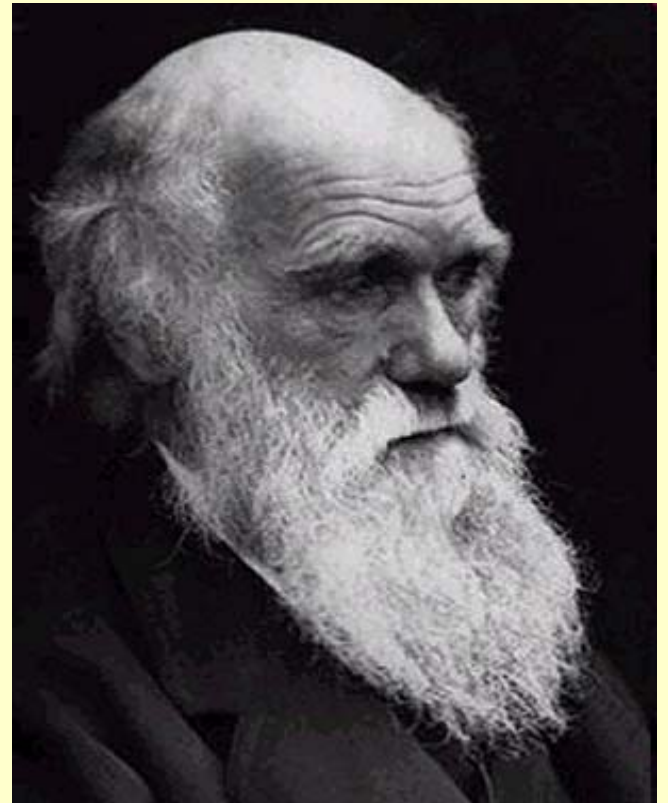
Tractatus (1923)

Charles Darwin

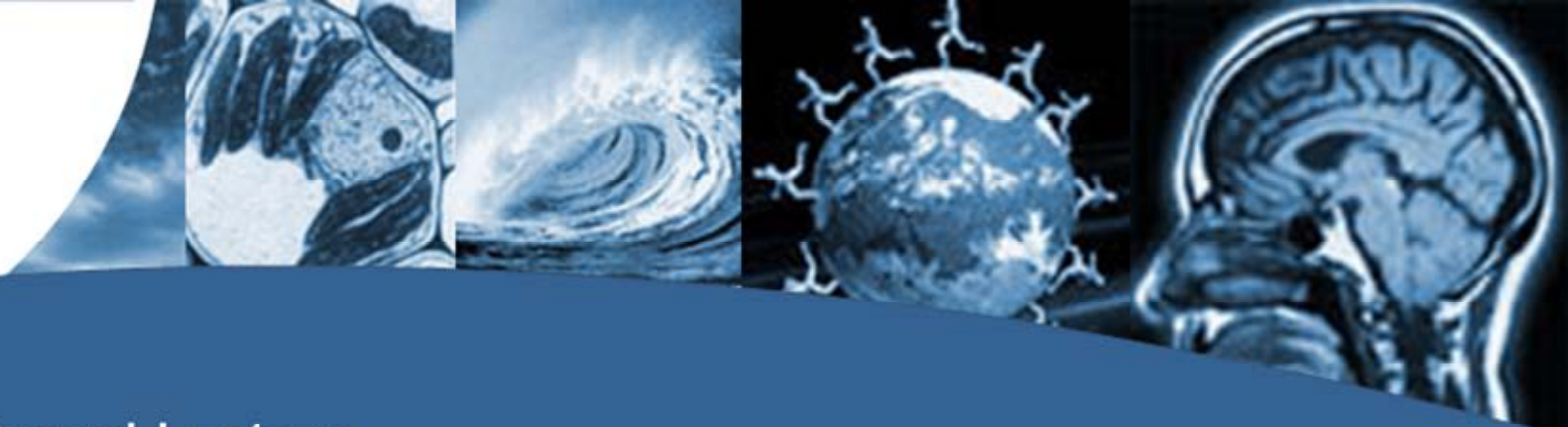"he who understands baboon would do more for metaphysics than Locke"

Notebooks (1838)

Acknowledgements

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