Developmental homology and the decoupling of levels of organization

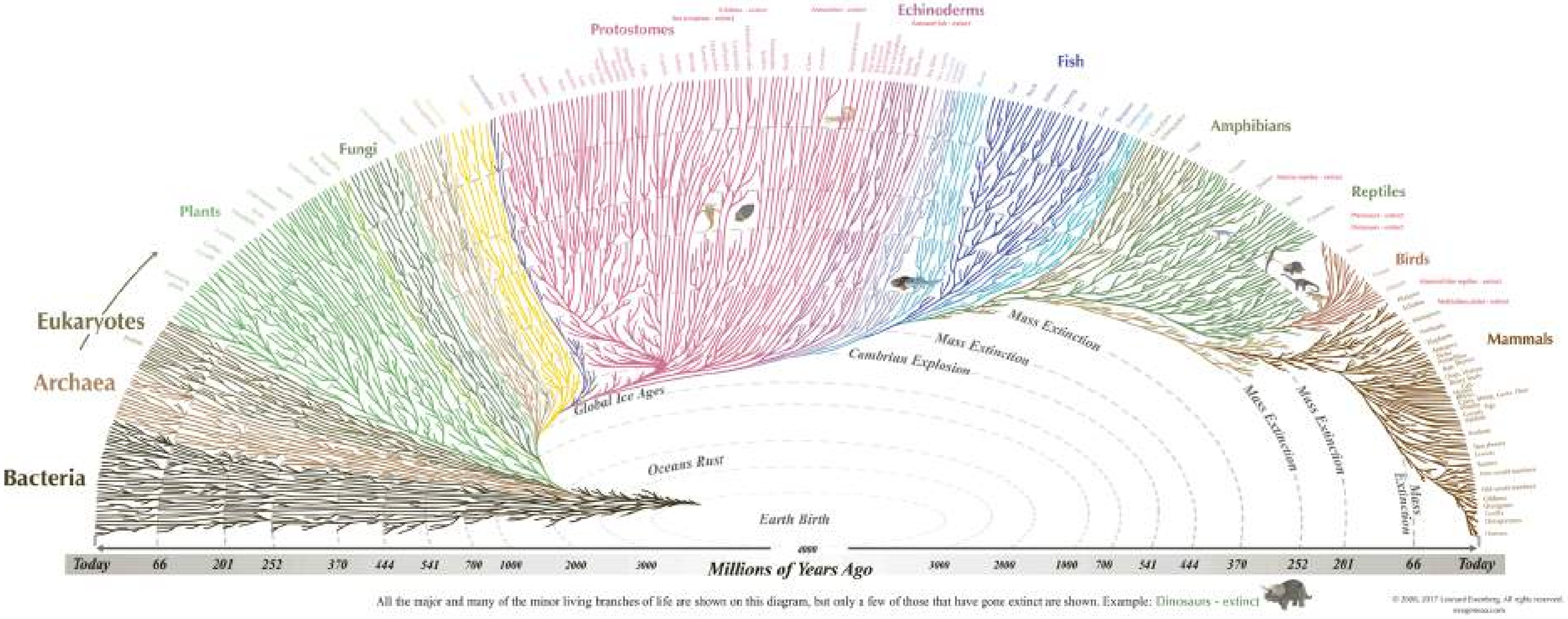
James DiFrisco

ThUMB, Croatia

17 July 2019

fwo Research Foundation
Flanders
Opening new horizons

KU LEUVEN



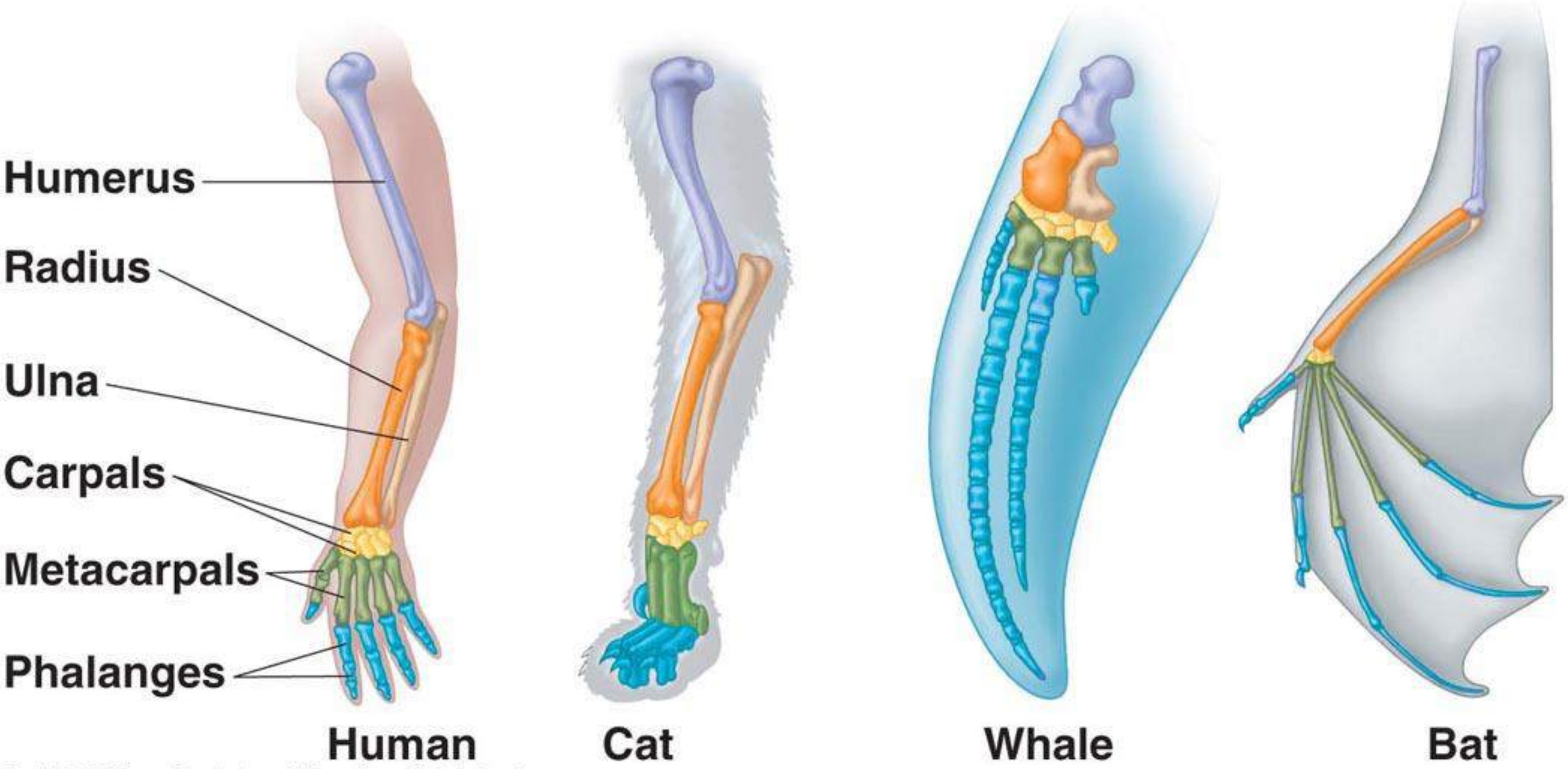
8.7 million eukaryotes known

An estimated 80 million species may exist

* Need for generalizable research *

Homology

Generic definition: Two characters in distinct organisms or taxa are homologous if they are genealogically connected by continuous descent from a common ancestor that had the same character.



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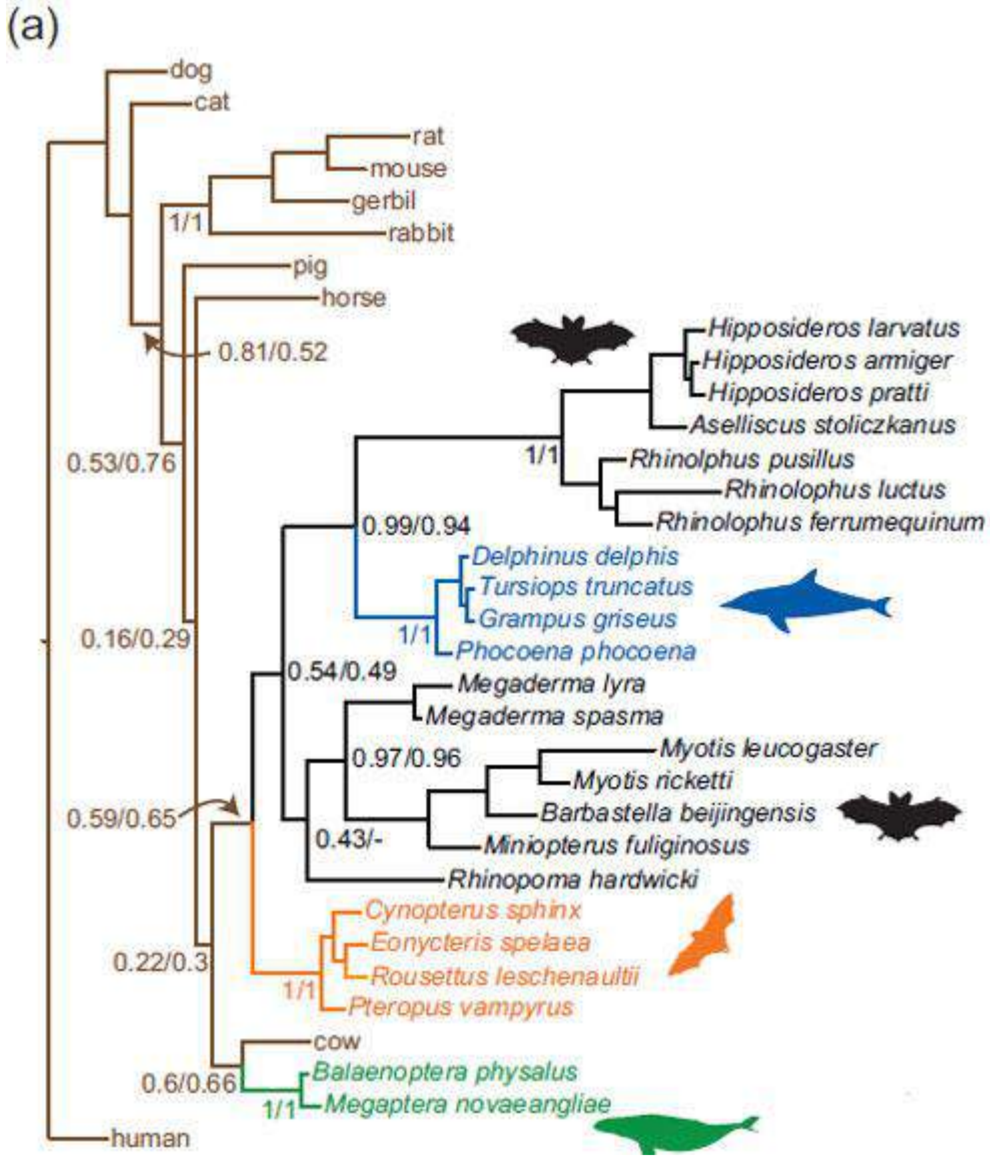
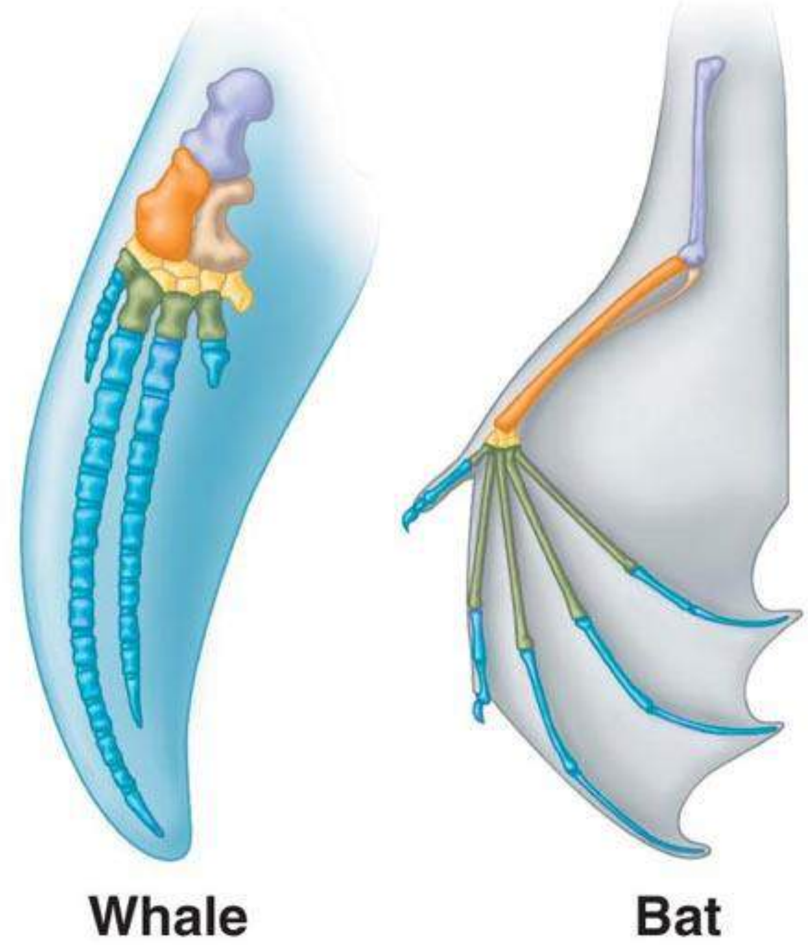
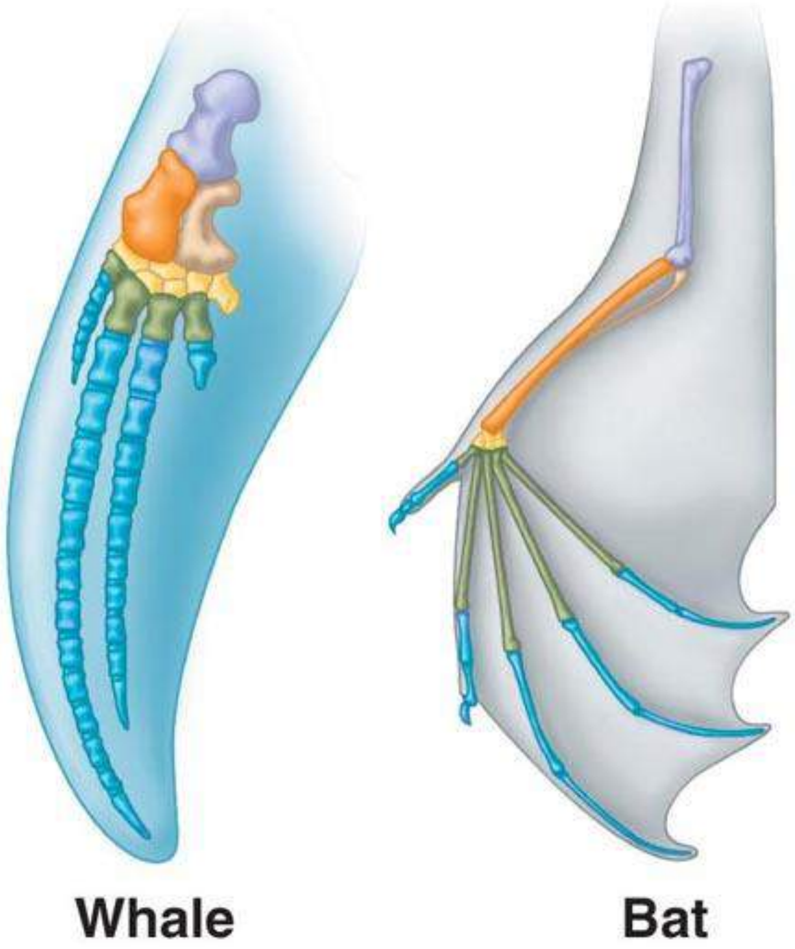
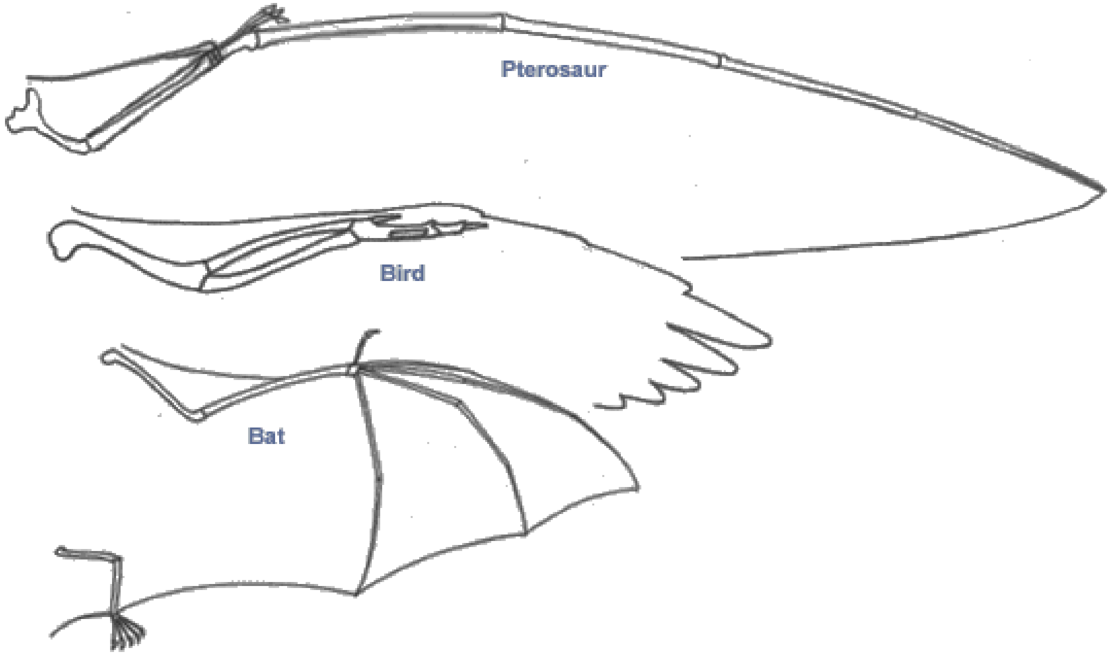

(a)
dog
cat
rat
mouse
gerbil
1/1
rabbit
pig
horse
0.81/0.52
Hipposideros larvatus
Hipposideros armiger
Hipposideros pratti
Aselliscus stoliczkanus
1/1
Rhinolphus pusillus
Rhinolophus luctus
Rhinolophus ferrumequinum
0.53/0.76
0.99/0.94
Delphinus delphis
Tursiops truncatus
Grampus griseus
1/1
Phocoena phocoena
0.16/0.29
0.54/0.49
Megaderma lyra
Megaderma spasma
0.97/0.96
Myotis leucogaster
Myotis ricketti
Barbastella beijingensis
0.59/0.65
0.43/-
Miniopterus fuliginosus
Rhinopoma hardwicki
Cynopterus sphinx
Eonycteris spelaea
Rousettus leschenaultii
0.22/0.3
1/1
Pteropus vampyrus
cow
Balaenoptera physalus
0.6/0.66
1/1
Megaptera novaeangliae
human


Whale
Bat


Whale
Bat


Pterosaur
Bird
Bat

Homology

Generic definition: Two characters in distinct organisms or taxa are homologous if they are genealogically connected by **continuous descent** from a common ancestor that had **the same** character.

Criteria of Homology

1. Similarity in descriptive properties of the character, especially complex properties that are unlikely to be independently evolved (homoplasies) (Riedl 1978; Remane 1956);
2. Similarity or sameness in the topological position of the character relative to other characters on the body, and in the relative positions of internal components of the character (Owen 1843; Jardine 1969);
3. "Congruence" or agreement with the most probable placement of other characters on a phylogenetic tree, such that homologies are *synapomorphies*, or characters that define a monophyletic group (Remane 1956; Bock 1974; Patterson 1982);
4. Similarity or sameness in the genetic and/or mechanistic generation of the character during development (Van Valen 1982; Roth 1984, 1988; Wagner 1989a, b, 2014).

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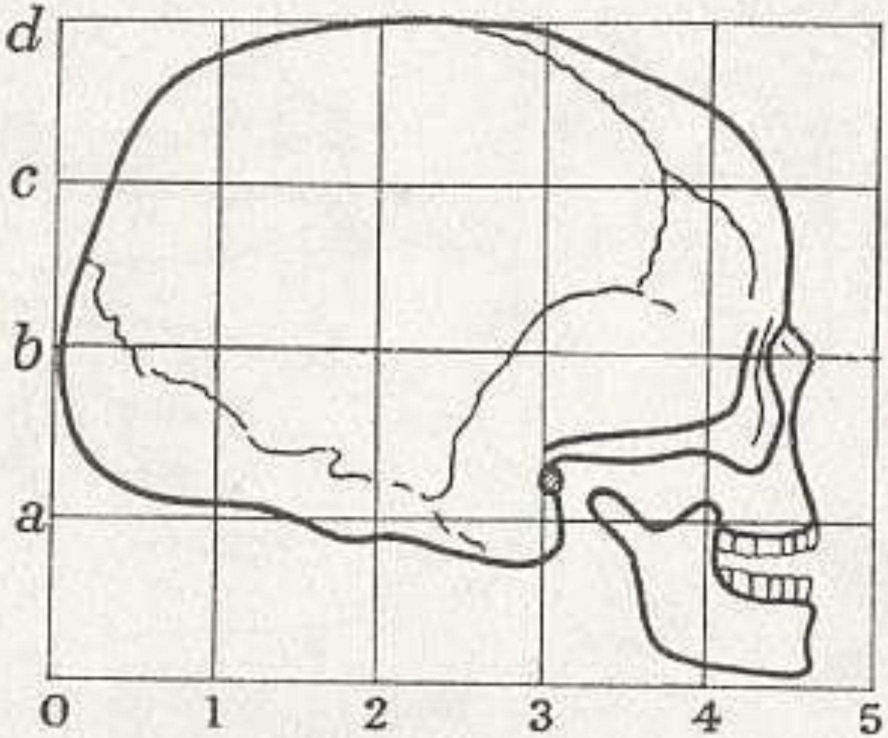

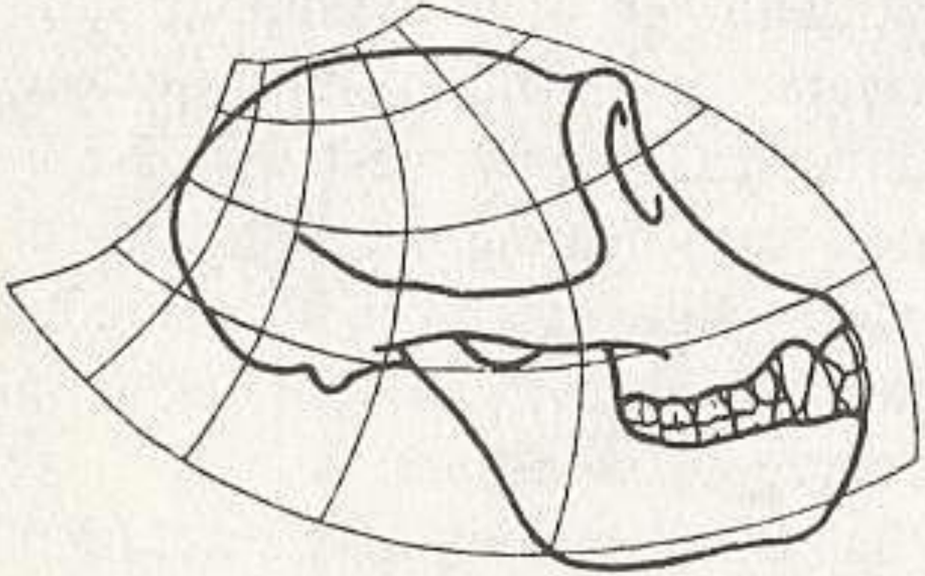

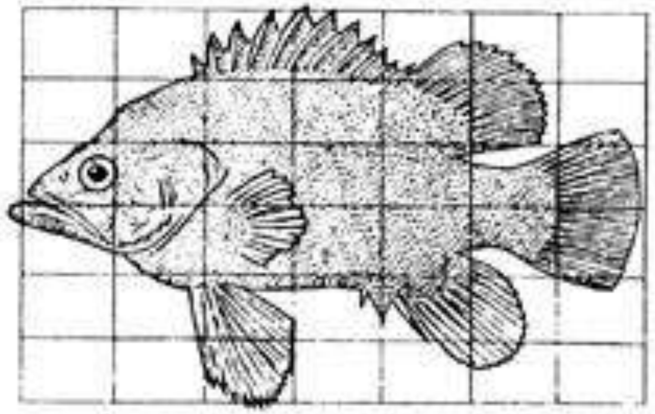

Fig. 150. *Polyprion.*

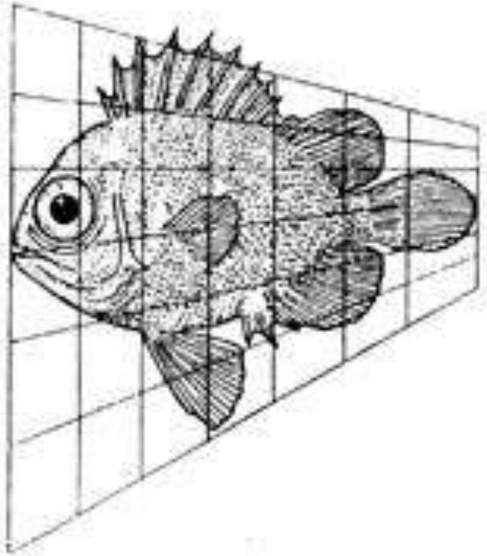

Fig. 151. *Pseudopriacanthus altus.*

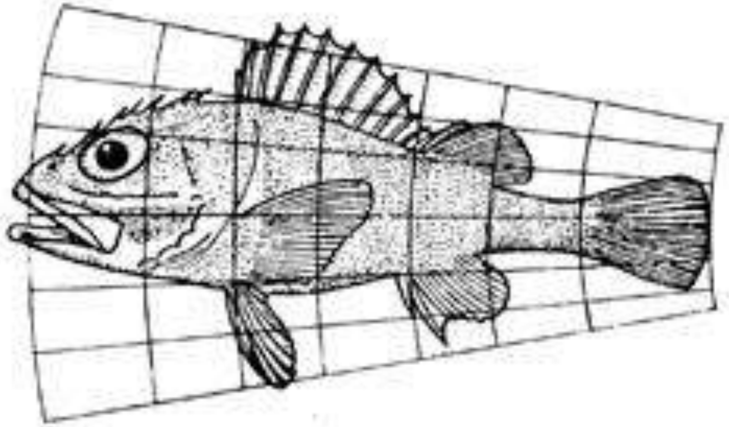

Fig. 152. *Scorpaena* sp.

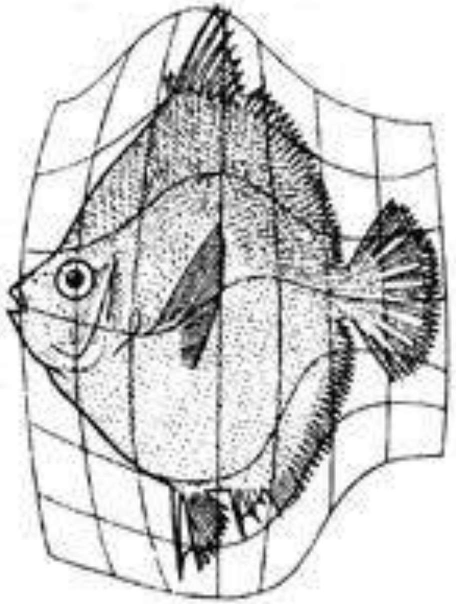

Fig. 153. *Antigonia capros.*

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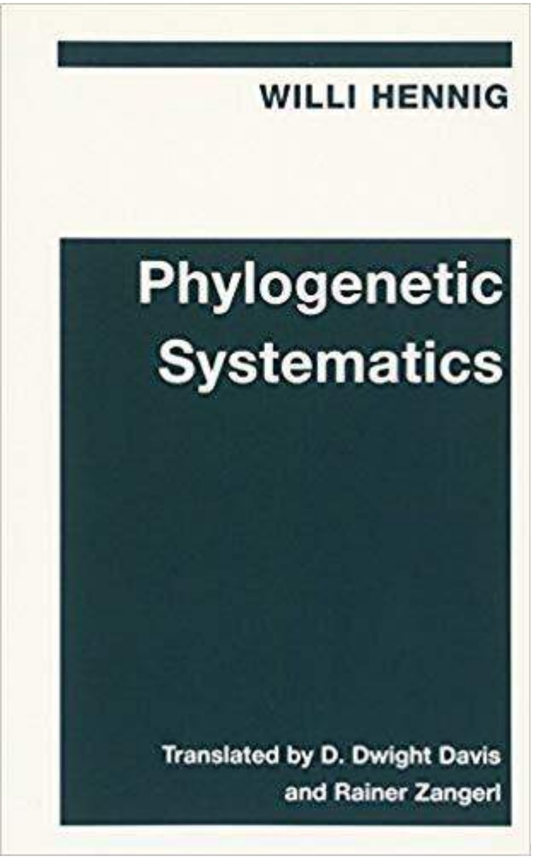
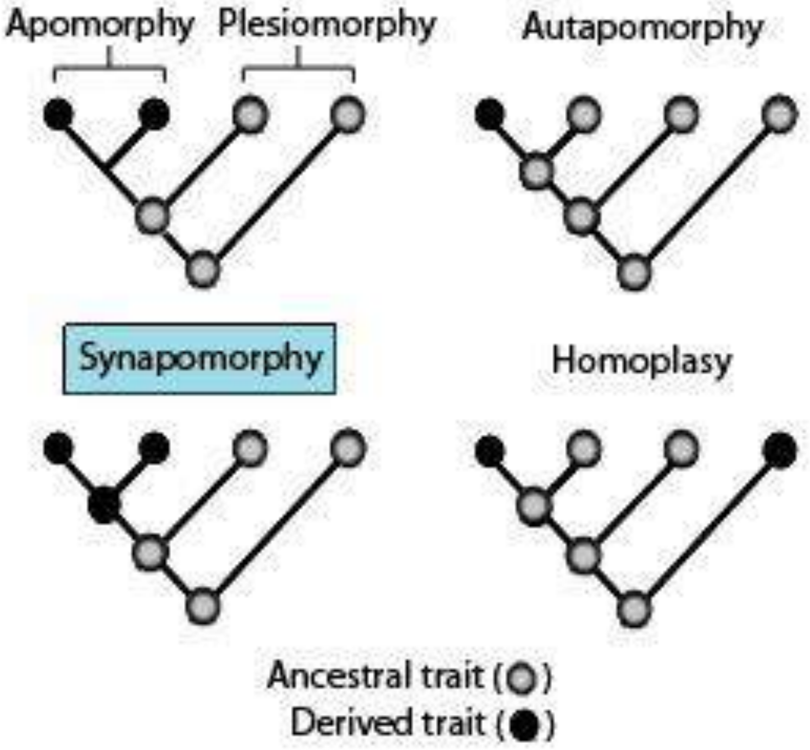
Congruence and synapomorphy





- Different possible distributions of characters into taxonomic groups are tested
- Phylogenetic view of homology
- Homology as **synapomorphy**: shared derived characters of a monophyletic group

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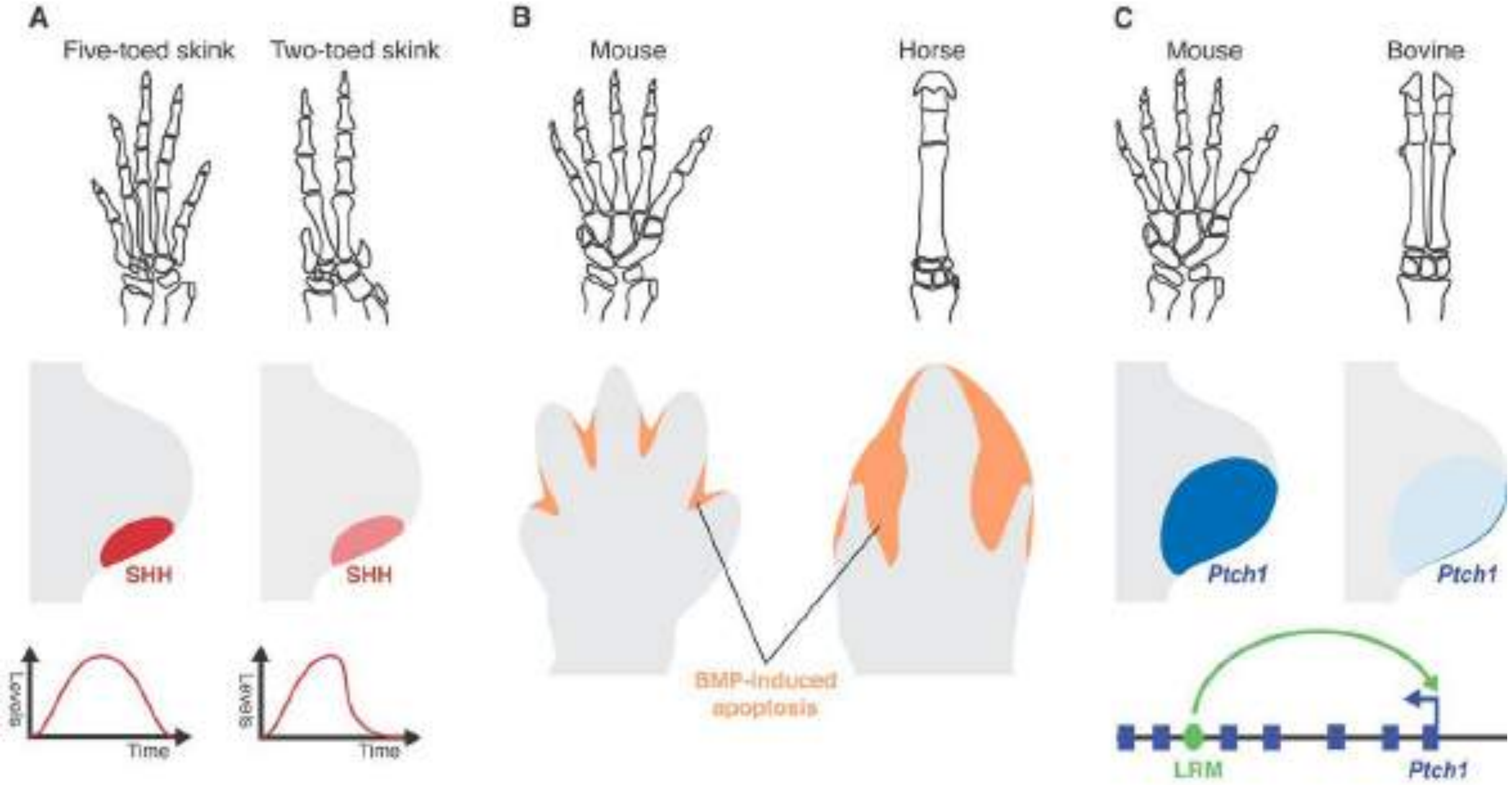
Developmental homology



- Homologues are characters that share the same causes or mechanisms of development

- The mechanisms are Gene Regulatory Networks (GRN)

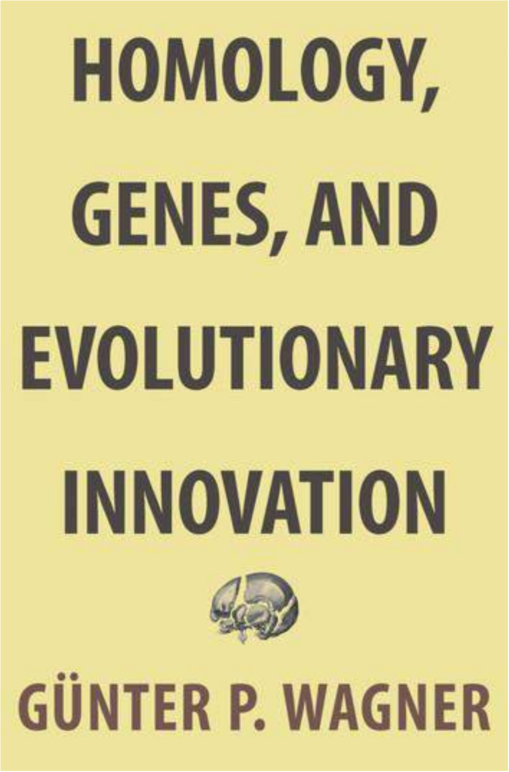
Developmental homology principle (DHP)

DHP: the identity and classification of homologues is determined by the specific developmental factors that cause them in ontogeny

Developmental homology

Core motivation: a developmental account is needed in order for homologues to be **individuated** and in order for homology to be **explained**

Individuation of homologues


HOMOLOGY,
GENES, AND
EVOLUTIONARY
INNOVATION

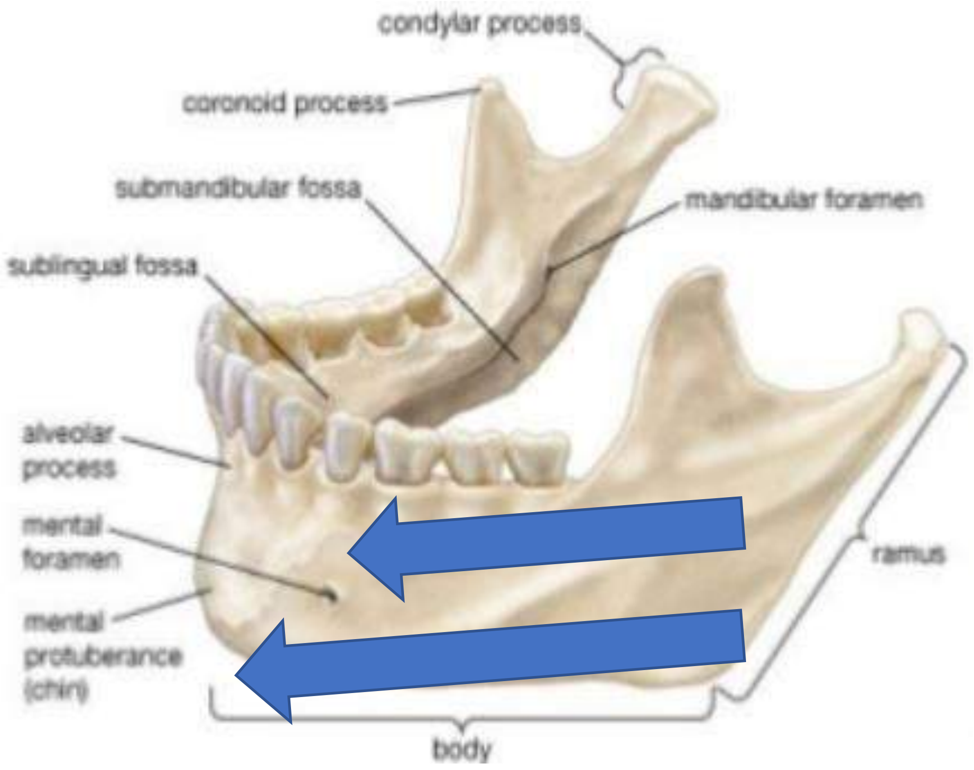
GÜNTER P. WAGNER

- Indefinitely many decompositions into traits
- Not all decompositions possess “evolutionary individuality”
- Homologues must share variational properties

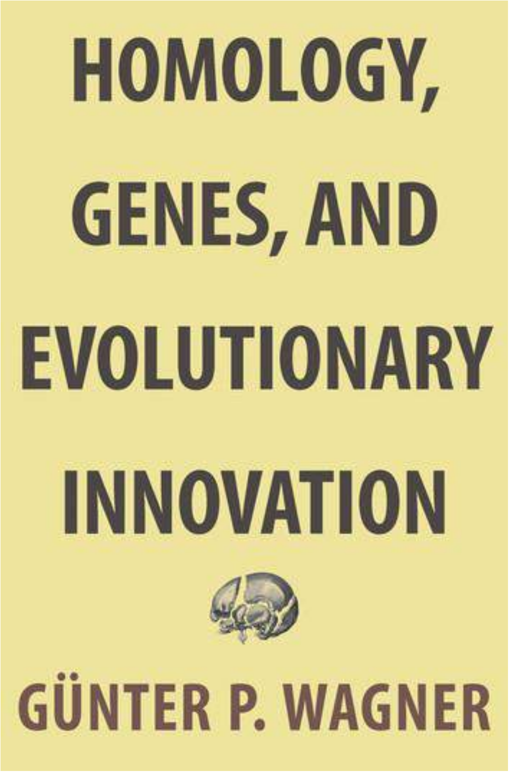
- DHP: homologues are individuated by their developmental causes

Non-character: human chin

The human chin lacks “developmental individuality”



Individuation of homologues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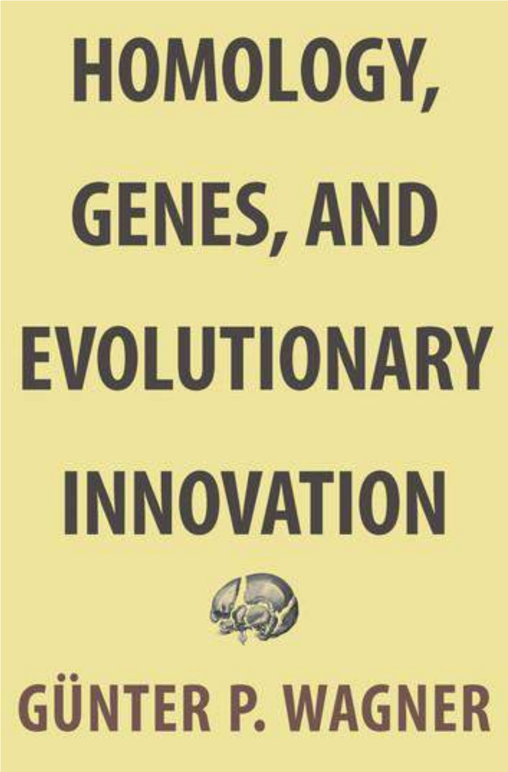
Individuation of homologues



HOMOLOGY,
GENES, AND
EVOLUTIONARY
INNOVATION

GÜNTER P. WAGNER

"The individuality of body parts, required for homology to make biological sense, requires specific genetic and developmental mechanisms to cause the distinctness of the body part during the life of an individual and continuity of distinctness in the course of evolution." (Wagner 2014, 44)

Individuation problems

- How are developmental causes/mechanisms individuated?
- No established criteria of individuation for GRNs
- It’s quite likely that there are no criteria capable of providing causes that are always historically coextensive with the associated characters
- Homologous characters can have different (non-homologous) causes

Developmental System Drift (DSD)

EVOLUTION & DEVELOPMENT 3:2, 109–119 (2001)

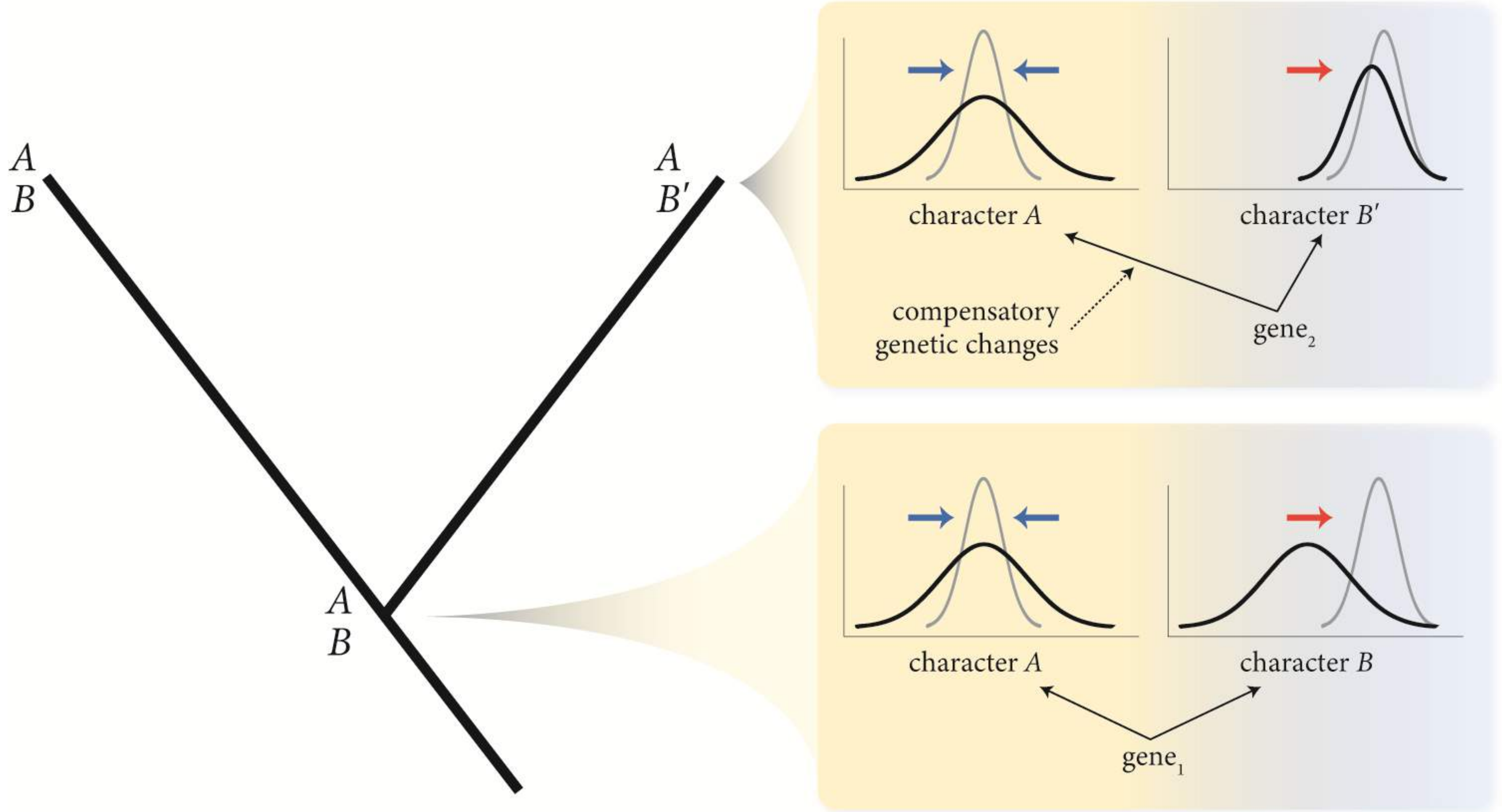
Developmental system drift and flexibility in evolutionary trajectories

John R. True[a,c,*] and Eric S. Haag[b,c]
[a]Laboratory of Molecular Biology, [b]Department of Biochemistry, and [c]Howard Hughes Medical Institute,
University of Wisconsin, Madison, WI 53706, USA
*Author for correspondence (email: jrtrue@facstaff.wisc.edu)

DSD occurs when there are changes in the genes and/or network underlying the same character in related taxa

Occurs because of (1) neutral drift; (2) selection on a correlated phenotype with pleiotropic genes; (3) drift and selection

Selectional DSD



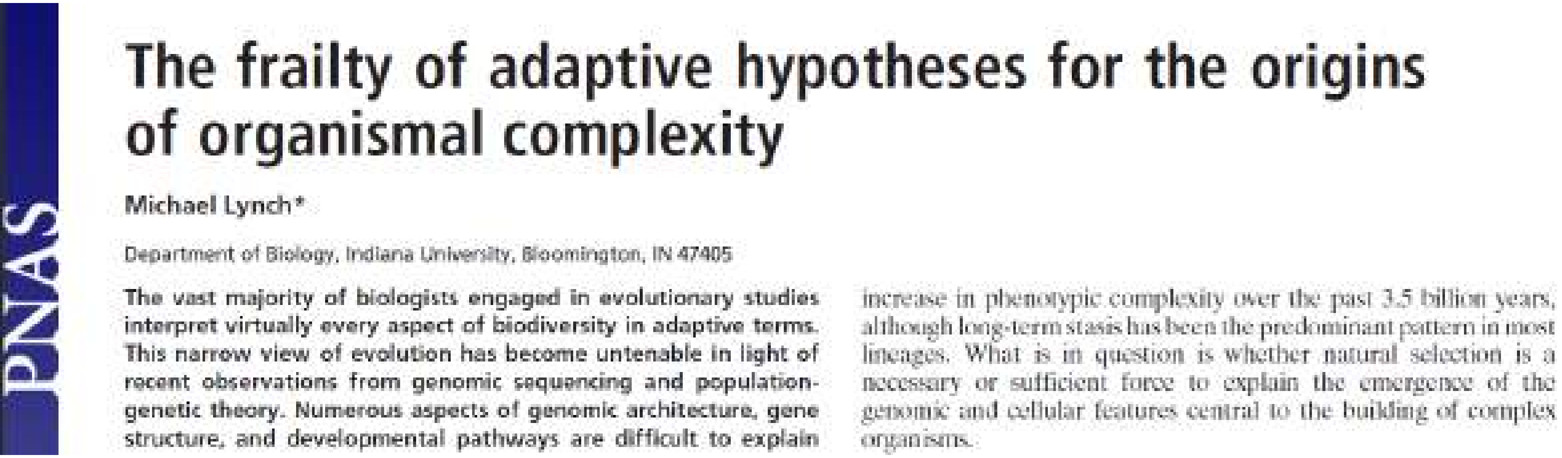
Neutral DSD

- Selection cannot discriminate between different ways of building the same trait

- Depends on strength of selection, N_e, total genetic variance, effect size, phylogenetic distance

Neutralist DSD

- Eukaryotic genome evolution dominated by non-adaptive processes
- Gene duplication + subfunctionalization + partitioning among paralogs
- Trait polygeny + small effect sizes → *most genetic changes beneath detection threshold of selection* (Rockman 2012; Kingsolver et al 2001)



PNAS

The frailty of adaptive hypotheses for the origins of organismal complexity

Michael Lynch*

Department of Biology, Indiana University, Bloomington, IN 47405

The vast majority of biologists engaged in evolutionary studies interpret virtually every aspect of biodiversity in adaptive terms. This narrow view of evolution has become untenable in light of recent observations from genomic sequencing and population-genetic theory. Numerous aspects of genomic architecture, gene structure, and developmental pathways are difficult to explain

increase in phenotypic complexity over the past 3.5 billion years, although long-term stasis has been the predominant pattern in most lineages. What is in question is whether natural selection is a necessary or sufficient force to explain the emergence of the genomic and cellular features central to the building of complex organisms.

Brit. J. Phil. Sci. **66** (2015), 505–536

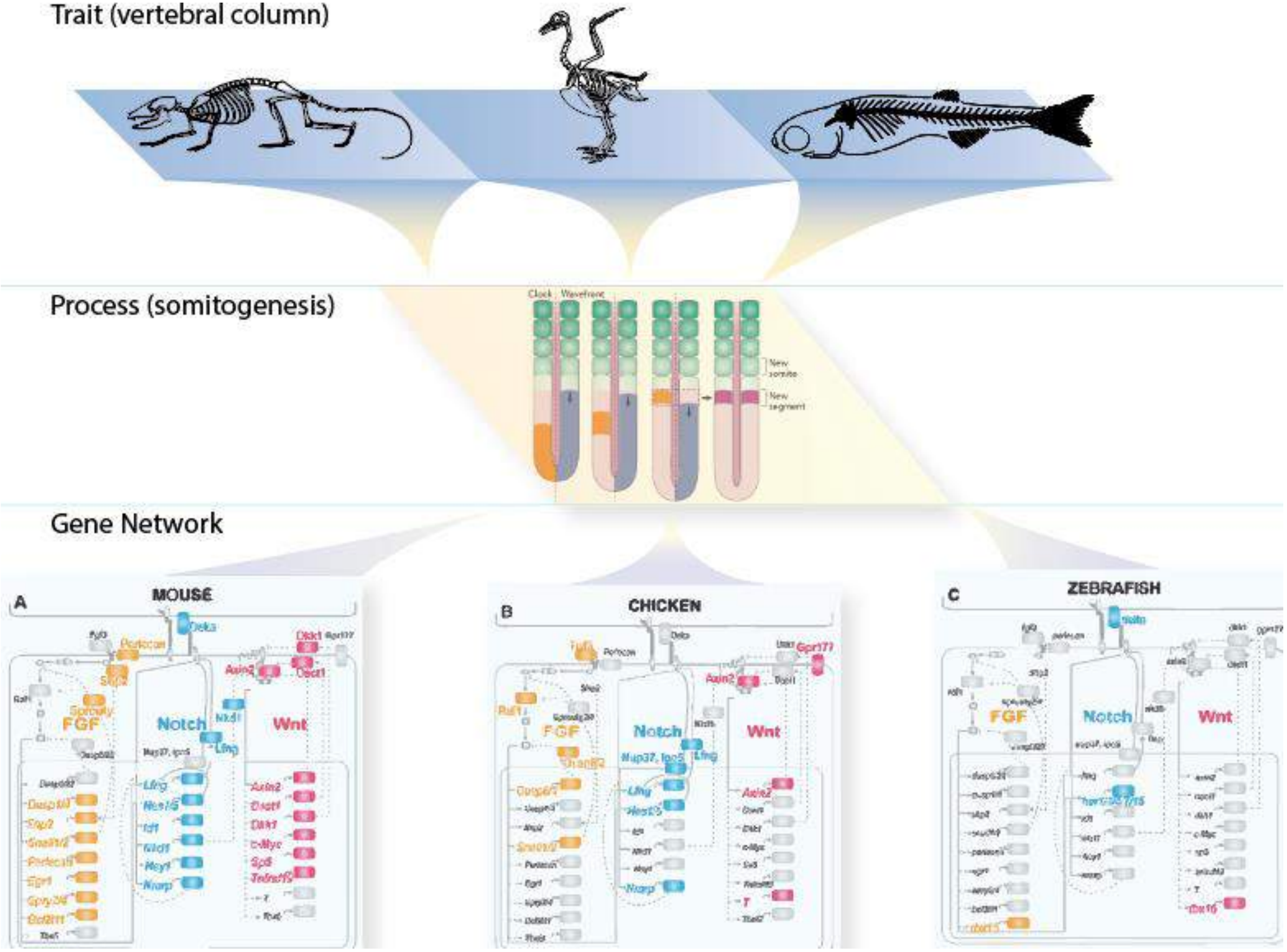
The Genomic Challenge to Adaptationism

Sahotra Sarkar

Trait (vertebral column)

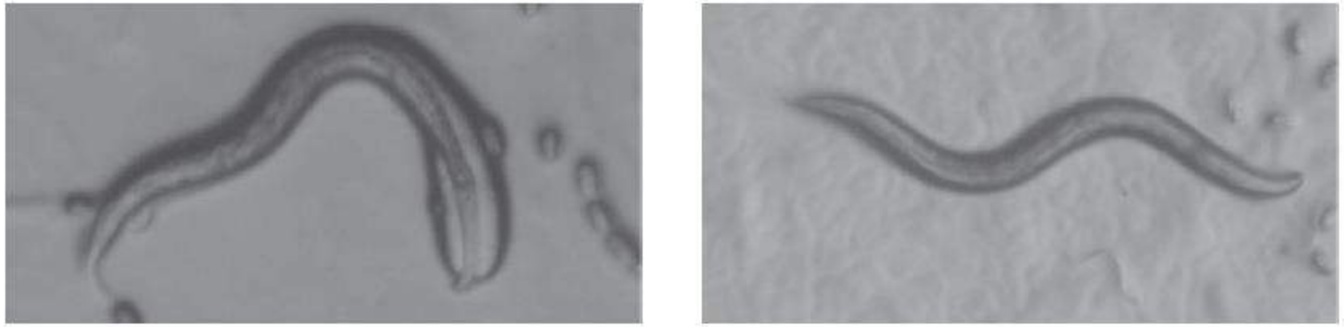
Process (somitogenesis)

Gene Network



Developmental System Drift (DSD)

- *C. elegans* and *C. briggsae* diverged 20 Mya
- Out of 1300 conserved genes, 25% had acquired different functions



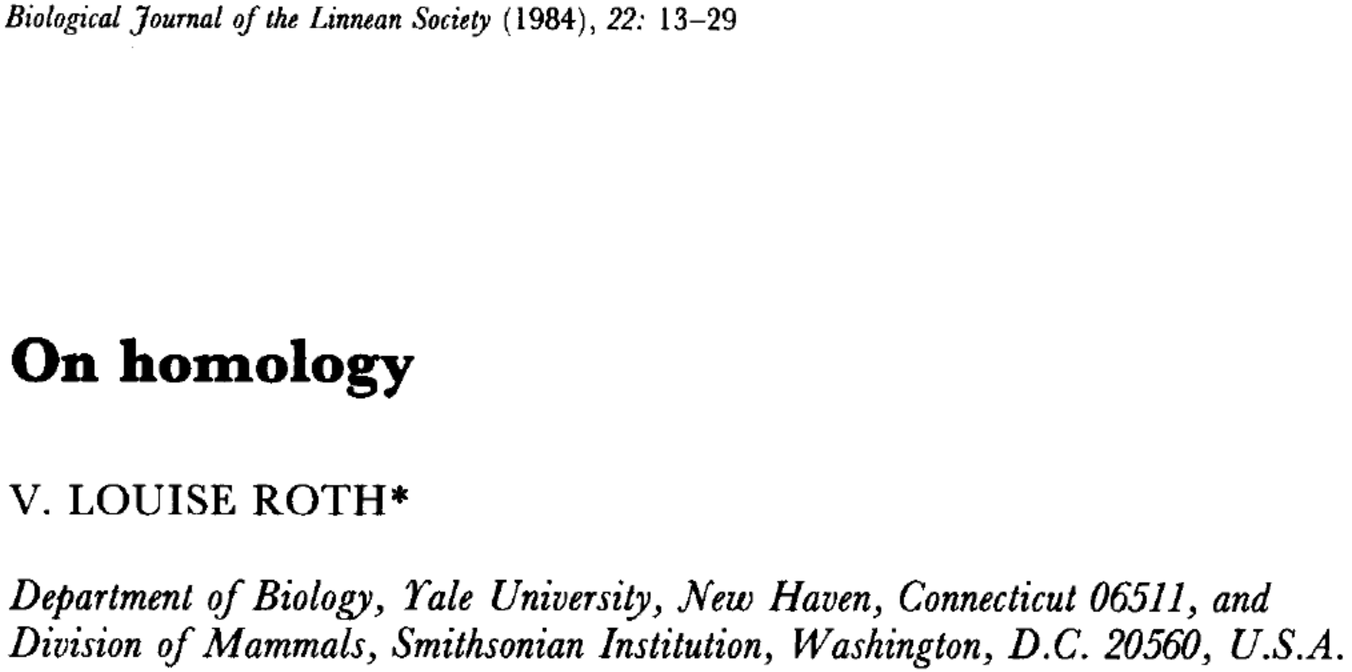
C. elegans
bli-5 (RNAi)

C. briggsae
bli-5 (RNAi)

Verster et al (2014) “Comparative RNAi Screens in *C. Elegans* and *C. Briggsae* Reveal the Impact of Developmental System Drift on Gene Function.” *PLOS Genetics* 10(2): e1004077.

Genes: thread of identity or meandering spoor?

“*Genetic relationship* provides the thread which unites all forms of biological homology into one concept, with one definition.”



Biological Journal of the Linnean Society (1984), *22:* 13–29

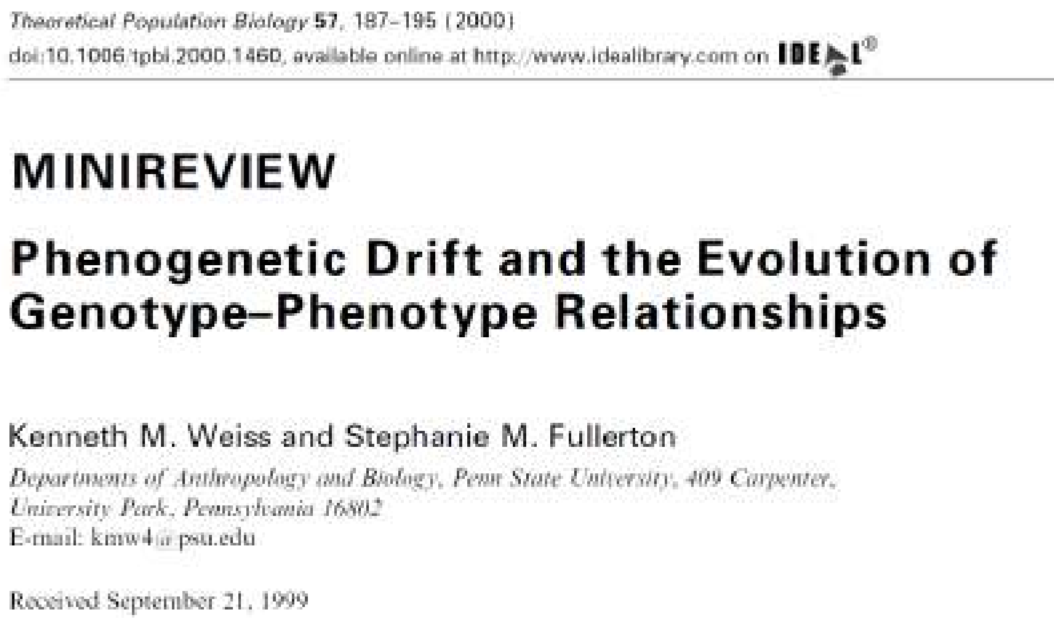
On homology

V. LOUISE ROTH*

Department of Biology, Yale University, New Haven, Connecticut 06511, and
Division of Mammals, Smithsonian Institution, Washington, D.C. 20560, U.S.A.

Genes: thread of identity or meandering spoor?

“It may seem mystical to suggest that biology is not ‘molecular’ at its core the way physics and chemistry are. But suppose it is not the genome that is especially conserved by evolution. Suppose the ephemeral phenotype really is what we need to understand and what persists over time. Genes would then be ‘only’ the meandering spoor left by the process of evolution by phenotype.”



Theoretical Population Biology **57**, 187–195 (2000)
doi:10.1006/tpbi.2000.1460, available online at http://www.idealibrary.com on IDEAL®

MINIREVIEW

Phenogenetic Drift and the Evolution of Genotype–Phenotype Relationships

Kenneth M. Weiss and Stephanie M. Fullerton
Departments of Anthropology and Biology, Penn State University, 409 Carpenter, University Park, Pennsylvania 16802
E-mail: kmw4@psu.edu

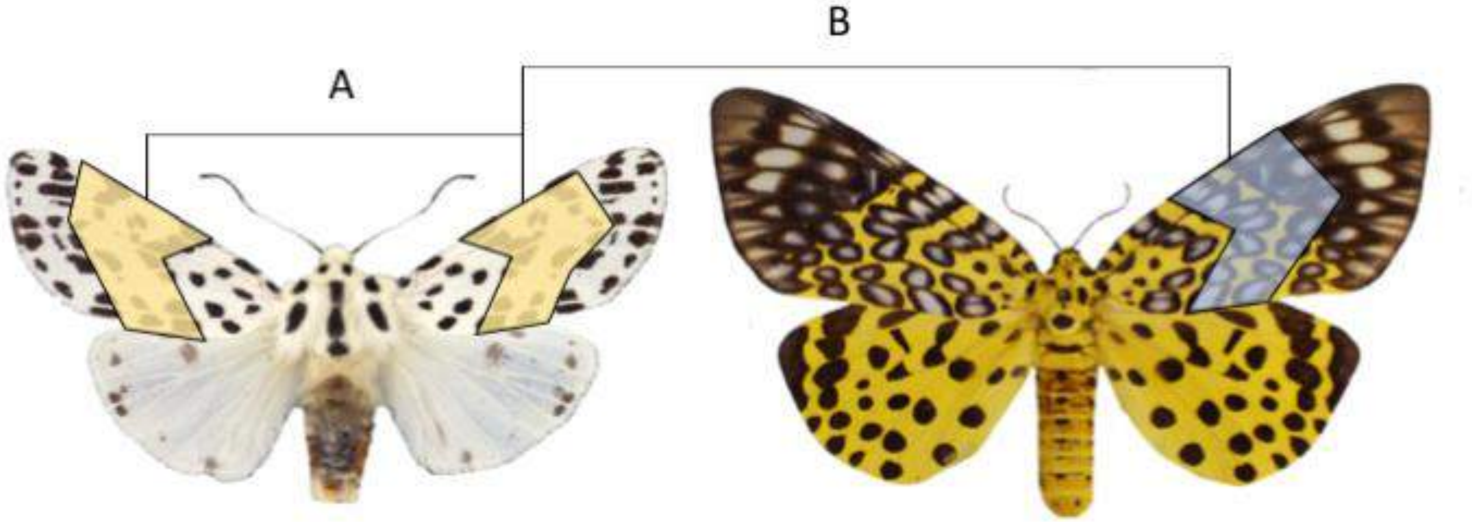
Received September 21, 1999

Explaining homology

DHP: the identity and classification of homologues is determined by the specific developmental factors that cause them in ontogeny

Why are the same characters present in diverse taxa at all?

* Developmental constraints explain the evolutionary stability of homologues*



Problems with developmental explanations of homology

(What explains the evolutionary distribution and stability of developmental constraints?—inheritance)

(1) Homologous characters can have non-homologous developmental constraints (DSD)

(2) Developmental mechanisms are not the only factors that explain character stability. There is also:
    (a) Stabilizing selection (incl. burden, generative entrenchment)
    (b) Inherent physical robustness
    (c) Phylogenetic niche conservatism

Impasse of definitions

- Does my argument beg the question against developmental views?

Different problem:

- If DHP is true, then it is true *by definition* that the evolutionary stability of homologues is explained by development

= only development can explain the stability of characters whose stability is explained by development

- Then development does not provide a better explanation of *<u>the same</u>* phenomenon (homology) than evolution

Developmental explanations of homology

- An account of homology that rejects DHP as an answer to the individuation problem still has access to developmental explanations of character stability

- Adopting a developmental definition of homology does nothing to improve our ability to explain homology in terms of development.

Concluding remarks

- Evolution at one level can be de-coupled from evolution at another

- The expectation that morphological homology will be definable in terms of developmental mechanisms (Brigandt 2002, 401; Griffiths 2007, 651; Wagner 2014, 50) should be met with skepticism

Metaphilosophy of science

- Conceptual analysis?
- It’s unrealistic to expect that any property or constitutive feature of homology is immune to the contingencies of evolutionary change
- We should not expect to find a definition of homology in terms of necessary and sufficient conditions

Definition pluralism?

- My position: development provides an important class of explanations of homology but does not define homology

What if we adopted pluralism about definitions?

- It wouldn't improve our ability to individuate homologues
- It wouldn't improve our ability to explain homology, and would actually hinder it

Explanatory pluralism requires definition monism

Costs: sacrifices the unity of the concept, increased cognitive load

From definitions to theories

- Take counterexamples as opportunities to revise the *theory* of homology
- Incorporate deviations from 1:1 correspondence into the theory as something to be expected under certain conditions

Examples

- DSD is more likely in reproductive organs, when pleiotropy is high, and when there are abundant functionally equivalent genes, low N_e, more phylogenetic distance, etc.
- Genetic specificity is more likely in later evolutionary epochs

- The refutation of generalizations by evolutionary contingency might not be an ultimate state of affairs

- Exceptions to one regularity might be signals of another regularity

- Towards a *hierarchical* theory of developmental evolution

Thank you!

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