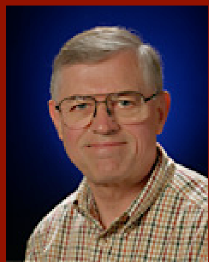
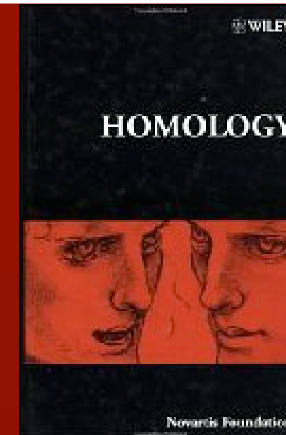
Assessing homology at different levels of the biological hierarchy

August, 16, 2011

Brian K. Hall





"I will grant that someone might be able to generate an original thought concerning homology, but I doubt it."

(Wake, 1999, In *Homology*. Novartis Foundation Symposium 222, Wiley, Chichester. p. 24)

A central Issue:

Does homology of the phenotype (structure, behaviour, physiology) depends upon the feature sharing common genetic/developmental pathways ?

i.e.,

Should (must) our (single) concept of homology apply to all levels in the biological hierarchy ?

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Richard Owen (1804–1892) — who gave us our ‘modern’ definition of homology did not think so.

Nor did Charles Darwin (1809–1882) who used Owen’s non-evolutionary definition/concept in his evolutionary writings

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Neither Owen nor Darwin based homology on shared development

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Owen

Homology "is mainly, if not wholly, determined by the relative position and connection of the parts, and may exist independently of...similarity of development"…"There exists doubtless a close general resemblance in the mode of development of homologous parts; but this is subject to modification, like the forms, proportions, functions and very substance of such parts, without their essential homological relationships being thereby obliterated"

(*Report on the Archetype*)

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Darwin

"Thus, community in embryonic structure reveals community of descent; but dissimilarity in embryonic development does not prove discommunity of descent, for in one of two groups the developmental stages may have been suppressed, or may have been so greatly modified through adaptation to new habits of life, as to be no longer recognizable

(*Descent of Man*)

Which one is the transformationist ?

2nd central Issue:

With what do we compare/contrast homology ?

Owen said analogy but that is ‘wrong’

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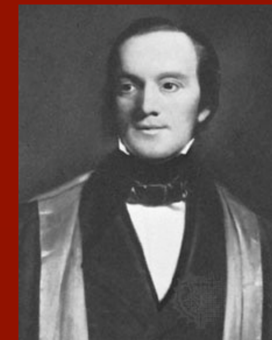


Owen

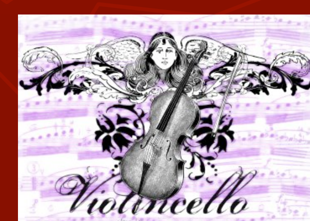
A tall man with great glittering eyes

Brilliant and politically astute

Incredibly charming but could be (usually was?) irascible, ruthless, condescending, egotistical, authoritarian, mean-spirited

Loved poetry, and the works of Dickens and Kingsley, whom he entertained to dinner

Passion for music and was a good performer on the violincello and flute



Performed music with Charles Dickens

Owen spends 31 years (1825-1856) with the Royal College of Surgeons as Conservator and Hunterian Professor

Obtained many specimens from the Zoological Society to dissect and becomes world expert on fossils

1856 (age 52) — Superintendent of the Natural History Department of the British Museum, culminating in removal (in 1881) of the natural history collections to South Kensington as the British Museum (Natural History).

Remained in office until 1884 (age 80)

Owen's analysis rarely extended beyond comparative anatomy, although he was well aware of the adaptation of form to function (Britain's Cuvier).

He was aware of and contributed enormously to descriptions of the geographical and geological distributions of animals

He did comment on geological succession of species and genera as possibly indicating a sequence of replacement and origin

But, he remained a defiant typologist and non-transformist

Richard Owen left a legacy that is fundamental and foundational.

It is the greatest Legacy of any non-Darwinian to modern biology

It is Homology

Criteria to reveal homology of structures were developed in the 18th C, esp. by the

French anatomist Etienne Geoffroy St.-Hilaire

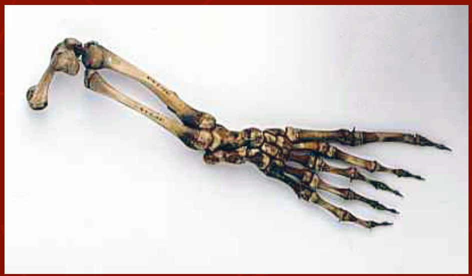
(a) position

(b) connections

[(c) intermediate stages]

human

seal



Owen did not change these criteria

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These criteria were developed to reveal homology of structures, not behaviours or physiology

They describe the final adult feature (pattern) not how that pattern arose

human

seal

Owen did not change this position

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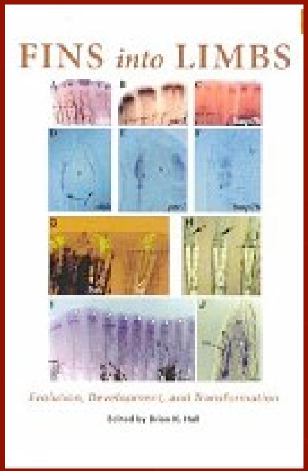
Fins into Limbs



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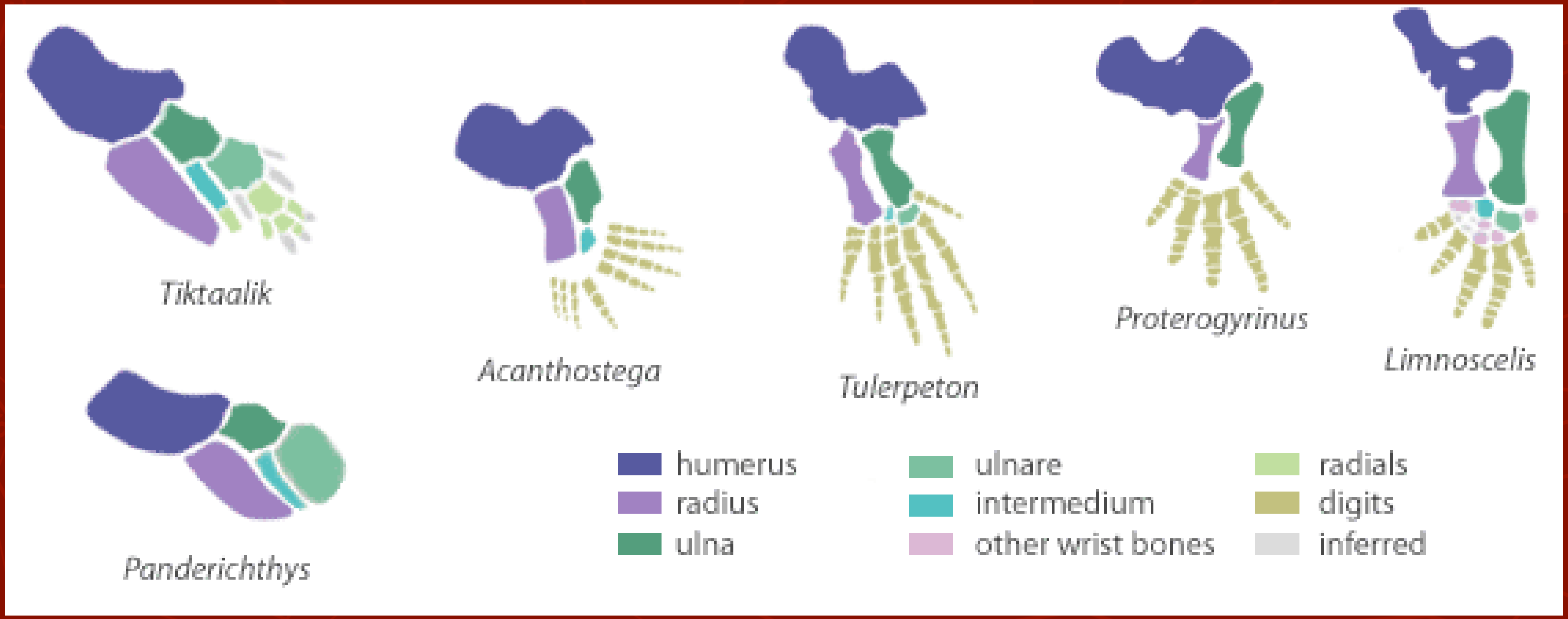


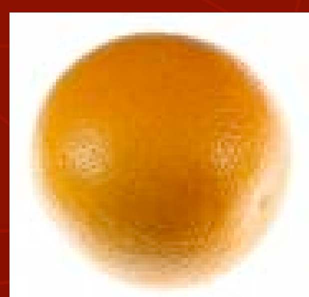
Although he provided much of the comparative anatomical basis for transformation of morphology, the transformations themselves were a closed book to Owen

Owen saw the homology of the elements of tetrapod limbs, of fins to limbs, indeed of elements of fundamental archetypes

He described changes in earlier forms leading to reptiles, birds, horses in terms of comparative anatomy not transformation

He saw "the nature and mode of operation of the laws governing life… as the great aim of the philosophical naturalist"

Nevertheless, because of Richard Owen we know that an apple is an apple and an orange an orange but that a bird is not a bat



Owen defined homology and distinguished homology from analogy

All Owen's comparative anatomy was based on assessment of homology

Owen used homology to build a zoology based on maintenance of the archetype

Darwin used Owen's definition of homology to build biology based on transformation

One is comparative anatomy, the other the science of life

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Owen defined homology (homologue) and analogy (analogue) in a glossary to the published version of his *Lectures on Comparative Anatomy and Physiology of the Invertebrate Animals, Delivered at the Royal College of Surgeons in 1843*

"Homologue...The same organ in different animals under every variety of form and function......

Analogue...A part or organ in one animal which has the same function as another part or organ in a different animal" (pp. 379, 374)

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Although after Darwin it could be stated that "a feature is homologous in two or more taxa if it can be traced back to the same feature in the presumptive common ancestor" (Mayr, 1982, pp. 45, 232), criteria for determining structural homology remain today what they were in pre-Darwinian times — position and connections

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Owen's analysis rarely extended beyond comparative anatomy, although

he was well aware of the adaptation of form to function (Britain's Cuvier).

He was aware of and contributed enormously to descriptions of the

geographical and geological distributions of animals

He did comment on geological succession of species and genera as

possibly indicating a sequence of replacement and origin

But, he remained a defiant typologist and non-transformist

(1) The first pairing/contrast

Owen contrasted homology with analogy — similar structure vs. superficial similarity but similar function

This is a pre-evolutionary pairing/contrast and should be discarded

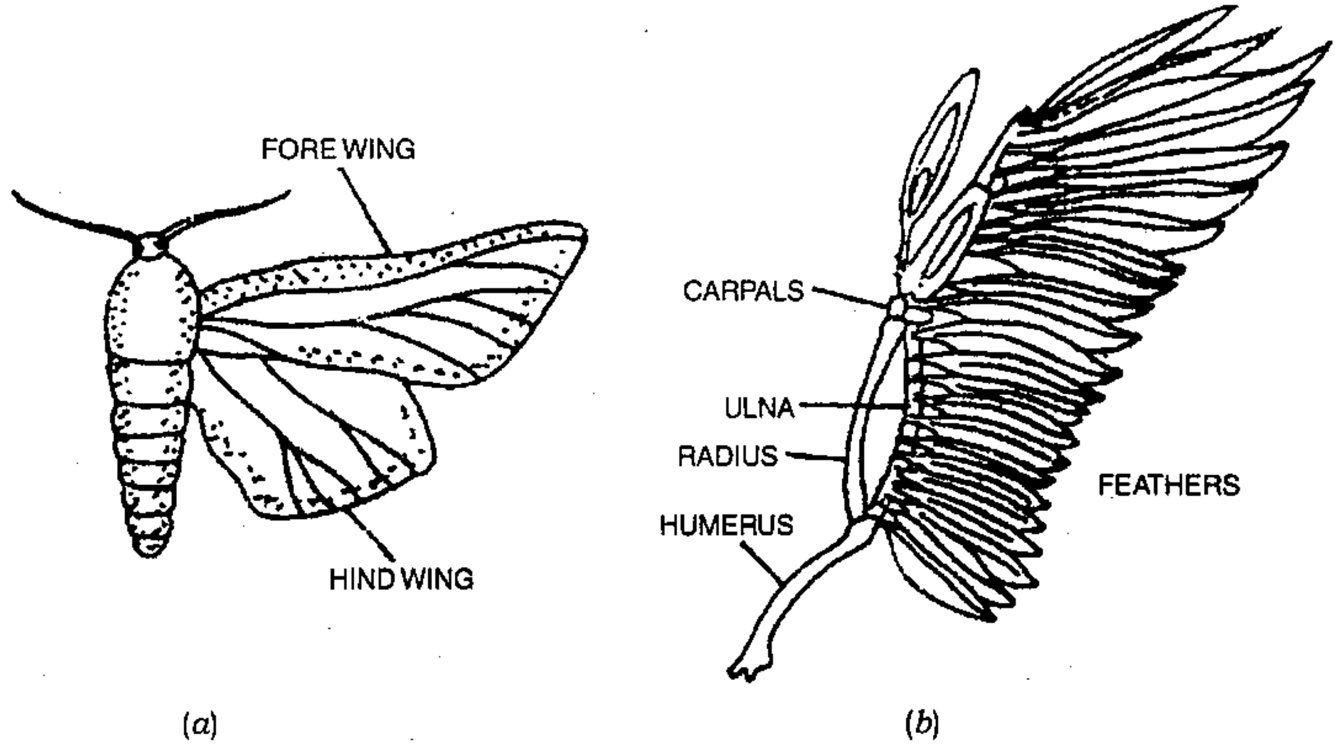


Fig. 8.17. Analogy in the wings of (*a*) insect (*b*) bird.

The first major shift in homology came in 1870 when the zoologists Karl Gegenbaur (1826–1903) and (E.) Ray Lankester (1847–1929) – 3rd director of the BM(NH) – independently sought to bring Owen's definitions (and concept) into line with evolutionary theory

Lankester edited and revised the English translation of Haeckel's *History of Creation* in 1876

A spellbinding teacher, Lankester

"was the only man in London who could hold his lectures at one o'clock, the sacred luncheon-hour, and have them crowded. His lecture-room, and Balfour's at Cambridge, were the two foci from which the new views on morphology and evolution were spread throughout the academic world.

(*Nature*, 1929, 129, p. 346)

Lankester advocated abandoning the term homology altogether, proposing in its place 'homogeny' for similarity resulting from shared ancestry

Structures which are genetically related, in so far as they have a single representative in a common ancestor, may be called homogenous. We may trace an homogeny between them, and speak of one as the homogen of the other... details not traceable to, and inherited from the ancestor cannot be homogenous

Lankester introduced 'homoplasy' for the second class of similarity resulting from independent evolution.

Both homogeny and homoplasy are classes of homology

Neither Gegenbaur nor Lankester were concerned with finding the antithesis of homology

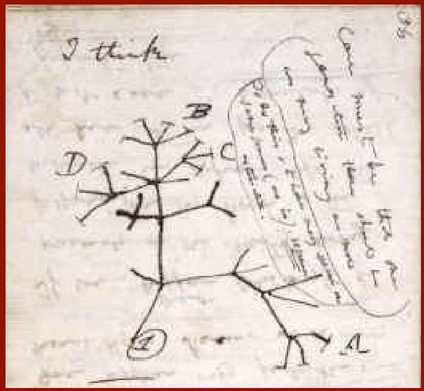
Both placed homology into an evolutionary framework because both were staunch Darwinians:

"in [the various] kinds of animals and plants [we see] simply the parts of one great genealogical tree, which have become detached and separated from one another in a thousand different degrees, through the operation of the great destroyer Time..." (Lankester, 1870)

(2) The second pairing/contrast

Homogeny and homoplasy are classes of homology for features derived from common ancestry or independent evolution, respectively

This is an evolutionary pairing/contrast and should be retained



Lankester's term homogeny did not take hold.

Homology – similarity because of common descent and ancestry

Homoplasy – similarity arrived at by independent evolution

Homoplasy traditionally as parallelism and convergence

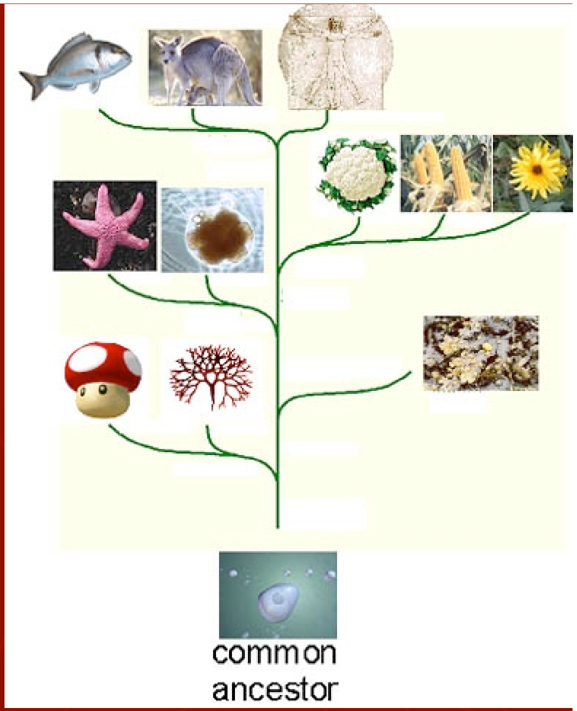
Homology: The same character continuously present in two taxa and in their most recent common ancestor (shared ancestry and usually shared development)

Reversals, atavisms, vestiges, rudiments: Feature, either fully formed or incomplete, and similar to a fully formed feature seen in ancestors within the lineage or in a related taxon

Parallelism: A feature present in closely related organisms but not present continuously in all members of the lineage (similar development)

Convergence: Similarity arising through independent evolution (most likely different development mechanisms)

However



There has been but one history of life

All organisms, and therefore all features of organisms
share some degree of relationship and similarity

Either by
Similarity or even identity of structure reflecting sharing of a most recent common ancestor (ape and human humeri)

or

Some (often small) degree of similarity, such as that between the wings of insects and the wings of birds because of deep shared ancestry

An expanded category of homology

Homology —> reversals —> rudiments —> vestiges —> atavisms —> parallelism

Convergence as the only class of homoplasy

as advocated by Lankester (1870) and independently by Gould (2002) and Hall (2003)

Goud, S. J. (2002). *The Structure of Evolutionary Theory*. The Belknap Press of Harvard University Press, Cambridge MA

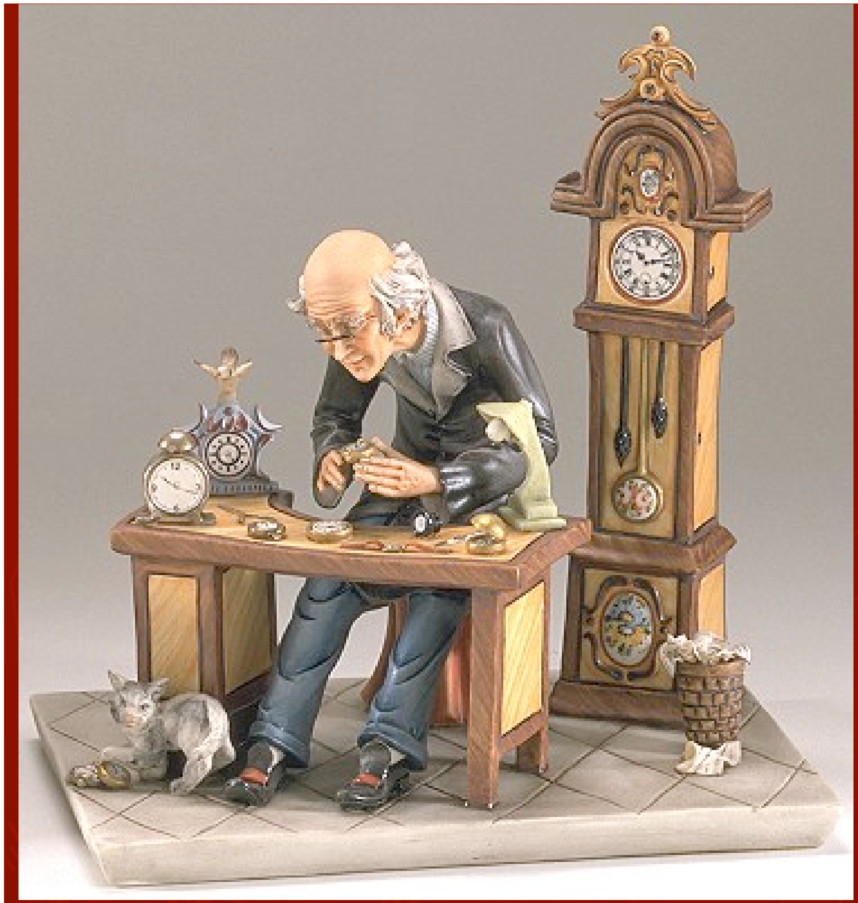
Hall, B. K. Descent with modification: the unity underlying homology and homoplasy as seen through an analysis of development and evolution. *Biol*. *Rev*. *Camb*. *Philos*. *Soc*. 78: 409-433.

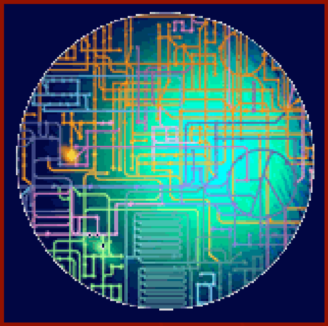
(3) The third pairing/contrast

Homology representing shared (most recent) common ancestor

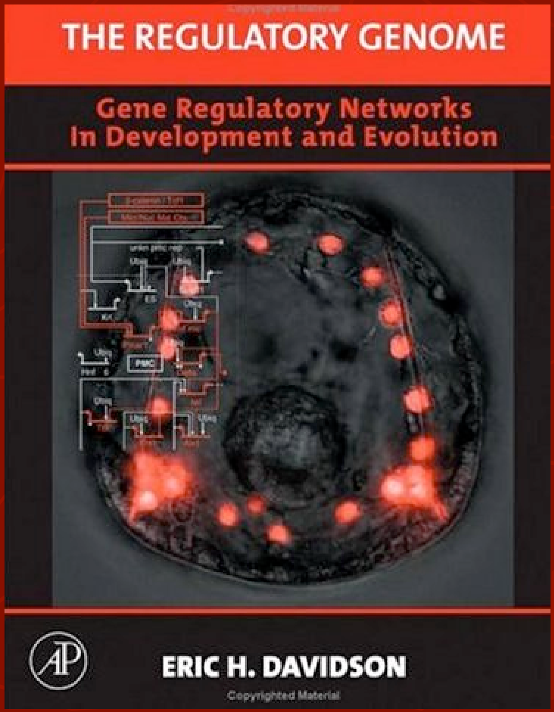
Homoplasy (convergence) representing ‘more distant’ ancestry

This is a expanded evolutionary synthesis pairing and should be retained





Tinkering



These relationships reflect the reality of evolution by **tinkering** (bricolage; Jacques Monod) and the **deep homology** of shared genetic, biochemical, cellular and developmental mechanisms across the animal kingdom

Homology has been approached at two levels

Structural / taxic homology reflects the presence of the same character in two lineages that share a common ancestor (a synapomorphy)

Developmental homology pertains to the 'same' developmental mechanisms producing a shared character.

Structural homology need not always equate with developmental homology. For instance developmental mechanisms, down to the level of gene regulation, can evolve, despite forming structurally homologous features.

This realignment bridges phylogenetic and developmental approaches to homology and homoplasy

It will not (and in a practical sense cannot) alter how homoplastic features are identified in phylogenetic analyses

It should allow us search for the common elements underlying the formation of the phenotype (what some have called the deep homology of genetic and/or cellular mechanisms), rather than discussing features in terms of shared or independent evolution

What are those common elements ?

Shared up-stream signaling genes (*Pax-6*)

a gene cascade

a gene network(s)

The same gene involved in the same feature

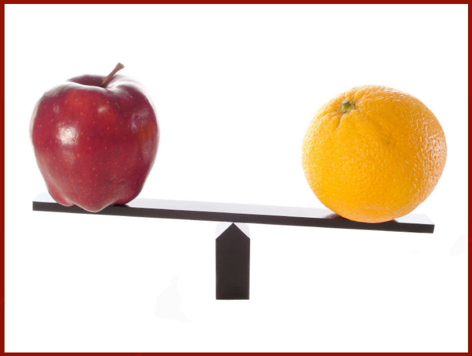
The same regulatory change (*cis-*) in different lineages ?




(4) The fourth pairing/contrast

Homology vs. Novelty

Analysis of novelty requires integrated phylogenetic, developmental, and molecular genetic analysis



Novelty is all about:

Similarity (homology and homoplasy)

Relationships (phylogenetic history)

Shared Development and Shared Gene Pathways/Networks (evolutionary history)

Definitions and Concept

(Müller and Wagner, 2003)

"A new constructional element in a body plan that neither has a homologous counterpart in the ancestral species nor in the same organism"

Hall (2005)

"A novelty (whether structure, function, or behaviour) is a new feature in a group of organisms that is not homologous to a feature in an ancestral taxon"

Westin Hotel knows what Novelty is

"Hotel invites guests to pick price of room"

"This is the first time that we are trying something like this and, as far as we know, it's the first time that a hotel has attempted this, so it's certainly novel"

Novelty is non-homology

A novelty (non-homologue) requires (by definition?) that the information to form the novelty not have been present in the lineage or have been present but unavailable/incomplete/latent

If the genetic (or other?) basis of the feature must be novel for the feature to be novel (non-homologous), then

Two mechanisms emerge as providing (genetic) bases for novelty (i.e. for non-homology)

Gene co-option followed by neofunctionalization

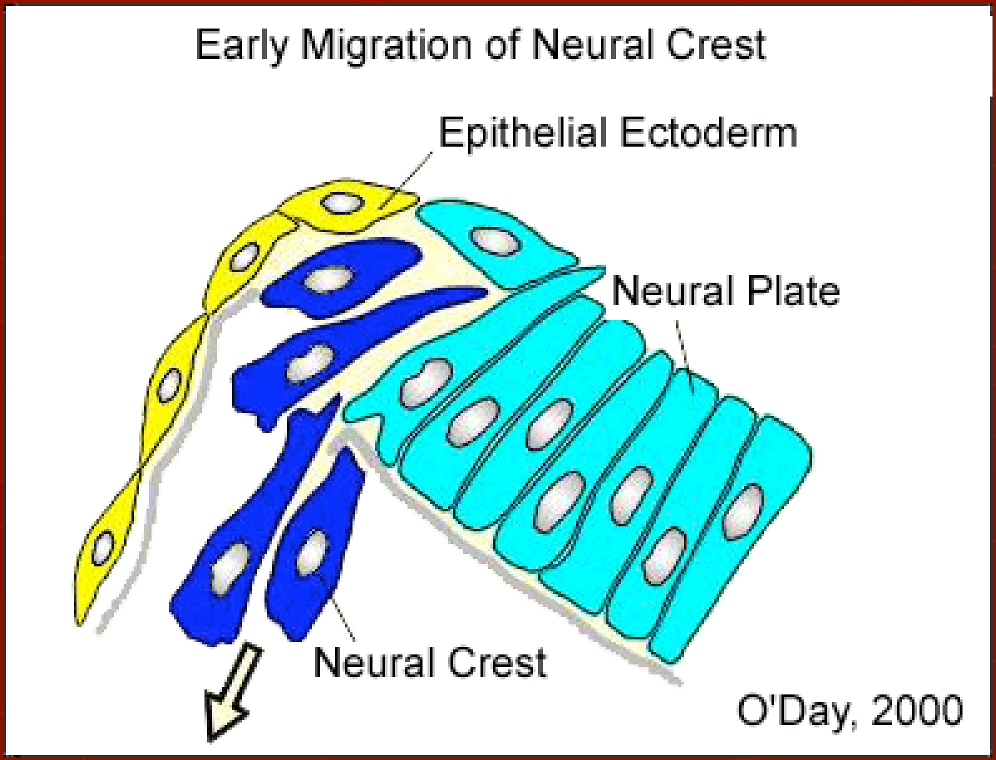
or

Lateral gene transfer

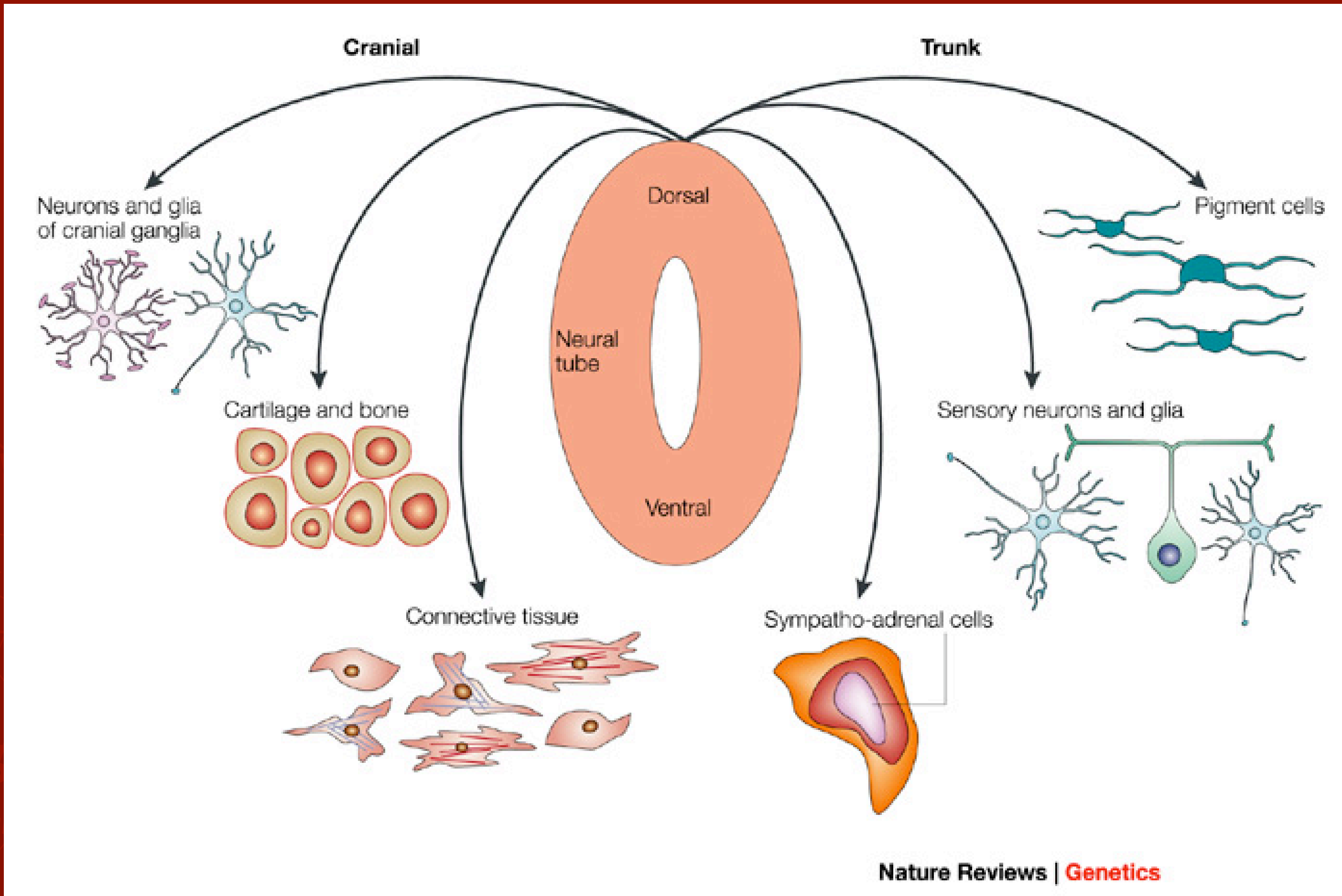
Hall, B. K., and Kerney, R. Levels of Biological Organization and the Origin of Novelty *J. Exp. Zool. (Mol. Dev. Evol.*) (early view).

Example of Gene co-option from other regions of the body

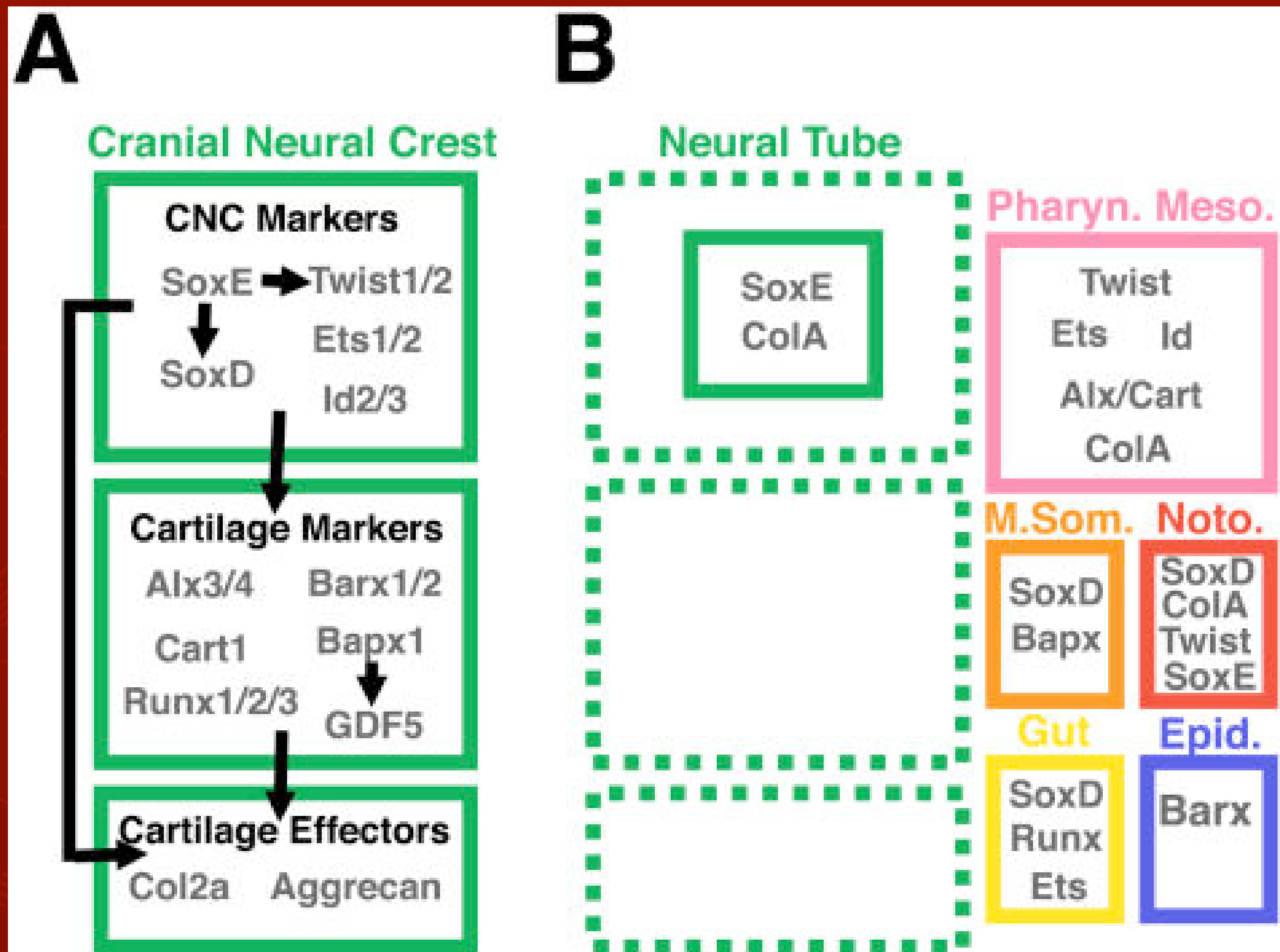
during evolution of neural crest



Derivatives of the Neural crest (NCCs)

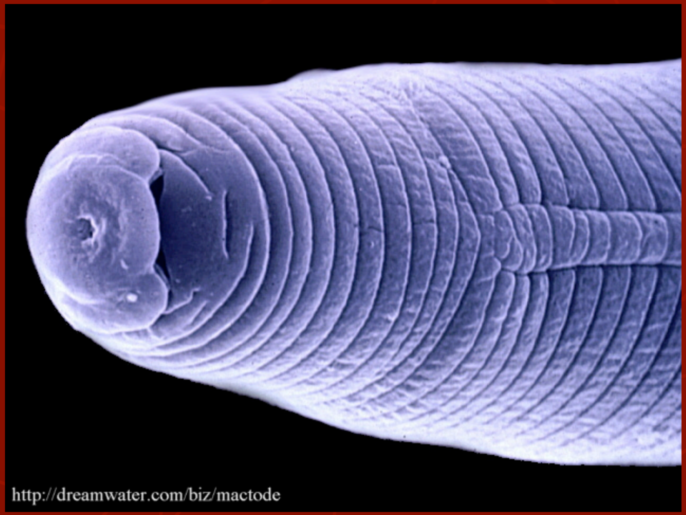


(A) Gene network in neural crest-derived cartilage. (B) Expression of network component homologs in amphioxus



Meulemans D, Bronner-Fraser M. (2005). Central role of gene cooption in neural crest evolution. *J Exp Zool* (*MDE*) 304, 298-303.

Digestion of Plant Products by the cotton root-knot nematode, *Meloidogyne incognita*

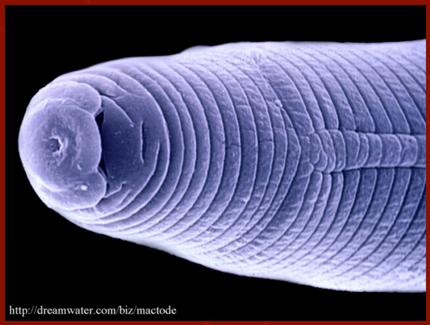


E. G. J. Danchin et al., Multiple lateral gene transfers and duplications have promoted plant parasitism ability in nematodes. PNAD (2010) doi/10.1073/pnas. 1008486107

60 genes in six protein families that degrade plant cell walls in genome of *M. incognita*

This novel although don't have detailed knowledge of related or ancestral taxa

(Cellulases, xylanases, hemicelluloses, polygalacturonases, pectata lysases, arabinanase)



E. G. J. Danchin et al., Multiple lateral gene transfers and duplications have promoted plant parasitism ability in nematodes. PNAD (2010) doi/10.1073/pnas. 1008486107

Table 1. Plant cell wall-modifying proteins in nematodes

Family	Activity	Closest relative
GH28	Polygalacturonase	Ralstonia: *Ralstonia solanacearum*
PL3	Pectate lyase	Actinomycetales
GH43	Putative arabinanase	Actinomycetales
GH5 (cel)	Cellulase	Coleoptera
GH5 (xyl)	Endo-1,4-β-xylanase	*Clostridium acetobutylicum*
EXPN	Loosening of plant cell wall	Actinomycetales

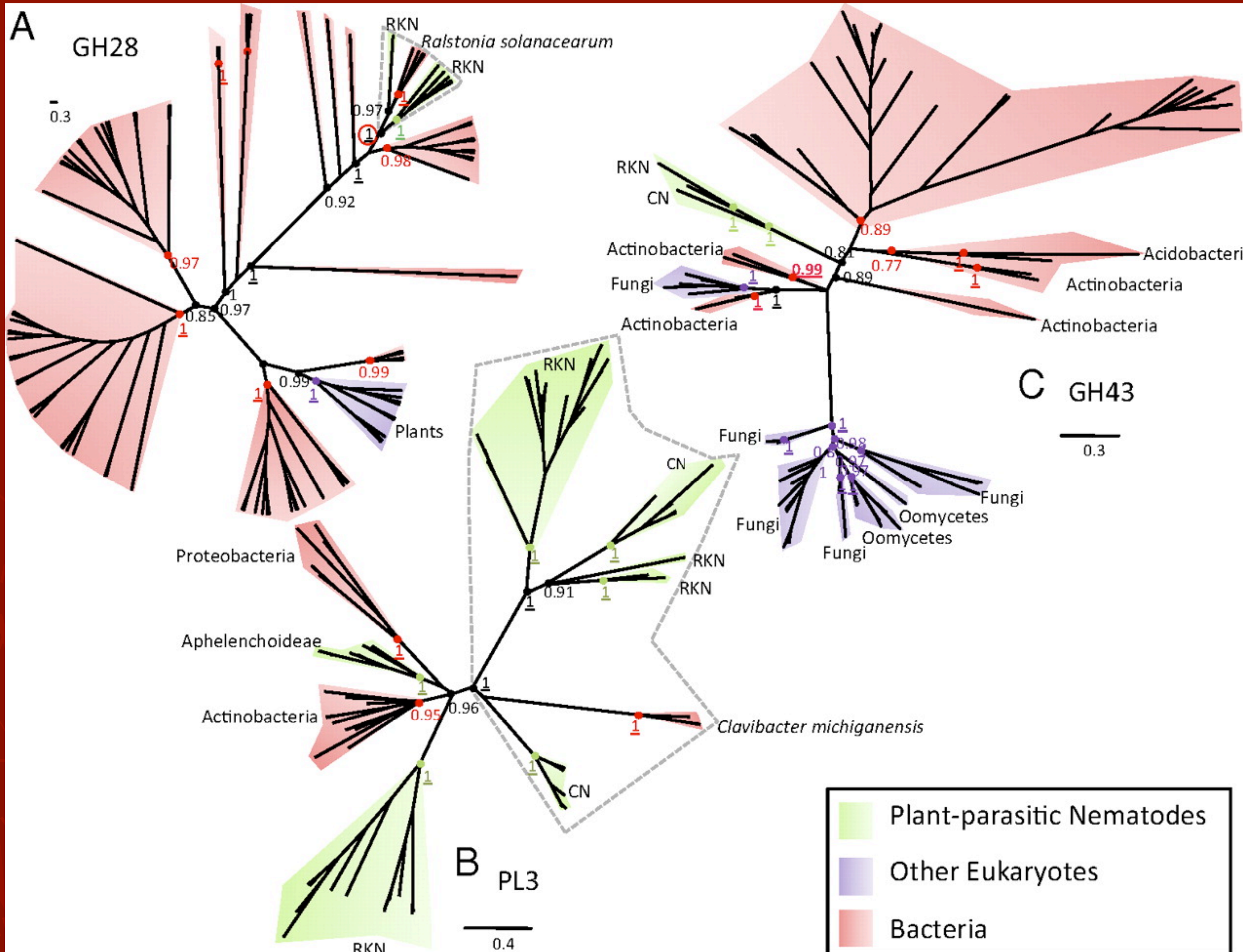
So What ? Where is the novelty ?

Arose from multiple, independent lateral gene transfers from different bacteria,

followed by

many gene duplications to form multigene families

E. G. J. Danchin et al., Multiple lateral gene transfers and duplications have promoted plant parasitism ability in nematodes. PNAD (2010) doi/10.1073/pnas. 1008486107



Phylogenetic trees of pectin-modifying proteins. (A) GH28 polygalacturonases; (B) PL3 Pectata lysase; (C) GH43 arabinase. Dashed lines delineate phylogenetic groupings of bacterial and plant-parasitic nematode

So, where are we ?

Homology — Analogy

Homology — Homoplasy

Homology — Convergence (homoplasy)

Homology — Novelty

Where do we go from here ?

Some discussion and then over to the philosophers

to wit: Paul Griffiths TBA