Developmental and Selectionist Approaches in 21st-Century Evolution

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Thanks to:

The Organizers

Marion Lamb

Anna Zeligowski (original pictures)

Students and Colleagues

I argue that developmental and selectionist approaches to evolution can be seen as aspects of a broader system-oriented perspective that is emerging in the 21st century.

The developmental aspect is associated with Lamarckism: it focuses on **developmental variation, and on the developmental aspects of heredity**. (**The arrival of the fittest**)

The selectionist approach is associated with Darwinism: it focuses on **selection as the direction giving process in evolution**. (**The survival of the fittest**)

I argue that in many cases the two aspects can be seen as manifestation of a common principle: selective stabilization.

I would like to discuss:

- The developmental and selectionist approaches to evolution: Lamarckism and Darwinism

  A short introduction
- The two approaches are joined within a framework that emphasizes:

  Plasticity, canalization, exploration and selective stabilization processes at different levels of biological organization, genetic assimilation, epigenetic inheritance.

Lamarck suggested that living organisms are the products of a long series of transformations starting from very simple beginning.

He suggested that life originated from complex chemical reactions in conditions of warmth and humidity. Processes of self organization led to the formation of the first fragile life forms.

The living beings became increasingly more complicated. He thought that self organization and self complication are the fundamental characteristics of living beings. As living entities become more complex they become more stable.

However, species do not form a ladder leading from simple to complex forms, but a tree. This is the result of different self-organizational responses to different, accidental, conditions of life, to different environments. Some organs are used (e.g. the giraffe's neck) others are not used (e.g. the eyes of cave animals). The effects of use and disuse are inherited. Acquired characters are inherited.

The accumulation of such effects leads to the specific (usually) adaptive features of living organisms. It also may lead to complexification.

Darwin worked for 20 years on his theory of evolution by natural selection. He published his book *On the Origin of Species* in 1859. The book revolutionized biology.

In the *Origin* he suggested the theory of descent with modification. He suggested that the main mechanism of evolutionary change was natural selection.

Evolution by natural selection

Results from the interactions between:

Multiplication (one entity begets others)

Heredity (entity A usually begets A descendants, entity B has B descendants)

Hereditary variation (entity A sometimes begets C which then begets C)

Hereditary variations affect the chances of multiplication

Accumulation of variation in a certain direction can lead to complex functional design

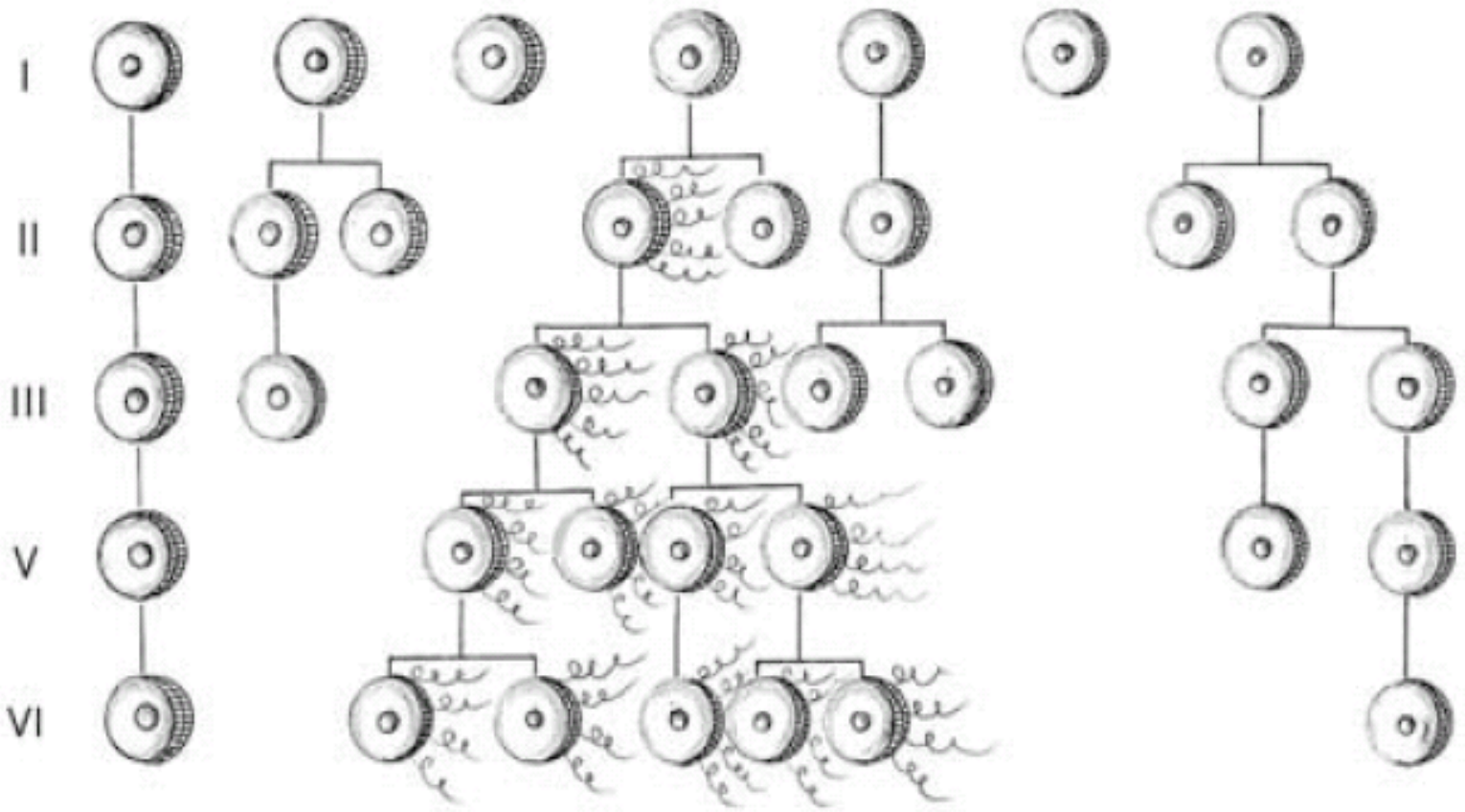


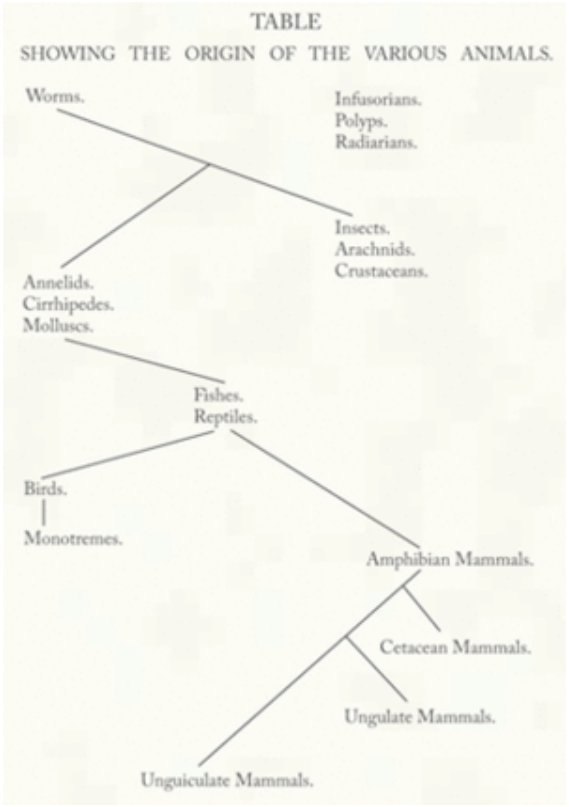
Figure 1.1

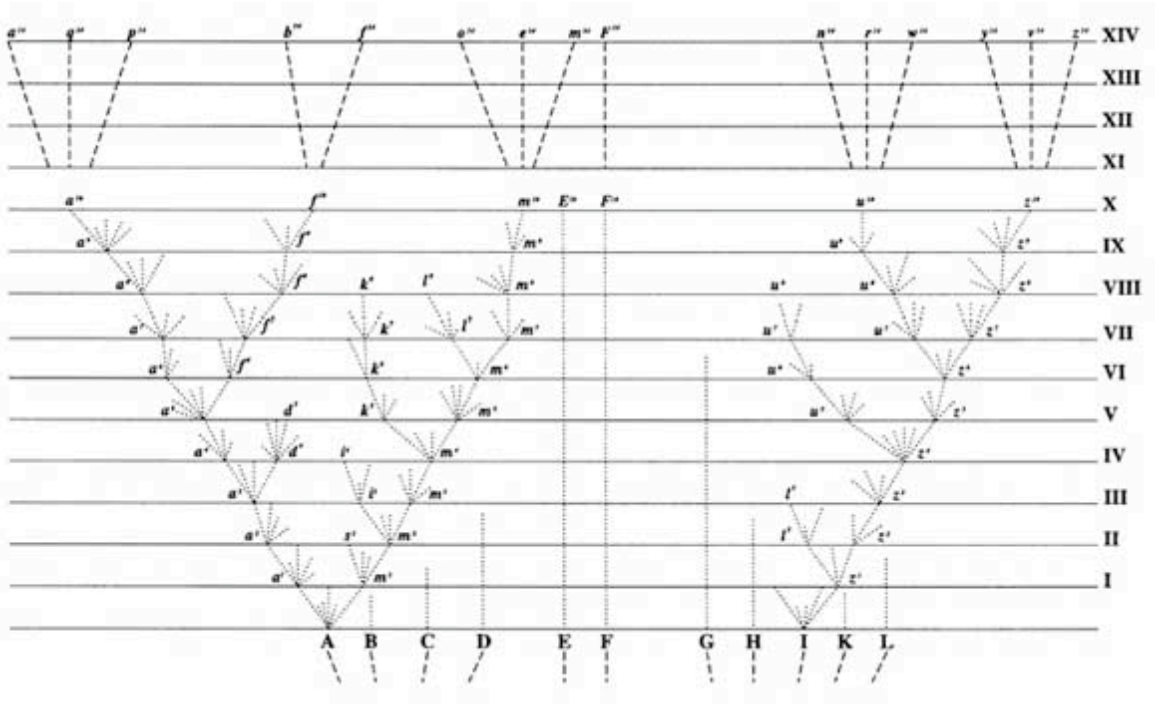
Universal Darwinism: the frequency of the hairy entity, which first appears in generation II, increases in subsequent generations because it survives better and multiplies more than its competitors.

Common assumptions:

Descent with modifications

gradualism



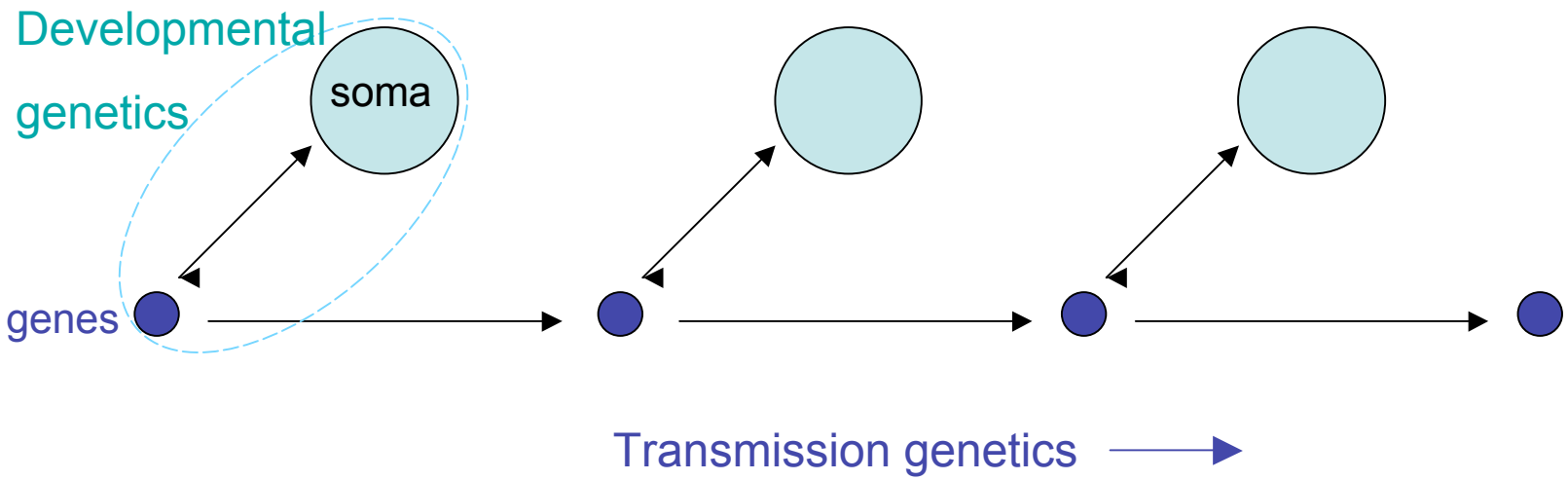


The decline of the developmental approach to evolution since the 1940s

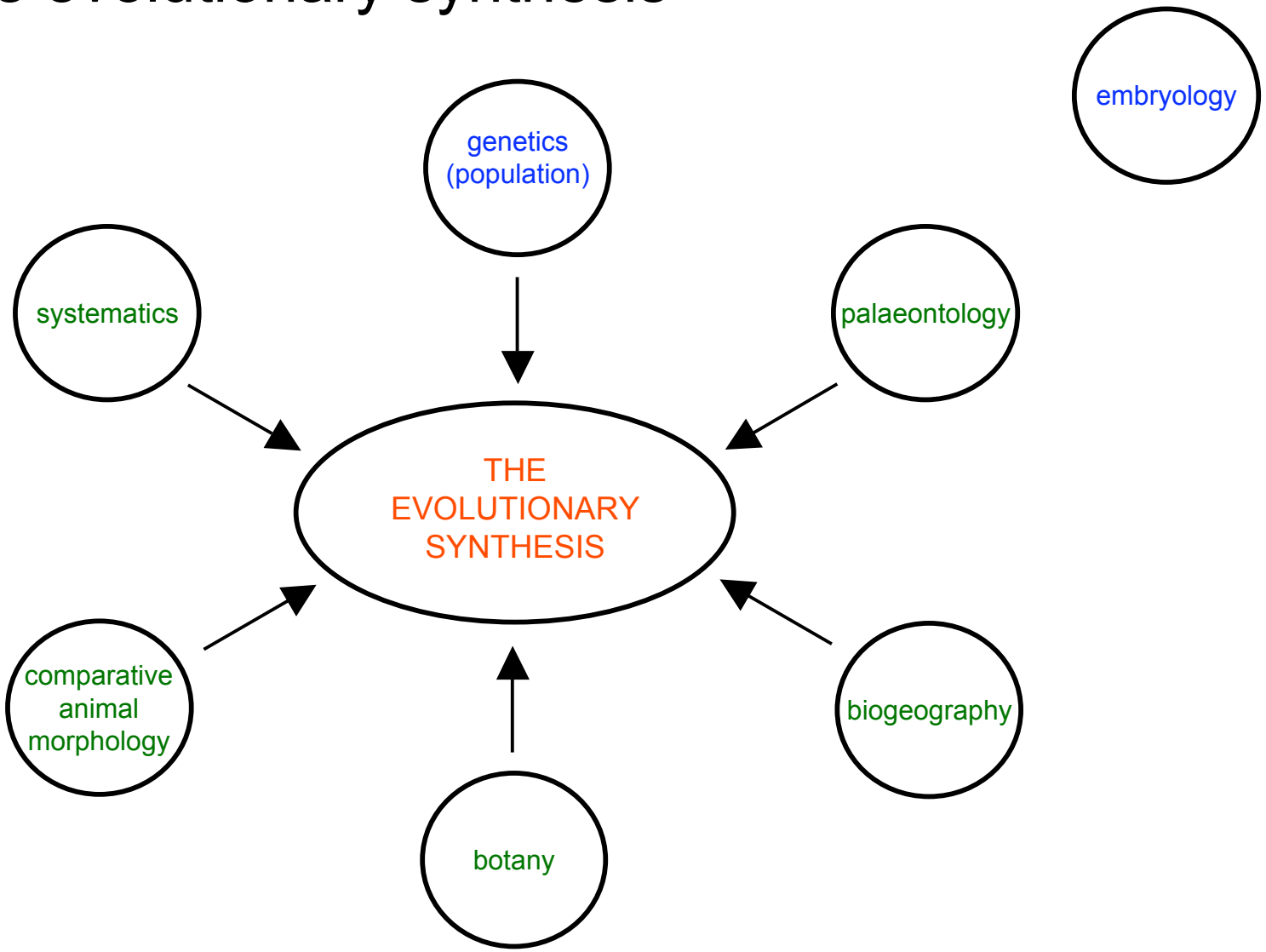
Heredity = the transmission of genes

Heredity is, in the last analysis, self-reproduction. The units of heredity, and hence of self-reproduction, are corpuscles of macromolecular dimensions, called genes. The chief, if not the only, function of every gene is to build a copy of itself out of the food materials; the organism, in a sense, is a by-product of this process of gene self-synthesis. [Dobzhansky 1958]

Transmission genetics and developmental genetics



Mayr's evolutionary synthesis



Some assumptions of the Modern Synthesis

(concerning heredity)

1. Heredity occurs through the transmission of germ-line genes. Hereditary variation is equated with variation in DNA base sequence. *There are no inherited non-DNA variations that cannot be reduced to DNA variations.*

2. Hereditary variation is the consequence of (i) the combinations of pre-existing alleles that are generated by the sexual processes; and (ii) new variations (mutations) that are the result of accidental changes in DNA. *Hereditary variation is not affected by the developmental history of the individual. There is no "soft inheritance".*

3. Heritable variations have small effects, and evolution is typically gradual. Through the selection of individuals with phenotypes that make them slightly more adapted to their environment than others individuals are, some alleles become more numerous in the population. *With a few exceptions, macroevolution is continuous with microevolution, and does not require any extra considerations beyond those operating during microevolution.*

Plasticity is seen as noise which obscures the role of selection.

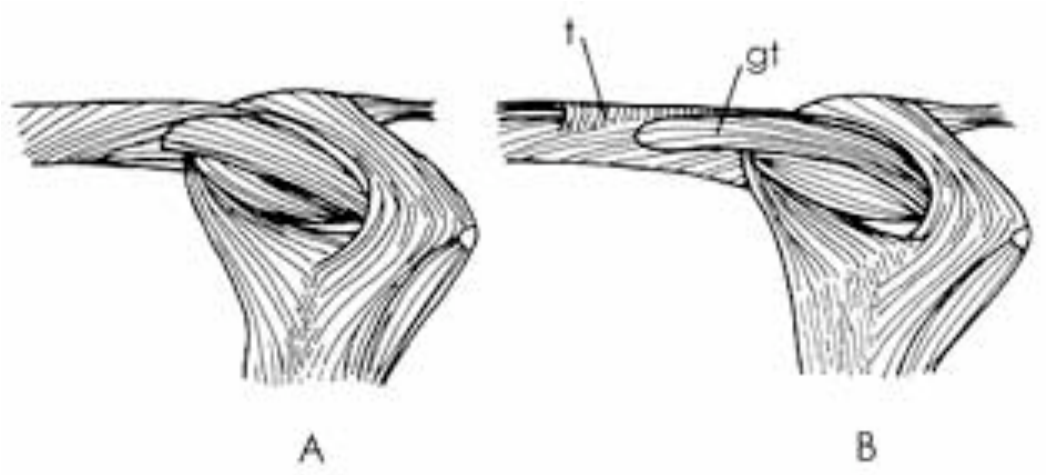
Plasticity

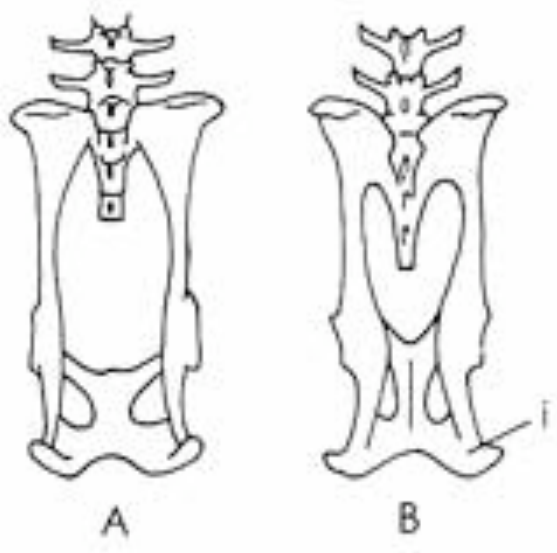
A single genotype can produce many phenotypes, depending on many contingencies encountered during development. That is, phenotype is an outcome of a complex series of developmental processes that are influenced by environmental factors as well as genes.

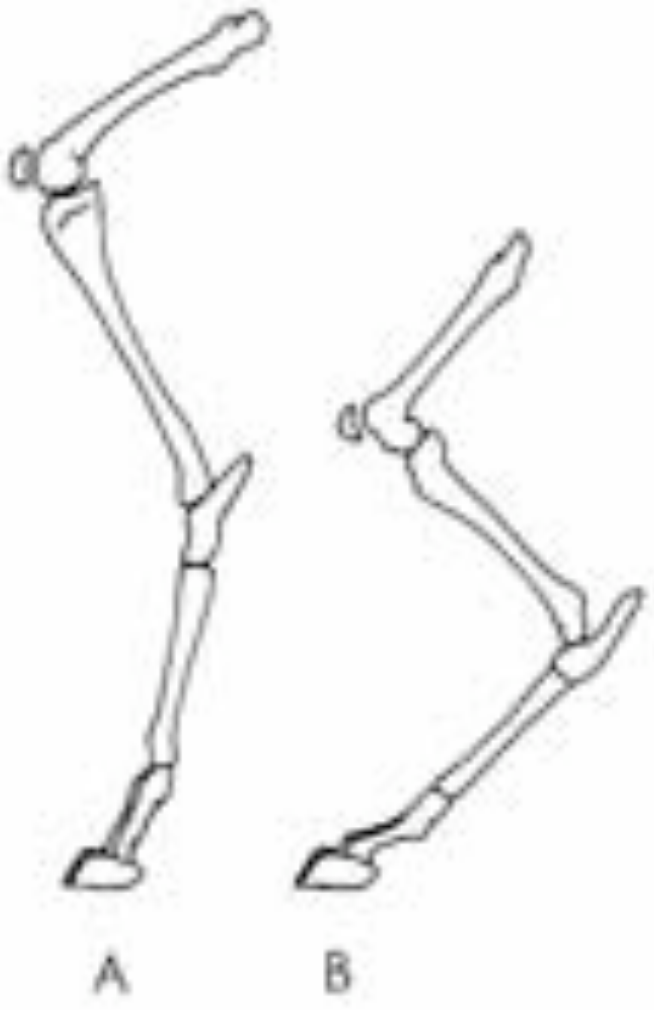
H. F. Nijhout, 1999

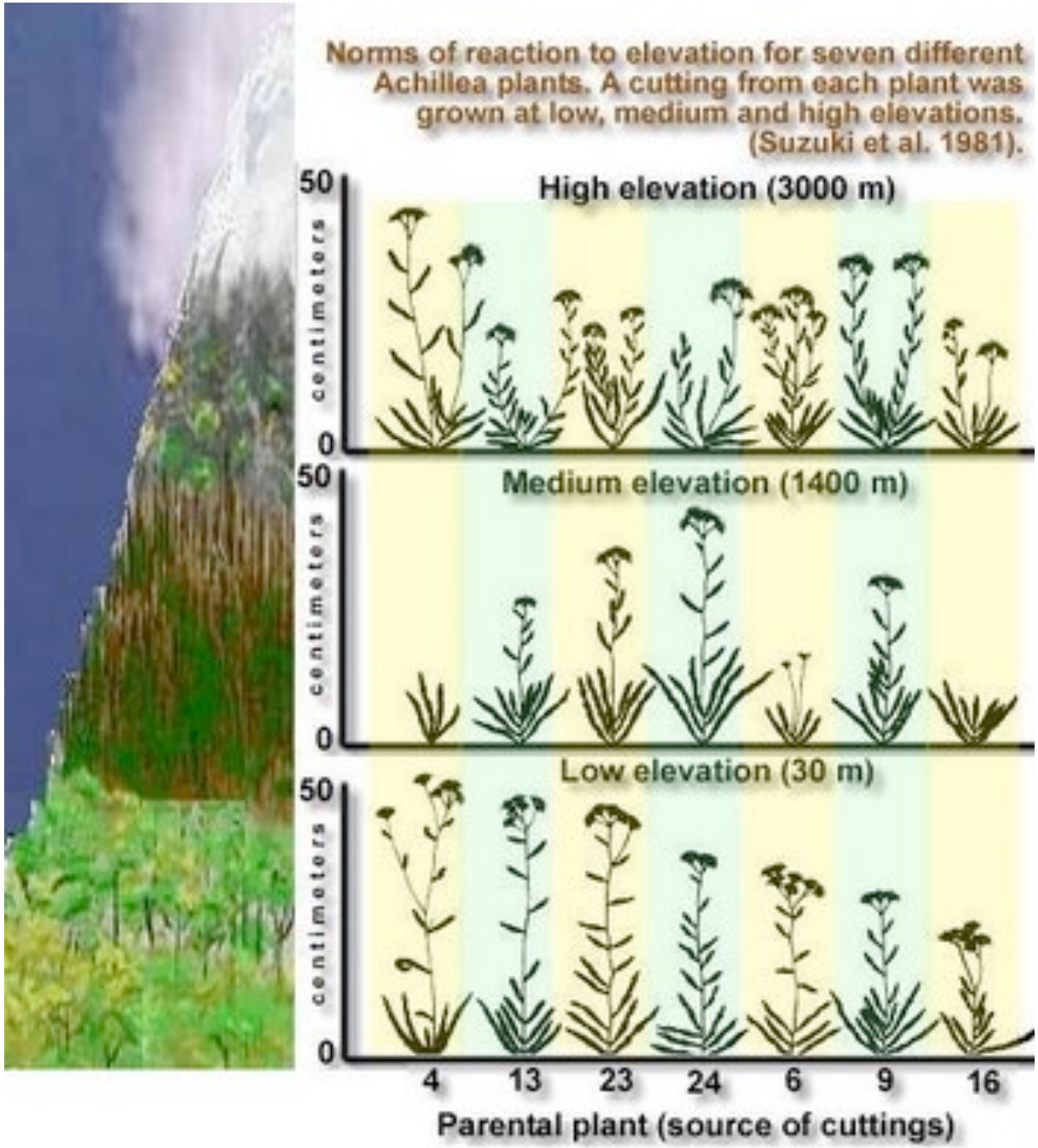
The two-legged goat

A: normal, B: bipedal








Norms of reaction to elevation for seven different Achillea plants. A cutting from each plant was grown at low, medium and high elevations. (Suzuki et al. 1981).
High elevation (3000 m)
Medium elevation (1400 m)
Low elevation (30 m)
50
0
centimeters
4
13
23
24
6
9
16
Parental plant (source of cuttings)

The Epigenetic Turn

The Waddington/Schmalhausen Approach: Gene's as followers.

The Structuralist Approach: Generative Plasticity

The Heredity-oriented Approach: Soft, Epigenetic Inheritance

Relations between Development and Evolution

It is not the changes of genotype that determine evolution and its direction. On the contrary, it is the evolution of the organism that determines changes of its genotype."

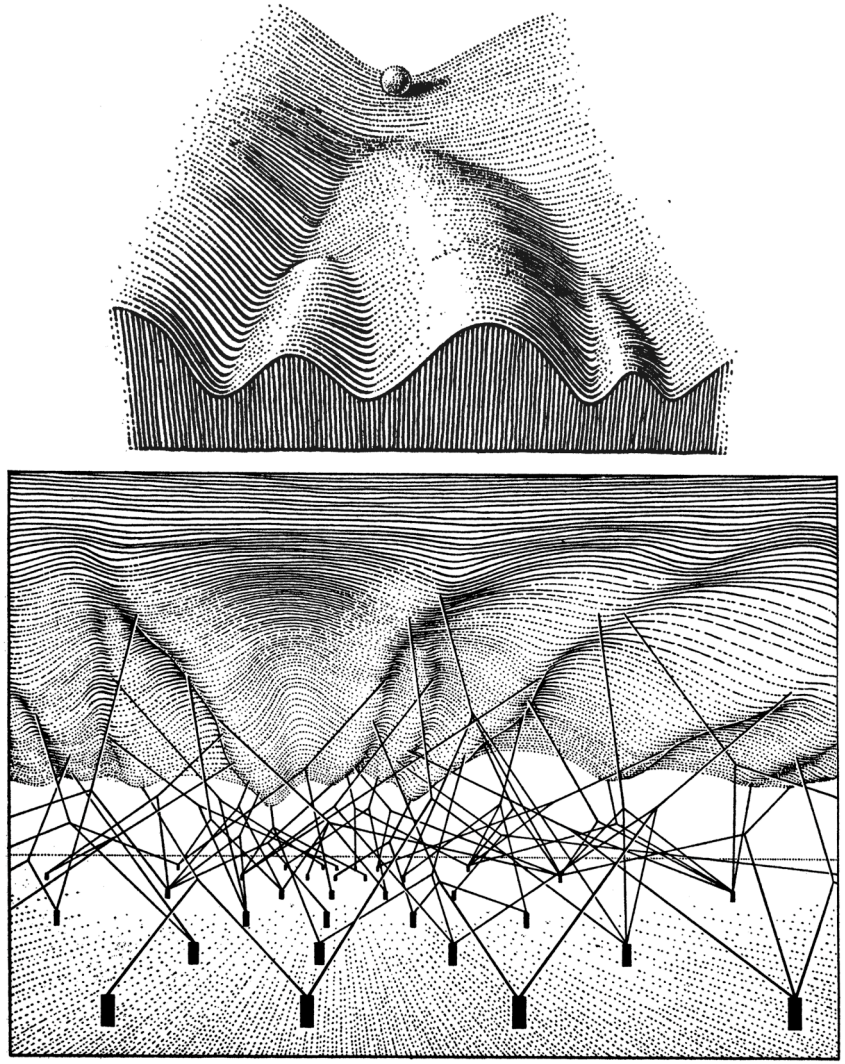
I.I.Schmalhausen, Stabilizing Selection. (1940) *J. of Gen. Biol.*

CANALIZATION OF DEVELOPMENT AND THE INHERITANCE OF ACQUIRED CHARACTERS

By Dr. C. H. WADDINGTON
Zoological and Strangeways Laboratories, Cambridge

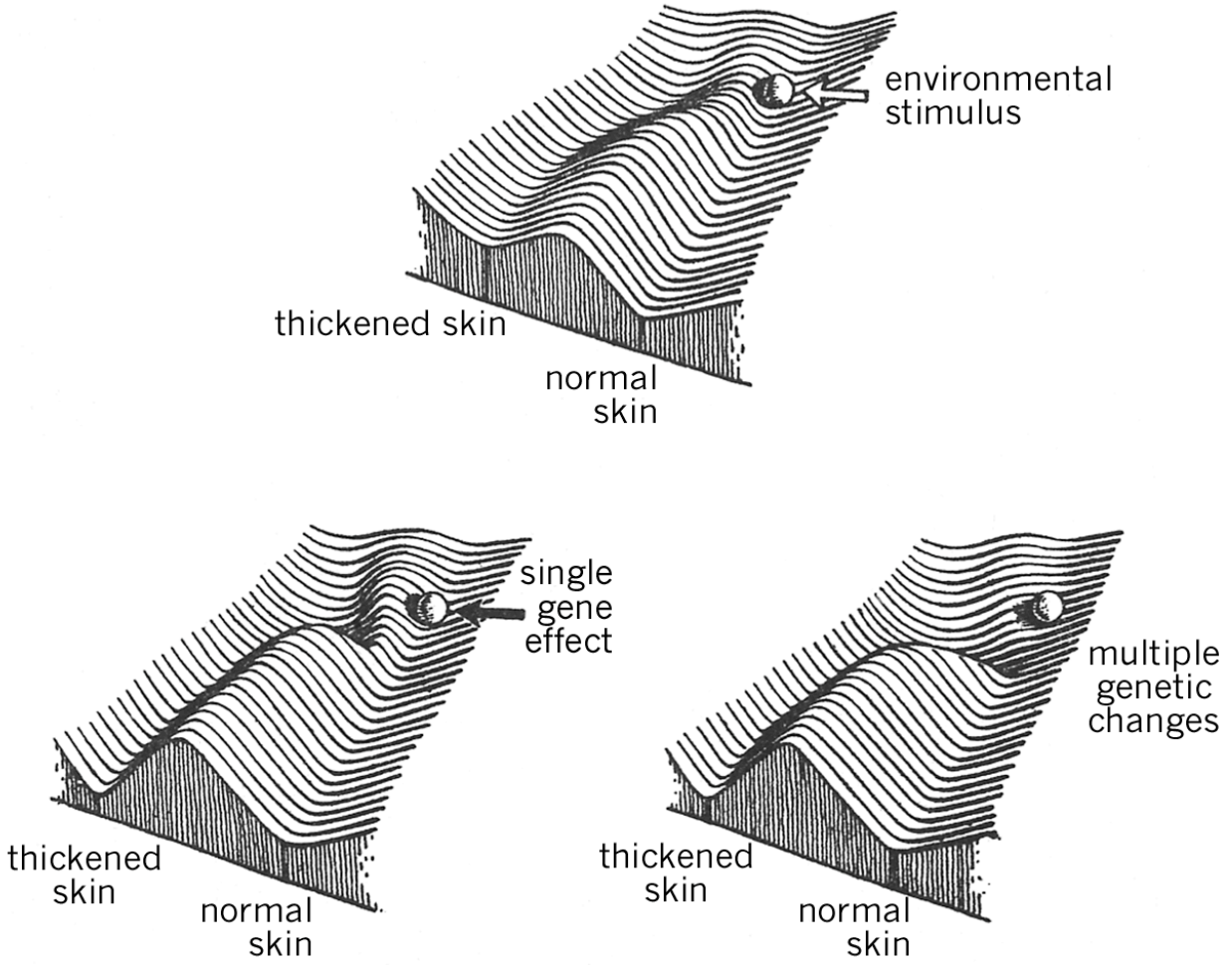
“If we are deprived of the hypothesis of the inheritance of the effects of use and disuse, we seem thrown back on an exclusive reliance on the natural selection of merely chance mutations.”

Waddington's epigenetic landscape



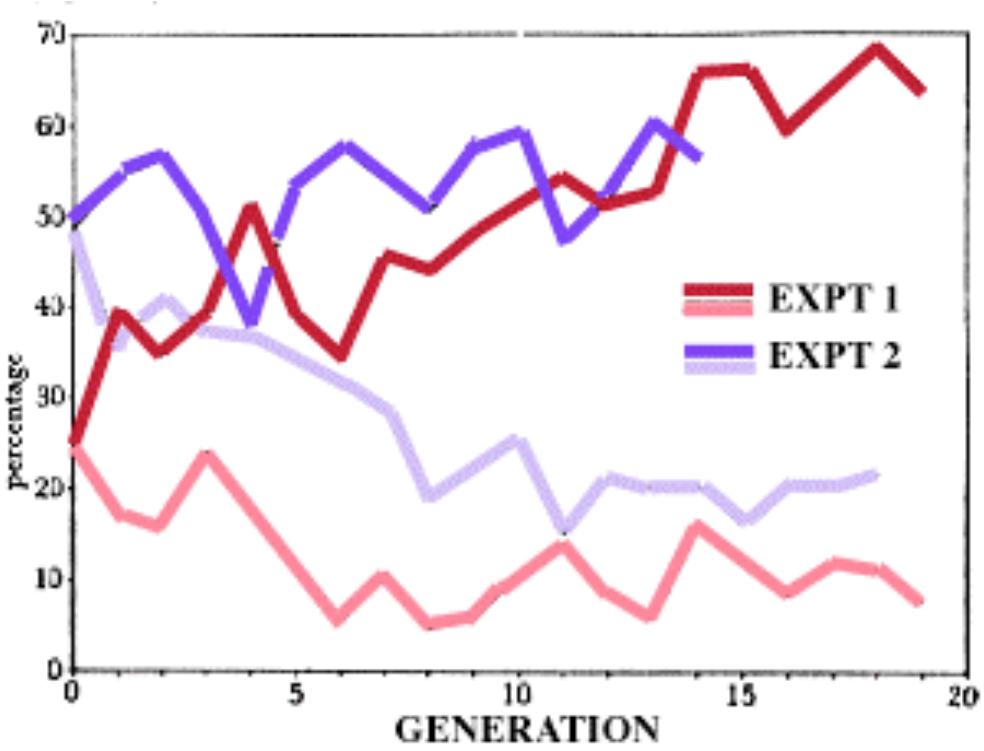
Waddington, *The Strategy of the Genes*, p 29 & 36, 1957

Genetic assimilation



Jablonka & Lamb *Evolution in Four Dimensions* 2005, p. 263

Phenocopy of the bithorax mutation. (A) A *bithorax* phenotype produced after treatment of the embryo with ether. The forewings have been removed to show the aberrant metathorax. This particular individual is actually from the "assimilated" stock that produced this phenotype without being exposed to ether. (B) Selection experiments for or against the *bithorax*-like response to ether treatment. Two experiments are shown (red and blue lines). In both cases, one group was selected for the trait and the other group was selected against the trait. (After Waddington 1956).



Gametes	A^1B^1	A^1B^2	A^2B^1	A^2B^2
A^1B^1	$A^1A^1B^1B^1$	$A^1A^1B^1B^2$	$A^1A^2B^1B^1$	$A^1A^2B^1B^2$
A^1B^2	$A^1A^1B^2B^1$	$A^1A^1B^2B^2$	$A^1A^2B^1B^2$	$A^1A^2B^2B^2$
A^2B^1	$A^2A^1B^1B^1$	$A^2A^1B^2B^1$	$A^2A^2B^1B^1$	$A^2A^2B^1B^2$
A^2B^2	$A^2A^1B^2B^1$	$A^2A^1B^2B^2$	$A^2A^2B^2B^1$	$A^2A^2B^2B^2$

Two genetic loci, A and B affect the expression of the trait (wing development). Each locus has two alleles: locus A, A^1 and A^2, locus B, B^1 and B^2. The gametes (sperms and eggs) have one allele of each gene, and the individuals are the result of the unification of the gametes. Assume that we select for genotypes with 2 or more type-2 alleles, i.e. those that when induced by the external stimulus develop a non-wild-type phenotype .If p, the frequency of A2 and B2 alleles, is 0.1, and q, the frequency of A^1 and B^1 alleles, is 0.9, then the overall frequency of genotypes with two or more type-2 alleles will be $6p^2q^2 + 4p^3q + p^4 = 0.0523$. It would be then likely to get the genotype with 4 type-2 alleles (darkest gray) – which is the genotype that develops the trait without induction Without selection for inducibility the frequency of such genotype is very small, 1/10000 and unlikely to be found.

Epigenetics (21st century definition)

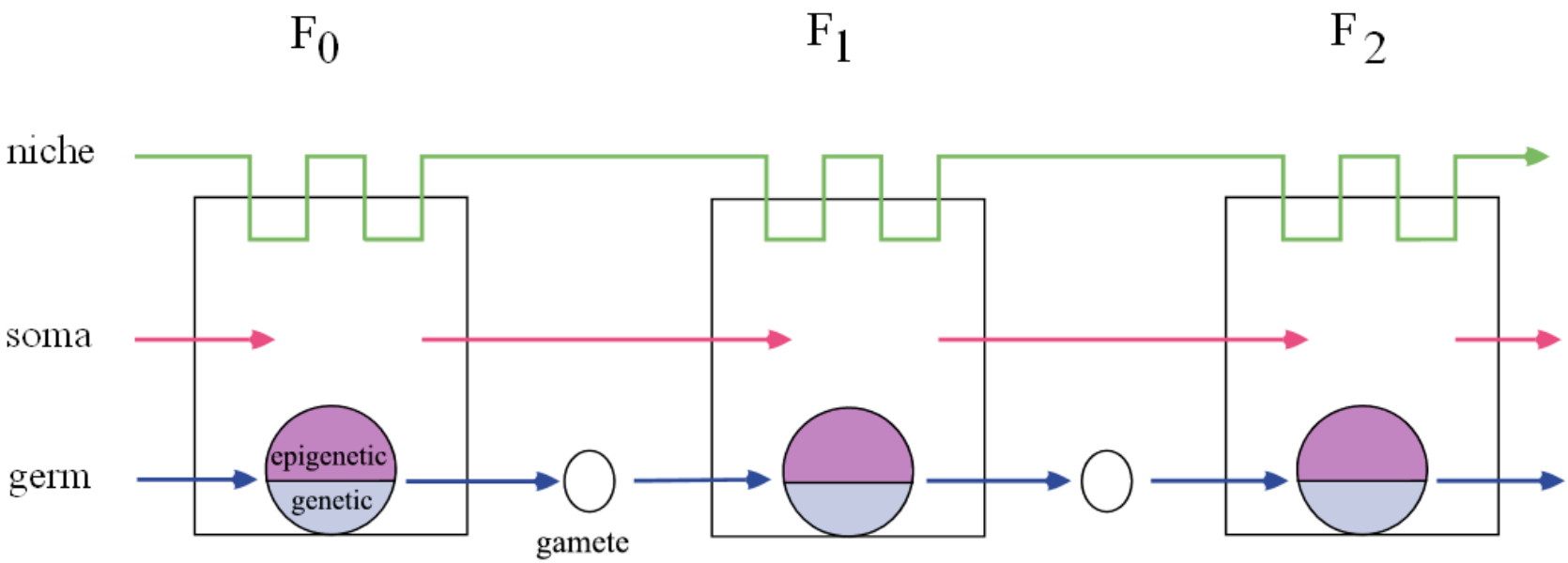
Epigenetics is the study, in both prokaryotes and eukaryotes, of the processes that lead to long-term, persistent developmental effects. At the cellular level these are the processes involved in cell determination and differentiation. At higher levels of biological organization, epigenetic mechanisms underlie self-sustaining interactions between groups of cells that lead to physiological and morphological persistence.

Epigenetic inheritance: the inheritance of plastic responses.

Epigenetic inheritance is a *component* of epigenetics. It occurs when phenotypic variations that do not stem from variations in DNA base sequence are transmitted to subsequent generations of cells or organisms.

It is used in a broad and a narrow (cellular) sense.

Epigenetic inheritance: broad and narrow conceptions



Cellular epigenetic inheritance

Cellular epigenetic inheritance is the transmission from mother cell to daughter cell of variations that are not the result of differences in DNA base sequence or the present environment. The cell is the unit of transmission. Transmission can be through

- self-sustaining metabolic loops
- self-reconstructing three-dimensional structures
- chromatin marks
- RNAs

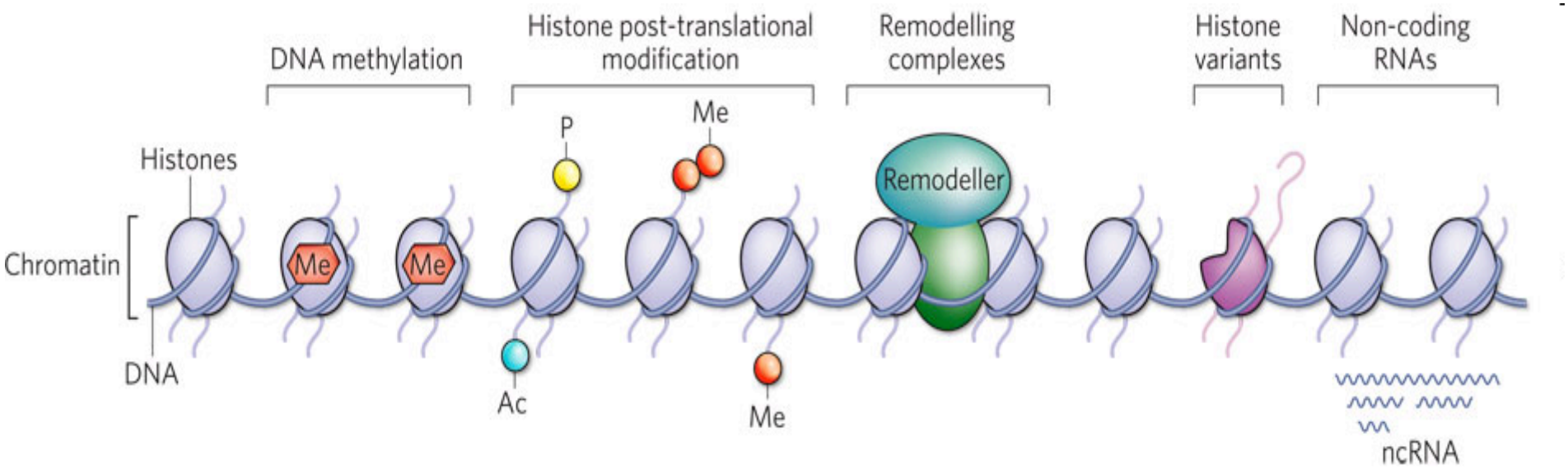
It occurs during cell division in prokaryotes, mitotic cell division in the soma of eukaryotes, and sometimes during the meiotic divisions in the germline.

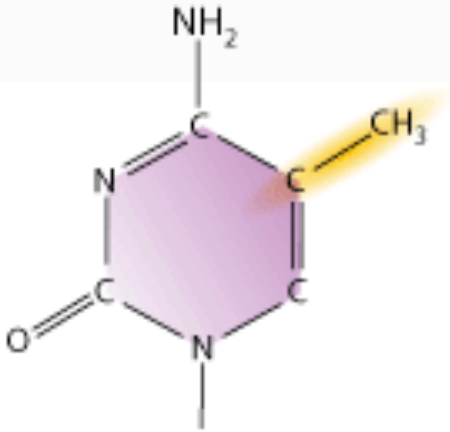
Figure 1: Mechanisms involved in chromatin modification

Brain function and chromatin plasticity

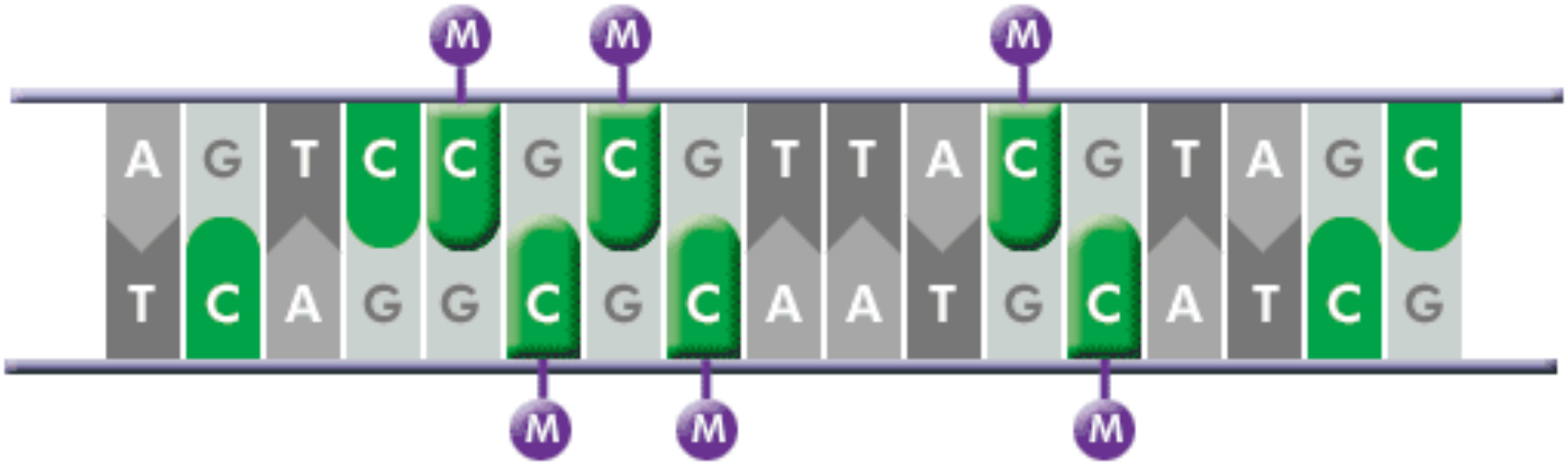
Catherine Dulac Nature 465:728–735, 2010

doi:10.1038/nature09231

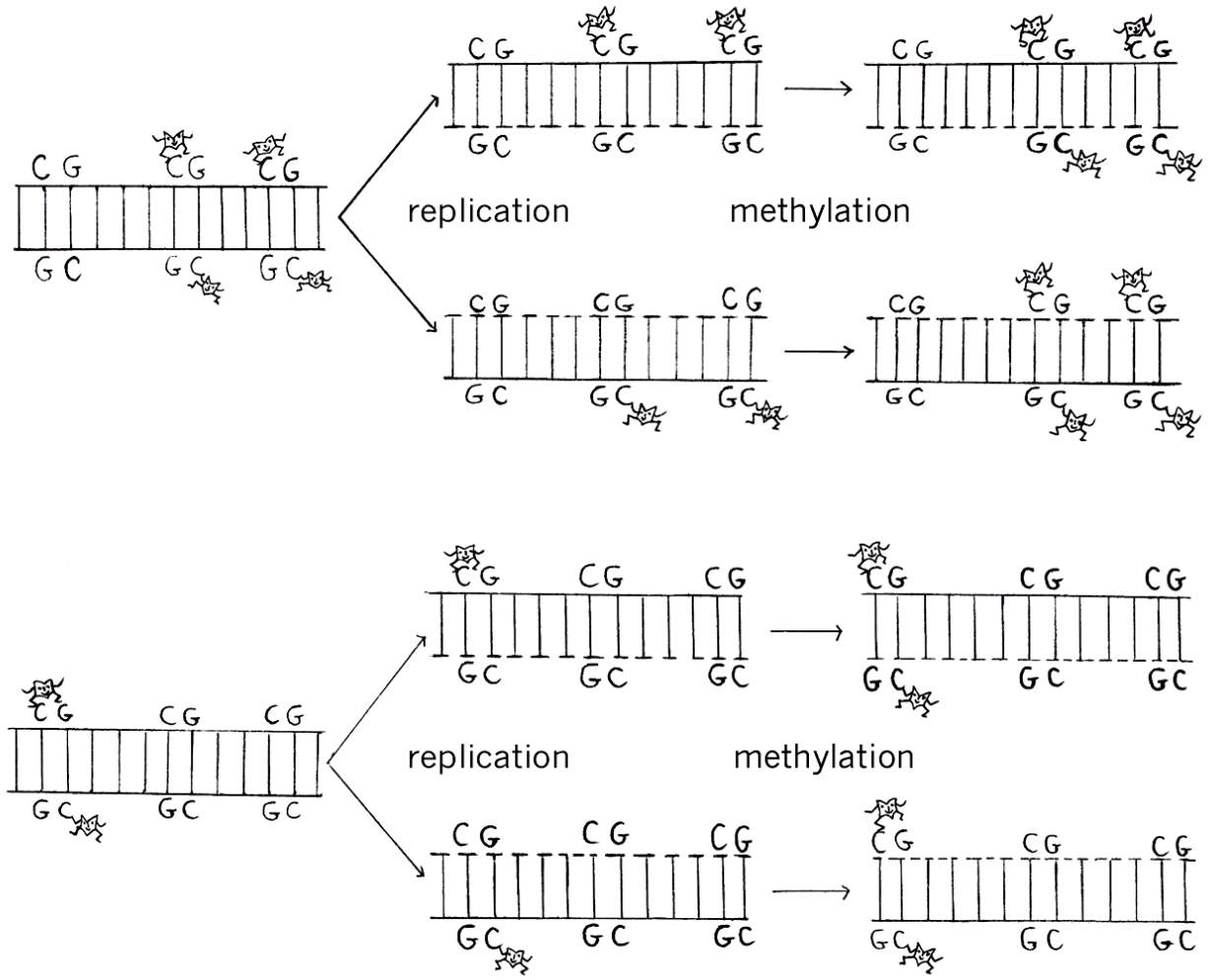




DNA Methylation is the addition of a methyl group (M) to the DNA base cytosine (C) in a CpG sequence.

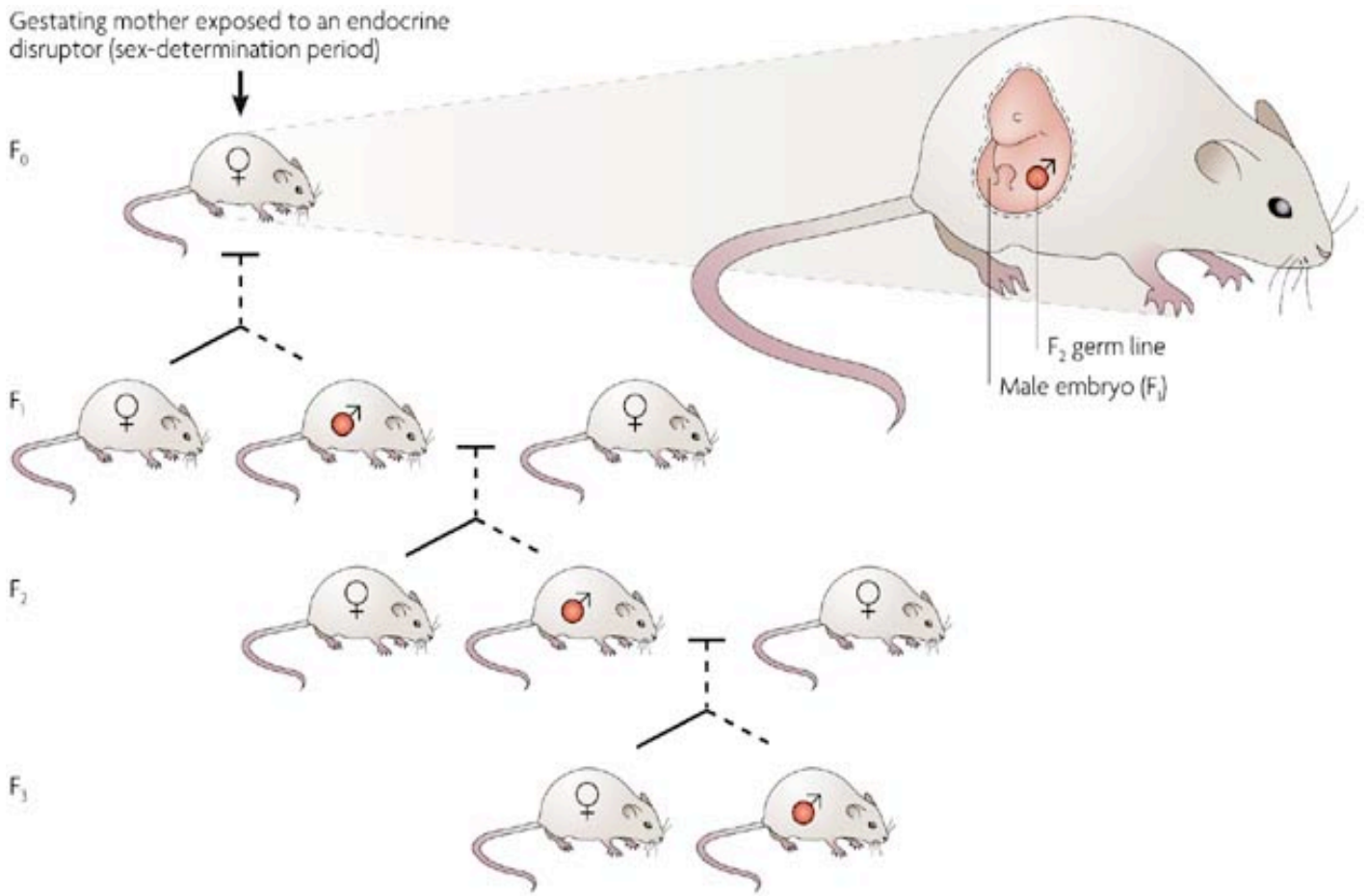


Replication of two DNA methylation patterns



Jablonka & Lamb *Evolution in Four Dimensions* 2005, p. 129

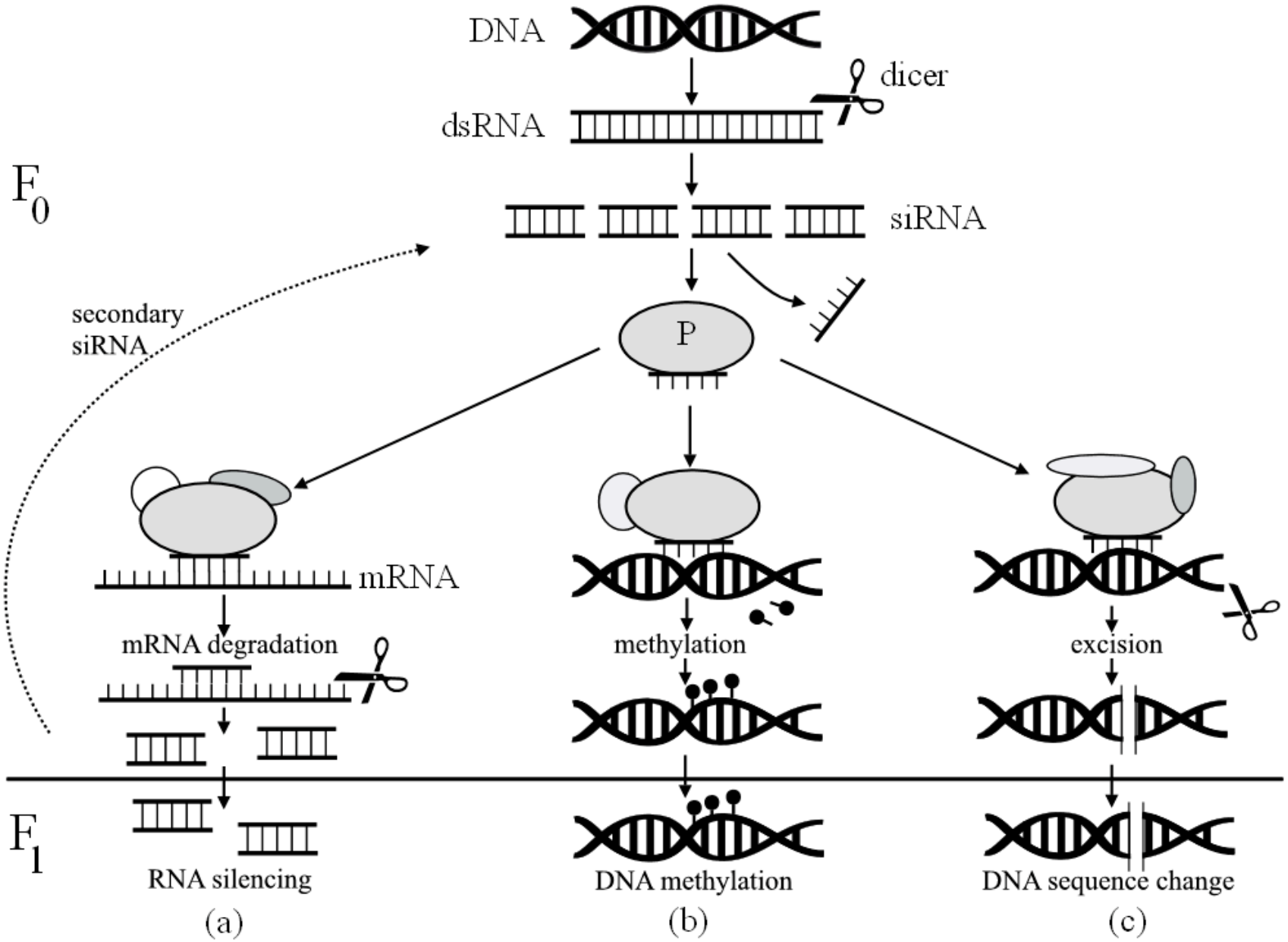
Germline transmission of induced changes



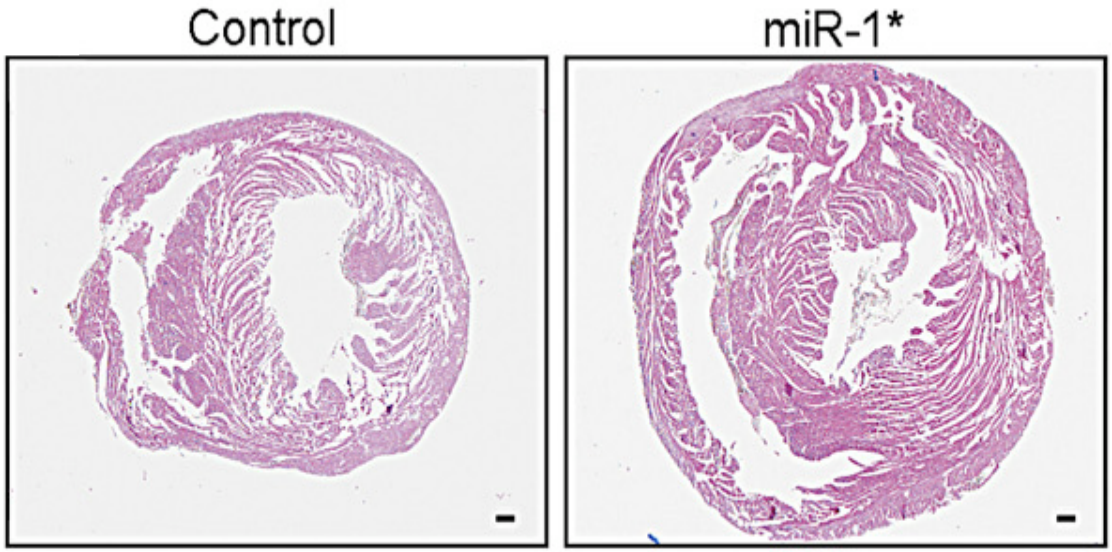
Jirtle and Skinner 2007

Transgenerational Disease Etiology - Vinclozolin

- Spermatogenic Defect (>90%)
- Male infertility (complete ~10%, severe 20%)
- Premature aging (~30%)
- Kidney disease (~40%)
- Prostate disease (~50%)
- Increase in tumor formation (~20%)
- Pre-eclampsia-like (hypertension) during late pregnancy (~15%)


DNA
dicer
dsRNA
F0
siRNA
secondary
siRNA
P
mRNA
mRNA degradation
methylation
excision
F1
RNA silencing
DNA methylation
DNA sequence change
(a)
(b)
(c)

Inherited cardiac hypertrophy induced by injection of early embryos with a specific microRNA



Sections of the ventricular walls

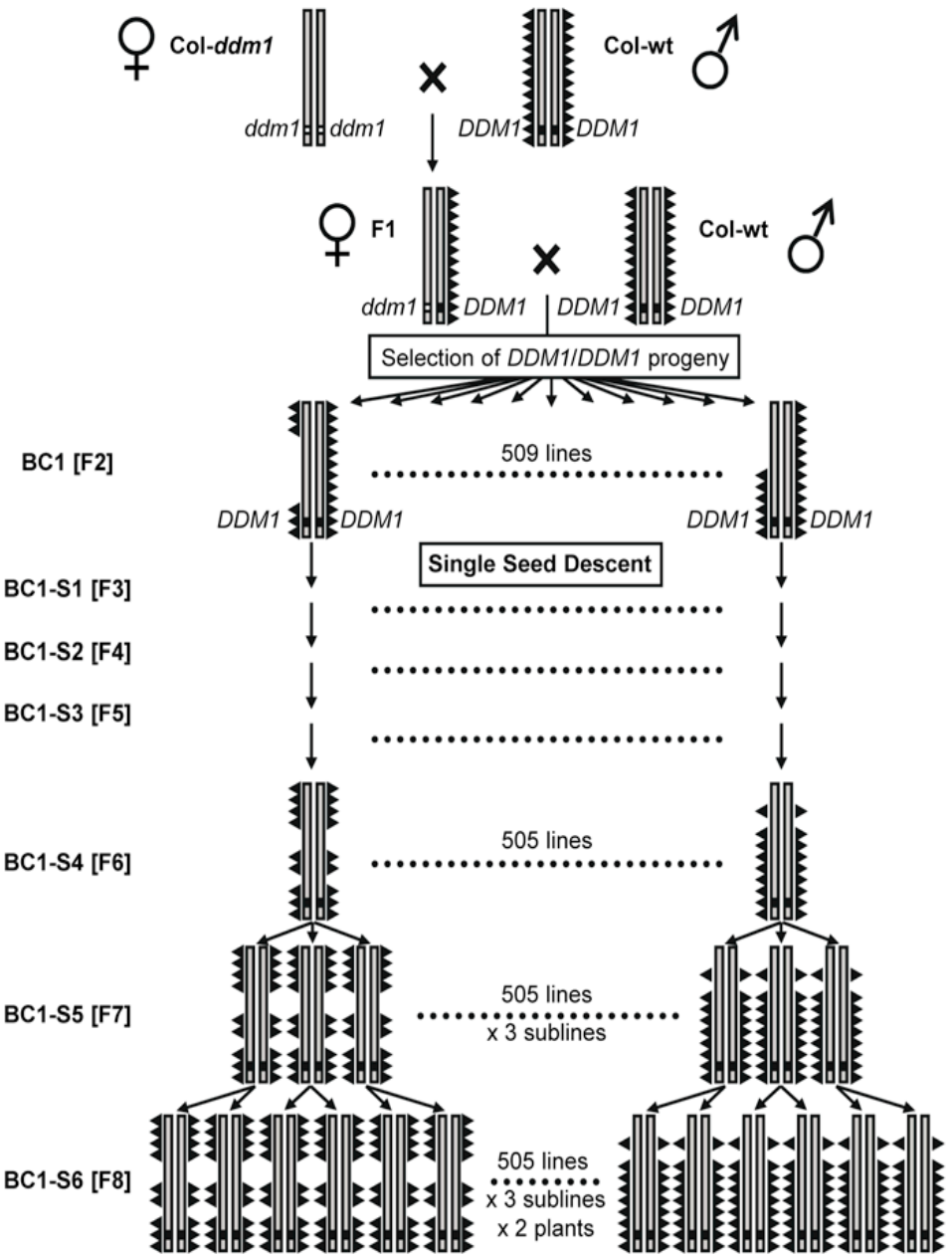
Wagner *at al*. *Developmental Cell* 14, 962, 2008

Cases of trans-generational epigenetic inheritance

Jablonka and Raz (2009) surveyed the literature on transgenerational epigenetic inheritance and found

- 12 cases of epigenetic inheritance in bacteria
- 8 cases of epigenetic inheritance in protists, mostly in ciliates where a large number of loci and traits have been studied
- 19 cases in fungi, involving many phenotypes and loci
- 38 cases in plants, involving many loci and many traits; often they were induced by genomic stresses
- 27 cases in animals, some involving many loci; stress sometimes induced multiple epigenetic changes

Many more!!!


Col-ddm1
ddm1 ddm1
Col-wt
DDM1 DDM1
F1
ddm1 DDM1
DDM1 DDM1
Selection of DDM1/DDM1 progeny
BC1 [F2]
509 lines
DDM1 DDM1
DDM1 DDM1
Single Seed Descent
BC1-S1 [F3]
BC1-S2 [F4]
BC1-S3 [F5]
BC1-S4 [F6]
505 lines
BC1-S5 [F7]
505 lines
x 3 sublines
BC1-S6 [F8]
505 lines
x 3 sublines
x 2 plants

Selection is part of development

Immune system

Nervous system

Somatic selection (could be inherited if gets to germline)

Within cell (spindle formation, promoter scrambling)

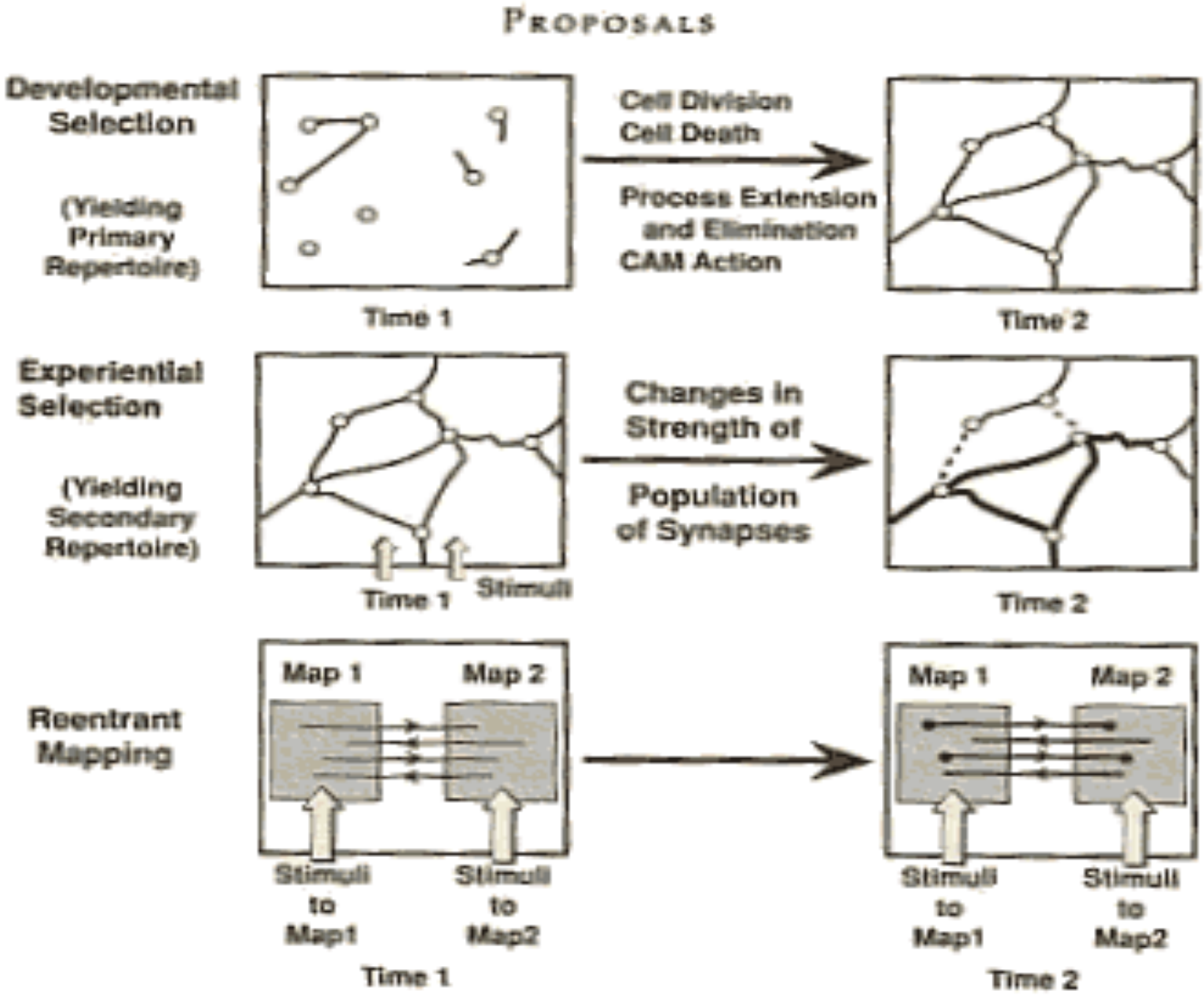
Behavior – trial and error learning (transmitted through social learning) .

In almost all these cases innovation is required. Exploration.

Selective stabilization may have been of crucial importance during chemical, pre-biotic evolution.

Open ended plasticity and the origins of phenotypic novelty

Exploration and selective stabilization: the generation of a large set of local variations and interactions, from which only a small subset is eventually stabilized and manifested. Which particular output is realized depends on the initial conditions, the ease with which developmental trajectories can be deflected away from their current paths, and the number of possible points around which development can be stably organized (attractors).


PROPOSALS
Developmental Selection
(Yielding Primary Repertoire)
Cell Division
Cell Death
Process Extension and Elimination
CAM Action
Time 1
Time 2
Experiential Selection
(Yielding Secondary Repertoire)
Changes in Strength of
Population of Synapses
Time 1
Stimuli
Time 2
Reentrant Mapping
Map 1
Map 2
Stimuli to Map1
Stimuli to Map2
Time 1
Map 1
Map 2
Stimuli to Map1
Stimuli to Map2
Time 2

An **attractor** is a set towards which a dynamical system evolves over time. That is, points that get close enough to the attractor remain close even if slightly disturbed. Geometrically an attractor can be a point, a curve, a manifold, or even a complicated set with a fractal structure known as a strange attractor.

Heritable plasticity following regulatory exploration

Braun and his colleageus engineered haploid strain in which the essential gene *HIS3*, which codes for an enzyme from the histidine biosynthesis pathway, was deleted from the chromosome and introduced back into the cell on a plasmid under the promoter of *GAL1*, a gene from the galactose utilization system. Histidine biosynthesis and galactose utilization are two evolutionarily conserved modules that are fundamentally different in their function and regulation. The GAL system, and with it the essential *HIS3*, are strongly repressed in glucose medium, so when histidine is not supplied, cells are severely challenged to produce histidine, and significant adaptation is required for their survival. It was found that after a lag 50% of the cells grown on glucose and without histidine started growing. In these cells the regulation of the *GAL1* promoter was altered and this altered regulation was inherited for hundreds of generations (Stolovicki et al. 2006; Stern et al. 2007).

Conclusions

Heredity may be developmentally constructed.

Development involves exploratory and selective mechanisms.

Natural selection can be seen as a special case of selective stabilization.

Questions???