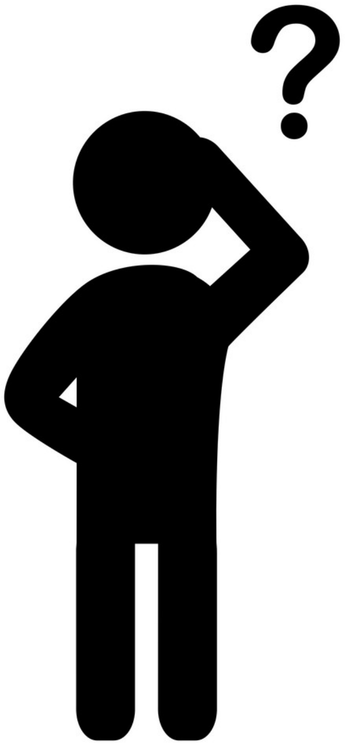
Níveis de Modularidade

‘Modularidade: Conectando padrões e processos em evolução multivariada’

Why study variation in biology?



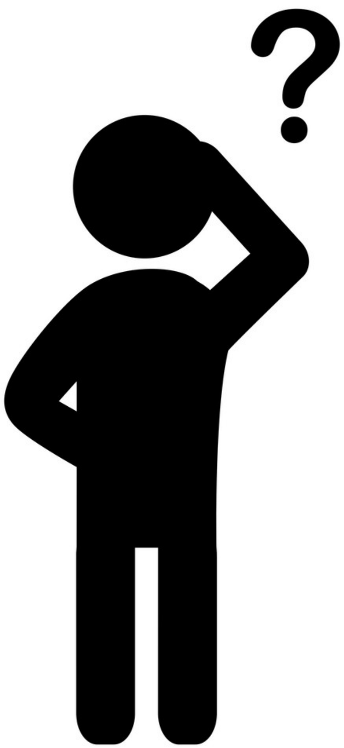
Where does variation comes from?

How is variation organized in populations?

What are the evolutionary consequences of a particular organization of variation?

Why study variation in biology?

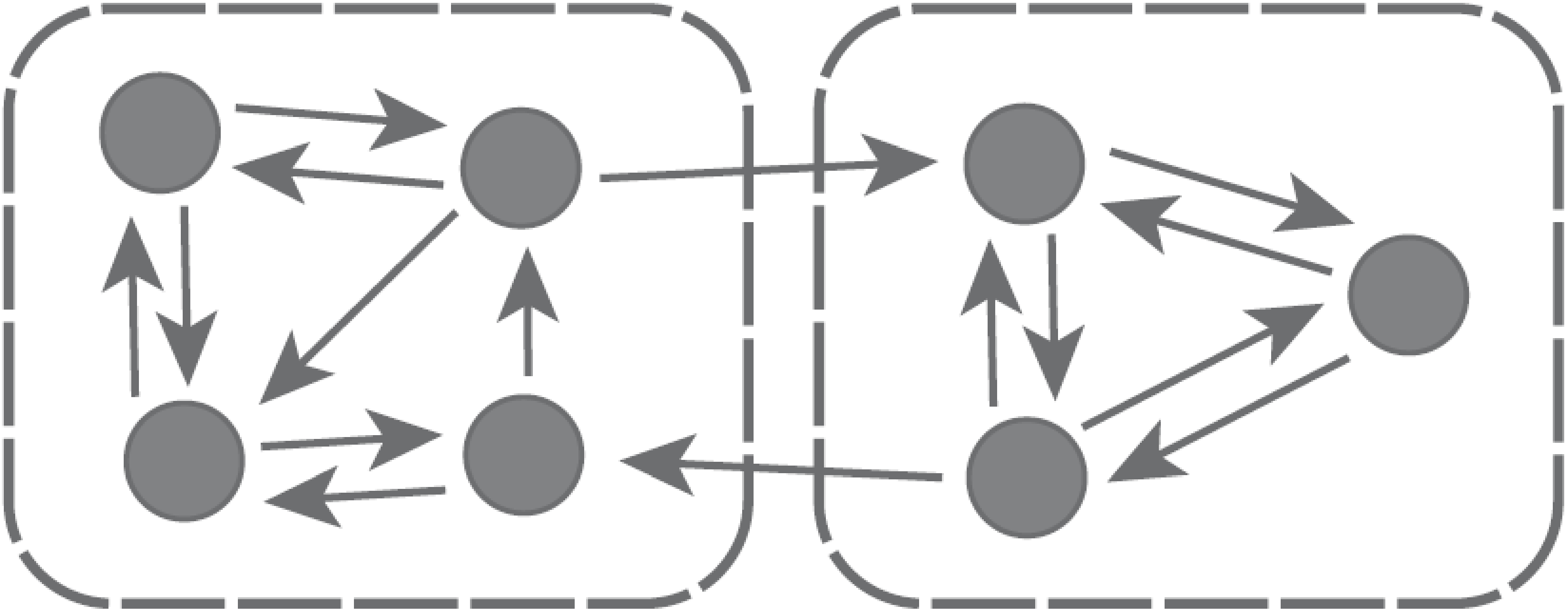
Where does variation comes from?



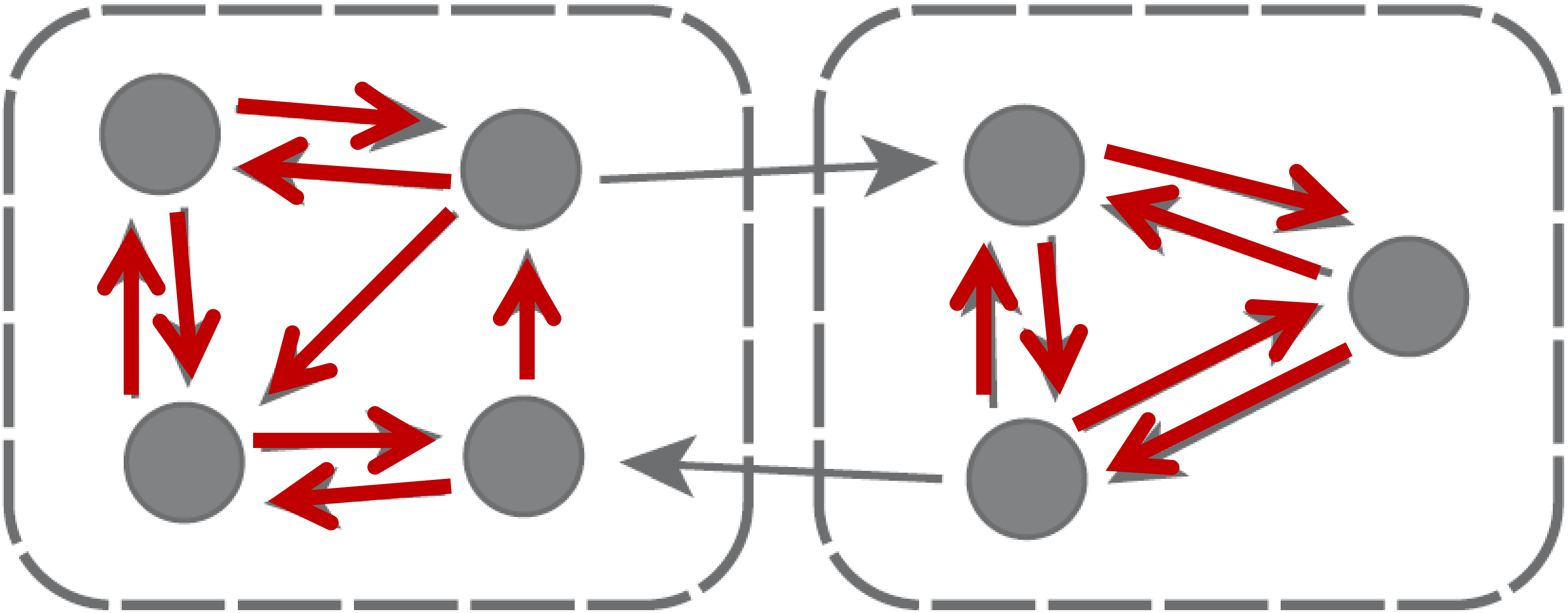
How is variation organized in populations?

What are the evolutionary consequences of a particular organization of variation?

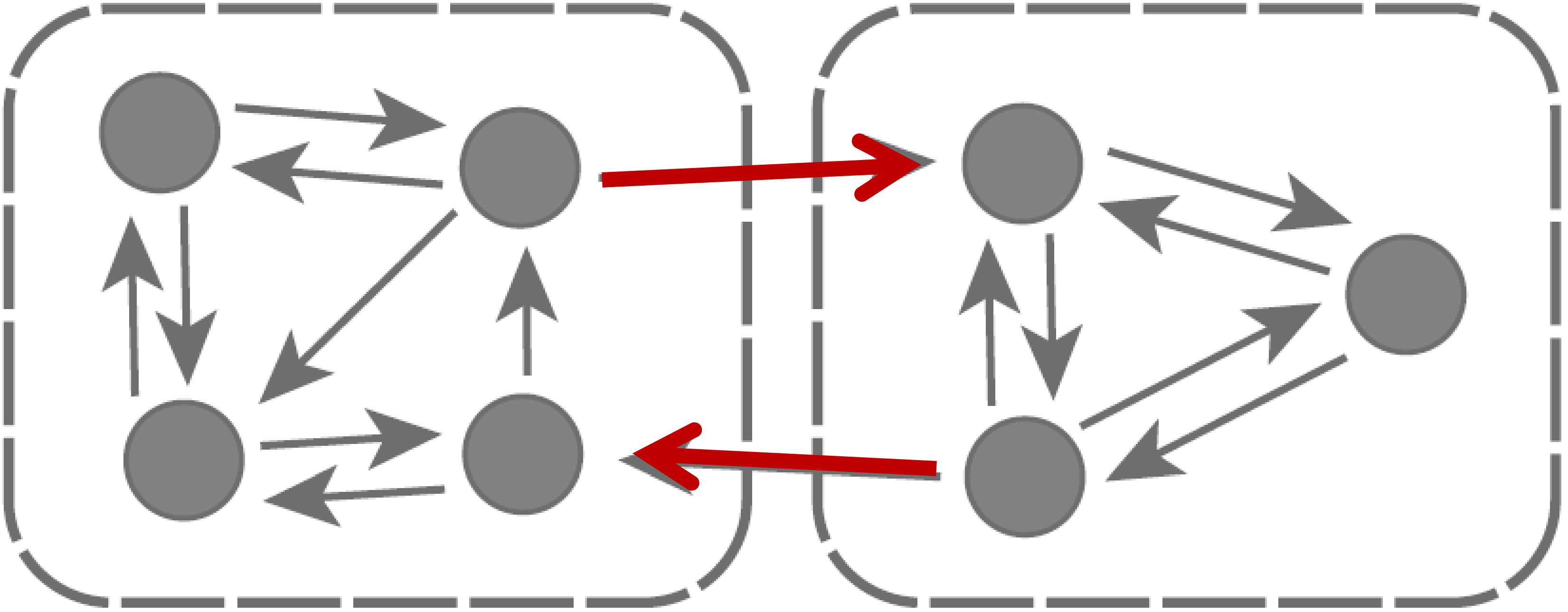
Integration within sets of traits



Integration within sets of traits

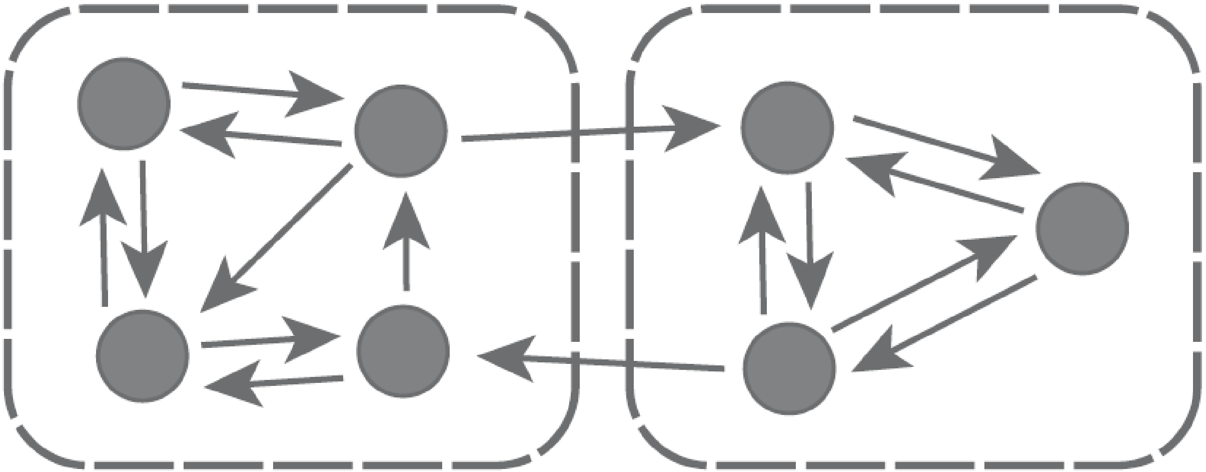


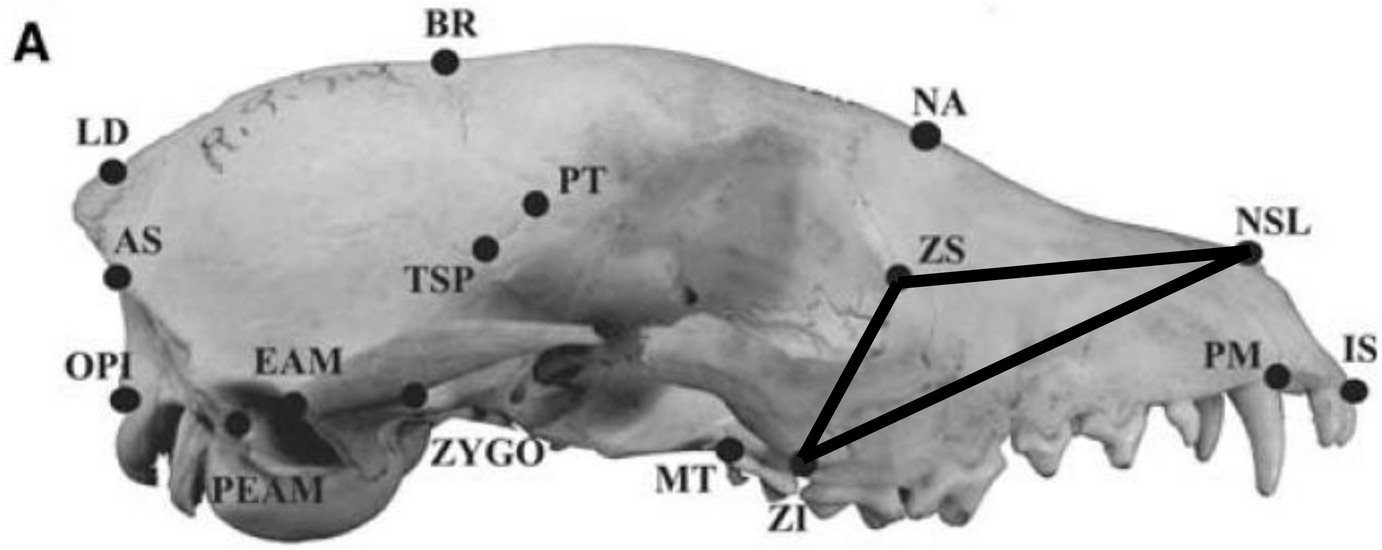
Modularity: semi-independence between sets



Why are these set of traits interpreted as modules??

Pattern and magnitude of integration

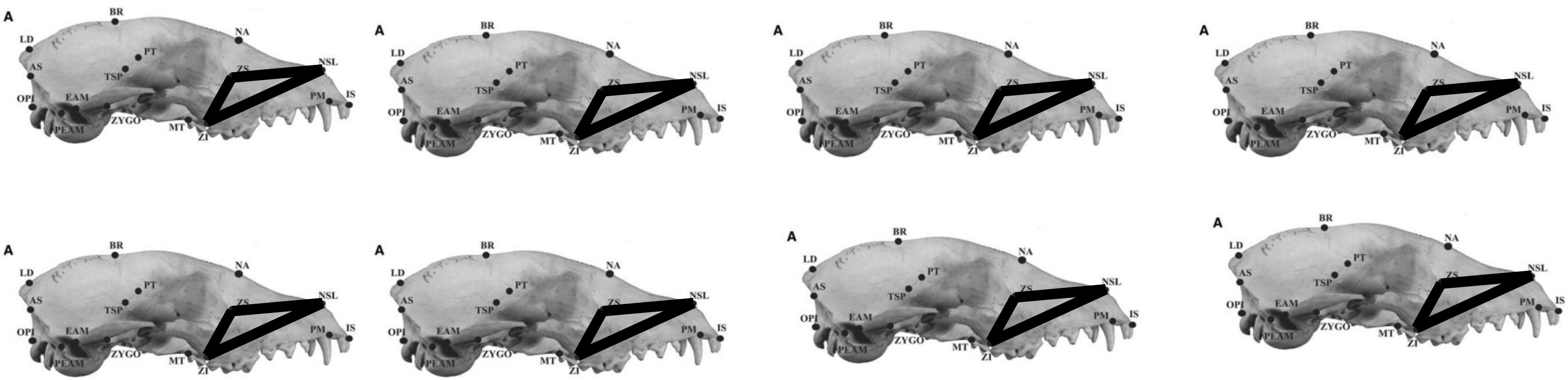


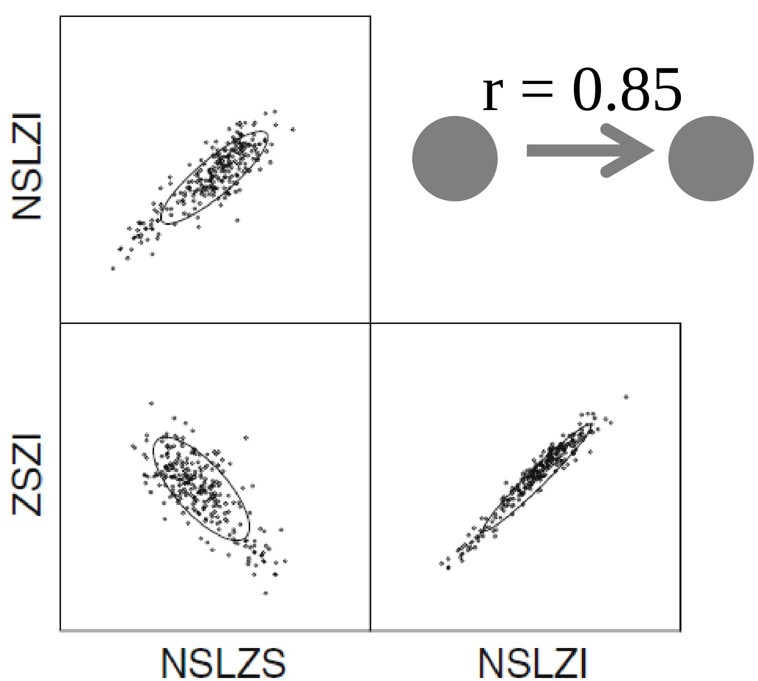


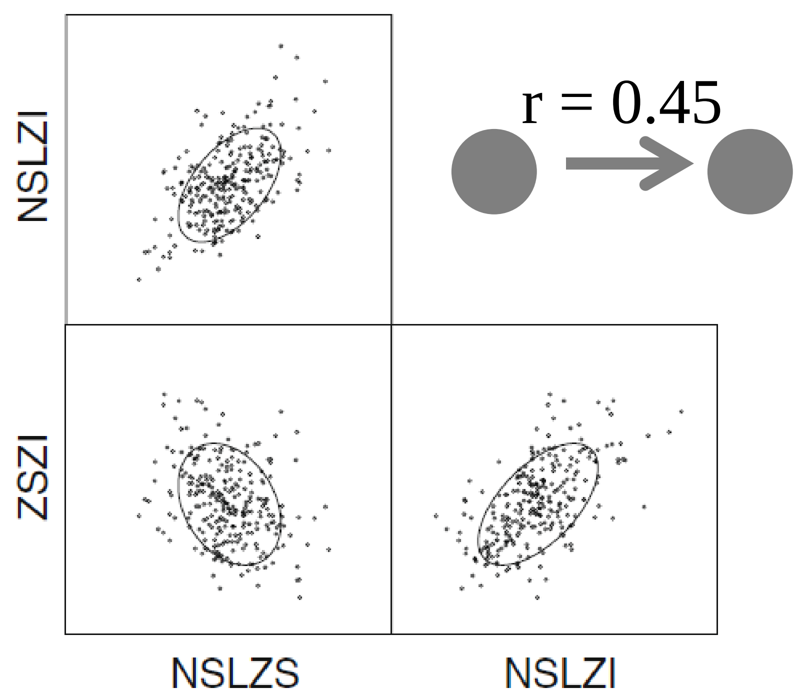
Porto et al. 2009

Same pattern, different magnitude of integration

Porto et al. 2009

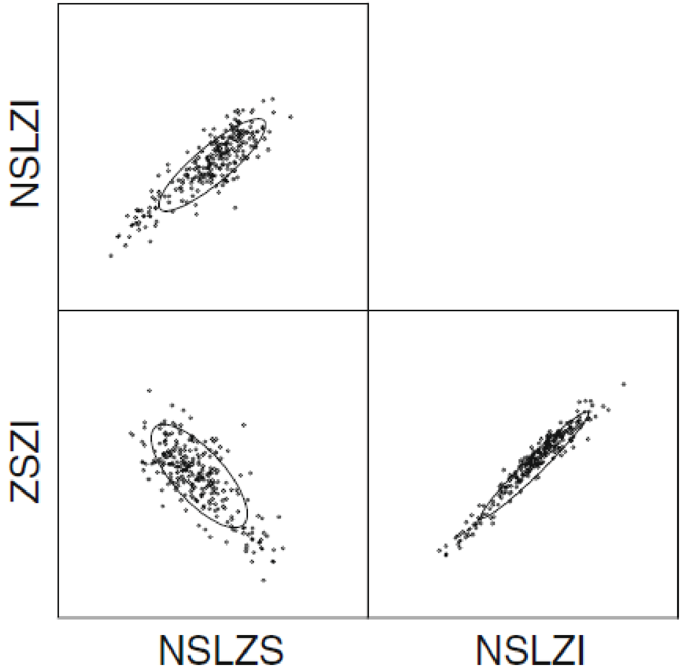


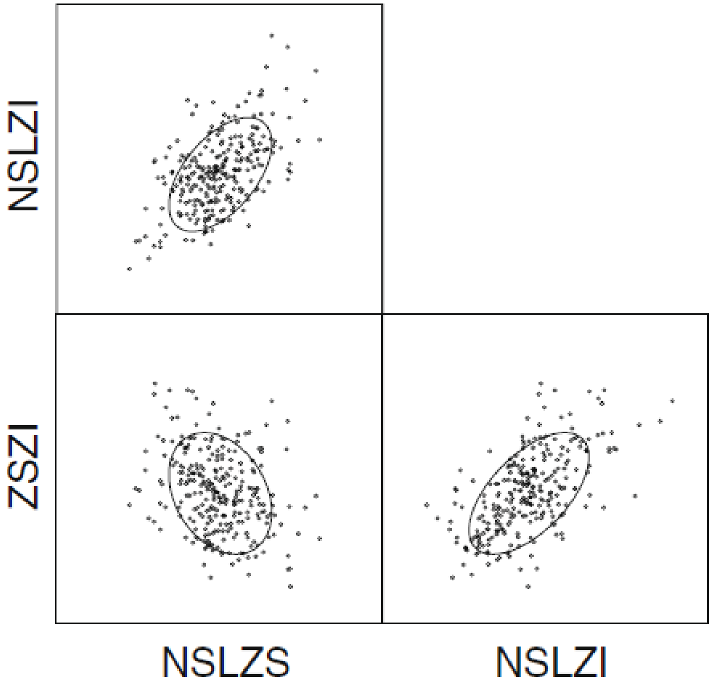




Same pattern, different magnitude of integration

Porto et al. 2009





A

	NSLZS	NSLZI	ZSZI
NSLZS	1		
NSLZI	0.85	1	
ZSZI	-0.70	0.90	1

B

	NSLZS	NSLZI	ZSZI
NSLZS	1		
NSLZI	0.45	1	
ZSZI	-0.30	0.50	1

How is variation organized in populations?

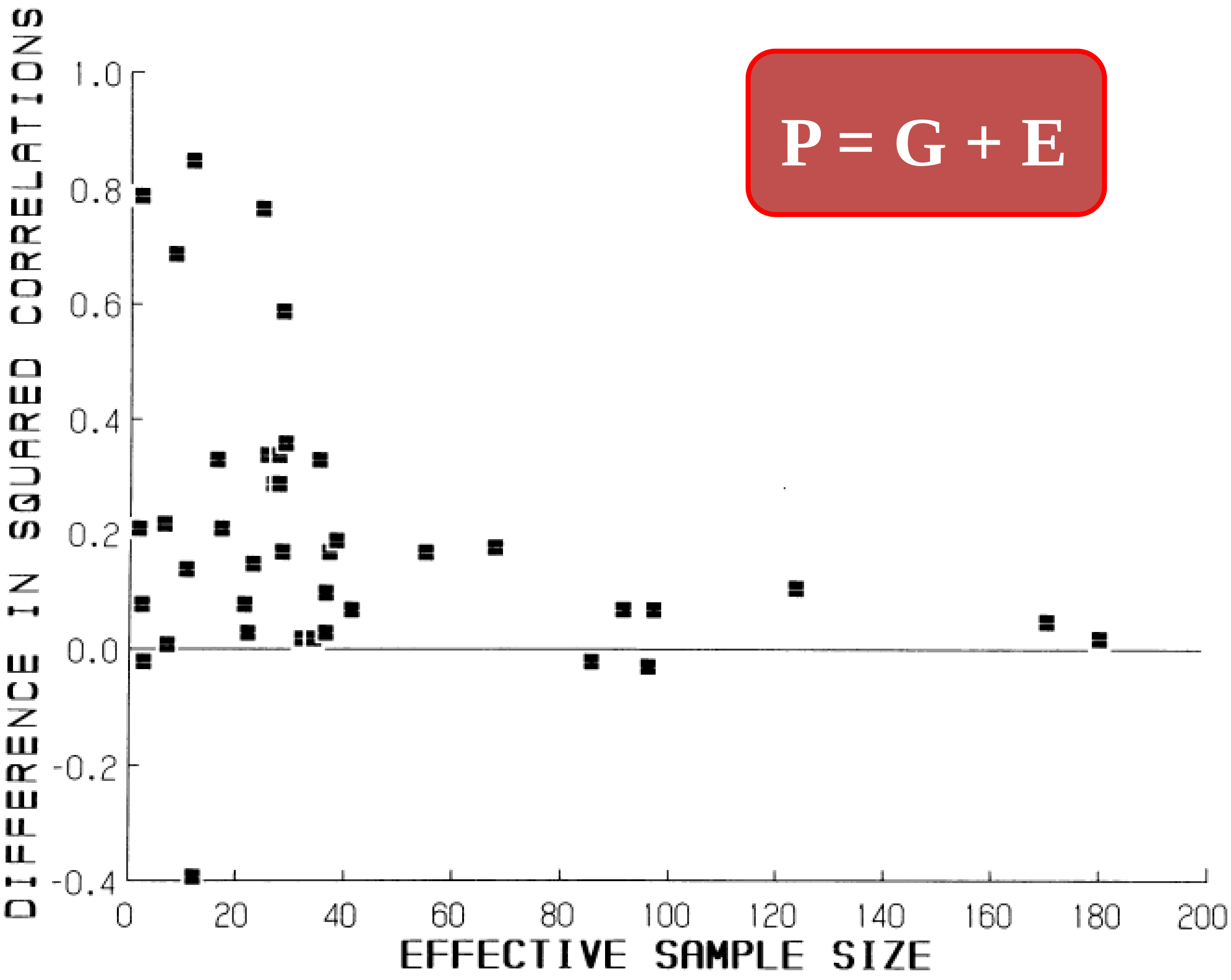
How is variation organized in populations?

A	NSLZS	NSLZI	ZSZI
NSLZS	1		
NSLZI	0.85	1	
ZSZI	-0.70	0.90	1

B	NSLZS	NSLZI	ZSZI
NSLZS	1		
NSLZI	0.45	1	
ZSZI	-0.30	0.50	1

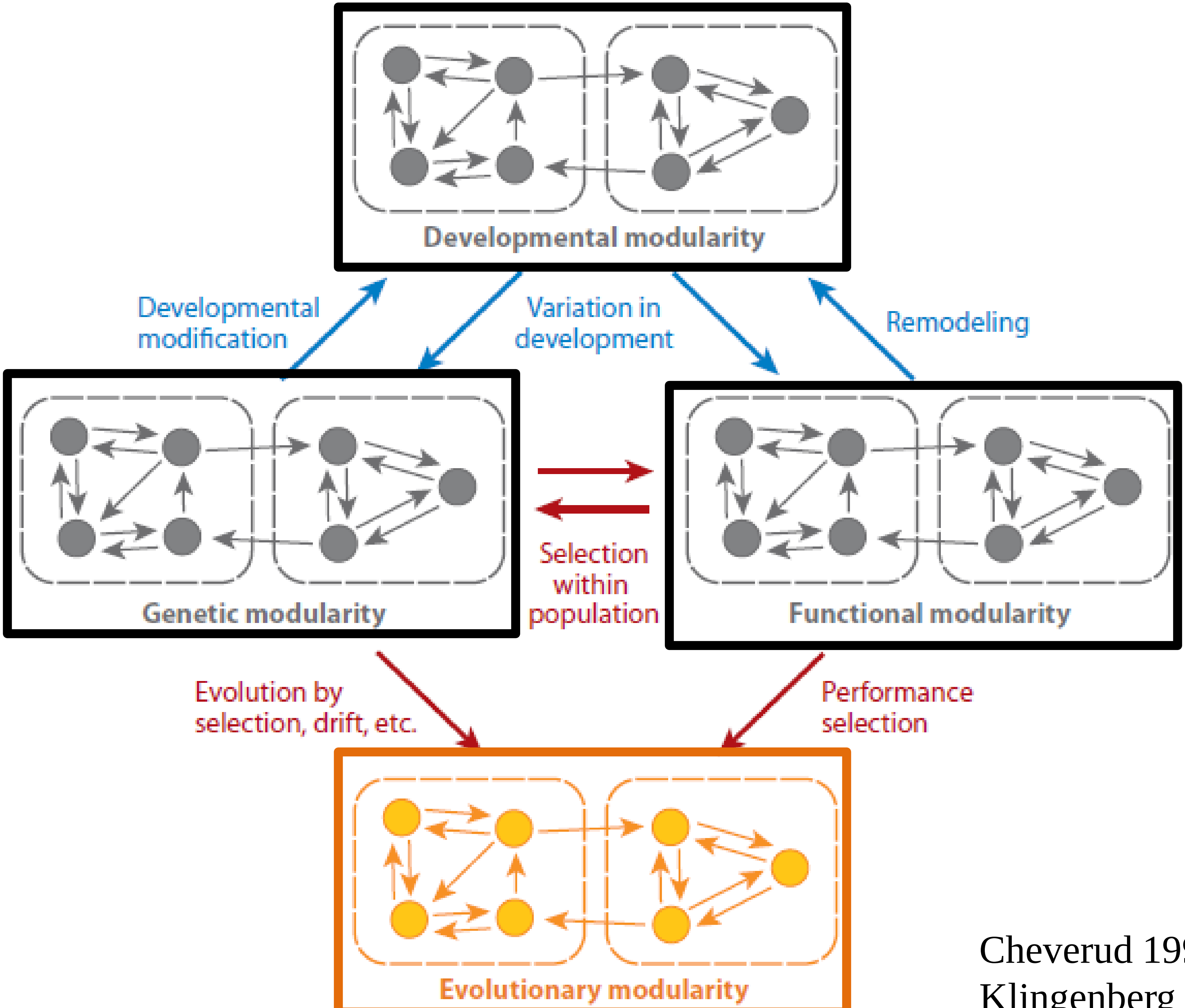
In G-matrices and P-matrices!

Cheverud's Conjecture (1988)



P = G + E

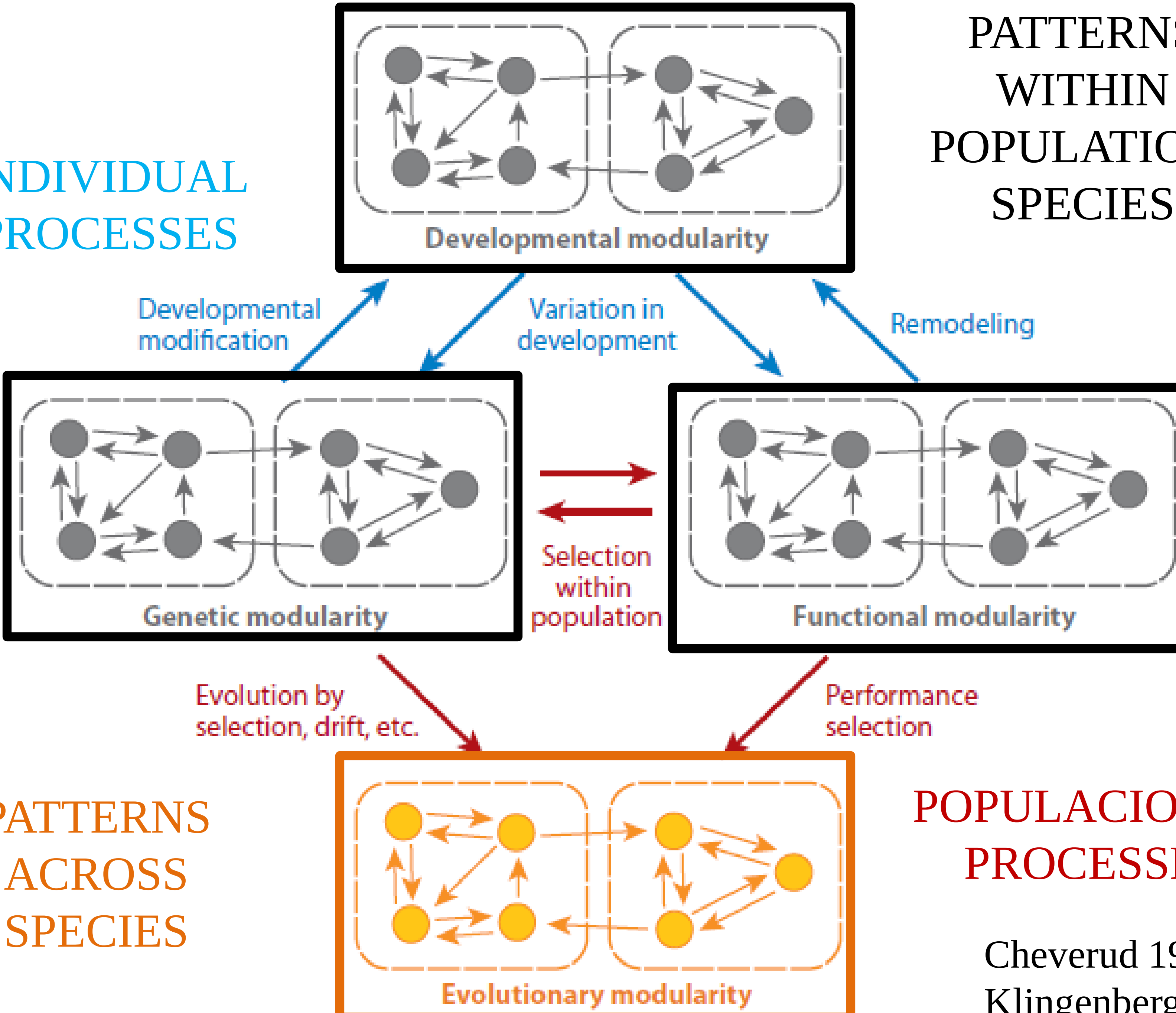
What processes determine the patterns and magnitudes of integration among traits???



Cheverud 1996
Klingenberg 2008

PATTERNS WITHIN POPULATION/ SPECIES

INDIVIDUAL PROCESSES

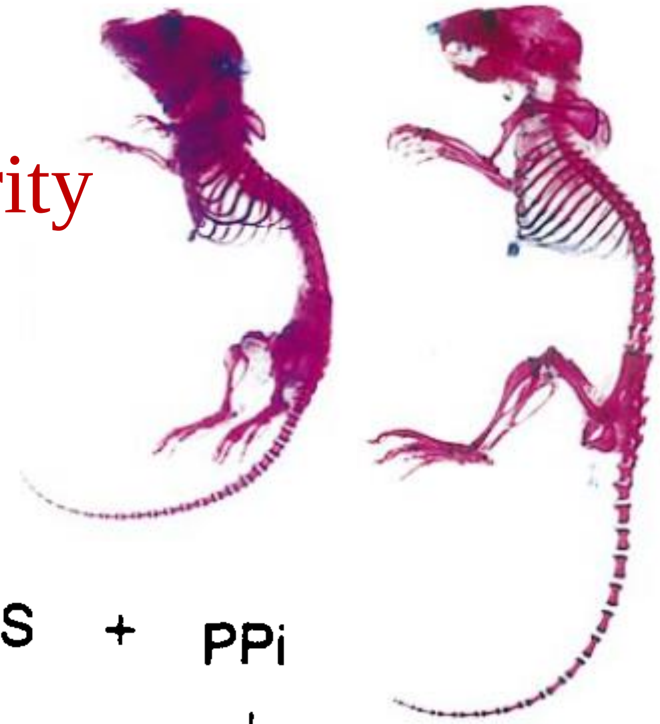


PATTERNS ACROSS SPECIES

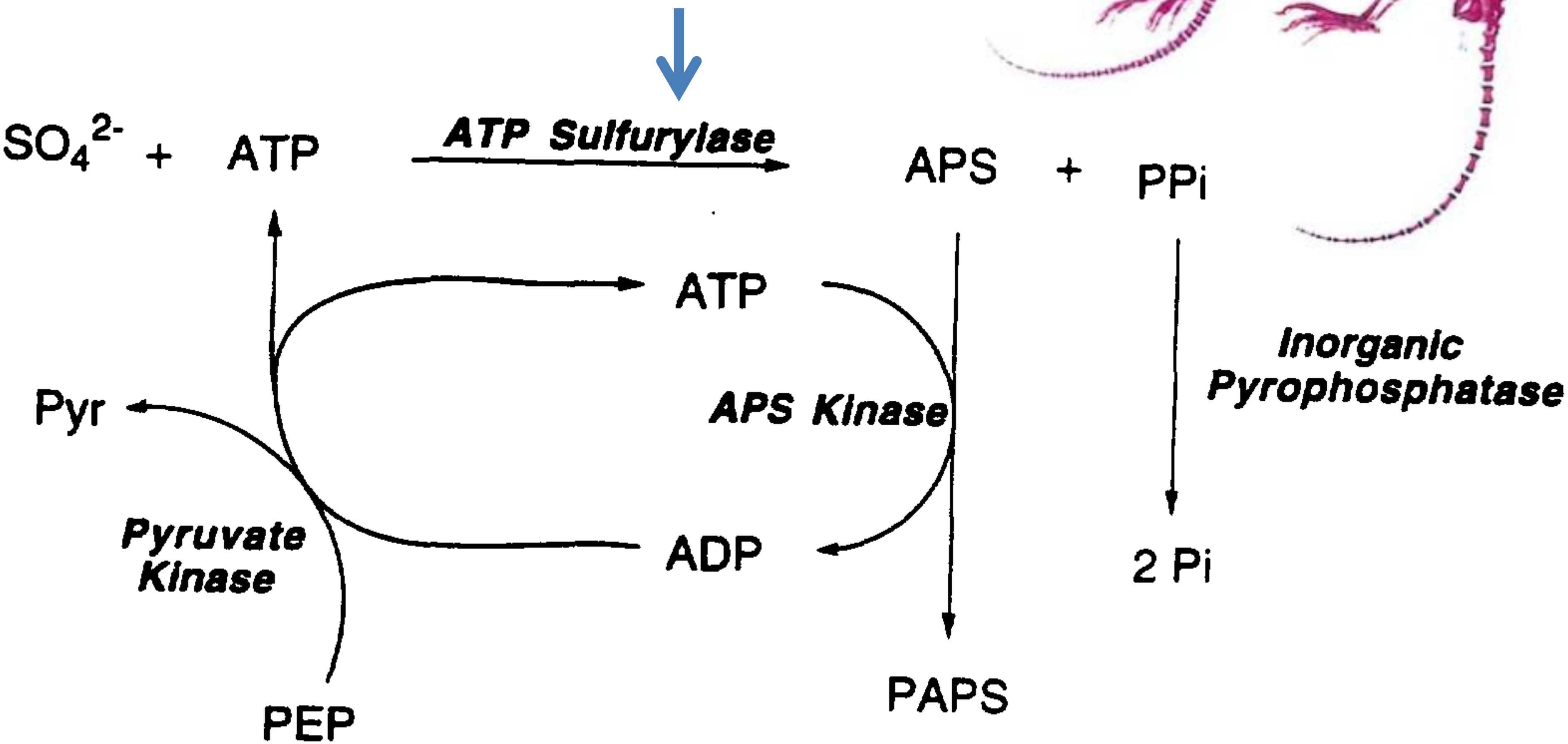
POPULACIONAL PROCESSES

Cheverud 1996
Klingenberg 2008

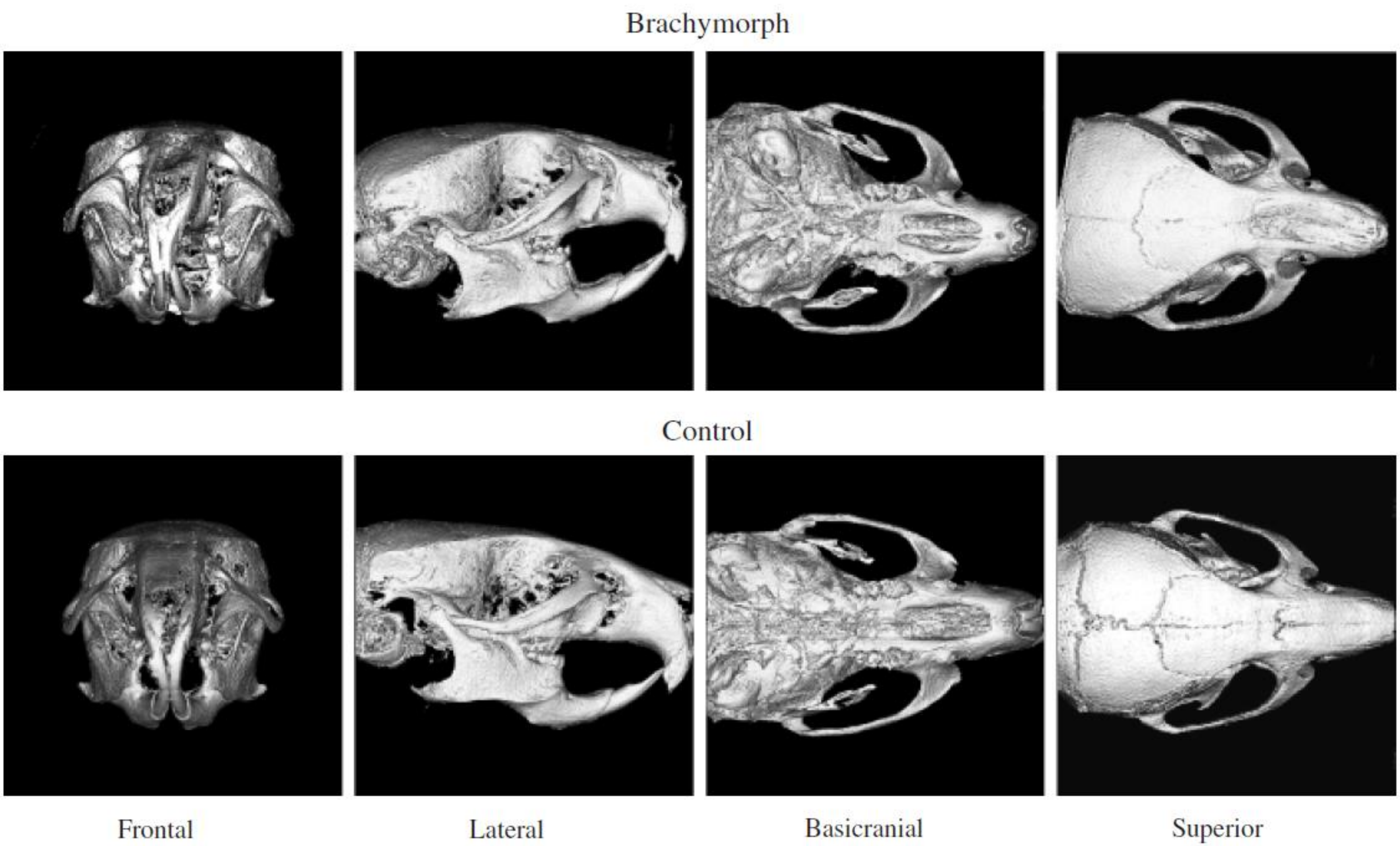
Developmental modification: genetic to developmental modularity



Single mutation

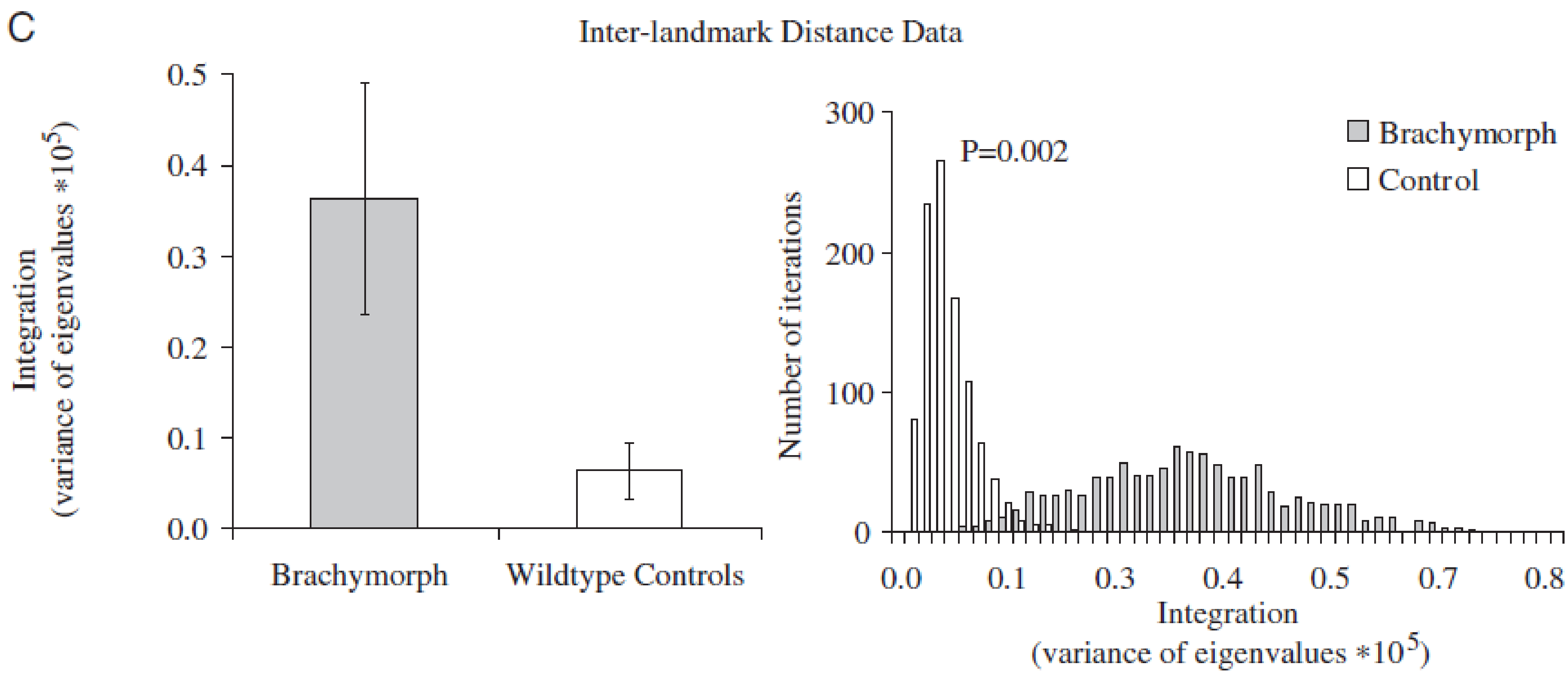


Brachyomorph phenotype

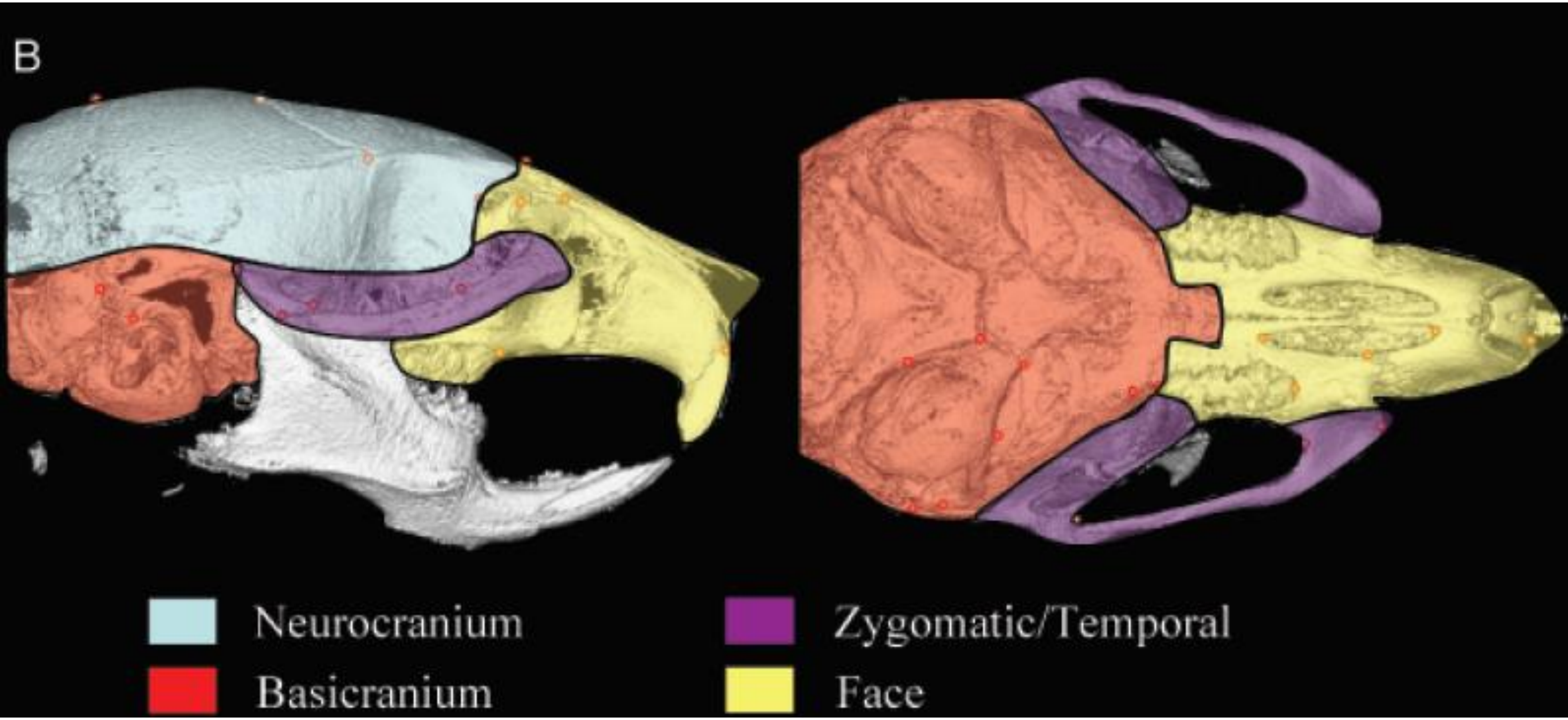


Hallgrímsson et al. 2006

Higher integration in the brachyomorph phenotype

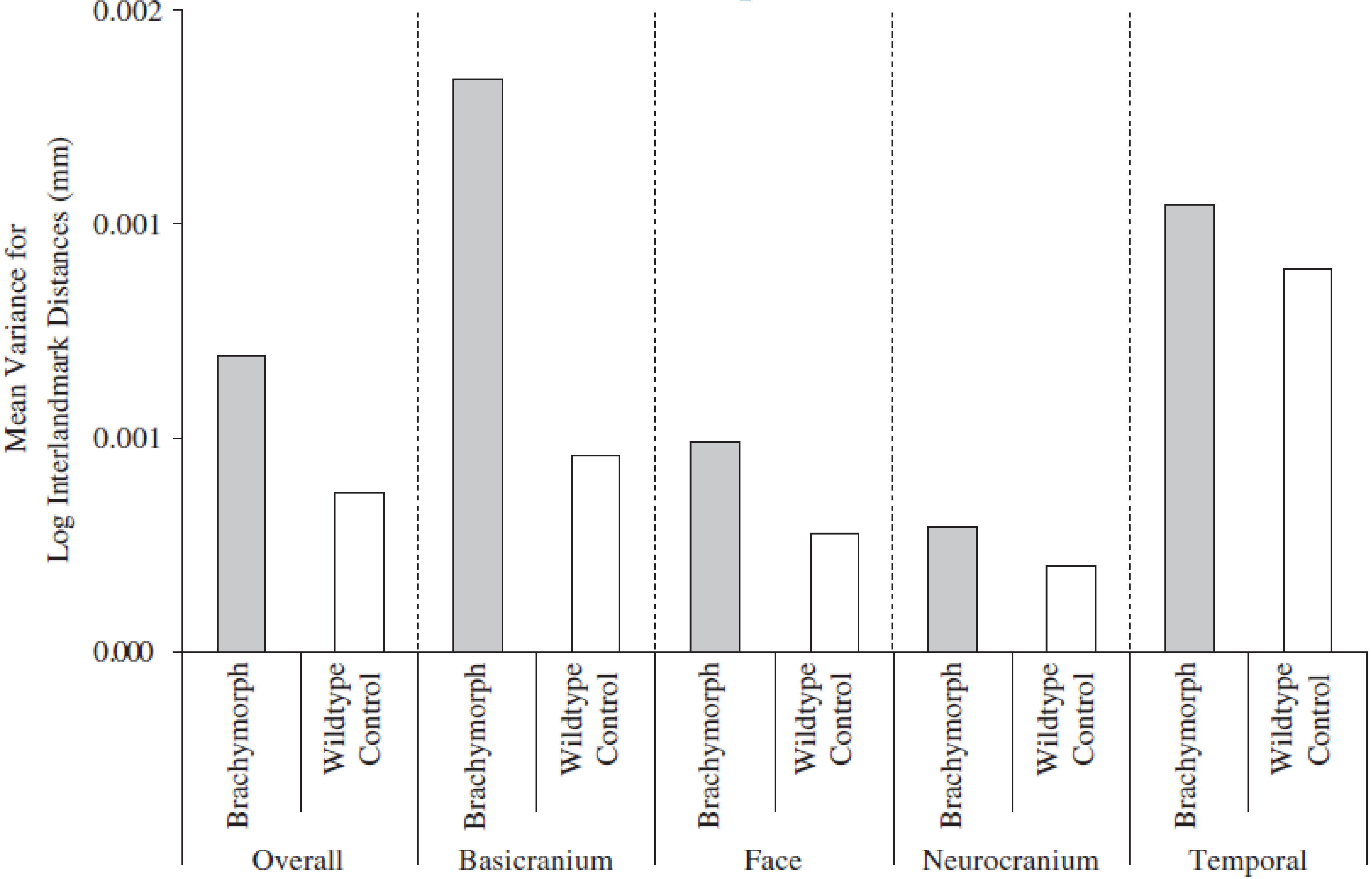


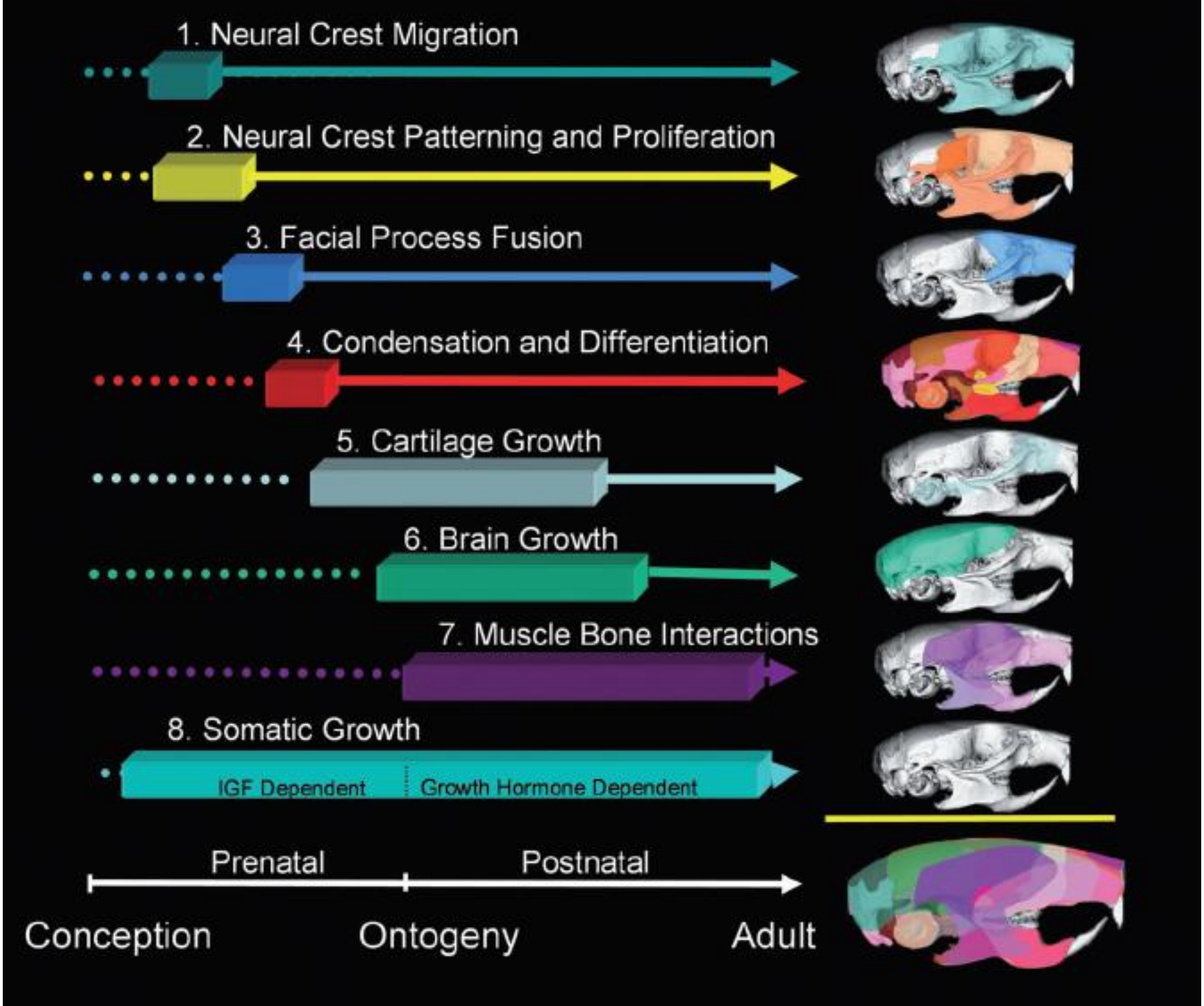
Developmental modules



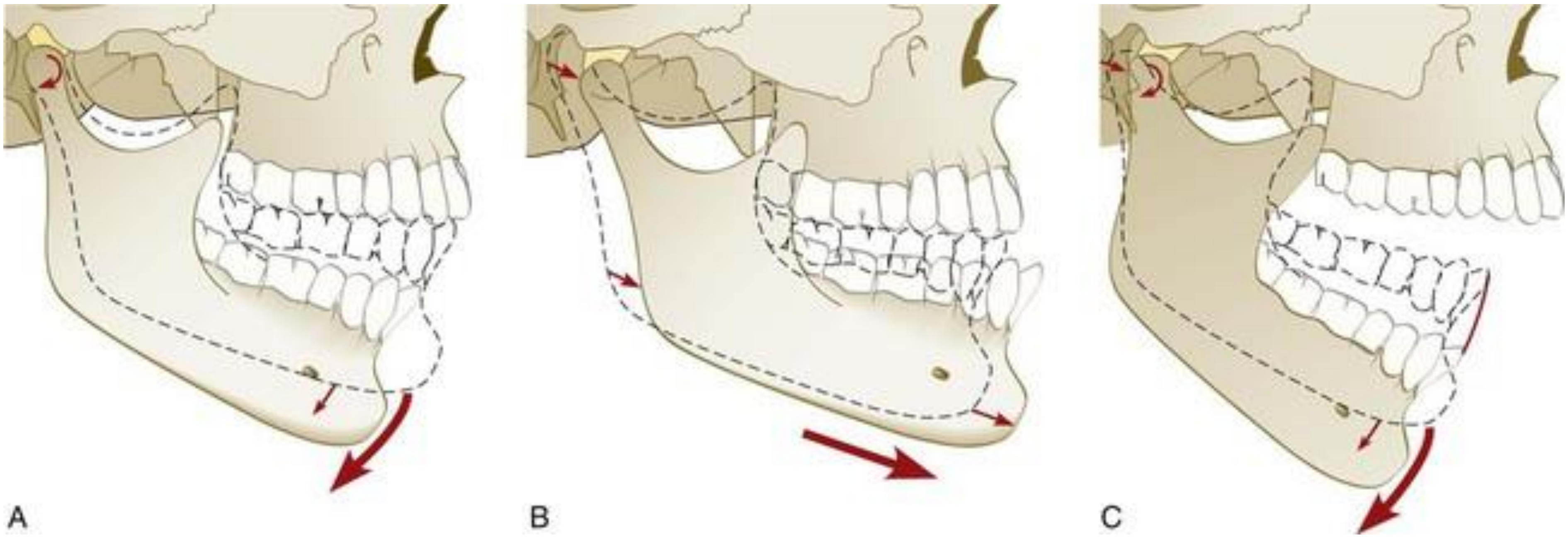
Divergent integration within developmental modules

WT and Bmp mutant matrix correlation = 0.3




1. Neural Crest Migration
2. Neural Crest Patterning and Proliferation
3. Facial Process Fusion
4. Condensation and Differentiation
5. Cartilage Growth
6. Brain Growth
7. Muscle Bone Interactions
8. Somatic Growth
IGF Dependent
Growth Hormone Dependent
Prenatal
Postnatal
Conception
Ontogeny
Adult

Remodeling:
functional to developmental modularity



Corruccini and Beecher 1982

Divergent masticatory demands and occlusal development

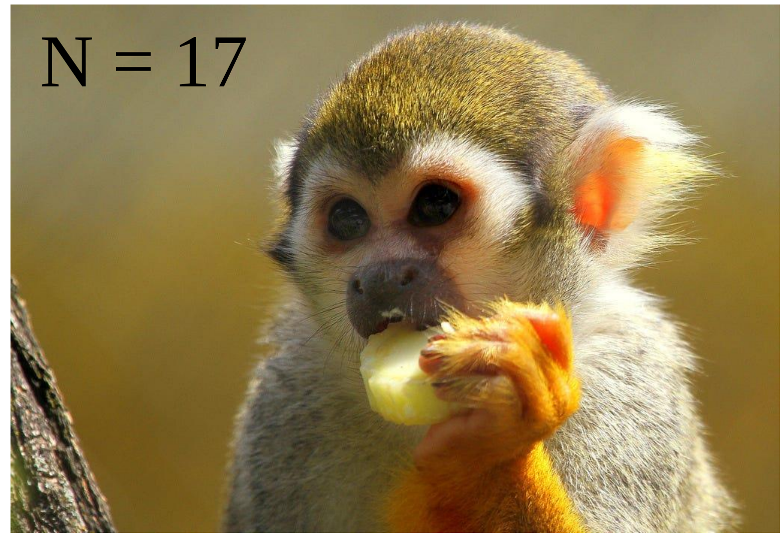


Table 1. Arch measurements of squirrel monkeys raised on natural hard diets (N = 24) and those raised on soft diets (N = 19). Values represent the mean ± standard deviation. Variance was homogeneous for all variables.

Variable	Measurement (mm)	
	Hard diet	Soft diet
Maxillary length to M^1	17.27 ± 0.83	17.49 ± 0.62
Maxillary length to C^1	9.76* ± 0.77	9.00 ± 0.76
Maxillary breadth at M^1	18.33* ± 0.83	17.57 ± 0.75
Maxillary breadth at P^3	17.12* ± 0.89	15.54 ± 0.65
Mandibular length to M_1	15.85 ± 0.87	15.51 ± 0.69
Mandibular breadth at M_1	14.38* ± 0.65	13.56 ± 0.58
Palate height	3.99* ± 0.38	3.44 ± 0.28
Maxillary (M^1) breadth/length ratio	1.056* ± 0.037	1.005 ± 0.045
Mandibular breadth/length ratio	0.908* ± 0.034	0.875 ± 0.028

*Mean significantly larger at P = .01.

Mean trait correlation in soft diet = 0.48

Mean trait correlation in hard diet = 0.68

Developmental plasticity: developmental to genetic modularity

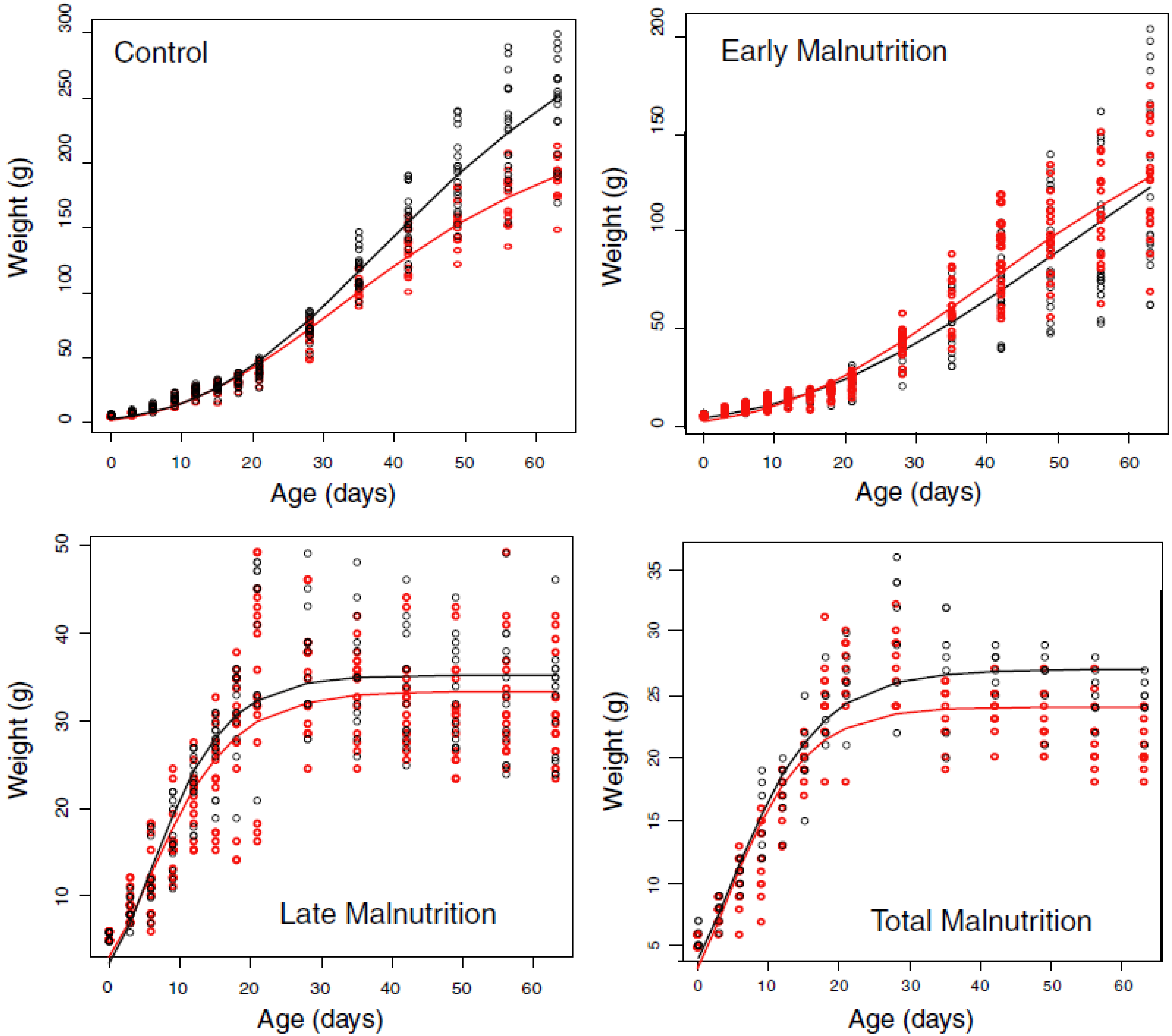
González et al. 2010

CONTROL:
diet *ad. libitum*

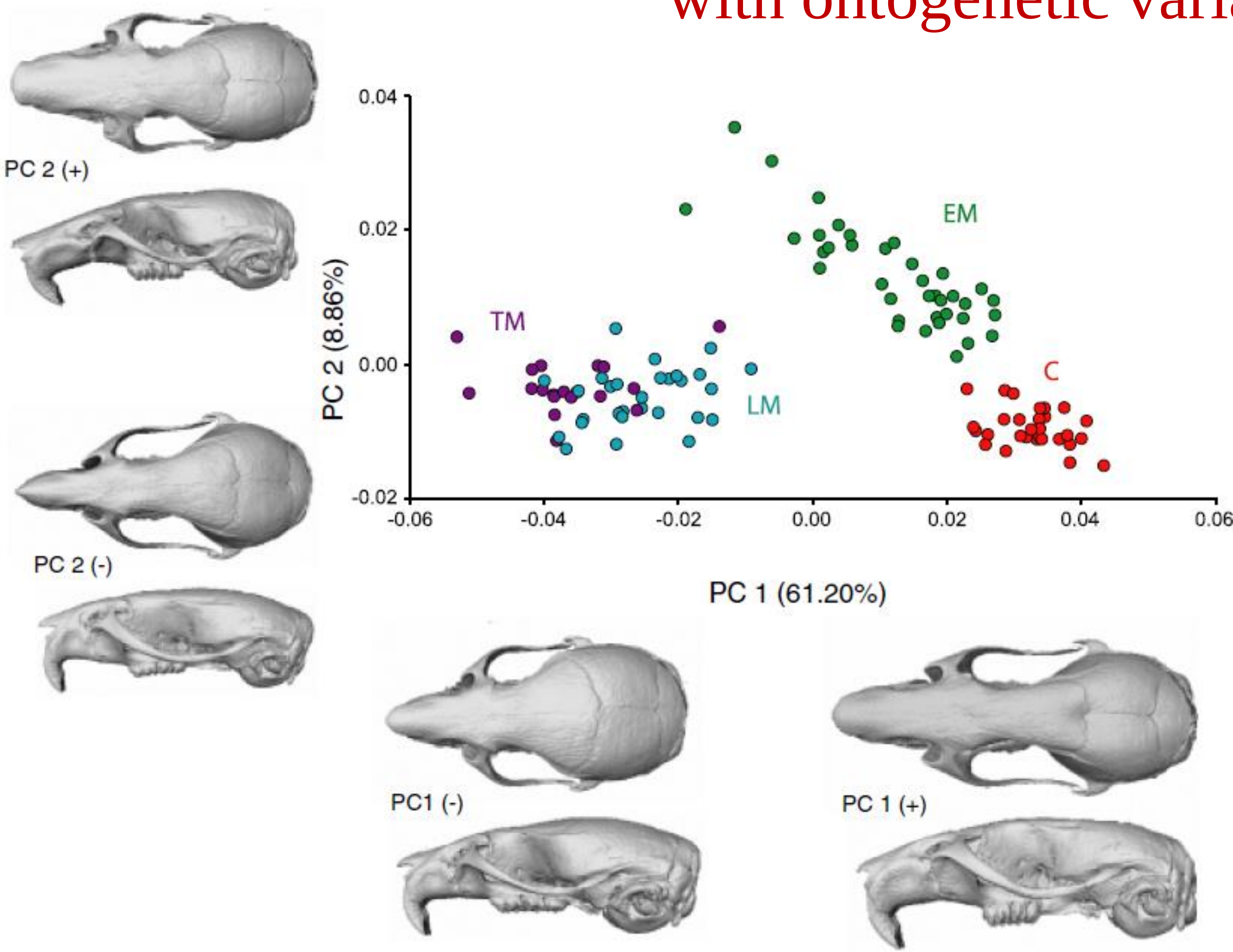
EARLY MALNUTRITION:
Dams: ½ control diet

LATE MALNUTRITION:
Pups: low protein diet

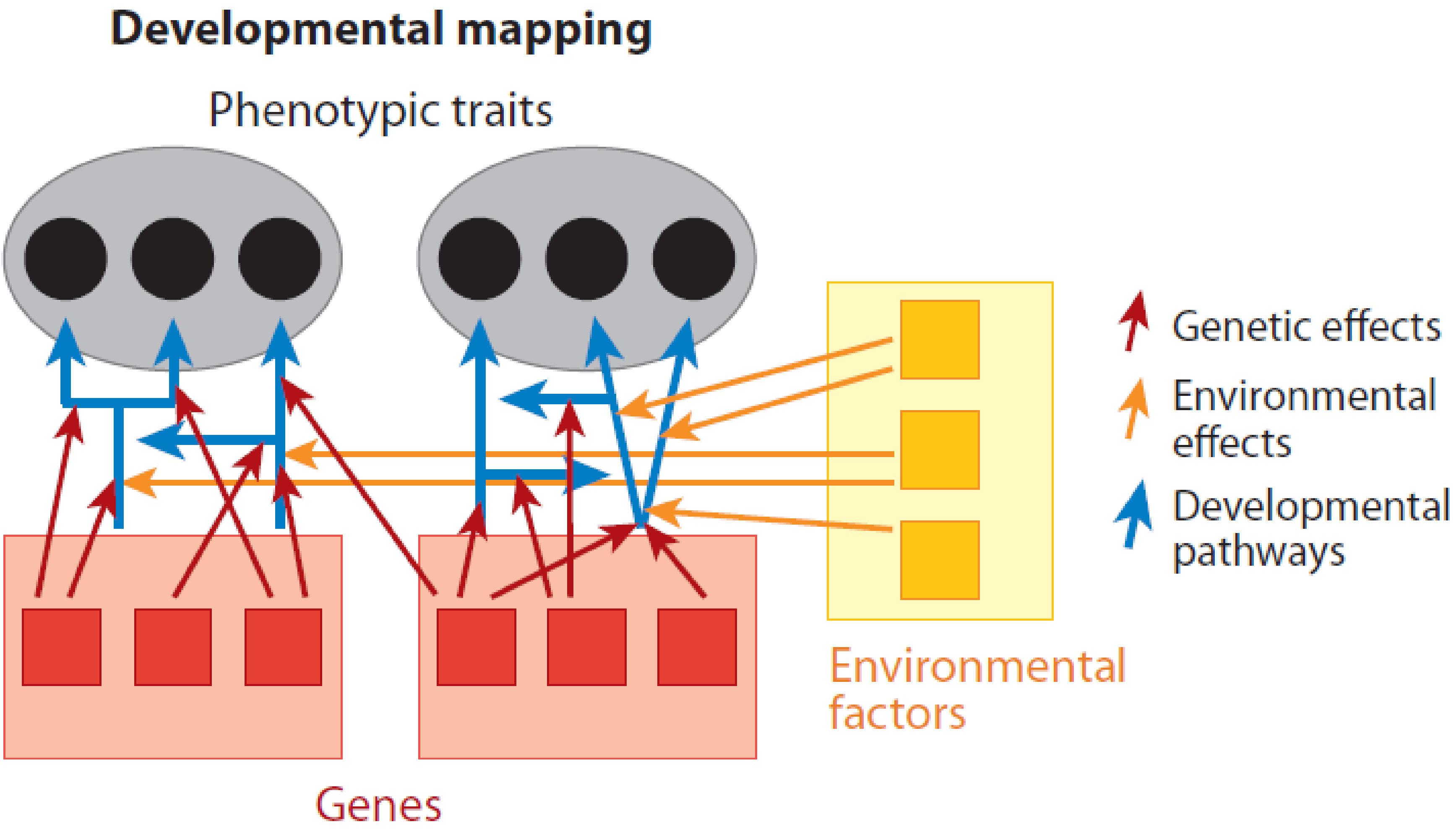
TOTAL MALNUTRITION:
Dams + pups

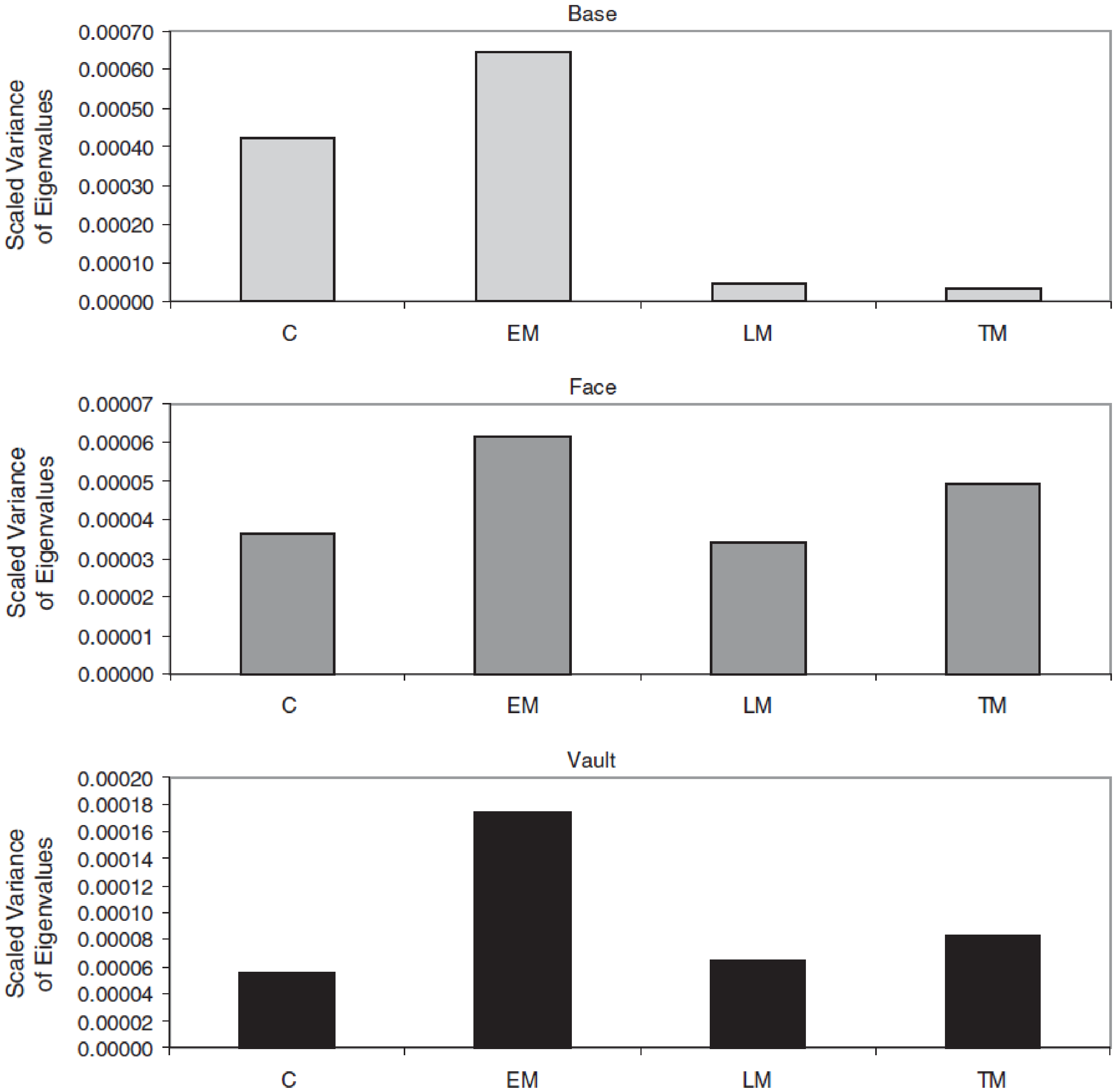

Control
Early Malnutrition
Late Malnutrition
Total Malnutrition
Weight (g)
Age (days)

Morphological changes aligned with ontogenetic variation

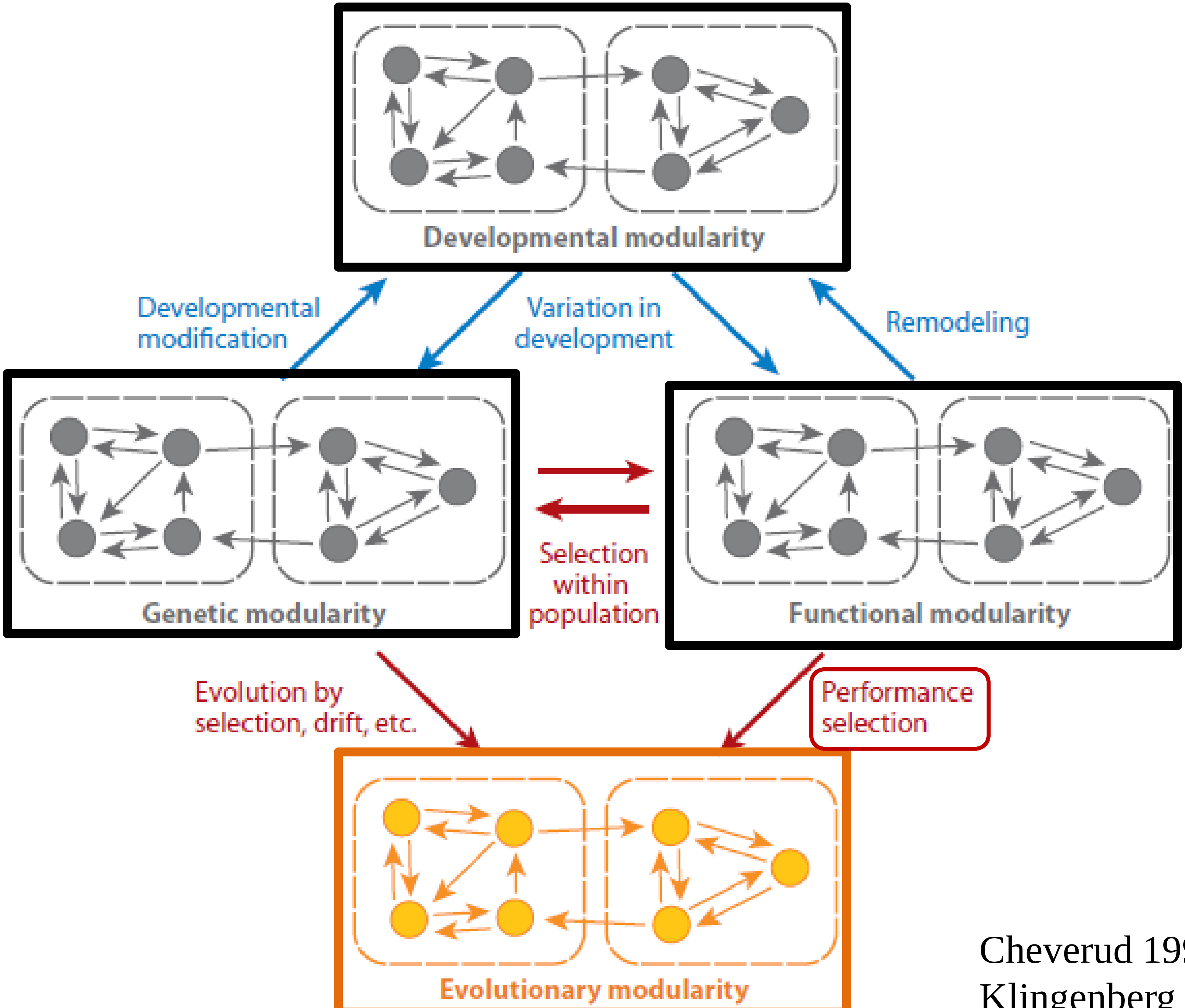


Genetic and environmental effects: same developmental pathways



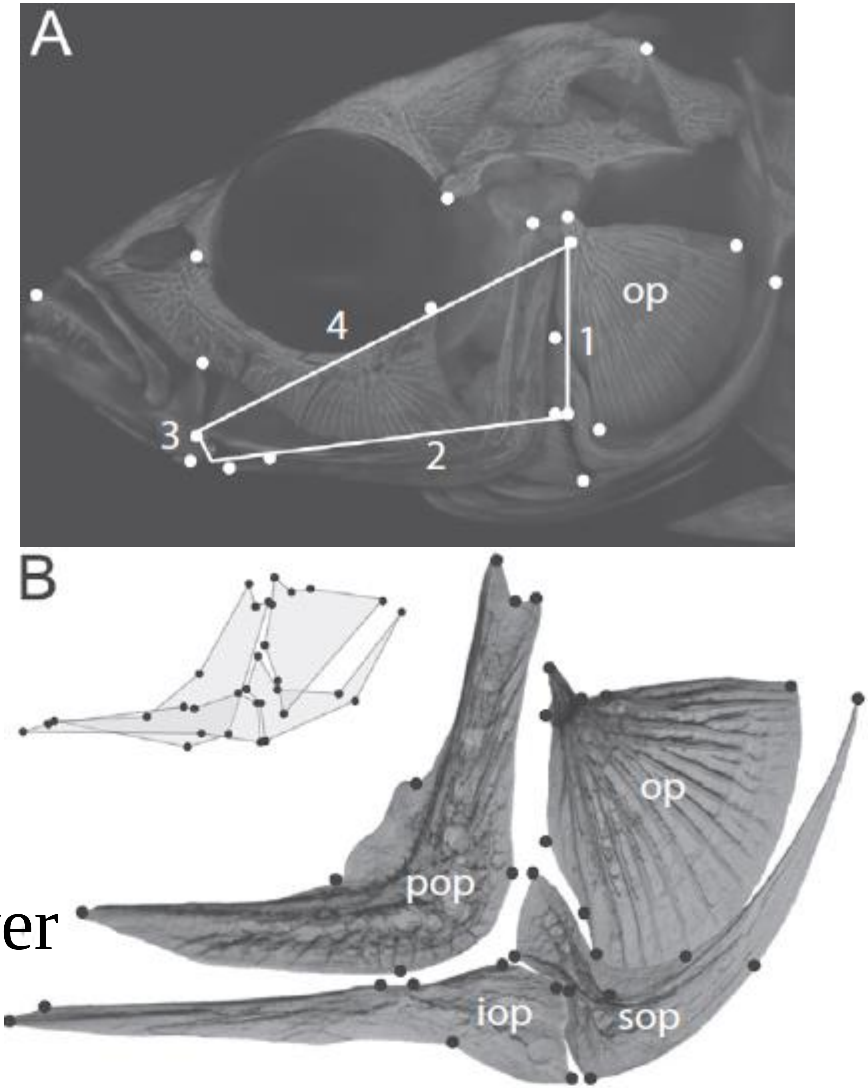


Base
Scaled Variance of Eigenvalues
0.00070
0.00060
0.00050
0.00040
0.00030
0.00020
0.00010
0.00000
C
EM
LM
TM
Face
Scaled Variance of Eigenvalues
0.00007
0.00006
0.00005
0.00004
0.00003
0.00002
0.00001
0.00000
C
EM
LM
TM
Vault
Scaled Variance of Eigenvalues
0.00020
0.00018
0.00016
0.00014
0.00012
0.00010
0.00008
0.00006
0.00004
0.00002
0.00000
C
EM
LM
TM



Cheverud 1996
Klingenberg 2008

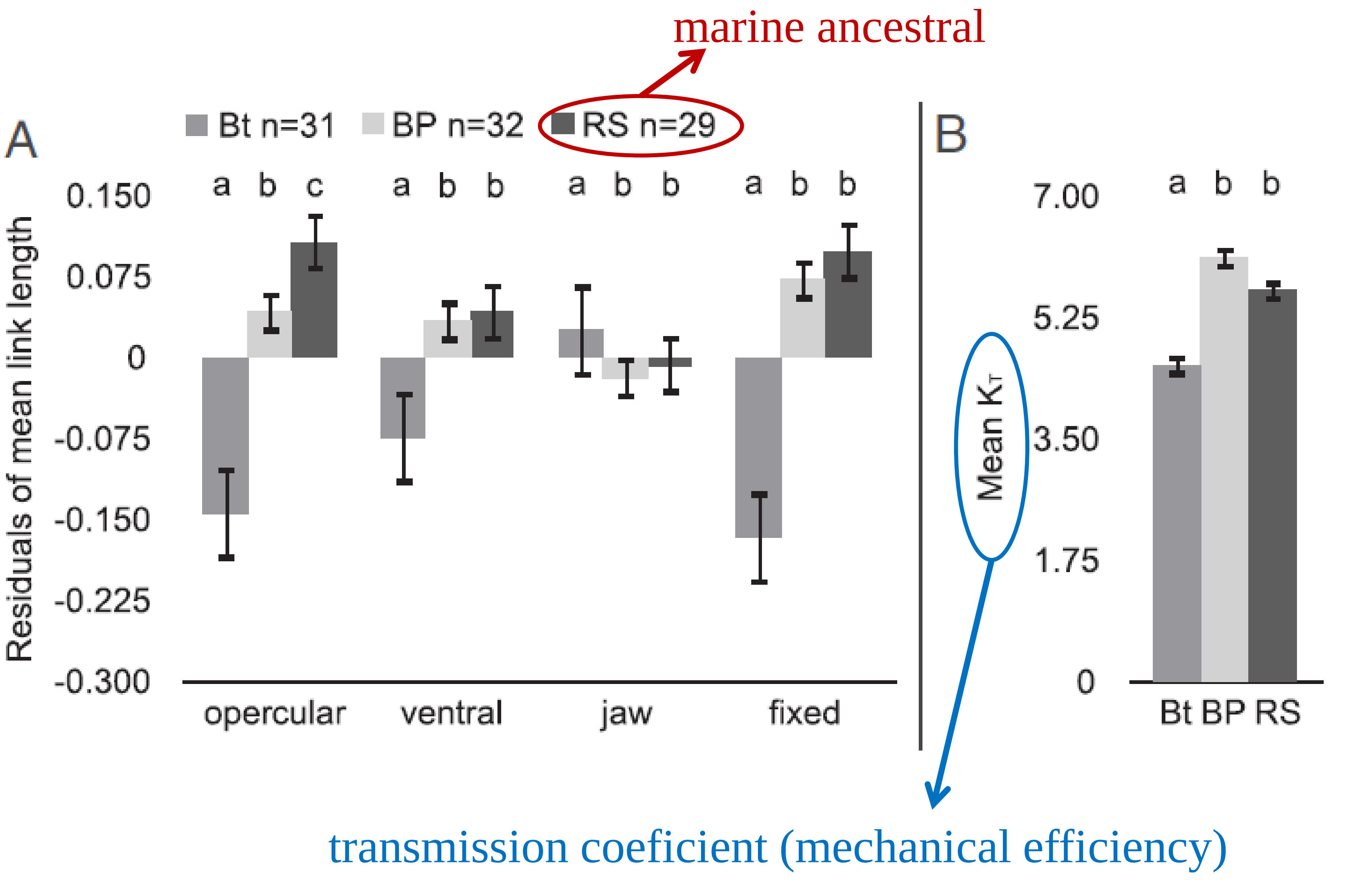
Performace selection:
functional to evolutionary modularity



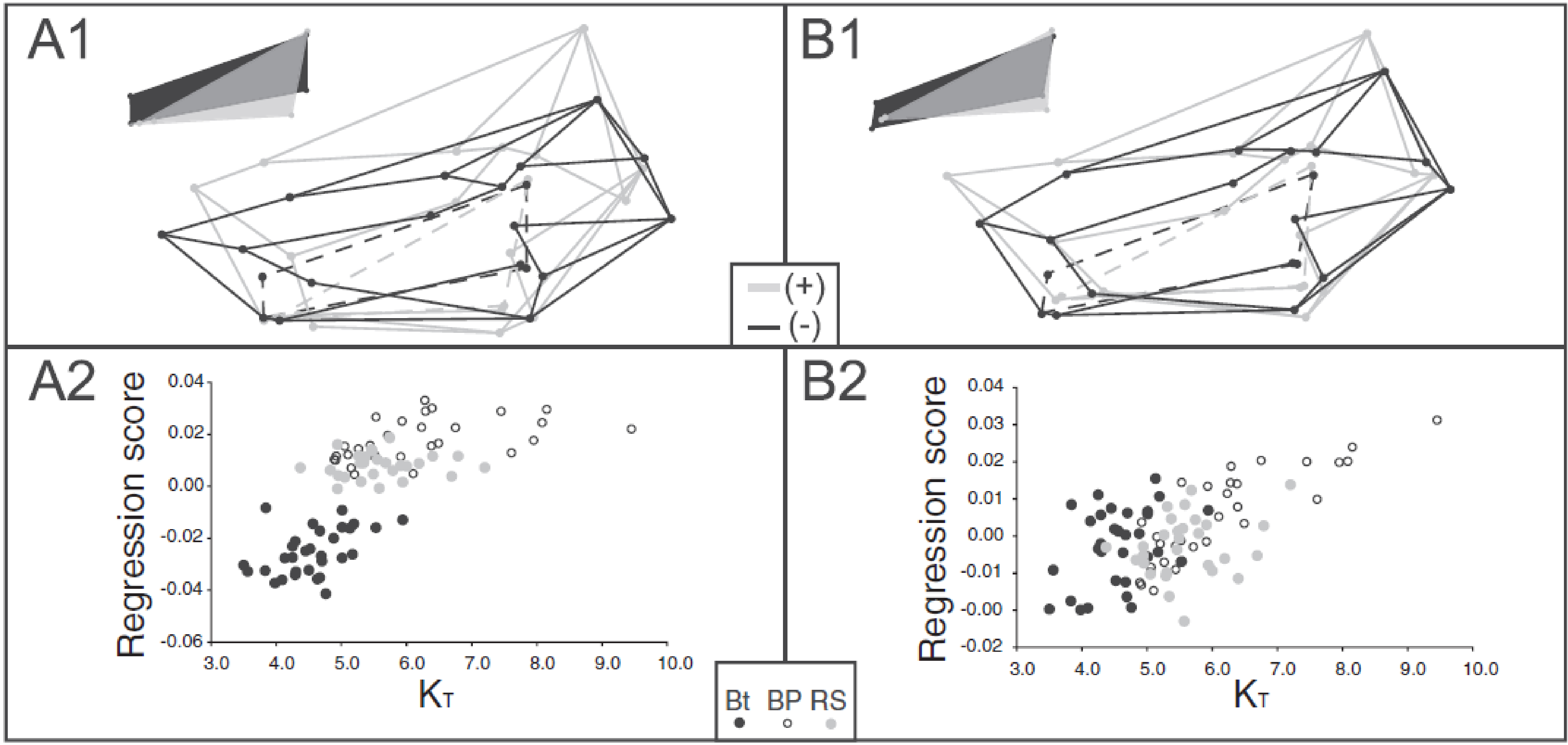
Opercular four bar lever

Jamnickzy et al.2014

Biomechanical differences in the 4-bar lever



Shape variation explains variation in K_T



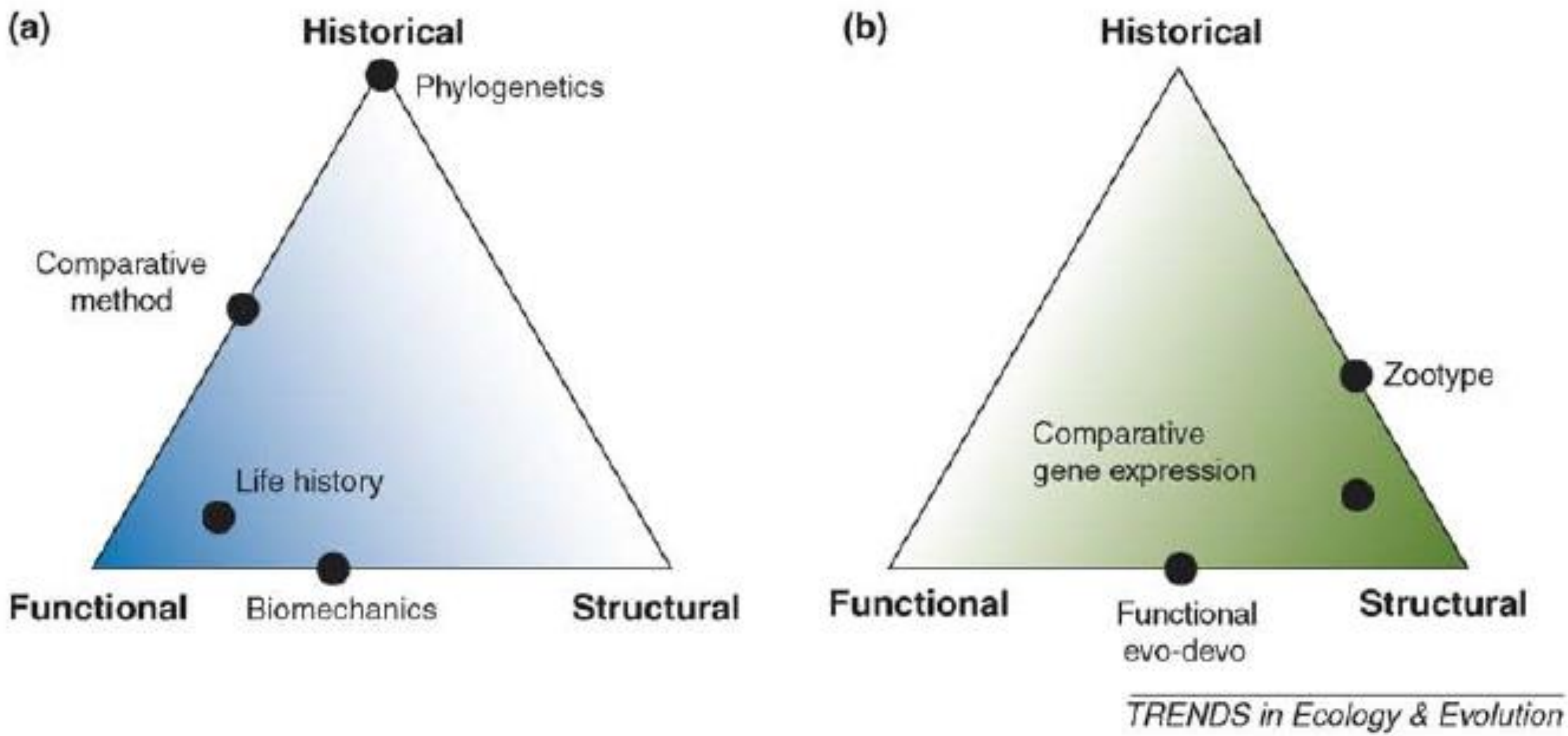
Stability of pattern and magnitudes across populations

Table 1. Covariance matrix comparison among populations for the whole-skull dataset

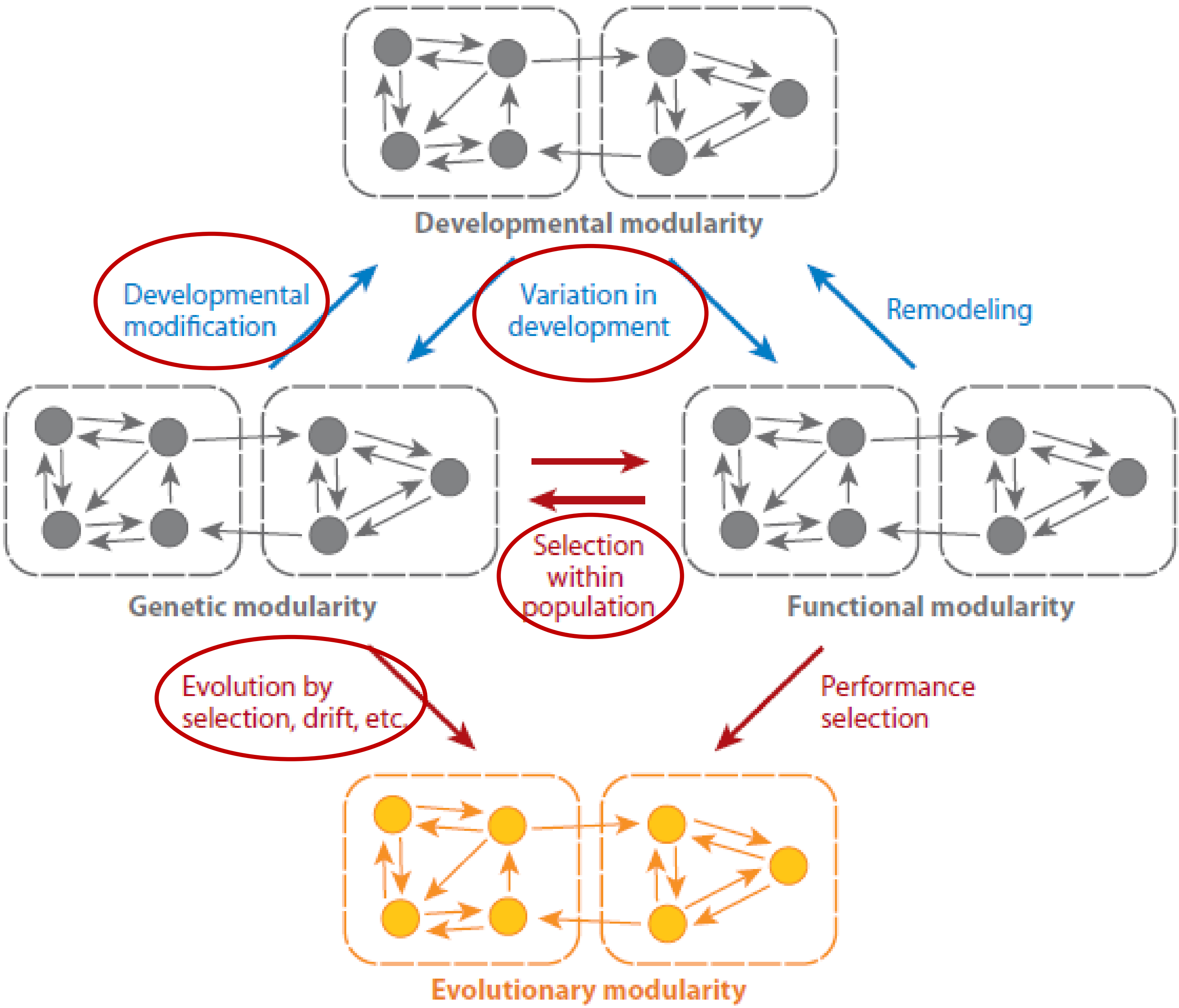
	Boot Lake	Bear Paw Lake	Rabbit Slough
Boot Lake	**0.8153**	0.8817	0.9021
Bear Paw Lake	0.7366	**0.8570**	0.7931
Rabbit Slough	0.6491	0.5850	**0.6349**

Population	Scaled variance of Eigenvalues	SD
Rabbit Slough	0.0012	0.0002
Boot Lake	0.0013	0.0001
Bear Paw Lake	0.0013	0.0002

Functional Evo-Devo



‘However, if the goal is to gain an integrated view of the role of development in evolution, the link to function is essential’. (Breucker et al. 2006)

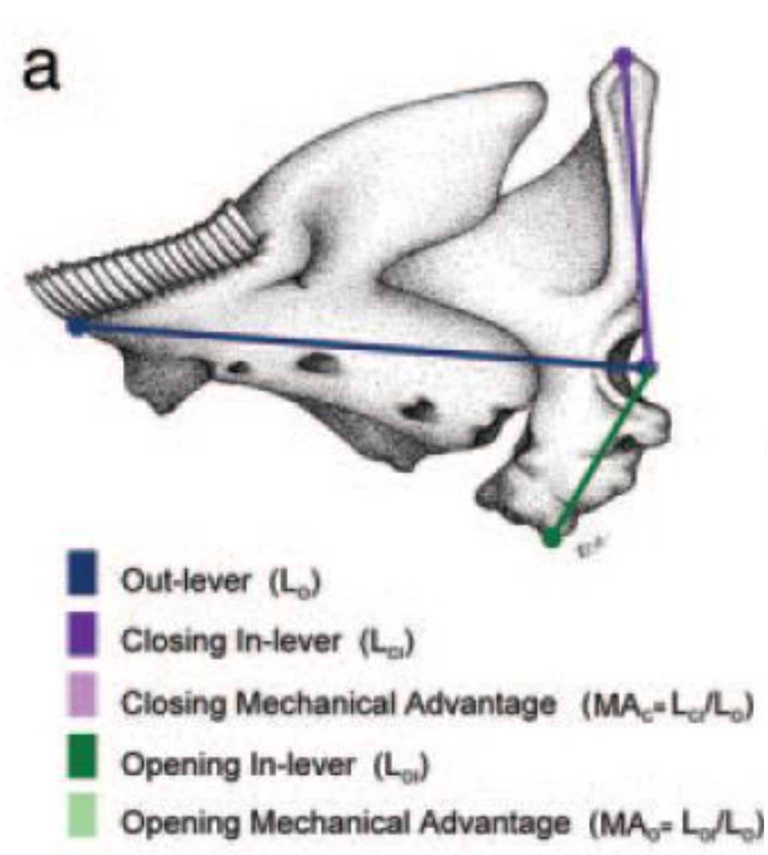


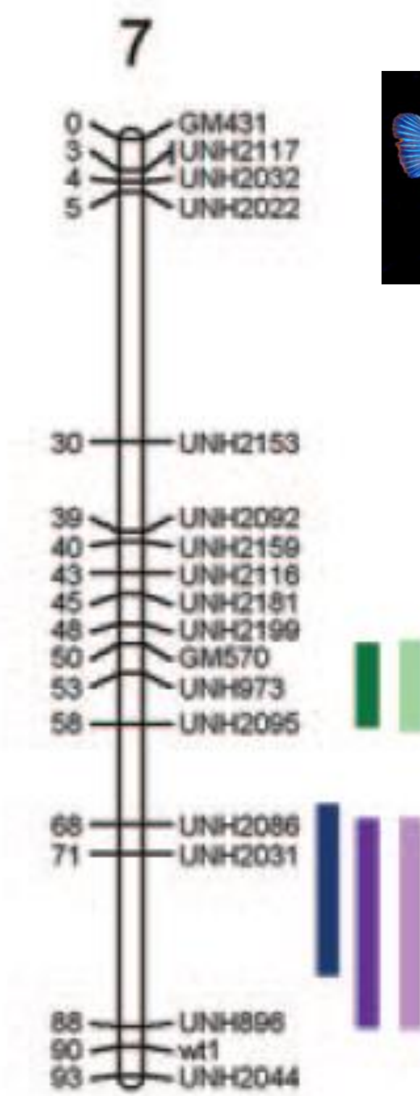
Developmental modularity
Developmental modification
Variation in development
Remodeling
Genetic modularity
Selection within population
Functional modularity
Evolution by selection, drift, etc.
Performance selection
Evolutionary modularity

Evolution by selection: functional to genetic to developmental modularity

Albertson et al.2005

Genetic basis of jaw opening and closing

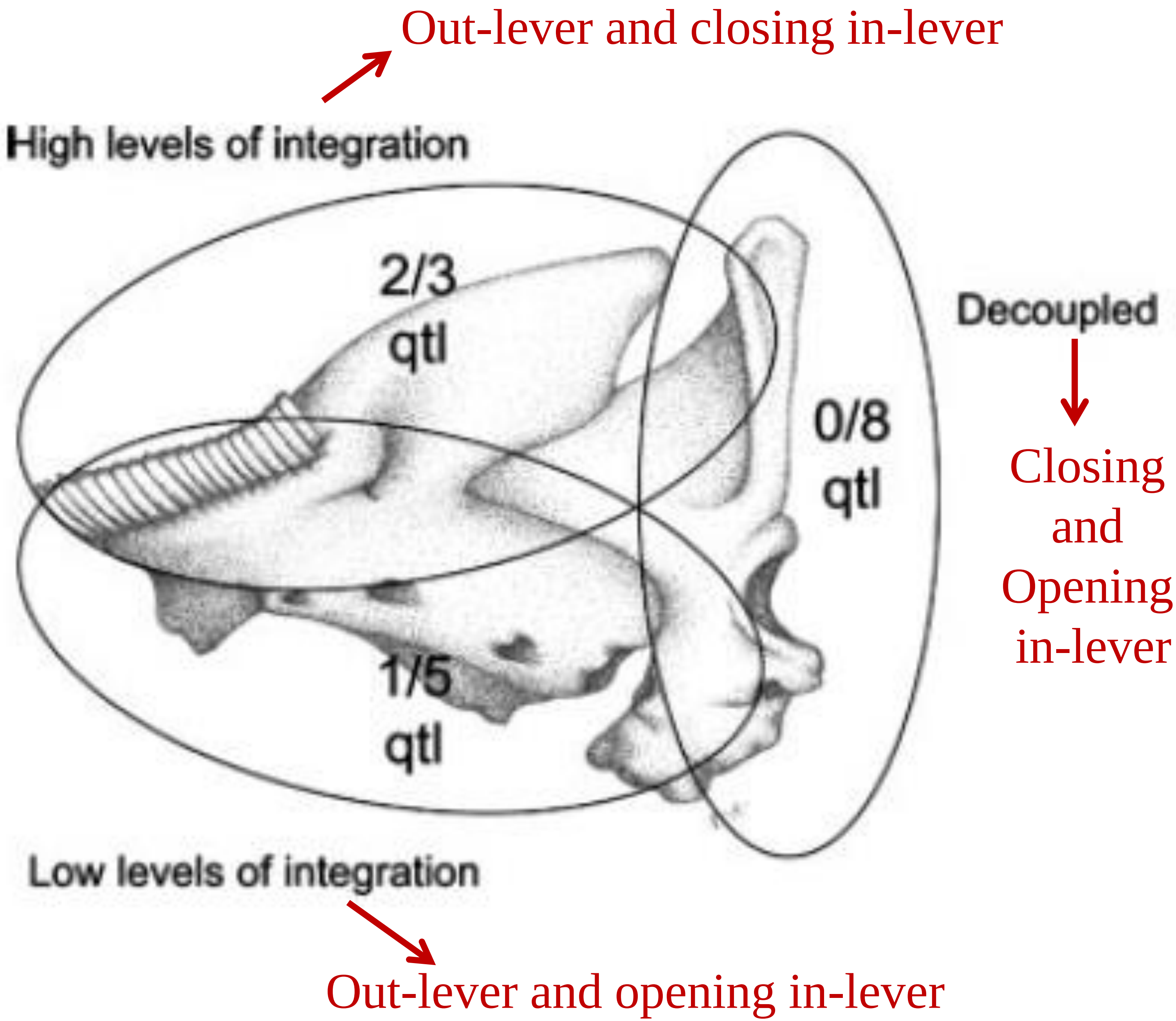




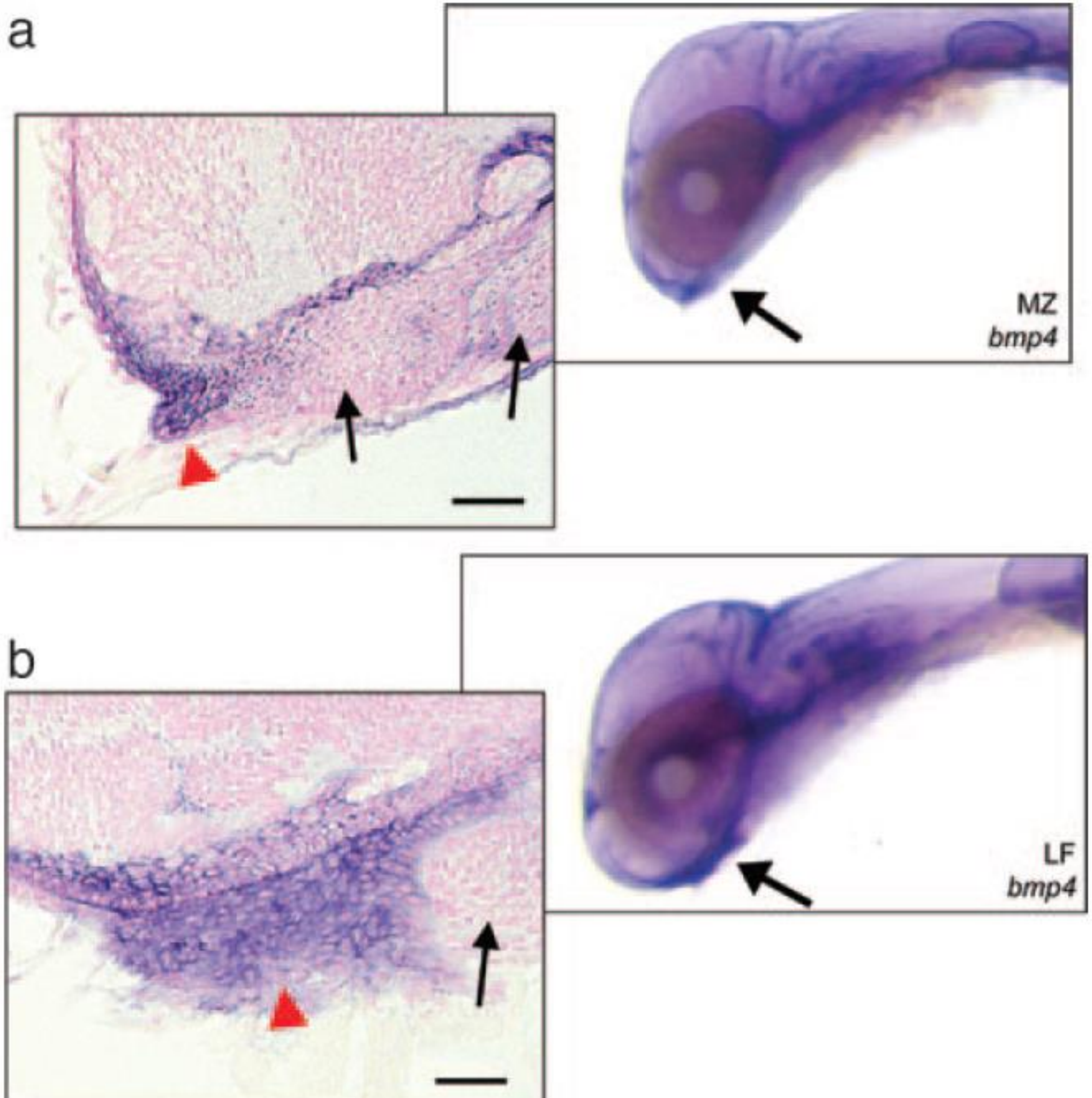
X

F2

QTL mapping


Out-lever and closing in-lever
High levels of integration
2/3
qtl
Decoupled
0/8
qtl
Closing
and
Opening
in-lever
1/5
qtl
Low levels of integration
Out-lever and opening in-lever

Divergent bone morphogenetic 4 expression



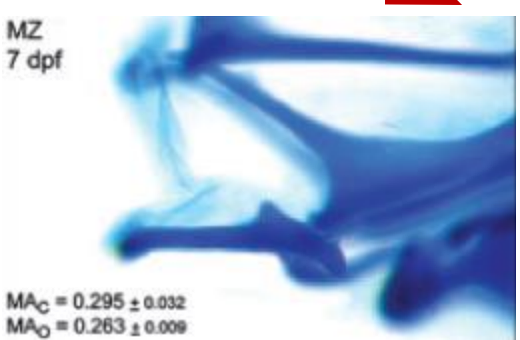
Divergent feeding biomechanics

Selection within populations

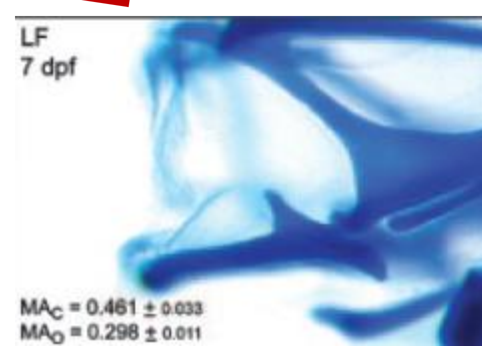
Genetic decoupling of functional modules

Developmental modification

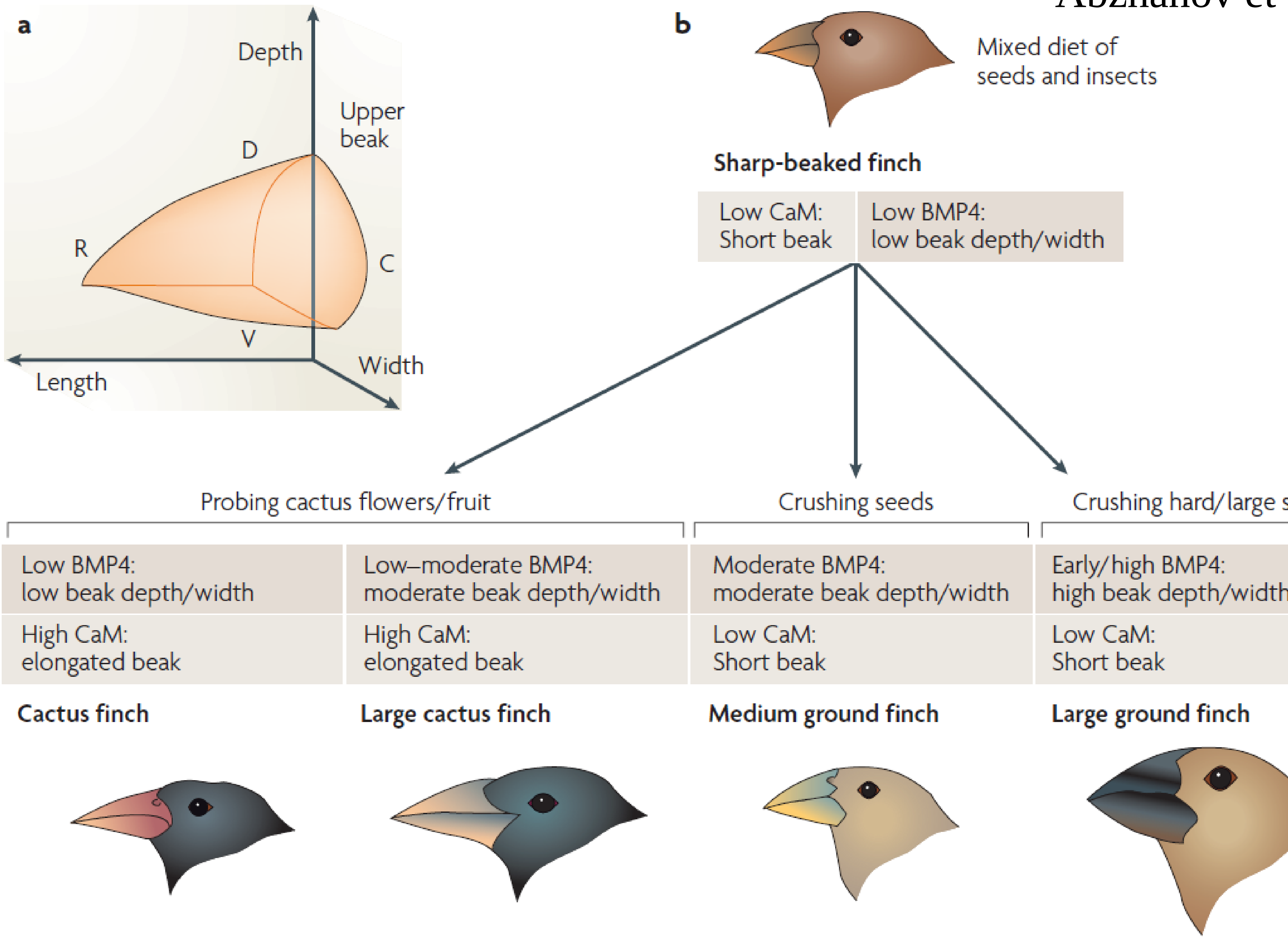
Differential expression of bmp4



Species differences

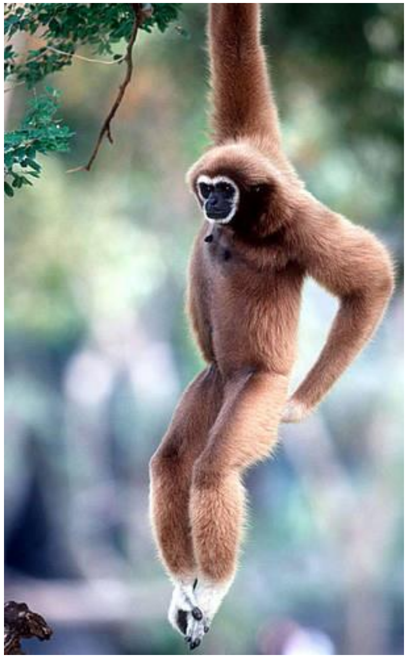


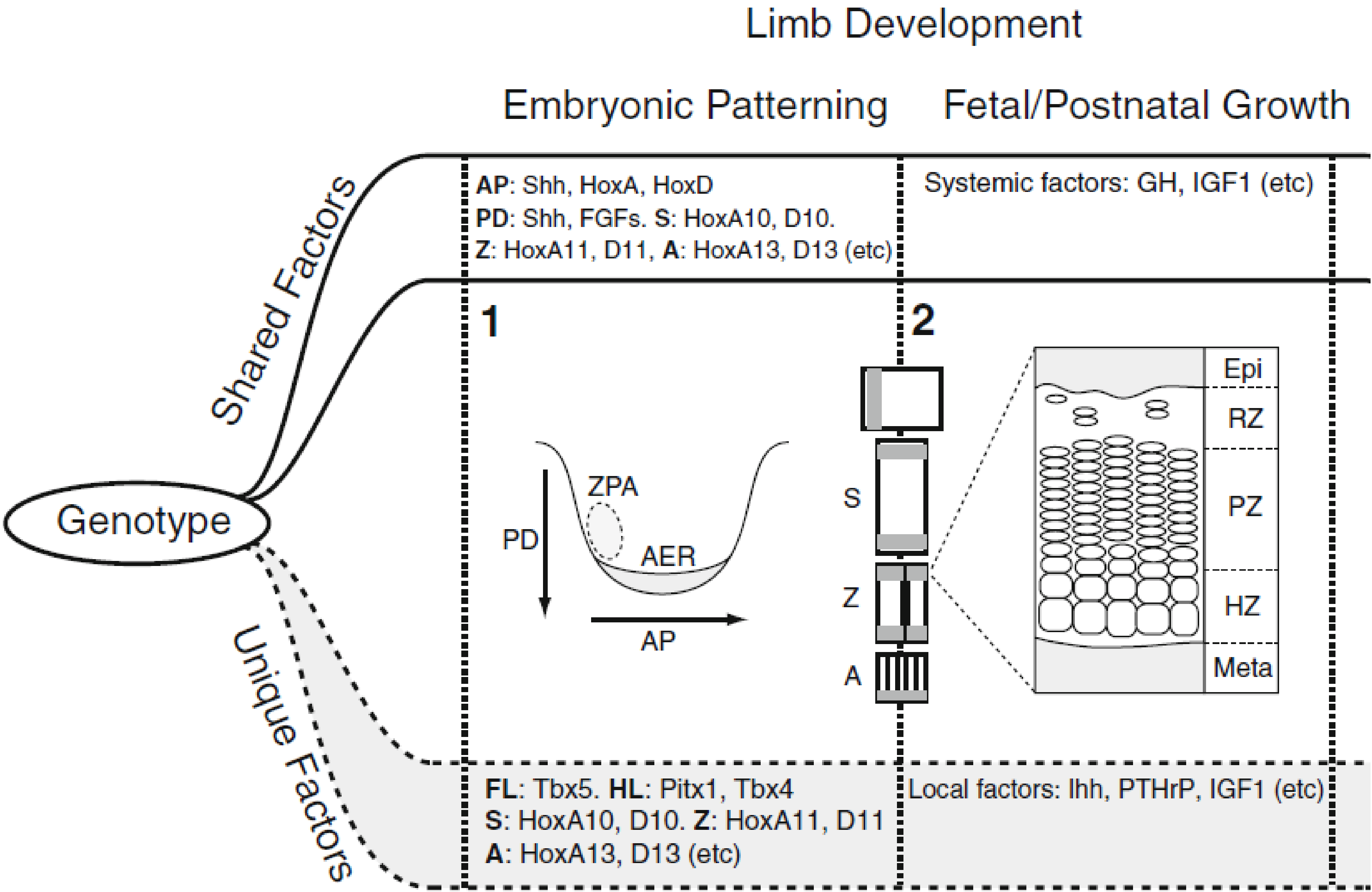
Abzhanov et

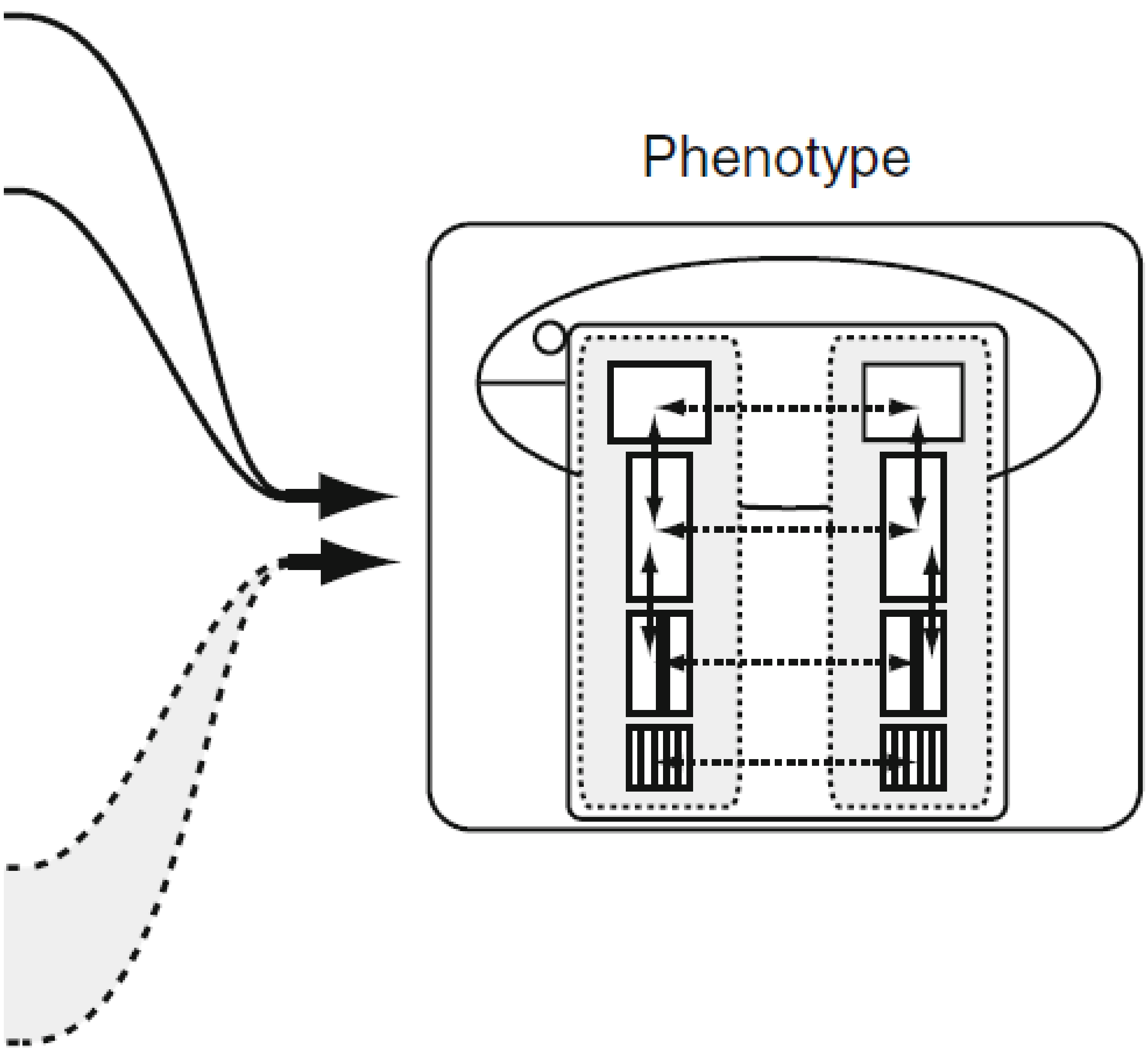

a
Depth
Upper
beak
D
R
C
V
Length
Width
b
Mixed diet of
seeds and insects
Sharp-beaked finch
Low CaM:
Short beak
Low BMP4:
low beak depth/width
Probing cactus flowers/fruit
Crushing seeds
Crushing hard/large s
Low BMP4:
low beak depth/width
High CaM:
elongated beak
Cactus finch
Low–moderate BMP4:
moderate beak depth/width
High CaM:
elongated beak
Large cactus finch
Moderate BMP4:
moderate beak depth/width
Low CaM:
Short beak
Medium ground finch
Early/high BMP4:
high beak depth/width
Low CaM:
Short beak
Large ground finch

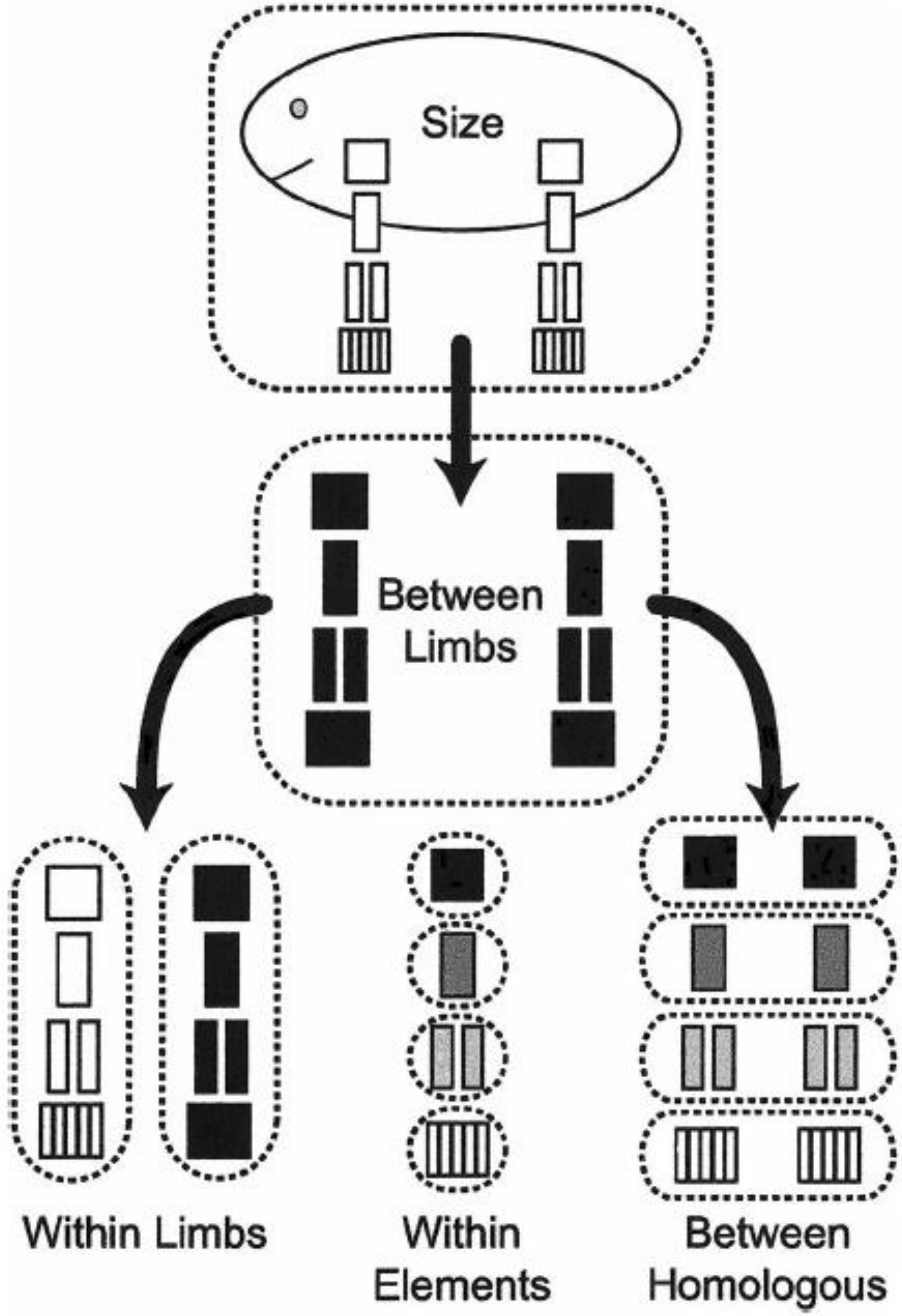
Young and Hallgrímsson 2005

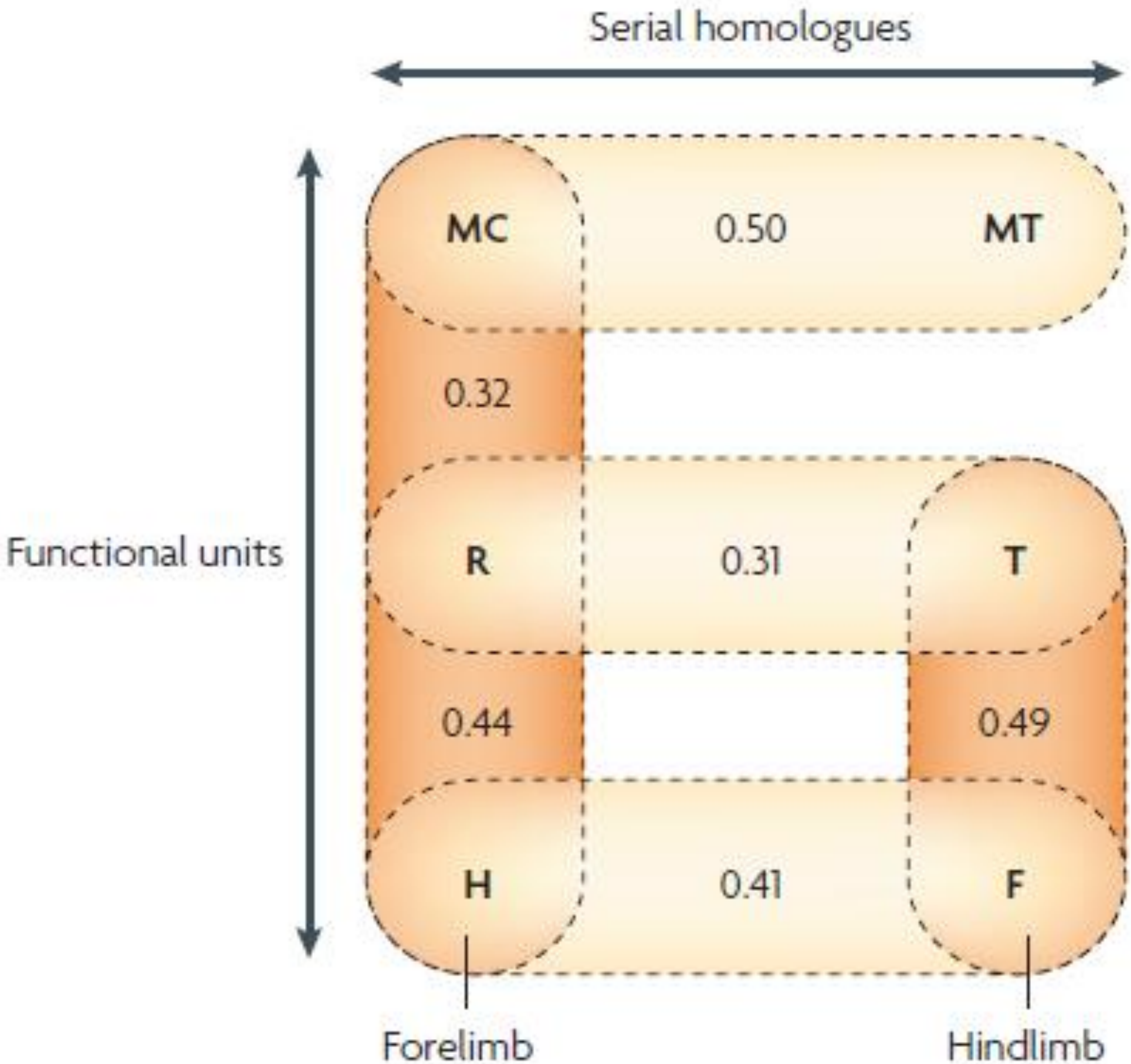
Evolution by selection: functional to developmental to evolutionary modularity



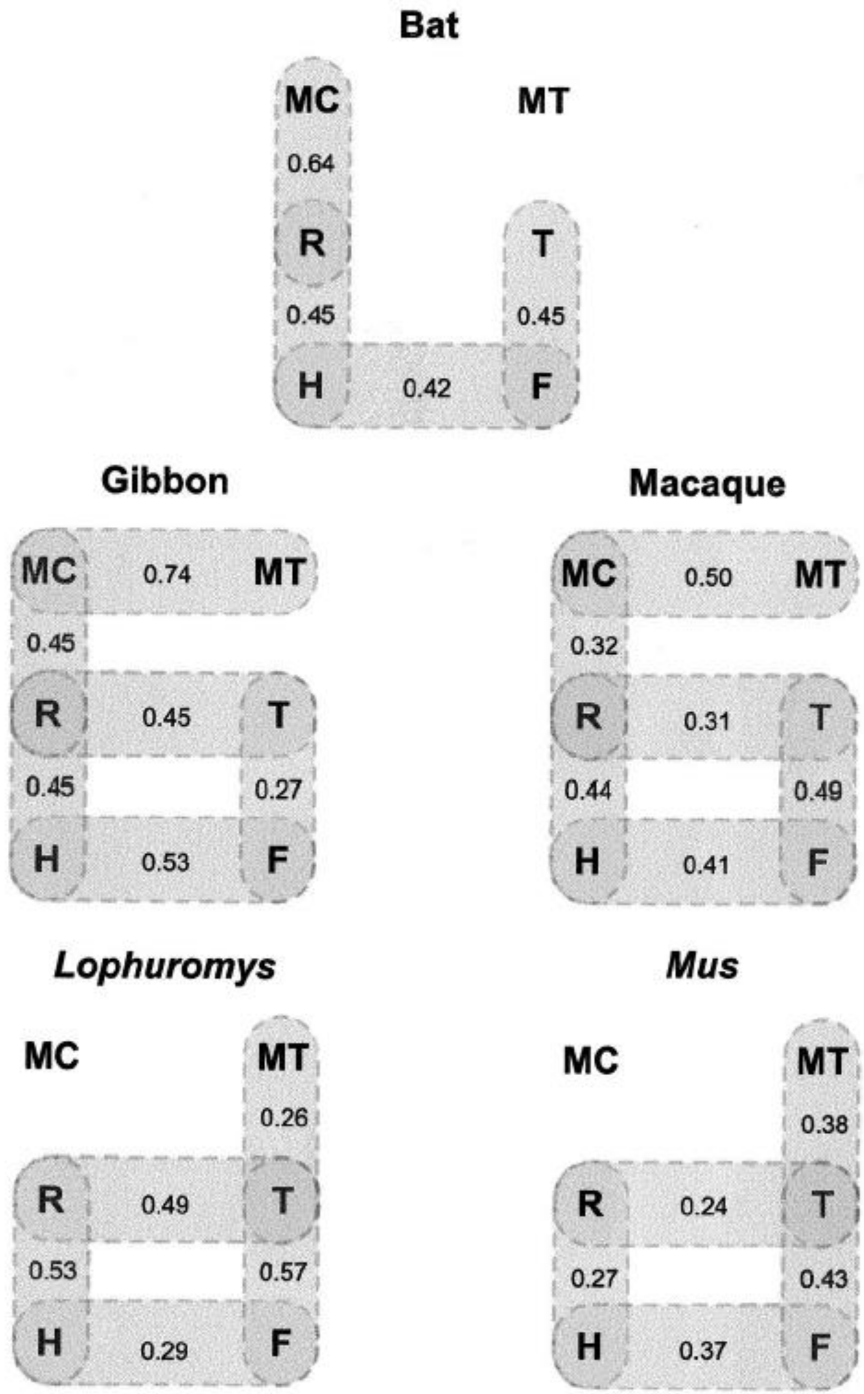

Limb Development
Embryonic Patterning
Fetal/Postnatal Growth
Shared Factors
Genotype
Unique Factors
AP: Shh, HoxA, HoxD
PD: Shh, FGFs. S: HoxA10, D10.
Z: HoxA11, D11, A: HoxA13, D13 (etc)
Systemic factors: GH, IGF1 (etc)
1
2
ZPA
PD
AER
AP
S
Z
A
Epi
RZ
PZ
HZ
Meta
FL: Tbx5. HL: Pitx1, Tbx4
S: HoxA10, D10. Z: HoxA11, D11
A: HoxA13, D13 (etc)
Local factors: Ihh, PTHrP, IGF1 (etc)

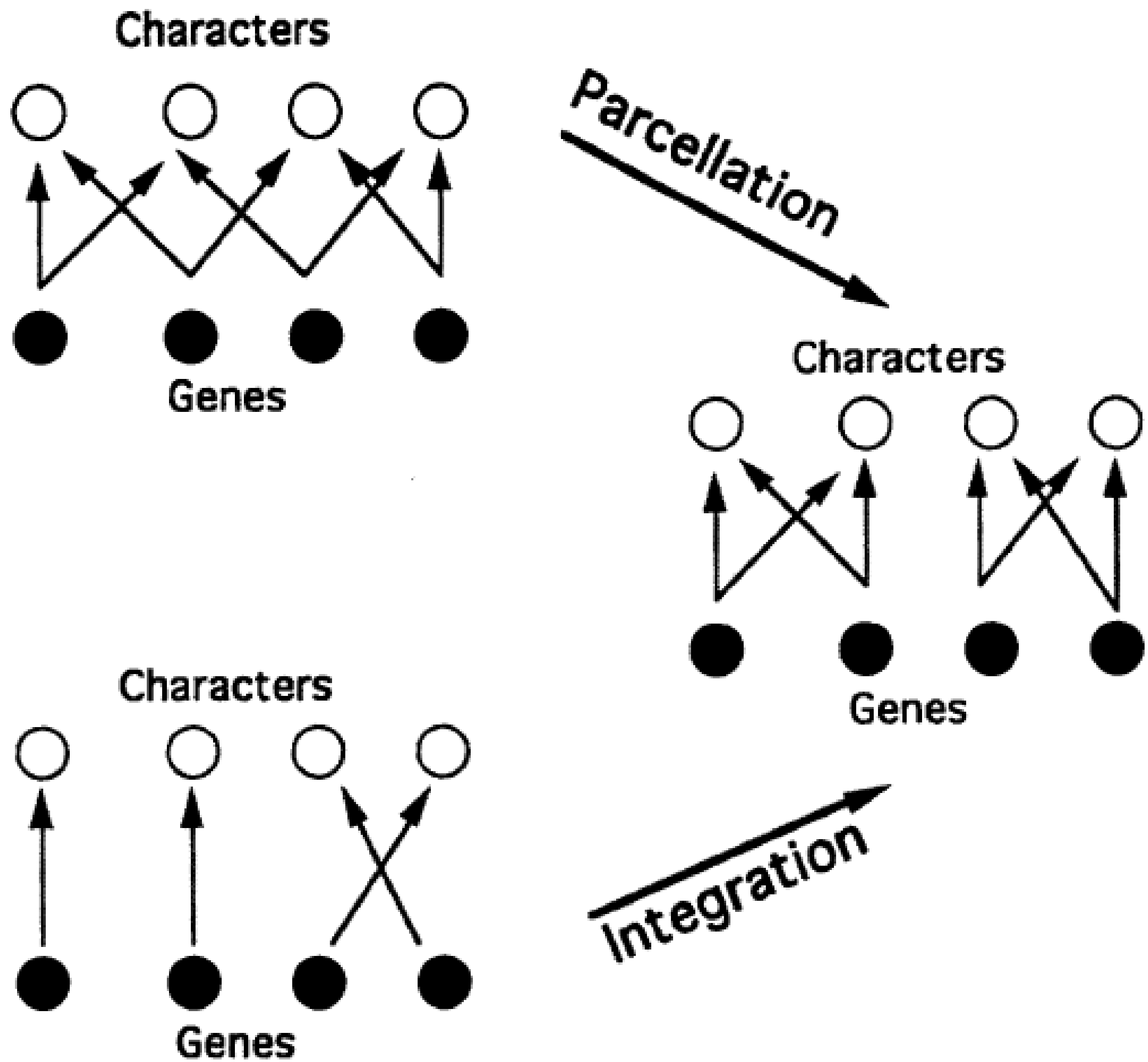

Phenotype


Size
Between
Limbs
Within Limbs
Within
Elements
Between
Homologous



Serial homologues
Functional units
MC
0.50
MT
0.32
R
0.31
T
0.44
0.49
H
0.41
F
Forelimb
Hindlimb


Bat
MC
MT
0.64
R
T
0.45
0.45
H
0.42
F
Gibbon
MC
0.74
MT
0.45
R
0.45
T
0.45
0.27
H
0.53
F
Macaque
MC
0.50
MT
0.32
R
0.31
T
0.44
0.49
H
0.41
F
Lophuromys
MC
MT
0.26
R
0.49
T
0.53
0.57
H
0.29
F
Mus
MC
MT
0.38
R
0.24
T
0.27
0.43
H
0.37
F


Characters
Genes
Parcellation
Characters
Genes
Characters
Genes
Integration

THE GENETIC COVARIANCE BETWEEN CHARACTERS MAINTAINED BY PLEIOTROPIC MUTATIONS

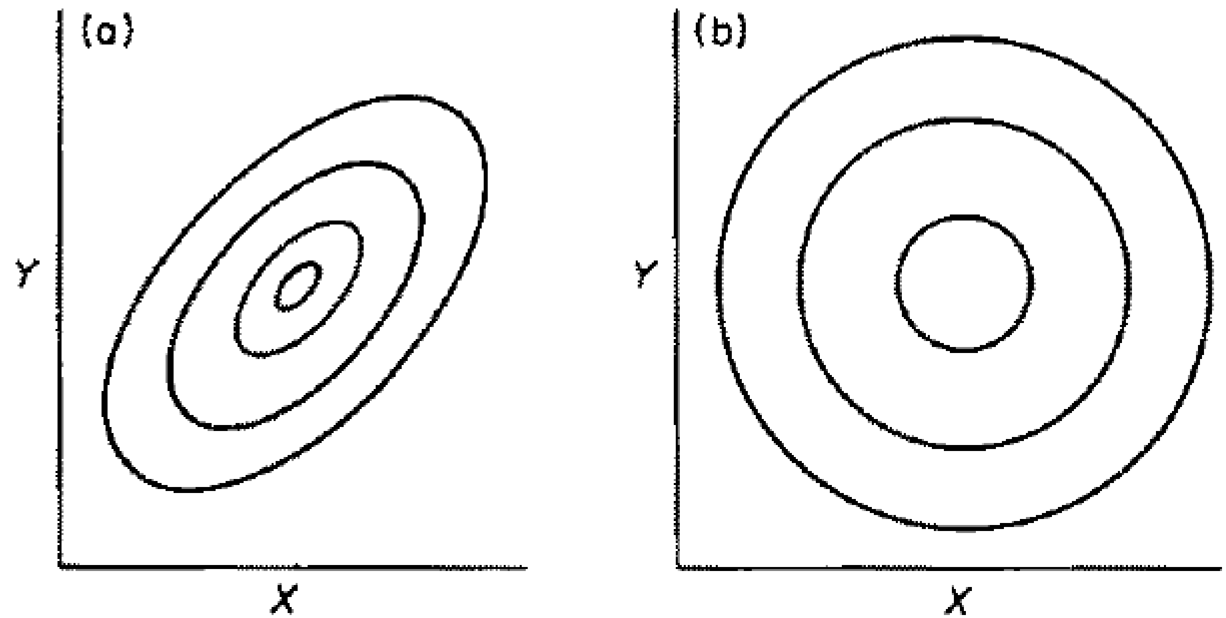
RUSSELL LANDE[1]

$$\mathbf{C} = \mathbf{W}^{1/2} (\mathbf{W}^{-1/2}\mathbf{U}\mathbf{W}^{-1/2})^{1/2} \mathbf{W}^{1/2}$$

Quantitative Genetics and Developmental Constraints on Evolution by Selection

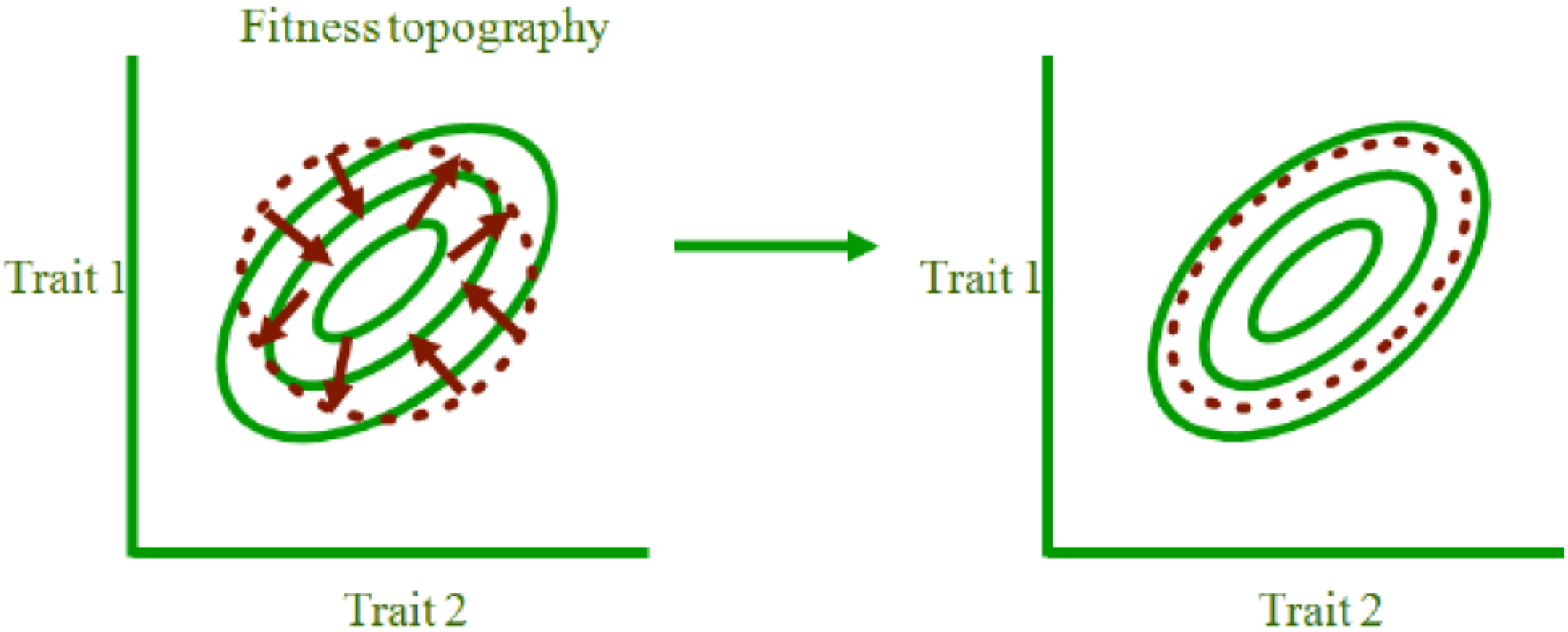
JAMES M. CHEVERUD

J. theor. Biol. (1984)



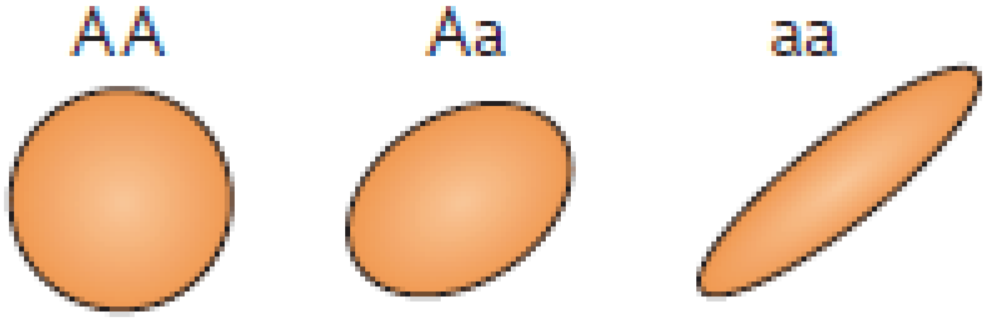
Stabilizing Selection!

Quantitative genetics models: Riedl's hypothesis

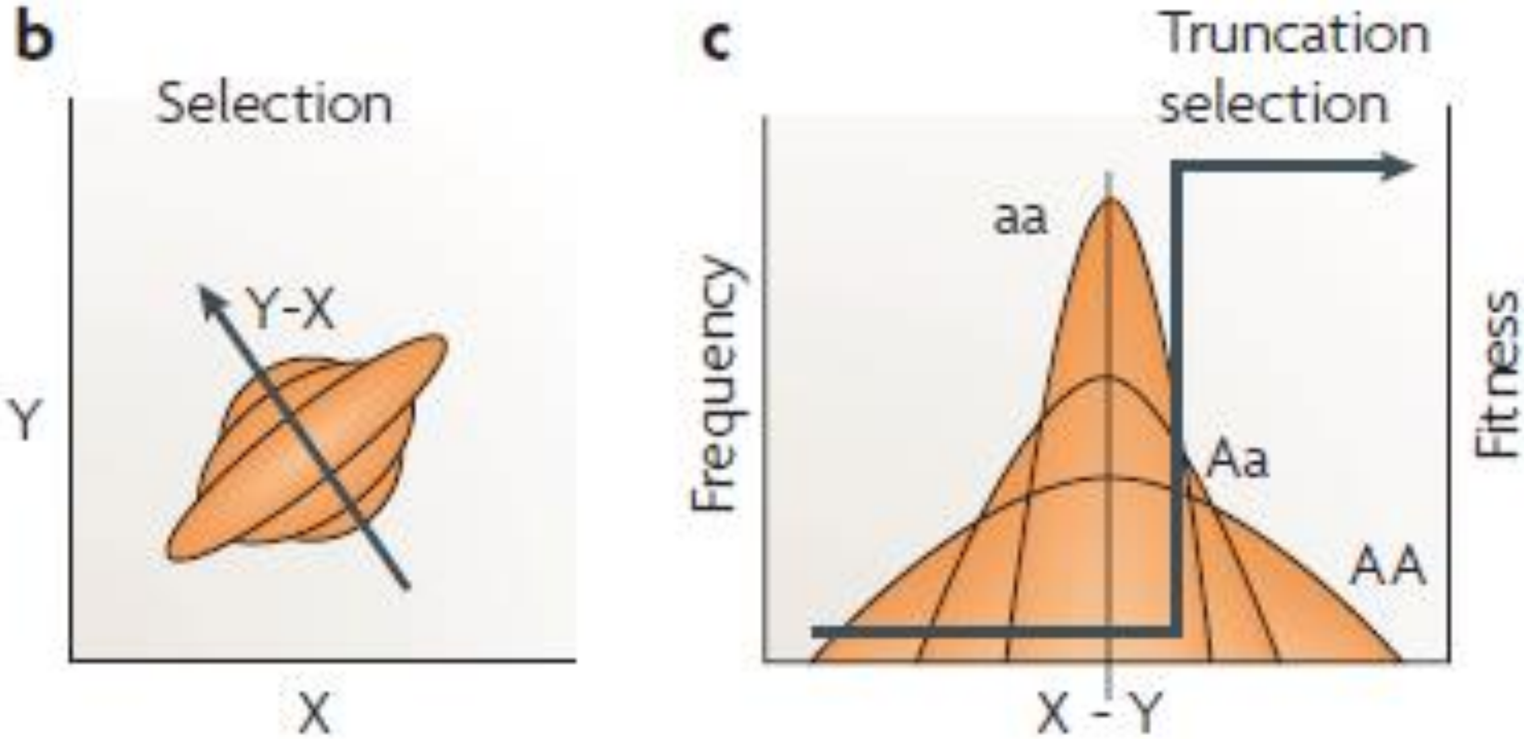


Riedl 1977; Lande 1980; Cheverud 1984

Pavlicev et al. (2008): relationship QTL

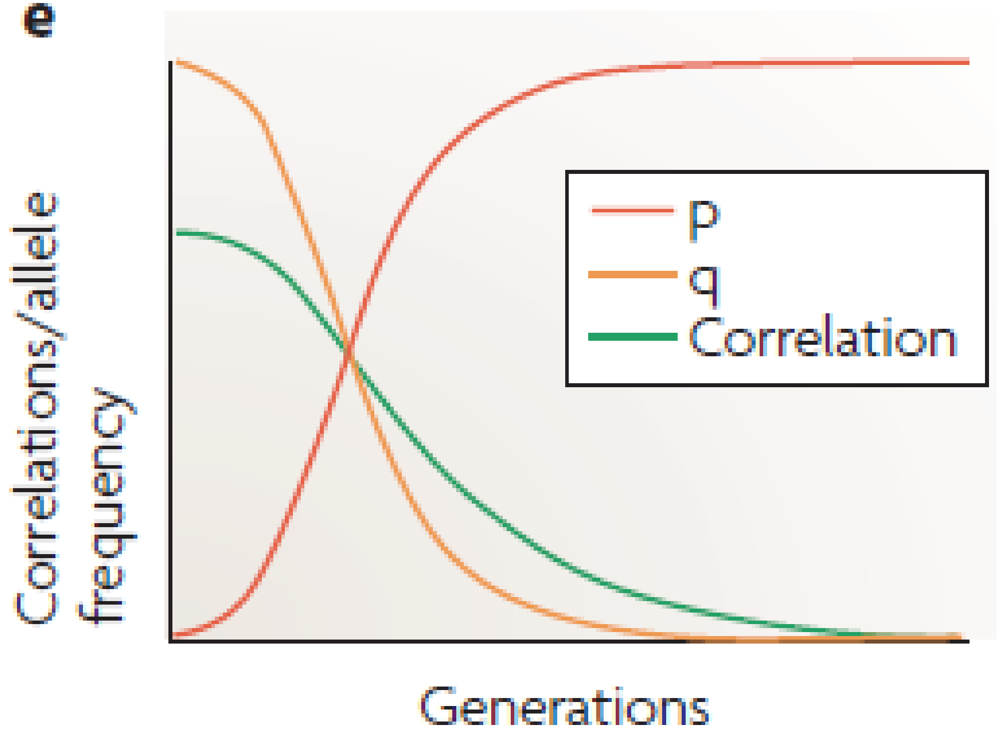


$$\begin{bmatrix} 1.0 & 0.0 \\ 0.0 & 1.0 \end{bmatrix} \quad \begin{bmatrix} 1.0 & 0.5 \\ 0.5 & 1.0 \end{bmatrix} \quad \begin{bmatrix} 1.0 & 0.7 \\ 0.7 & 1.0 \end{bmatrix}$$



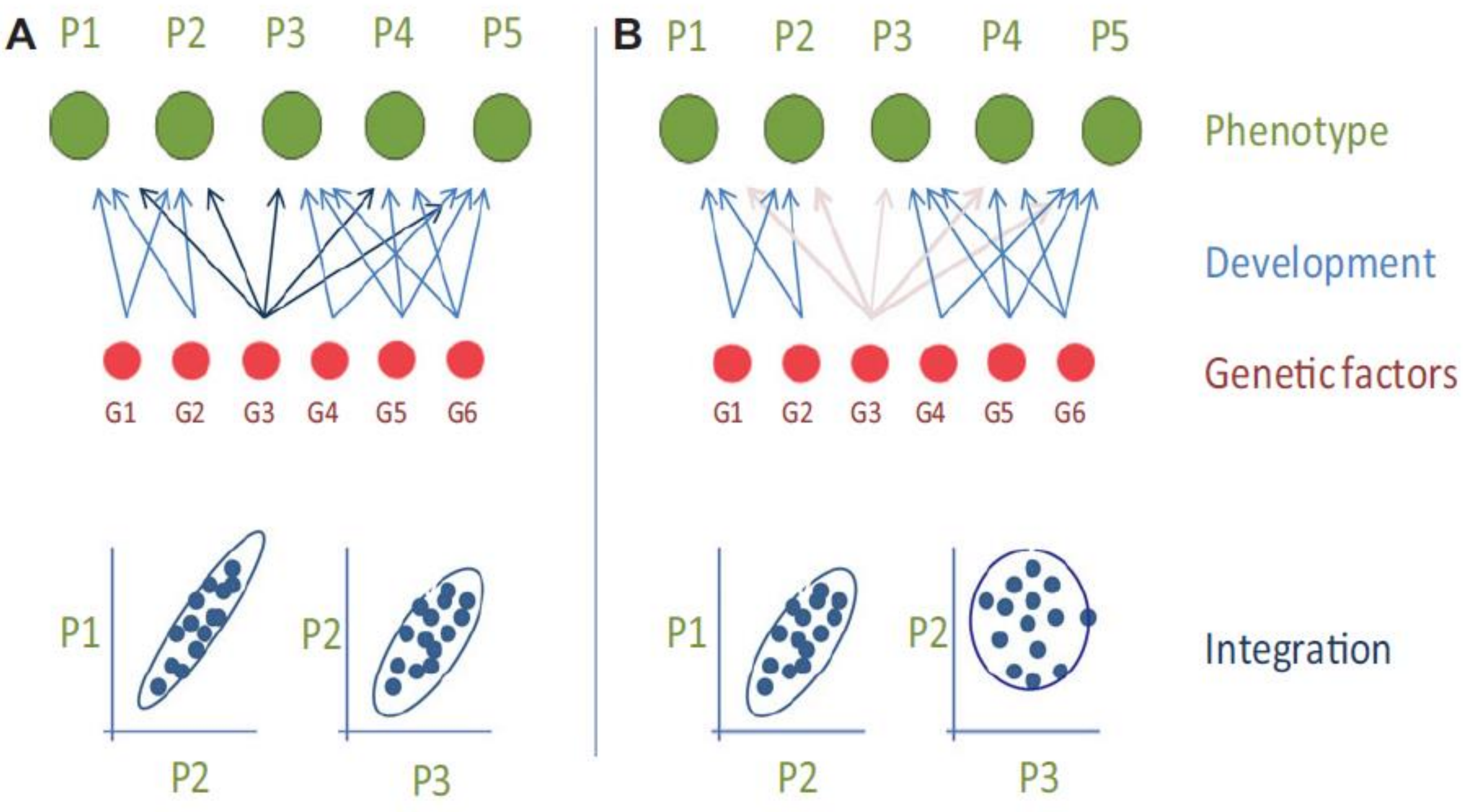
b
Selection
Y-X
Y
X
c
Truncation selection
aa
Frequency
Aa
AA
Fitness
X - Y

e


p
q
Correlation
Correlations/allele frequency
Generations

Genotype – Phenotype Map and Integration/Modularity

Porto et al. 2013



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Quiz

What is a modular genotype-phenotype map?