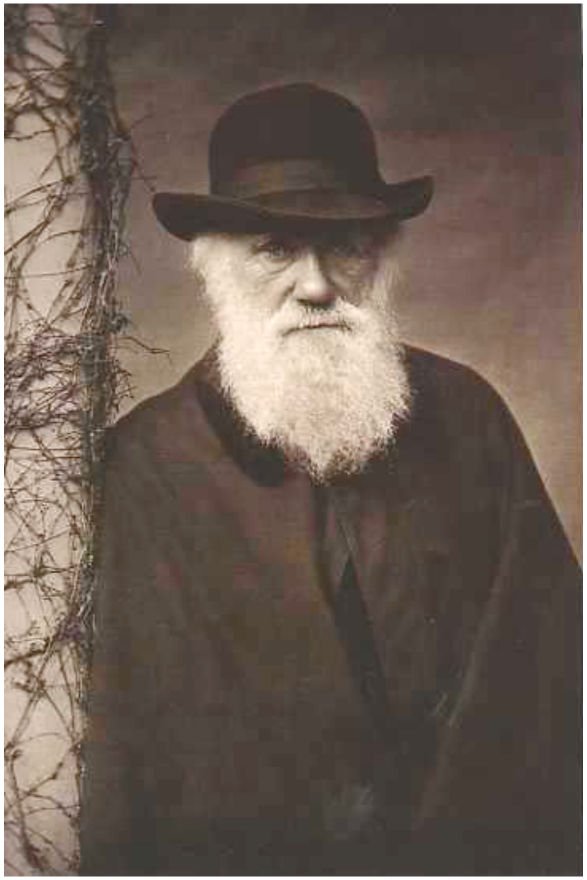
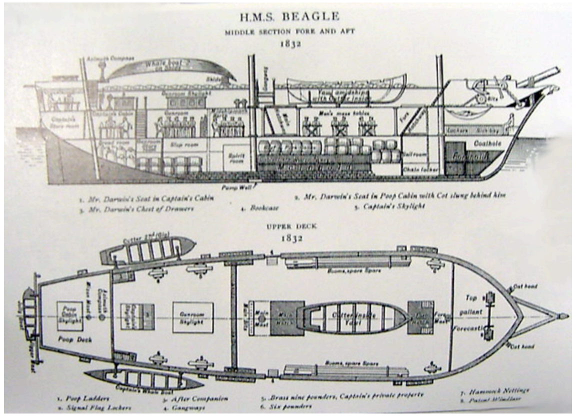
My Favorite (Current) Evolution Stories – An Emphasis on What We Know and How We Know It



Rob Phillips
California Institute of Technology
A Special Lecture: Darwin 200
Feb. 12, 2009

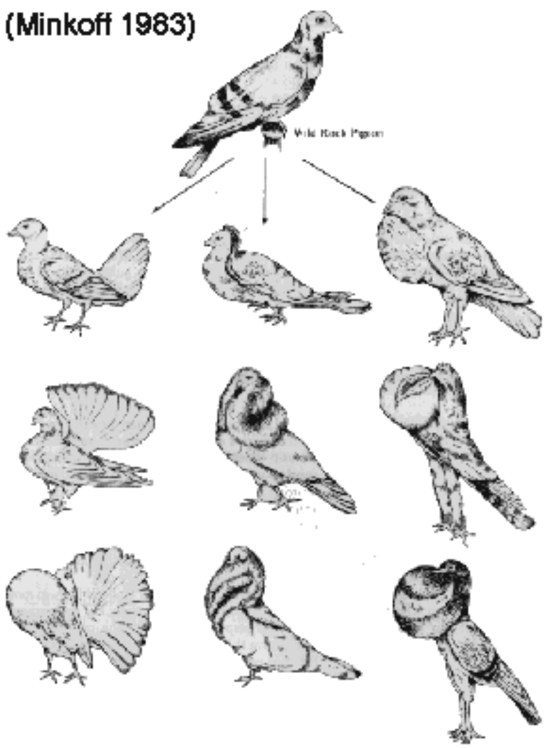
Biology's Greatest Idea

- *In physics we often celebrate the unity of phenomena. In biology, a compelling and exciting alternative is to embrace the diversity of phenomena.*
- *Fascinating essay of T. Dhobzhansky entitled: ``Nothing in biology makes sense except in the light of evolution." - the phrase has become hackneyed, but the idea has not.*
- *Darwin found data led to inescapable conclusion, ``it was like confessing a murder" he wrote.*



Lagrange on Newton: he was "the most fortunate, for we cannot find more than once a system of the world to establish." The same can be said of Darwin and Wallace.

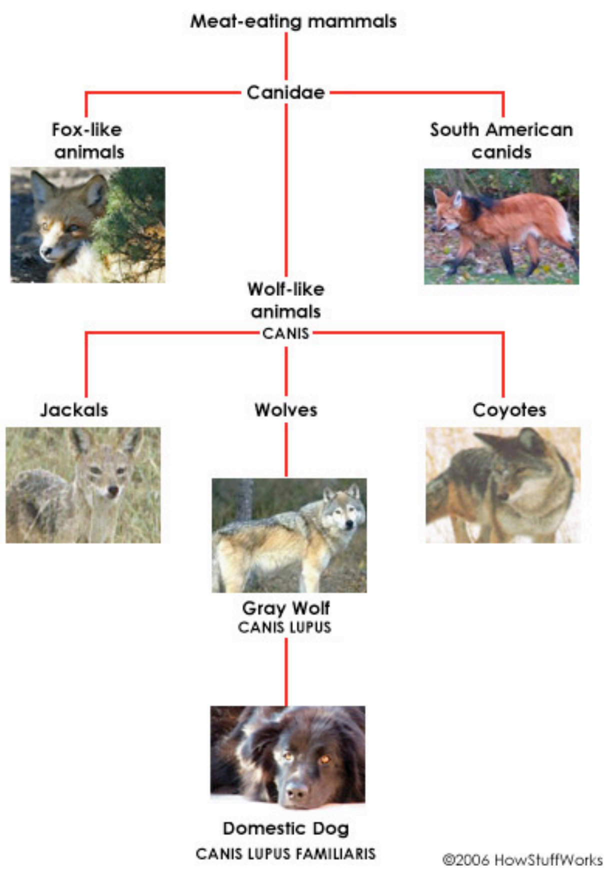
The Ingredients of Evolution: Heritable Variation



- *One ingredient for evolution is variation, differences between the parents and their offspring.*
- *Though Darwin is famous for finches, if you read ``The Origin of Species" you will see that it starts by talking about domestication of animals and how breeders exploit variation (Darwin was way into pigeons).*
- *The ``struggle for existence" - you do the numbers on a bacterial culture!*

Are You Living With Wolves? The Wonder of Artificial Selection

- *A classic story of artificial selection is provided by man's best friend.*
- *All dogs descended from only one of the more than 20 canine species: WOLVES.*



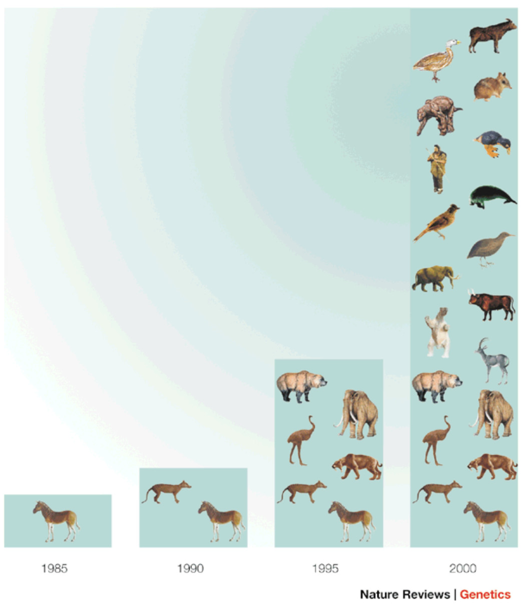
Biology's Uniquely Beautiful Approach to Heritable Variation: Genetics

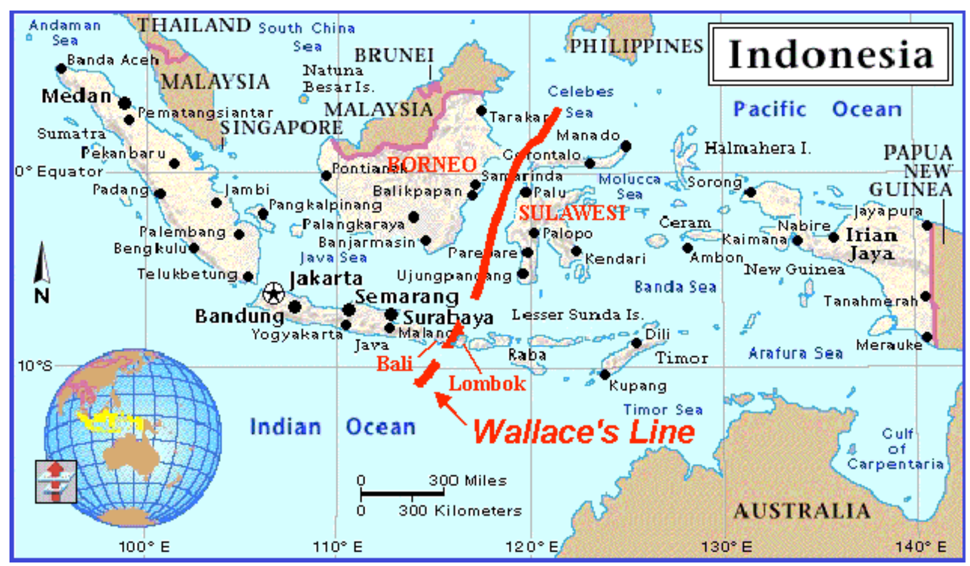
- *Genetics, as discovered by Mendel, provided the mechanistic underpinnings for the observed variations in organisms.*
- *Controlled study of variation in fruit flies (Drosophila melanogaster)provided a host of interesting insights into development and heredity.*

Female (left) and male (right) flies with the mutation eyeless

Evolution: How Do We Know? !!!!!!!!!

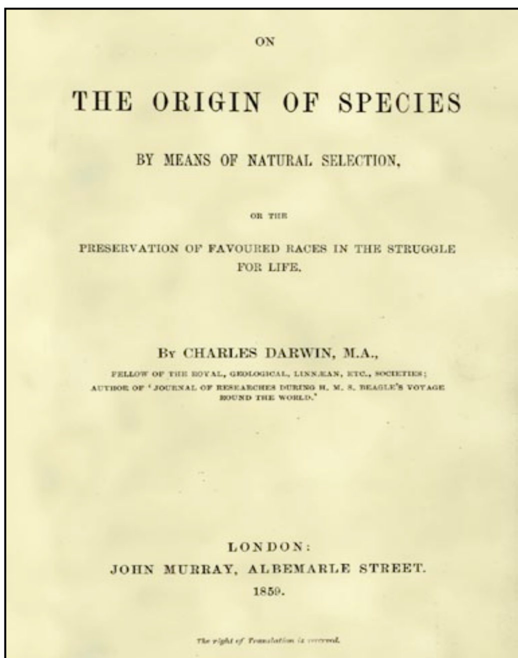
- *The family tree of life - the classification of organisms (both living and extinct) makes most sense when viewed as a family tree.*
- *Vestigial structures - whales, snakes, humans with tails*
- *Biogeography - distributions of species reveal patterns that only make sense in light of evolution. See the Wallace line.*
- *Fossils (The Earth is replete with vast evidence of the long history of life)*
- *Molecules as documents of evolutionary history (comparing sequences and structures from different organisms). Also, now DNA from extinct organisms.*
- *Evolution in real time (Peter and Rosemary Grant and the Galapagos finches, antibiotic resistance, flu each year, etc.)*





Darwin's Chapter 6: How Science is Done!

- *Chapter 6 of ``The Origin of Species" outlines the challenges to the idea of variation by natural selection.*
- *"Difficulties on Theory" - Darwin emphasized perfectly correctly the role of skeptical thinking in science.*



ON

THE ORIGIN OF SPECIES

BY MEANS OF NATURAL SELECTION,

OR THE

PRESERVATION OF FAVOURED RACES IN THE STRUGGLE FOR LIFE.

BY CHARLES DARWIN, M.A.,

FELLOW OF THE ROYAL, GEOLOGICAL, LINNÆAN, ETC., SOCIETIES;
AUTHOR OF 'JOURNAL OF RESEARCHES DURING H. M. S. BEAGLE'S VOYAGE ROUND THE WORLD.'

LONDON:
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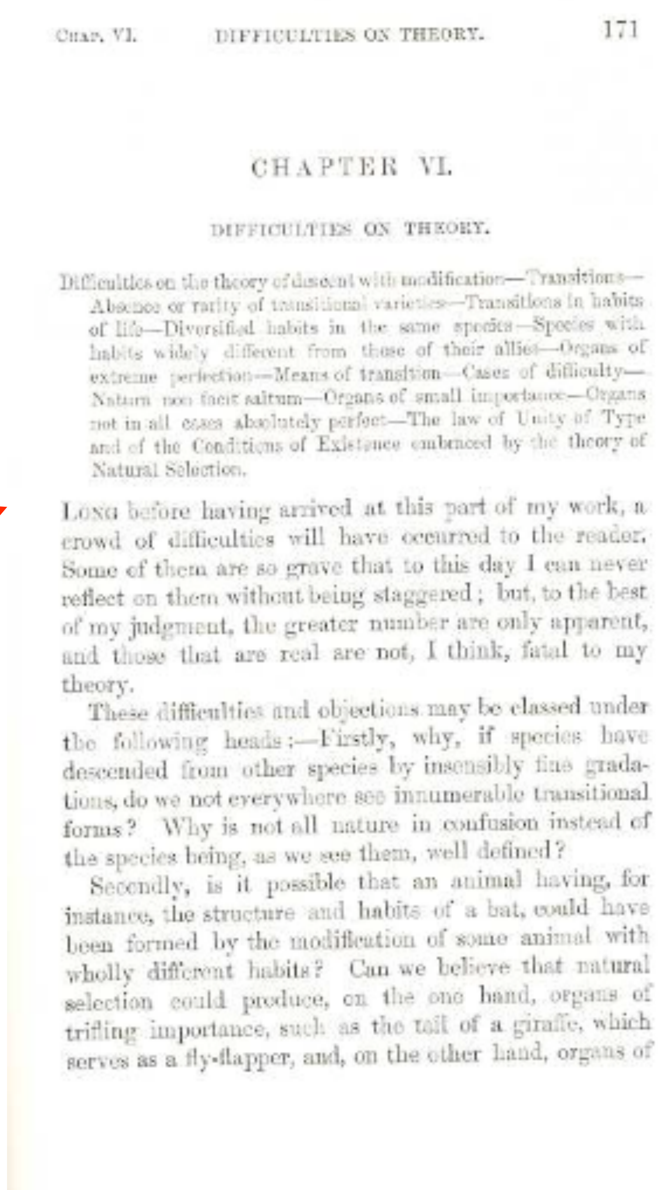


CHAP. VI. DIFFICULTIES ON THEORY. 171

CHAPTER VI.

DIFFICULTIES ON THEORY.

Difficulties on the theory of descent with modification—Transitions—Absence or rarity of transitional varieties—Transitions in habits of life—Diversified habits in the same species—Species with habits widely different from those of their allies—Organs of extreme perfection—Means of transition—Cases of difficulty—Natura non facit saltum—Organs of small importance—Organs not in all cases absolutely perfect—The law of Unity of Type and of the Conditions of Existence embraced by the theory of Natural Selection.

LONG before having arrived at this part of my work, a crowd of difficulties will have occurred to the reader. Some of them are so grave that to this day I can never reflect on them without being staggered; but, to the best of my judgment, the greater number are only apparent, and those that are real are not, I think, fatal to my theory.

These difficulties and objections may be classed under the following heads:—Firstly, why, if species have descended from other species by insensibly fine gradations, do we not everywhere see innumerable transitional forms? Why is not all nature in confusion instead of the species being, as we see them, well defined?

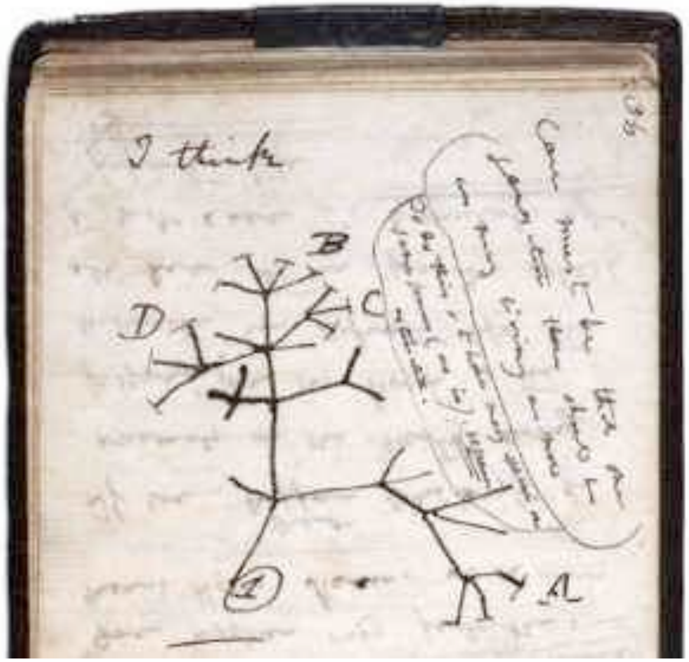
Secondly, is it possible that an animal having, for instance, the structure and habits of a bat, could have been formed by the modification of some animal with wholly different habits? Can we believe that natural selection could produce, on the one hand, organs of trifling importance, such as the tail of a giraffe, which serves as a fly-flapper, and, on the other hand, organs of

Biological Diversity and Adventure: Who Is Out There?

Key lesson: field biologists have undertaken adventures to the farthest corners of the world to look for previously unknown forms of life. From Van Leeuwenhoek to Darwin to Stetter, each new round of exploration tells us about new "biological dark matter".

Universal Tree of Life

- ***Diversity of living organisms is enormous.***



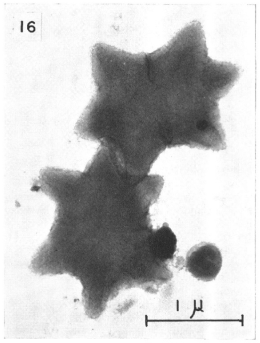
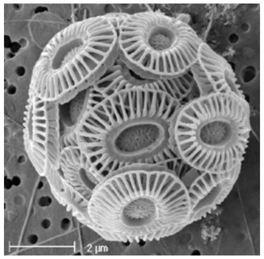
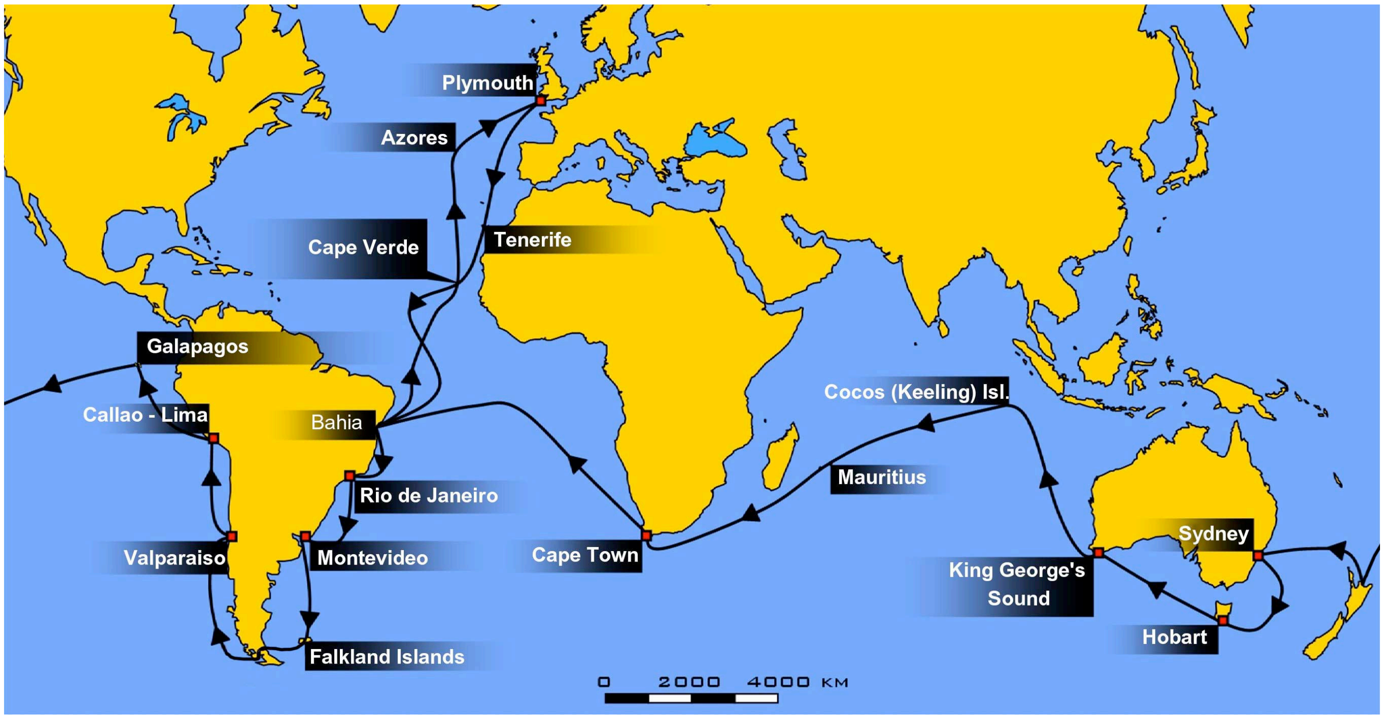
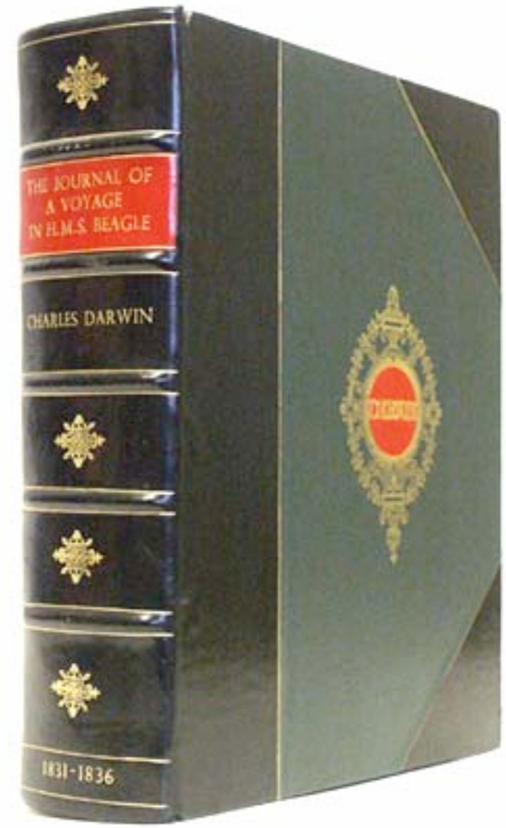


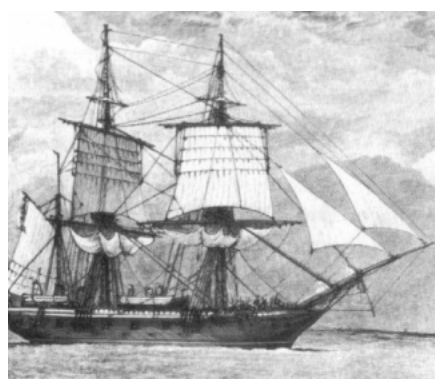
Fig. 16. Electron micrograph of star-shaped cells (form 8) observed in a negatively stained preparation from a crude culture. Note the division planes.



Darwin's Five Year Adventure: The Diversity of Life





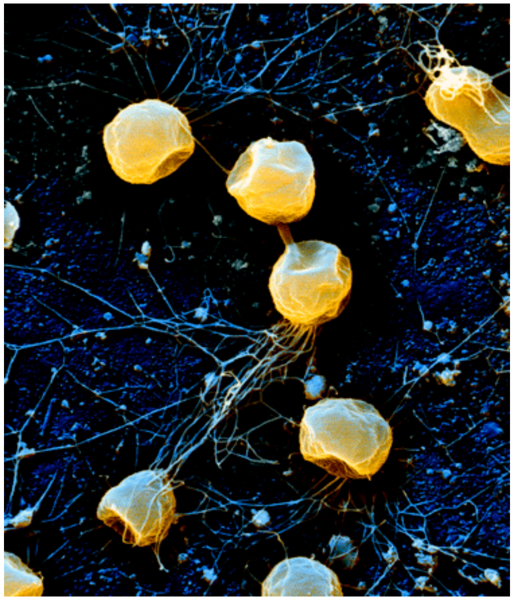


Wallace's Adventures

This map from Wallace's 1876 book shows his Oriental biogeographic region, broken into four subregions (outlined in red). "Wallace's Line" is indicated by the arrow.

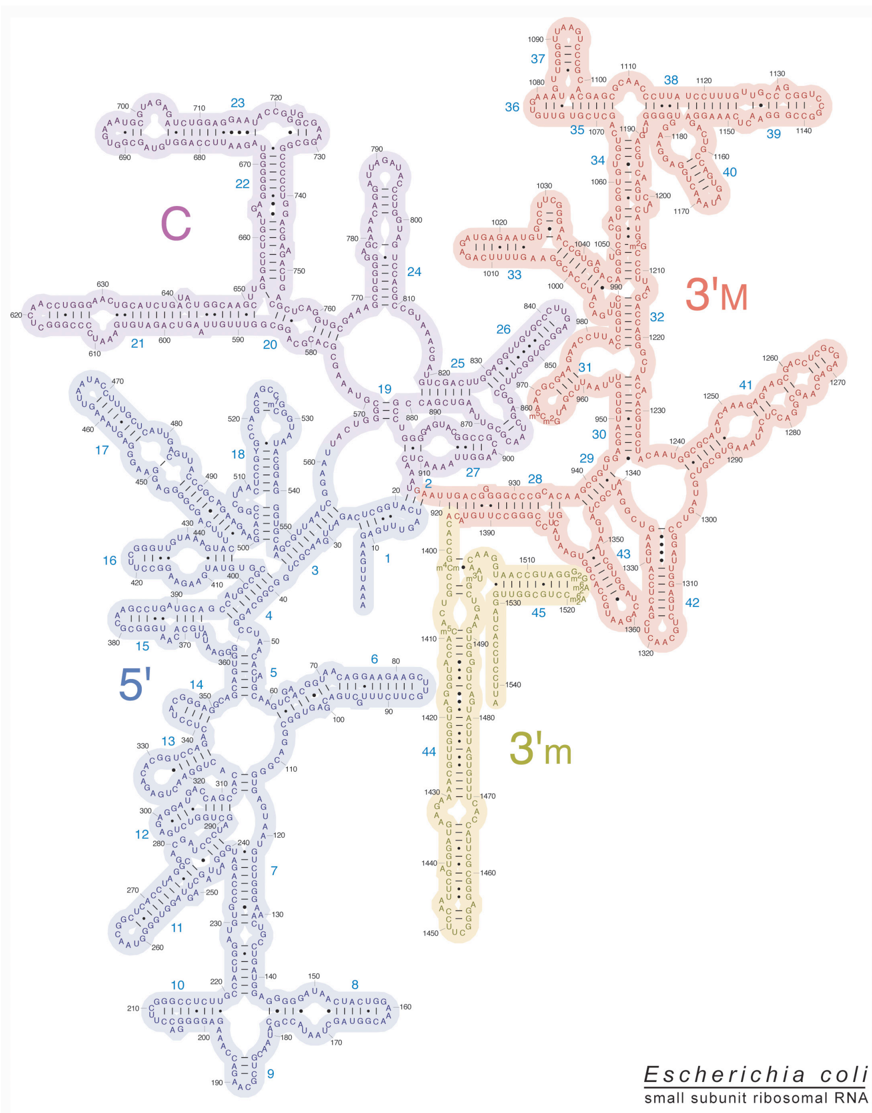
Biological Diversity and Adventure: Who Is Out There?

- *Karl Stetter has spent his life searching for new and bizarre classes of extremophiles.*



The archaeon Pyrococcus furiosus ("rushing fireball") was named for its ability to swim very rapidly at temperatures above 80|SDC. Up to 70 flagella per cell have been observed on its surface. These flagella are multifunctional structures; they are used not only for swimming but also for adhesion to various surfaces to establish biofilms. Cells shown here adhere to sand grains from the natural habitat, the coast of Vulcano Island, Italy. In addition, flagella can aggregate into compact cables, establishing cell-cell connections. The image is a scanning electron micrograph of superimposed back-scattered and secondary electron signals.

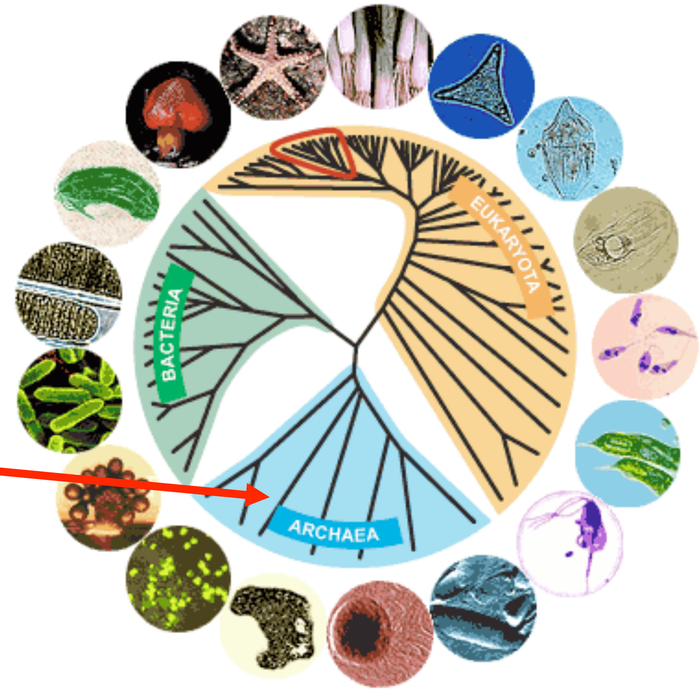
Biological Diversity and Adventure: Who Is Out There?

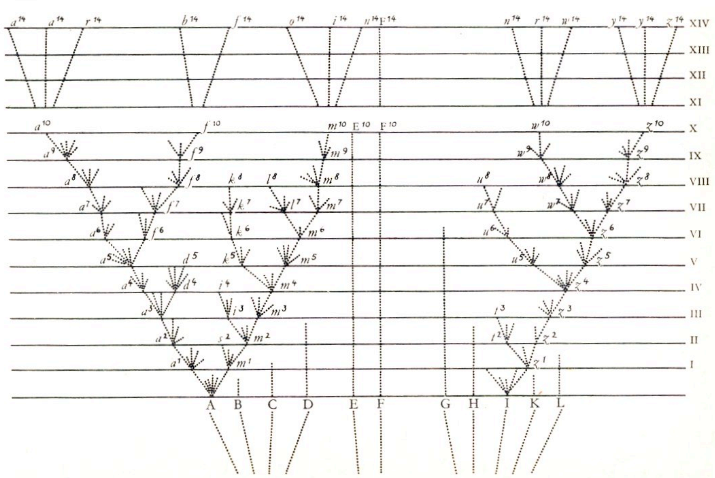


- *Carl Woese has used the ribosomal RNA associated with the small ribosomal subunit to provide a molecular measure of relatedness.*

Ribosomes and the Tree of Life

- *The idea: compare RNA sequences for small subunit from different organisms as basis for comparing species and examining their relatedness.*
- *A beautiful use of this idea by Carl Woese - molecular analysis of the tree of life.*
- *For the engineers in the house: build me extremophiles!*
- *Within the last 30 years we have discovered a previously unknown domain of life!*





Only figure in Darwin's ``Origin"

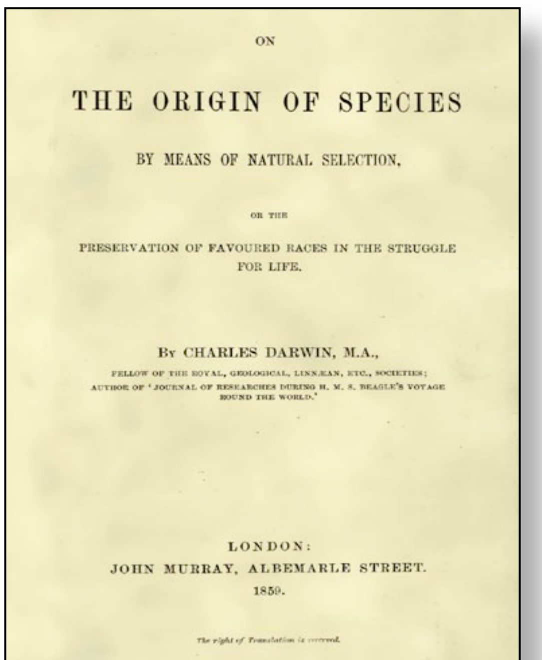
Biological Diversity and Adventure: Who Is Out There?

A Fossil Story: From Fins to Limbs and Back Again

Key Lesson: Fossils are one of the key windows of evidence into evolution. Since the time of Darwin, the imperfections of the fossil record have been filled in and several of the great transitions (fins to limbs, limbs to fins) have been elucidated with great fossil finds.

Darwin's Chapter 9: The Fossil Record

- *Chapter 9 of ``The Origin of Species" outlines Darwin's worries about the fossil record.*
- *Not surprisingly, there has been enormous and continual progress on this front in the time since.*
- *Biggest qualitative message: life has changed over time!*



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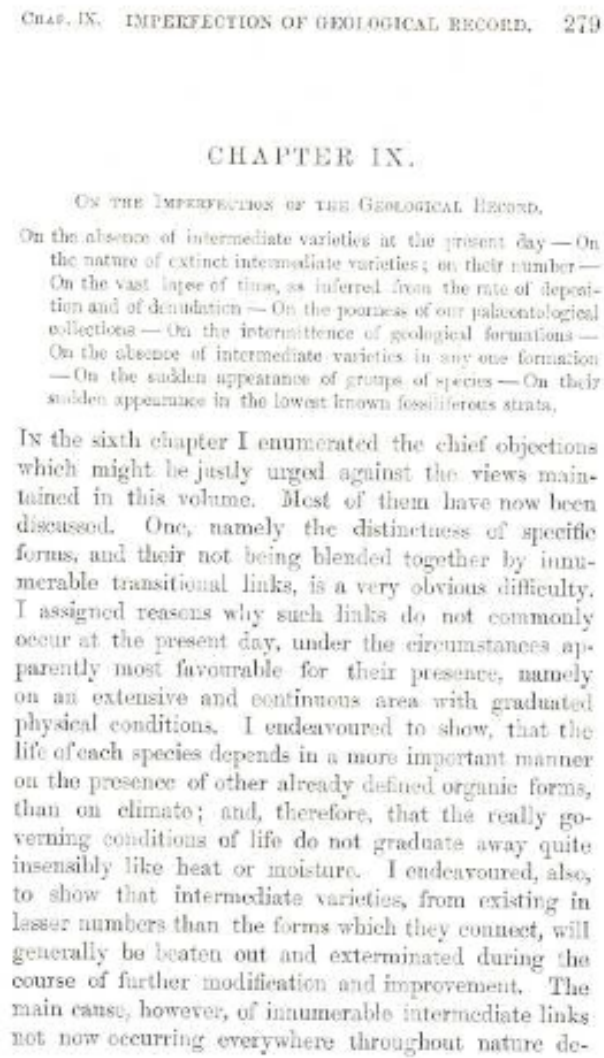


CHAP. IX. IMPERFECTION OF GEOLOGICAL RECORD. 279

CHAPTER IX.

ON THE IMPERFECTION OF THE GEOLOGICAL RECORD.

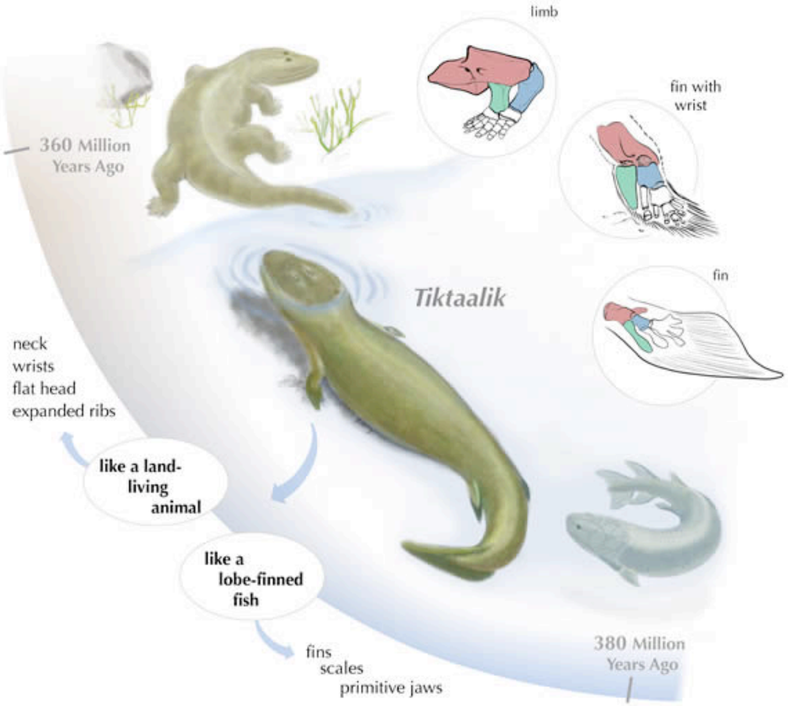
On the absence of intermediate varieties at the present day — On the nature of extinct intermediate varieties; on their number — On the vast lapse of time, as inferred from the rate of deposition and of denudation — On the poorness of our palæontological collections — On the intermittence of geological formations — On the absence of intermediate varieties in any one formation — On the sudden appearance of groups of species — On their sudden appearance in the lowest known fossiliferous strata.

IN the sixth chapter I enumerated the chief objections which might be justly urged against the views maintained in this volume. Most of them have now been discussed. One, namely the distinctness of specific forms, and their not being blended together by innumerable transitional links, is a very obvious difficulty. I assigned reasons why such links do not commonly occur at the present day, under the circumstances apparently most favourable for their presence, namely on an extensive and continuous area with graduated physical conditions. I endeavoured to show, that the life of each species depends in a more important manner on the presence of other already defined organic forms, than on climate; and, therefore, that the really governing conditions of life do not graduate away quite insensibly like heat or moisture. I endeavoured, also, to show that intermediate varieties, from existing in lesser numbers than the forms which they connect, will generally be beaten out and exterminated during the course of further modification and improvement. The main cause, however, of innumerable intermediate links not now occurring everywhere throughout nature de-

How Do We Know?: From Fins to Limbs

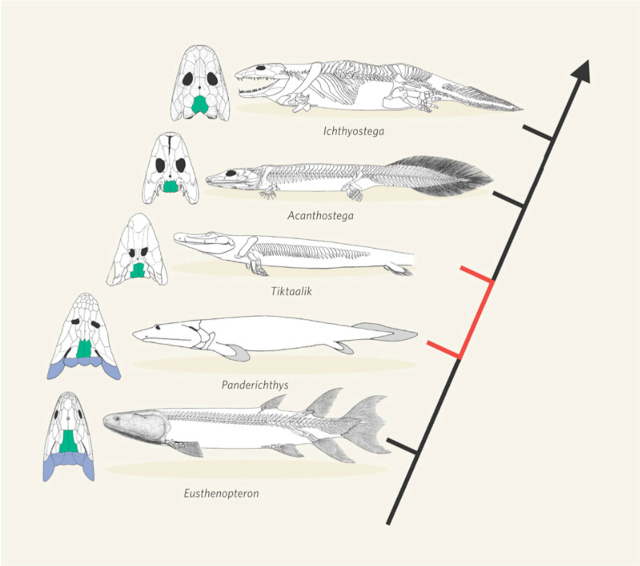
- *Shubin calls Tiktaalik ``a mosaic of primitive fish and derived amphibian”.*
- *Another example of filling in the transitional forms that are demanded by the theory of evolution.*
- *Note: there was a predictive element - they were looking for this in a place where they expected to find it. Theories make falsifiable predictions.*

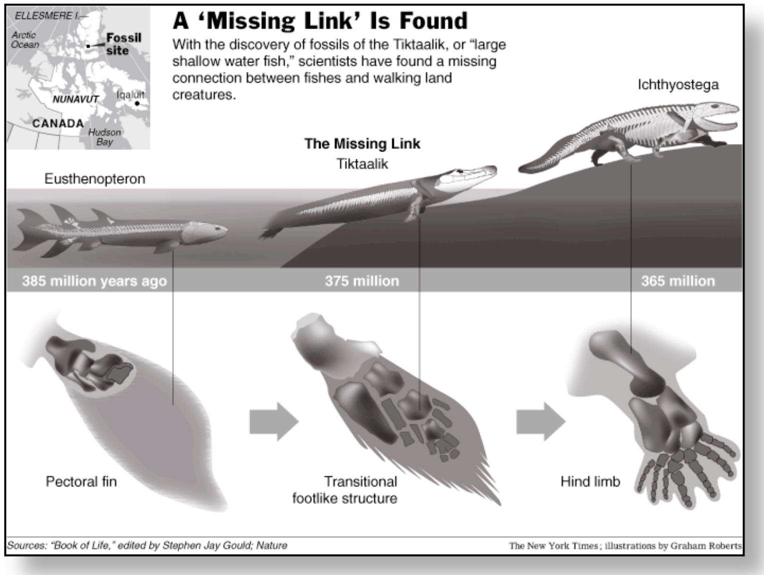
Fossil hunting in Arctic Canada



How Do We Know?: From Fins to Limbs

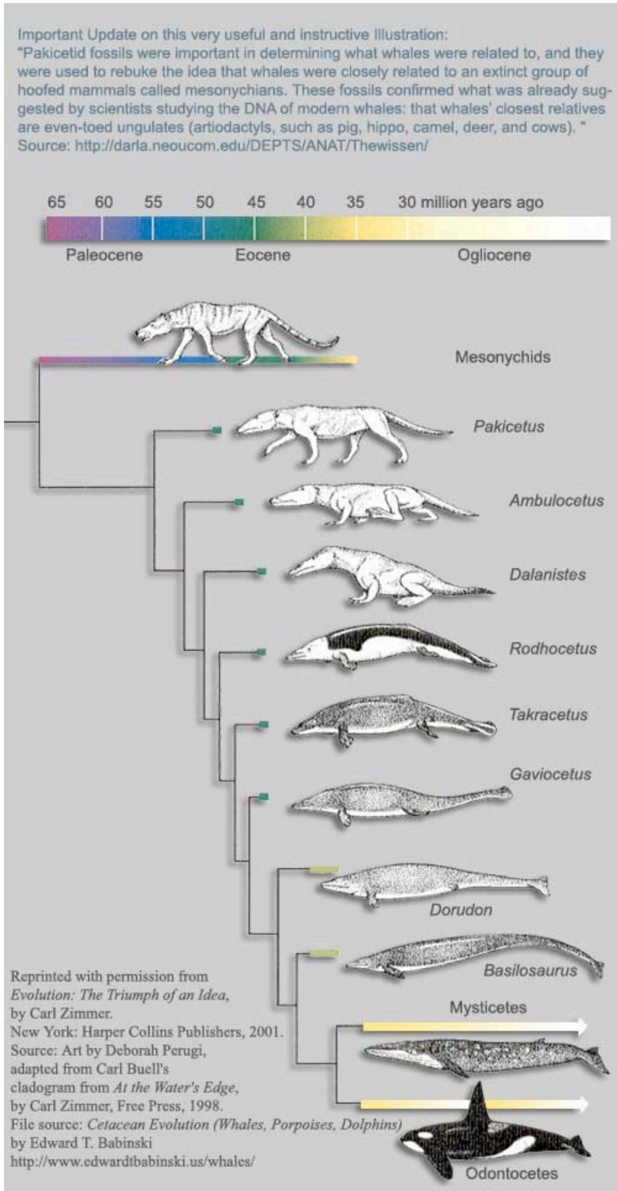
The lineage leading to modern tetrapods includes several fossil animals that form a morphological bridge between fishes and tetrapods. Five of the most completely known are the osteolepiform Eusthenopteron16; the transitional forms Panderichthys17 and Tiktaalik1; and the primitive tetrapods Acanthostega and Ichthyostega. The vertebral column of Panderichthys is poorly known and not shown. The skull roofs (left) show the loss of the gill cover (blue), reduction in size of the postparietal bones (green) and gradual reshaping of the skull. The transitional zone (red) bounded by Panderichthys and Tiktaalik can now be characterized in detail. These drawings are not to scale, but all animals are between 75 cm and 1.5 m in length. They are all Middle–Late Devonian in age, ranging from 385 million years (Panderichthys) to 365 million years (Acanthostega, Ichthyostega). The Devonian–Carboniferous boundary is dated to 359 million years ago18.



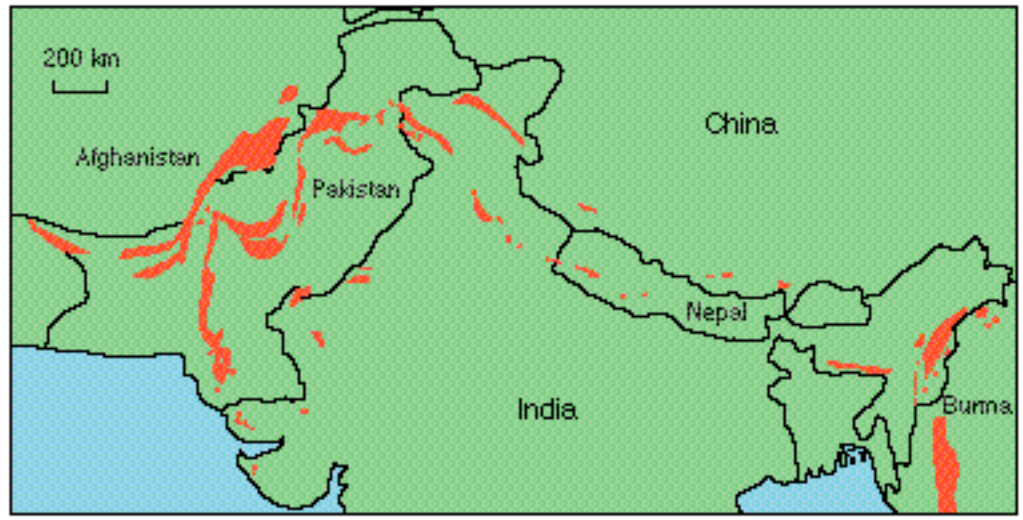


See the book "Gaining Ground" by Jennifer Clack

How Do We Know? Back Into the Water

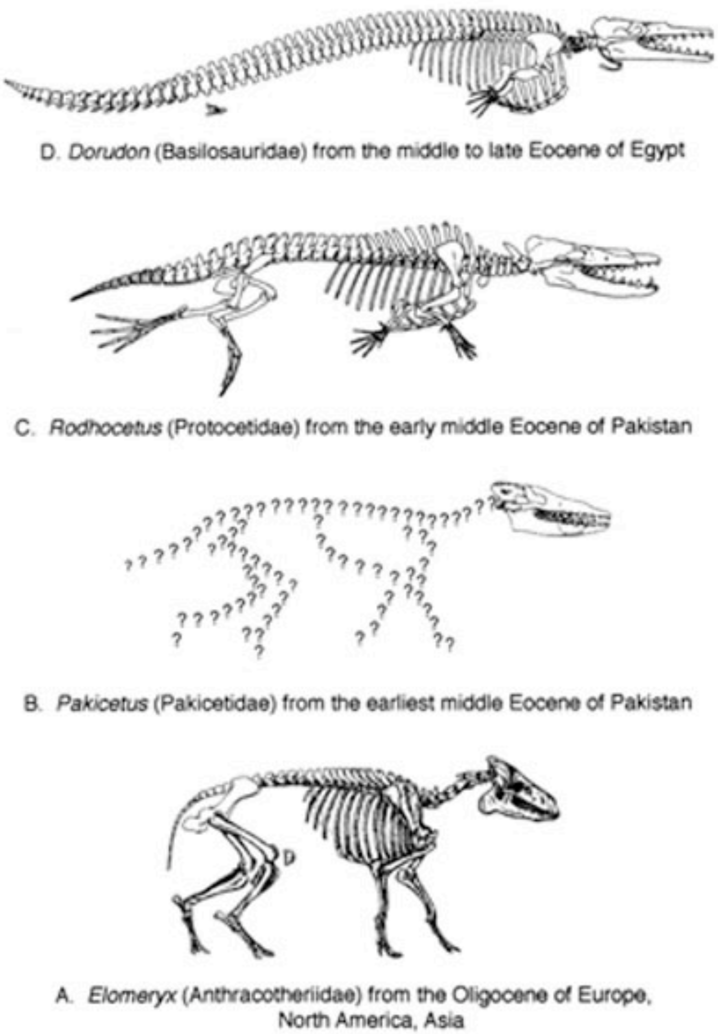


http://darla.neoucom.edu/DEPTS/ANAT/Thewissen/



- *Perhaps even more intriguing than animals leaving the water is mammals going back in.*
- *Amazing record in the ancient seas at the interface between India and the Asian continent.*
- *The transitional forms are instructive and very complete. Claims about missing transitional forms are oversold.*
- *See the video on Philip Gingerich.*

Work of Philip Gingerich



http://www-personal.umich.edu/~gingeric/PDGwhales/Whales.htm

http://en.wikipedia.org/wiki/Wadi_Al-Hitan

Egyptian Whale With Hind Limbs and Feet

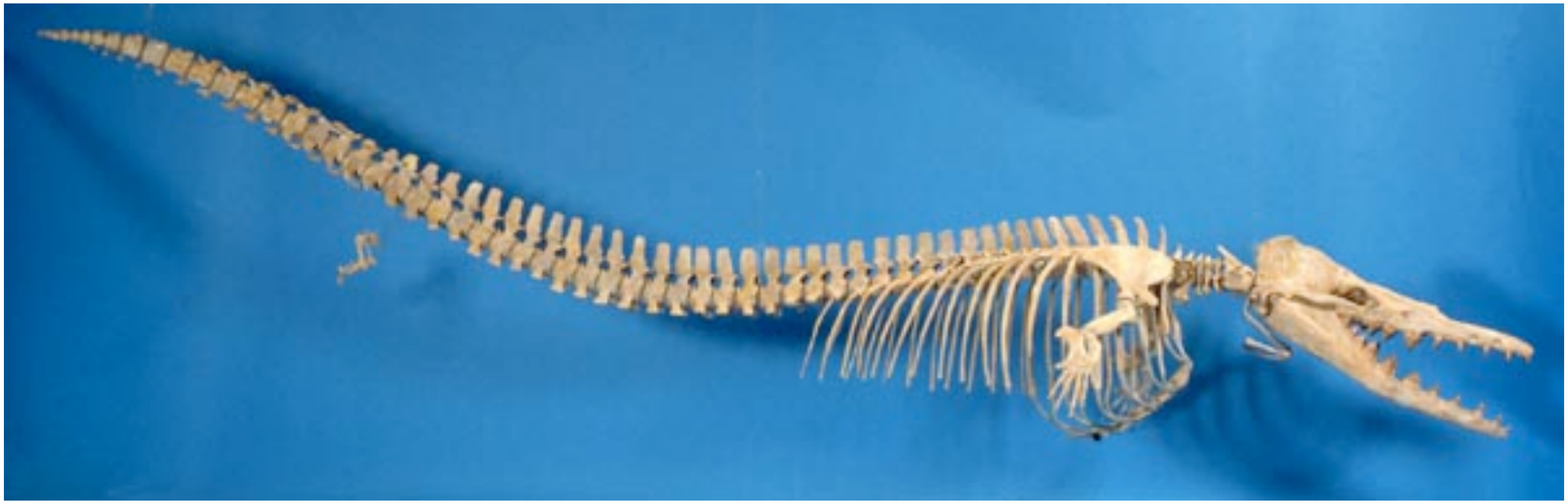
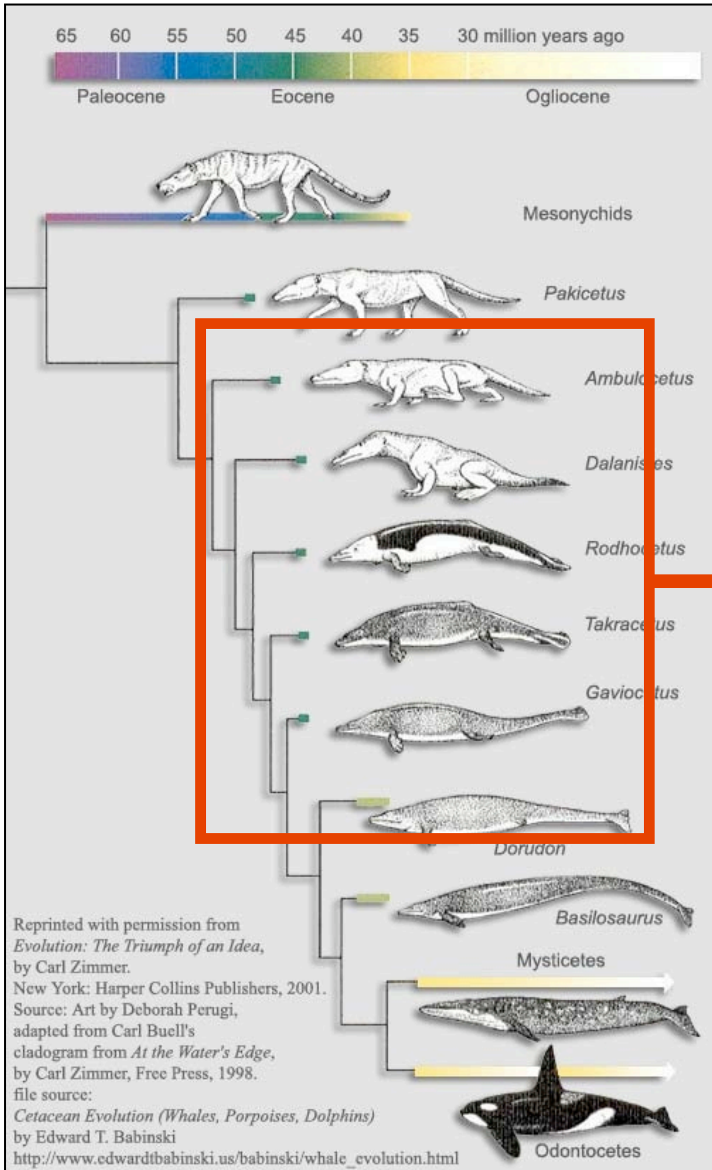


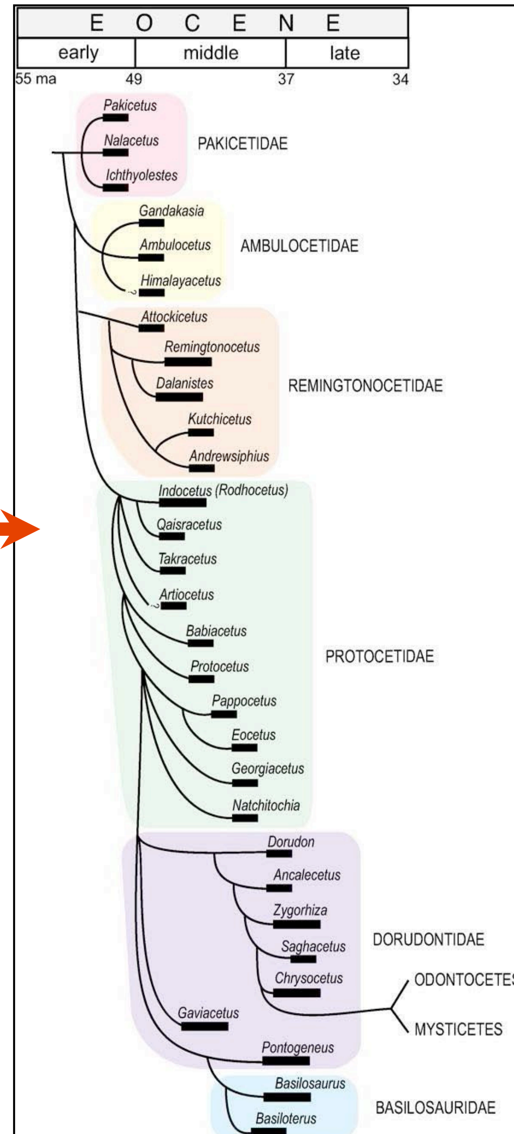
Figure 5. Virtually complete skeleton of *Dorudon atrox* excavated in Wadi Hitan, Egypt. Note the retention of hind limbs, feet, and toes like those found in Basilosaurus. This find is described in Uhen (1996, 2004). The skeleton is approximately 5 m long.

A Closer Look at the Limbs

Figure 4. Ankle, foot, and toes of *Basilosaurus isis* excavated in Wadi Hitan, Egypt. This find was described in Gingerich et al. (1990). The foot as shown is approximately 12 cm long. Photograph ©1991 Philip Gingerich. Figure may be reproduced for non-profit educational use.

How Do We Know? Missing Transitional Forms?





Evolution By Molecules and Genome Science

Key lesson: Molecules are one of the most important documents that we have of evolutionary history (and everything else). Genome science makes it possible to look over evolutionary times in the same way that new generations of telescopes allow us to look farther back in the history of the universe.

Molecules as Documents of Evolutionary History

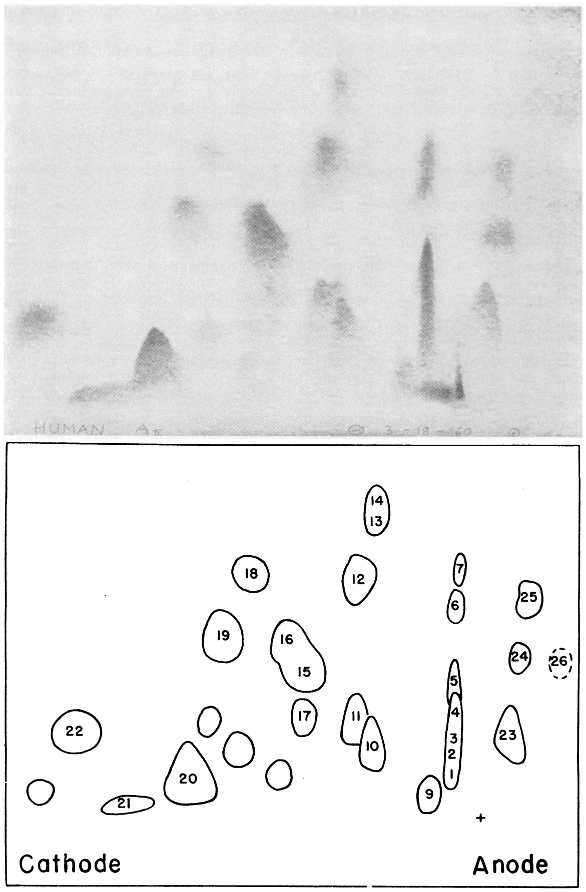


Fig. 1.—A tryptic peptide pattern of adult human hemoglobin and its schematic representation. The spots are numbered according to the convention introduced by Ingram.[2] The site of spot 26 is shown on the diagram, although not seen on the pattern represented. The locations of four hitherto undescribed spots usually found on patterns obtained in our laboratories are indicated.

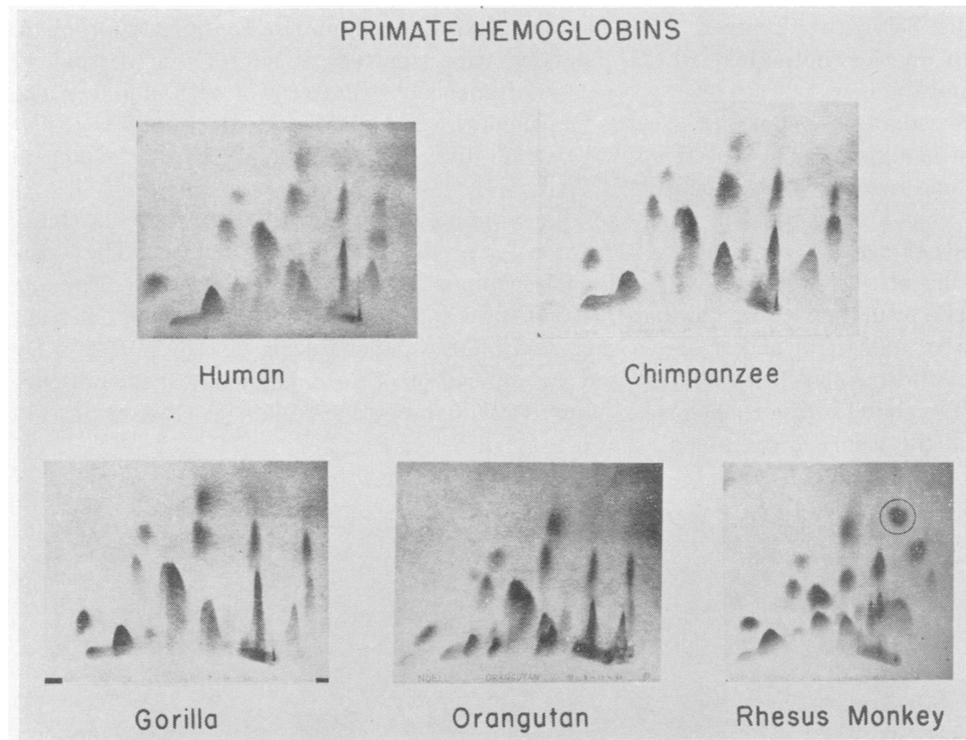


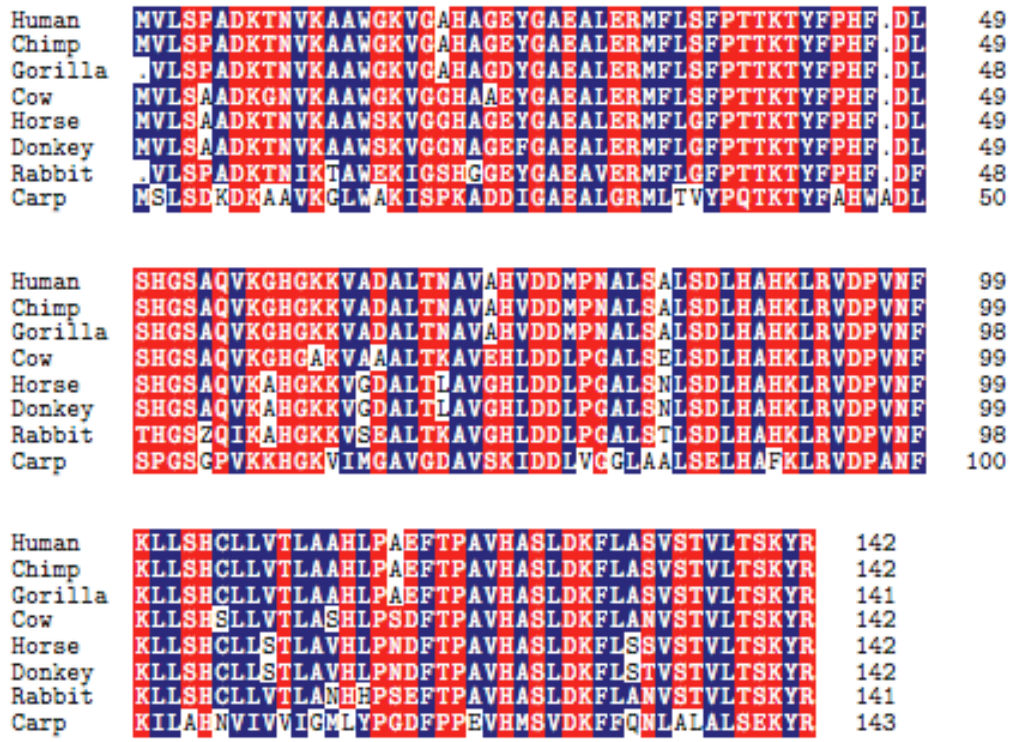
Fig. 2.—Tryptic peptide patterns of primate hemoglobins. The circled spot on the Rhesus monkey pattern represents phenylalanine added two and a half inches to the anodal side of the point of application of the peptide mixture.

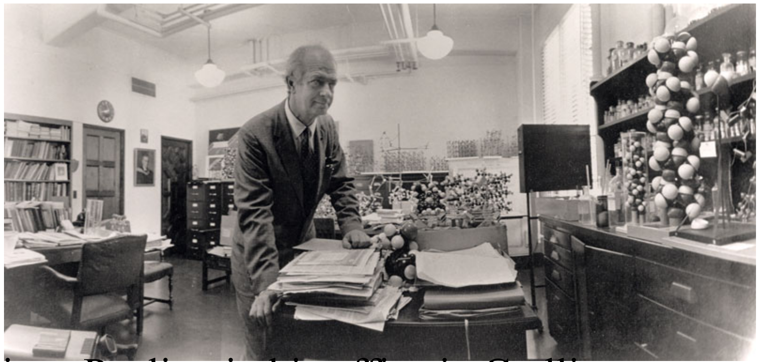
A Comparison of Animal Hemoglobins by Tryptic Peptide Pattern

Emile Zuckerkandl, Richard T. Jones, and Linus Pauling

Modern Molecular Analysis of Evolution

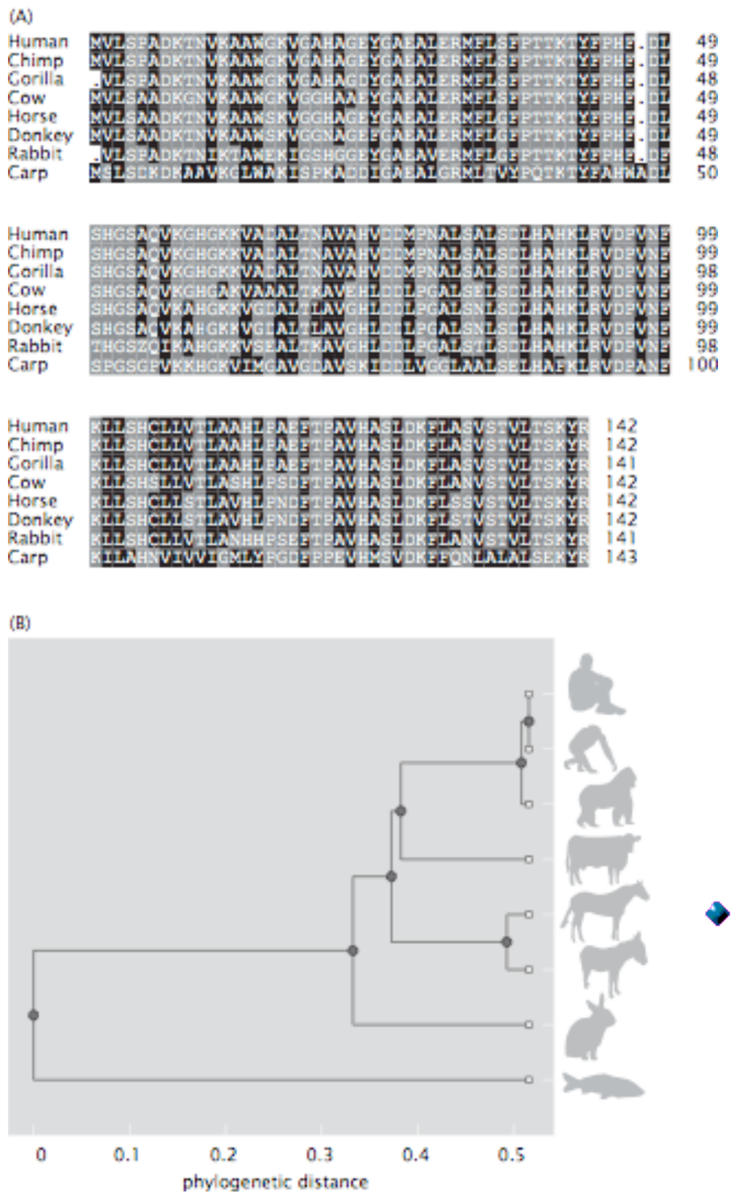
- *Sequence comparisons as a tool for exploring relatedness.*
- *This page: rudimentary sequence comparison of alpha chain of hemoglobin from different species. Pauling undertook this analysis in the early 60s.*
- *A similar story unfolded using cytochrome C as the basis of the comparison.*



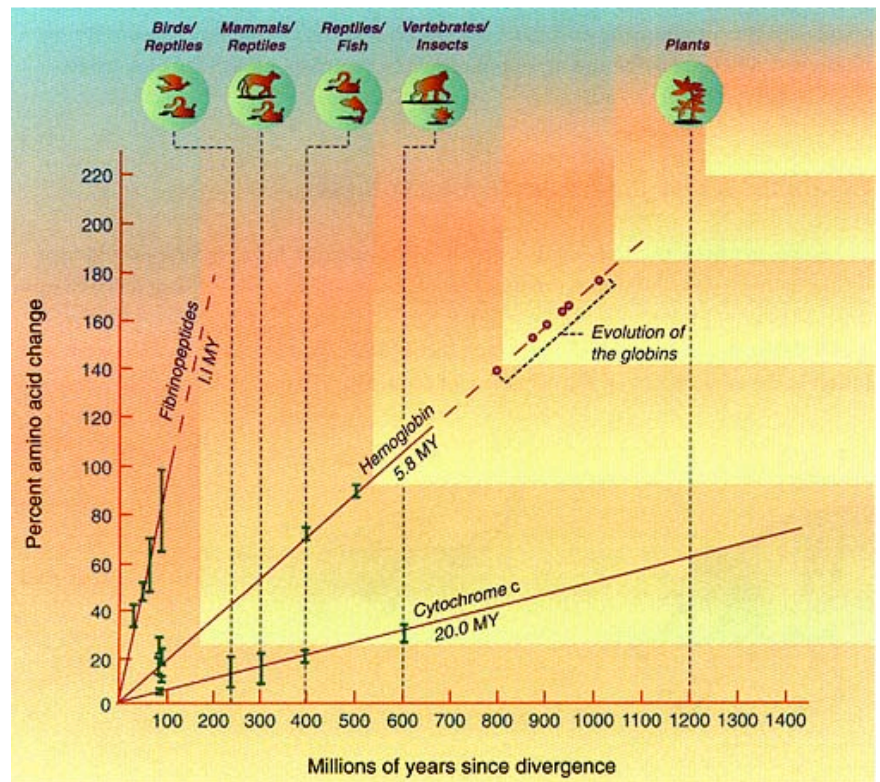


Linus Pauling in his office in Crellin

Stopwatches for the Very Fast and the Very Slow



(Dickerson, Scientific American, 1972)

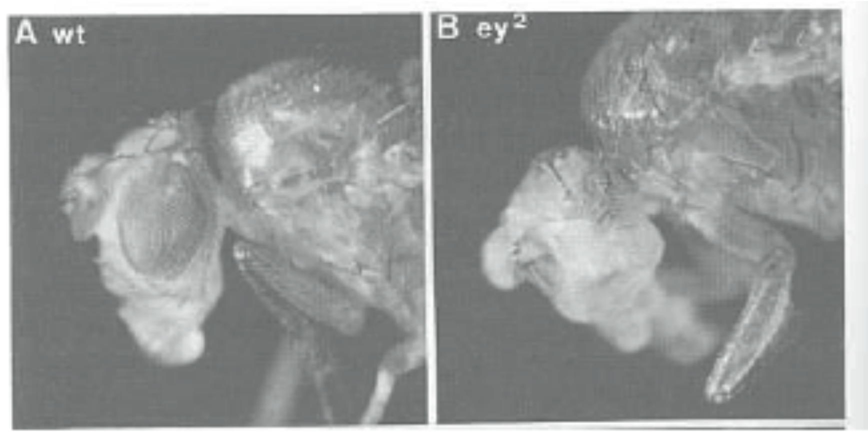


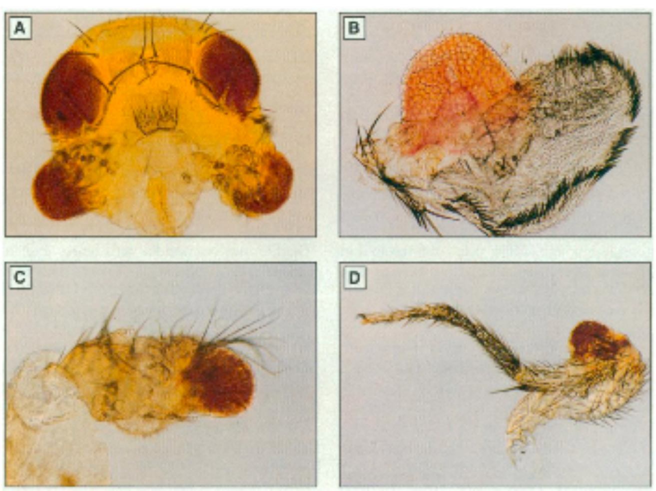
- *Molecules as stopwatches. Proteins are strings of amino acids. By comparing the same protein in different species, we can clock the timescale associated with evolutionary divergence.*

How Do We Know: Molecular Evidence

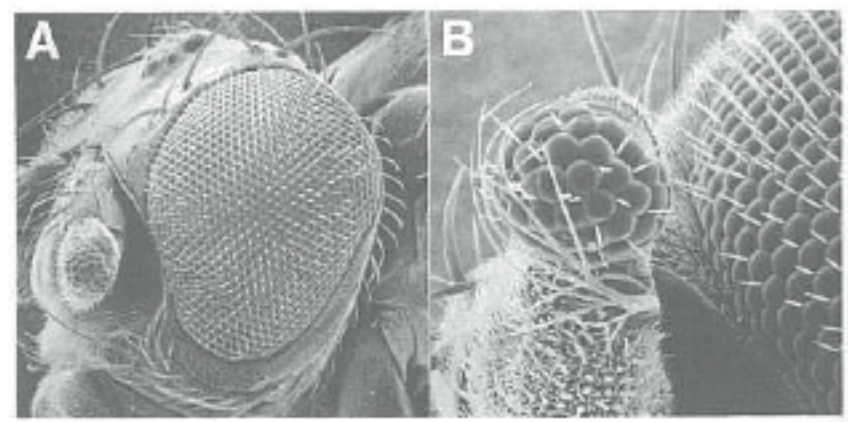
- *Eye development is one of the most beautiful examples of commonality of origins.*
- *Comparison of Pax6 (i.e. mouse) and eyeless (i.e. flies) sequences we can see the relation between these genes.*
- *Interestingly, expression of Pax6 in flies results in development of eye tissues where they don't normally belong.*

Eyeless mutant on right





Eyes on wings and legs



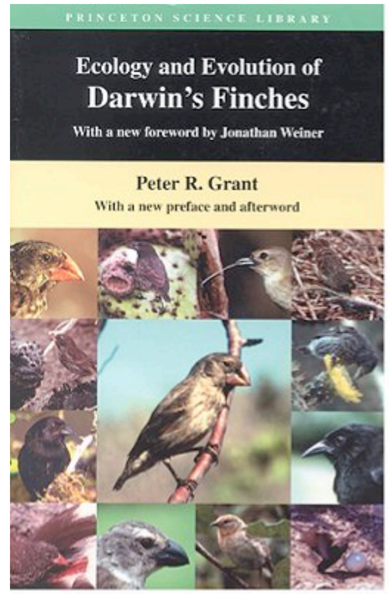
Mouse Pax6 gene used to drive formation of eyes

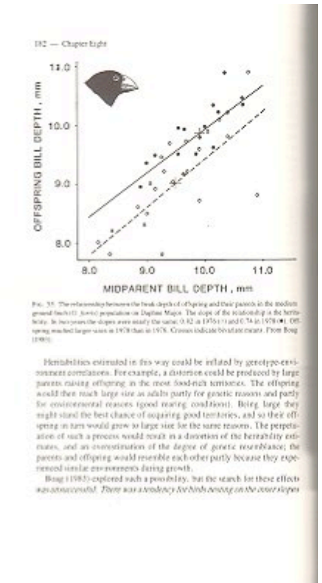
Evolution in Real Time: From Microbes to Darwin's Finches

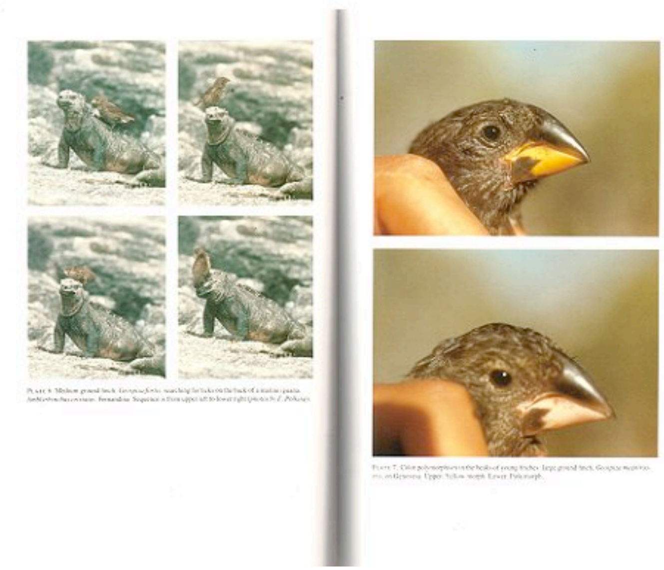
Key lesson: Many current studies have revealed evolution taking place in real time. Two of the most impressive studies involve detailed observations over more than 20 years of two totally different situations: Darwin's finches and E. coli. Evolution happens much faster than Darwin thought!

Evolution in Real Time: The Beak of the Finch

- *Peter and Rosemary Grant have spent since 1973 going to the Galapagos and making measurements on the birds and their habitat.*
- *Their observations reveal that measurable differences occur on the year time scale induced by environmental perturbations such as the amount of rain.*







Evolution in Real Time: From Microbes to Darwin's Finches

Grants' Finch Study Data

Figure 1

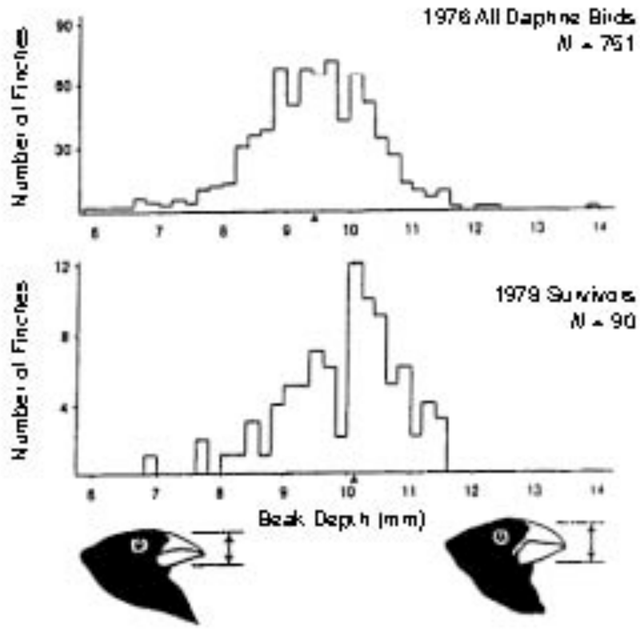
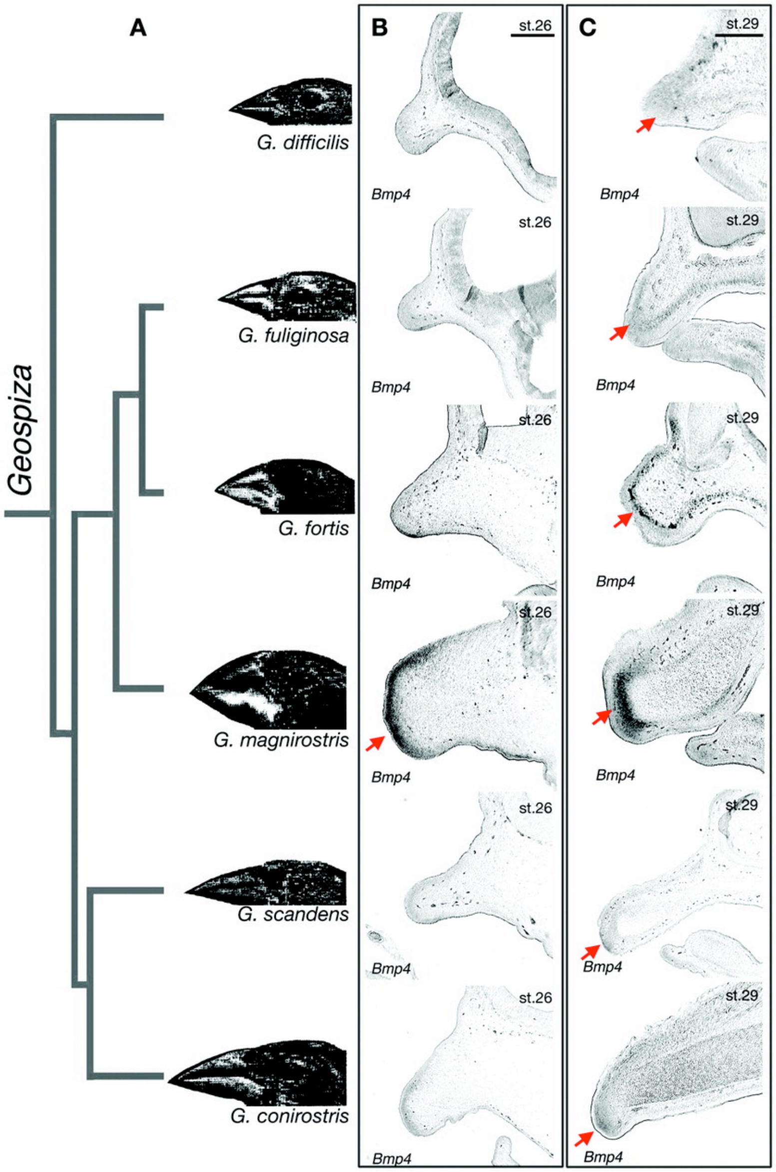


Figure 1: Histogram of distribution of beak depth of medium ground finches (*Geospiza fortis*) on Daphne Major, before and after the drought of 1977 (Grant 1986). Reprinted by permission of Princeton University Press.

In their natural laboratory, the 100-acre island called Daphne Major, the Grants and their assistants watched the struggle for survival among individuals in two species of small birds called Darwin's finches. The struggle is mainly about food -- different types of seeds -- and the availability of that food is dramatically influenced by year-to-year weather changes. – From PBS "Evolution" series.

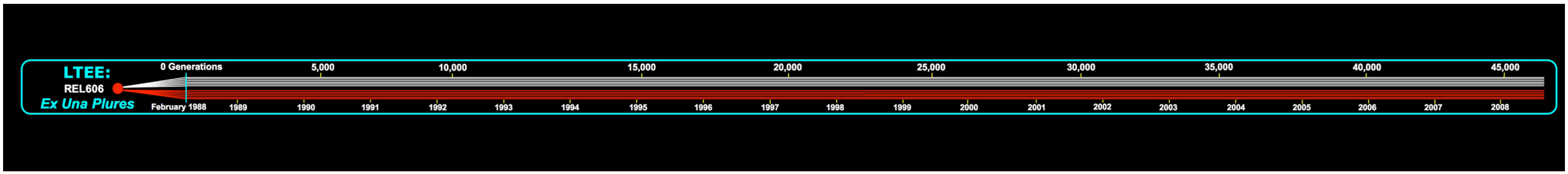
Evolution in Real Time: From Microbes to Darwin's Finches



Science. 2004 Sep 3;305(5689):1462-5.

Fig. 1. (A) Previous studies suggest that G. difficilis is the most basal species of the genus Geospiza, and the rest of the species form two groups: ground and cactus finches, with distinct beak morphologies. (B) At stage (st.) 26, Bmp4 is strongly expressed in a broad distal-dorsal domain in the mesenchyme of the upper beak prominence of G. magnirostris and at significantly lower levels in G. fortis and G. conirostris. No Bmp4 was detected in the mesenchyme of G. difficilis, G. fuliginosa, and G. scandens. (C) At stage 29, Bmp4 continues to be expressed at high levels in the distal beak mesenchyme of G. magnirostris. Broad domains of Bmp4 expression are detectable around prenasal cartilages of G. fuliginosa and G. fortis. A small domain of strong Bmp4 expression is also found in the most distal mesenchyme of G. conirostris, and weaker expression is seen in G. scandens and G. fortis (red arrows). Scale bars: 1 mm in (B) and 2 mm in (C).

Richard Lenski Long Term Evolution Experiment



The inexorable rhythm of the project is as follows:

1. *Every day, the cultures are propagated;*
2. *Every 75 days (500 generations), mixed-population samples are frozen away; and*
3. *Mean fitness, relative to the ancestor, is estimated using the mixed-population samples.*

Richard Lenski Long Term Evolution Experiment

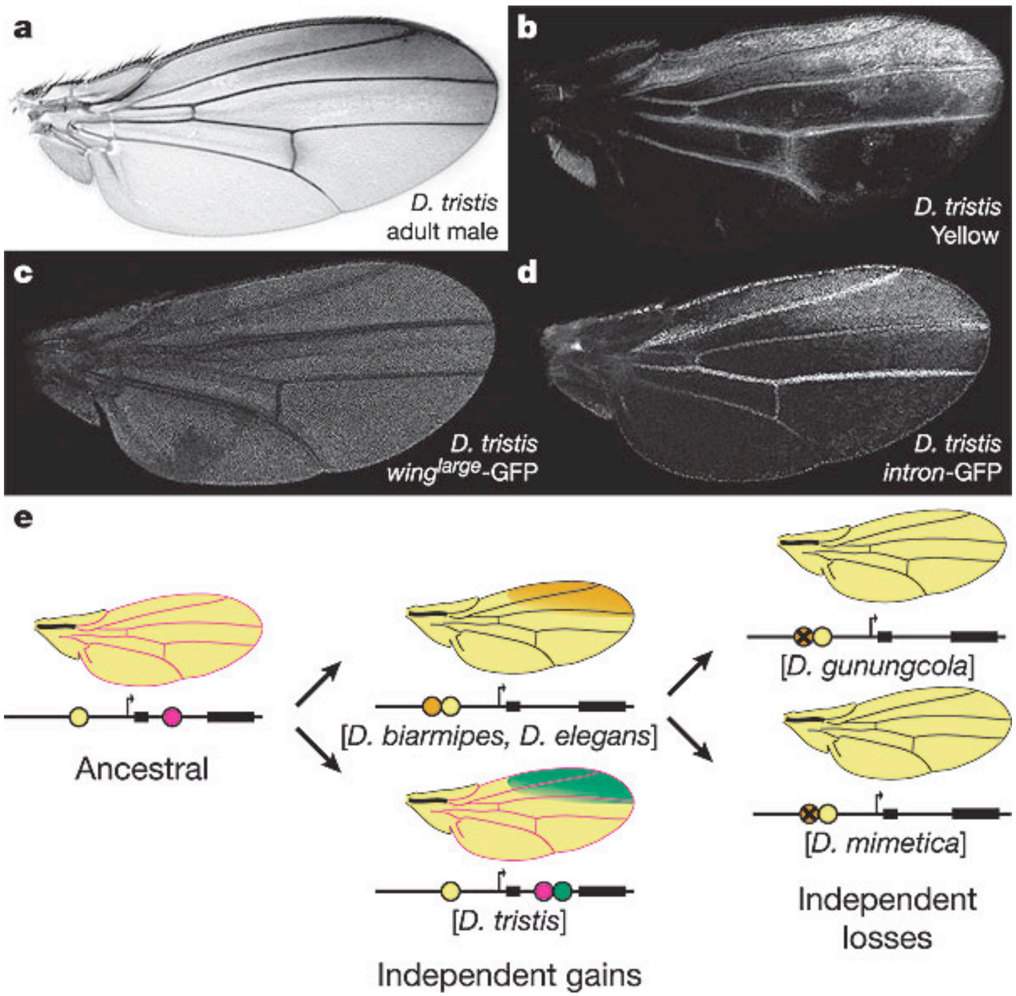
These 12 flasks contain separate populations of E. coli, all evolved from a single ancestor. Only the bacteria in flask A-3 evolved the ability to eat citrate.

Evo-Devo

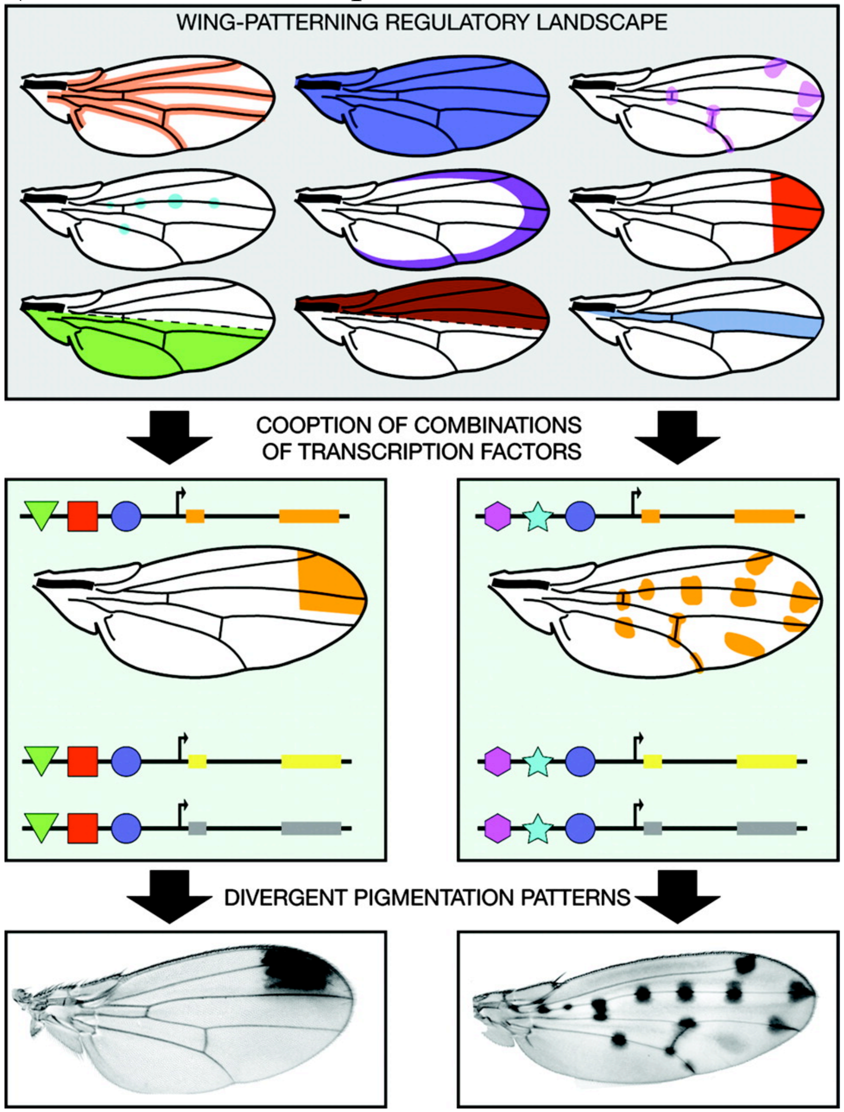
Key lesson: Developmental pathways are one of the primary substrates for evolutionary change. Molecular methods have resulted in the ability to perturb these developmental pathways and dissect the agents of evolutionary change.

Chance Caught on a Wing: Decision Making and Evolution

(Prud'homme, Gompel and Carroll, et al., Nature, 2006)



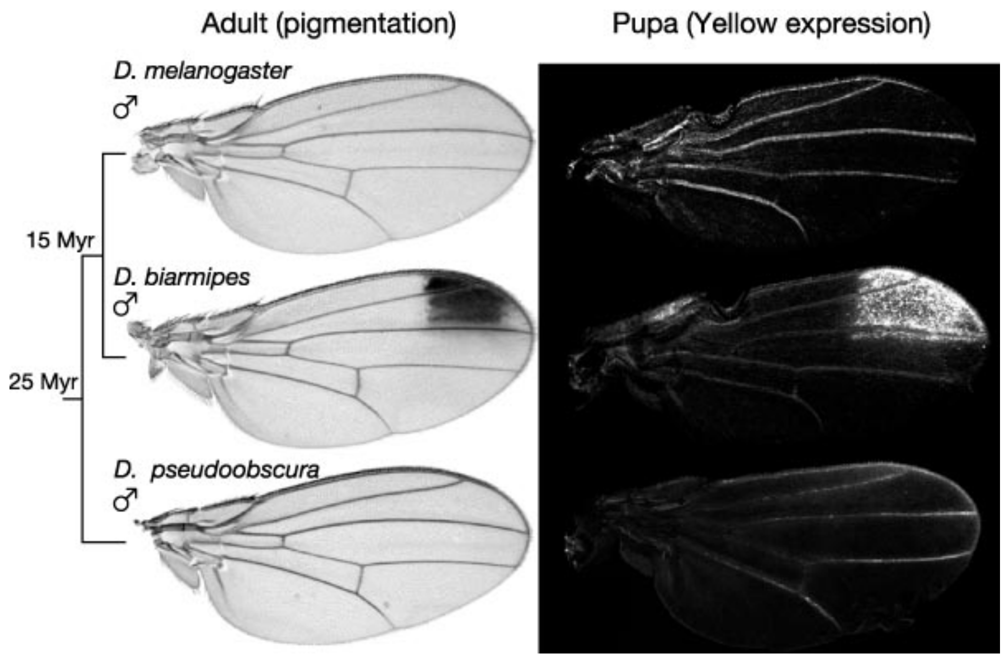
(Prud'homme, Gompel and Carroll, PNAS, 2007)

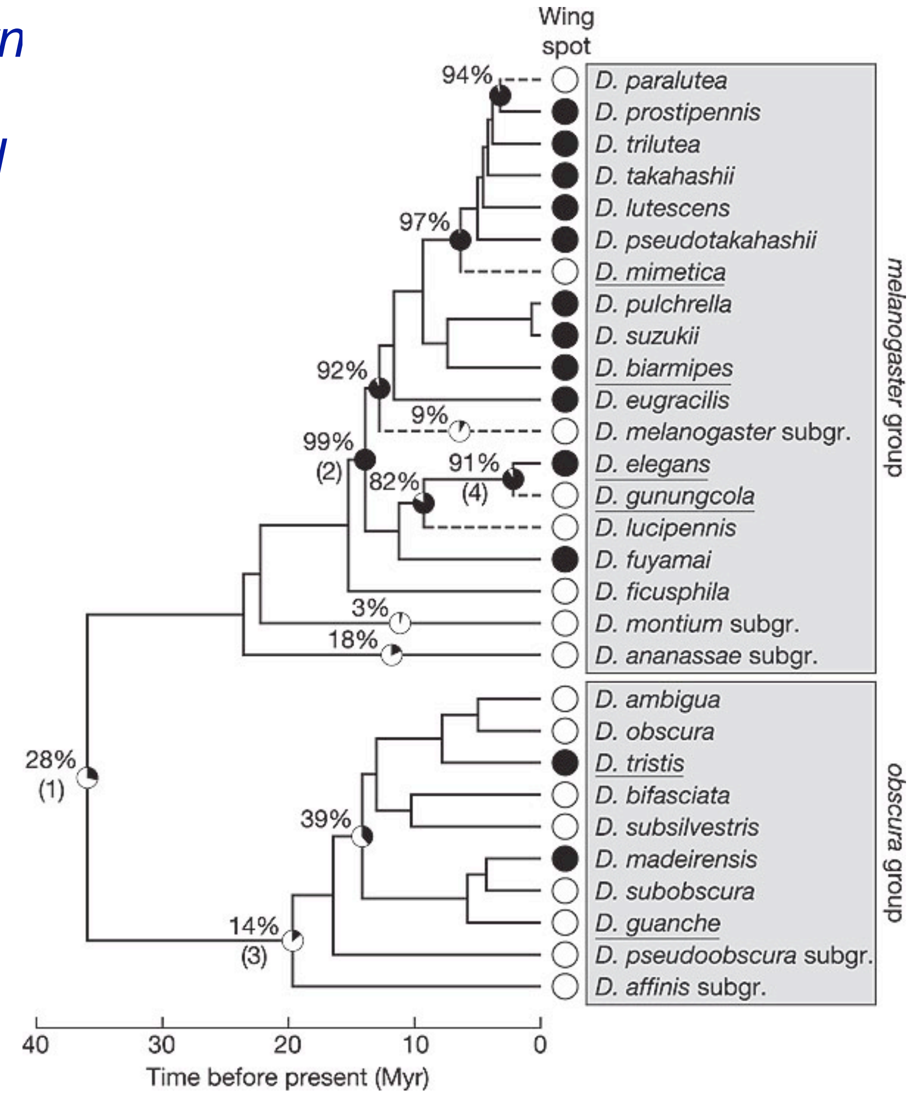


DNA molecules as "documents of evolutionary history" - these sequences are a stopwatch!

Fun Case Studies: Color of Wings

- *Different species of fly have different pattern of coloration on their wings.*
- *Fantastic conclusion - changes not induced by changes in protein coding regions. Rather, it is all in the ``regulation and feedback" circuits.*

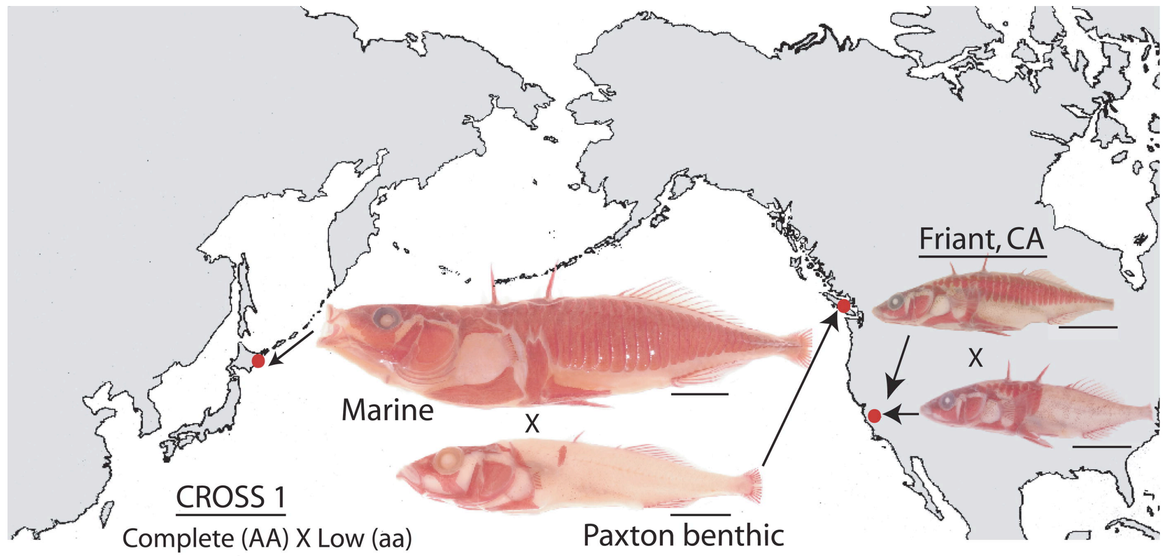




Gompel, Carroll *et al.*

Fun Case Studies: Changes in Body Plan in Fish

- *Stickleback fish separated after last ice age more than 10,000 years ago.*
- *Morphologically, fresh water and salt water versions all differ. Some of the interesting features include pelvic reduction and the nature of their armor.*
- *Fantastic conclusion - changes not necessarily induced by changes in protein coding regions.*
- *These studies merge genetics with molecular analysis and evolutionary biology. Stunning window onto how novelty is generated in body plans.*



CROSS 1

Complete (AA) X Low (aa)

↓

F1 (Aa) X F1 (Aa)

↓

360 F2 progeny

Genotype @ Gac4174	Plate Morph: Low	Partial	Complete
AA	0	3	79
Aa	6	66	104
aa	90	2	0

CROSS 2

Complete (Aa) X Low (aa)

↓

58 F1 progeny

Genotype @ Gac4174	Plate Morph: Low	Complete
Aa	2	24
aa	30	2

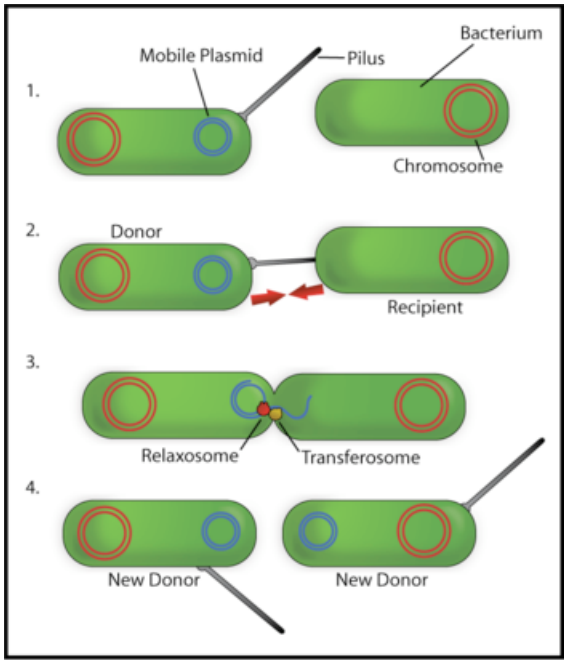
David Kingsley group, Stanford University

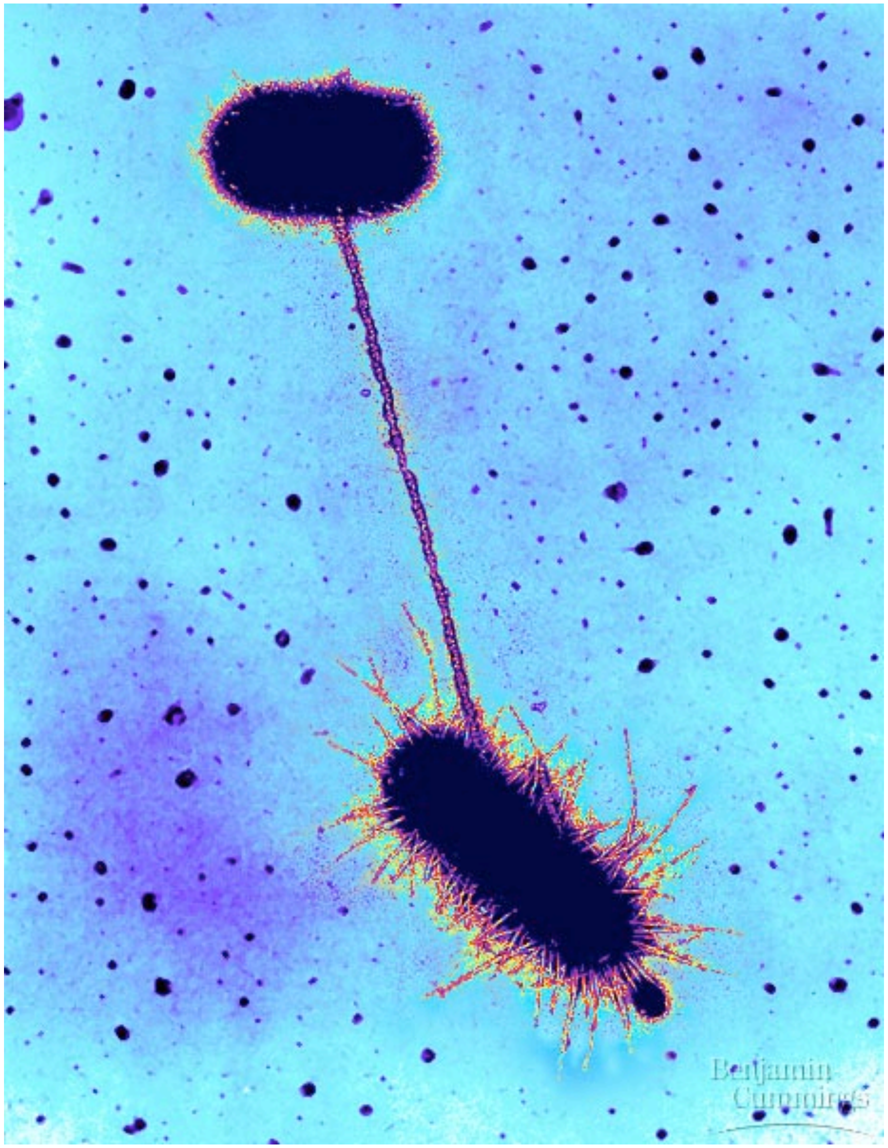
Horizontal Gene Transfer

Key lesson: Genes are transferred between different species. This clouds both the species concept and the interpretation of molecular phylogeny. The Darwin viewpoint was built upon vertical transfer. Woese and others are calling for a vigorous investigation of the significance of horizontal processes.

Horizontal Gene Transfer

- *Microbes swap genes.*
- *The pilus permits this transfer.*





Horizontal Gene Transfer

Science 14 March 2008:
Vol. 319. no. 5869, pp. 1533 – 1536
Direct Visualization of Horizontal Gene Transfer
Ana Babic,1,2* Ariel B. Lindner,1,2 Marin Vulic,1,2{dagger} Eric J. Stewart,1,2{dagger} Miroslav Radman1,2,3{ddagger}

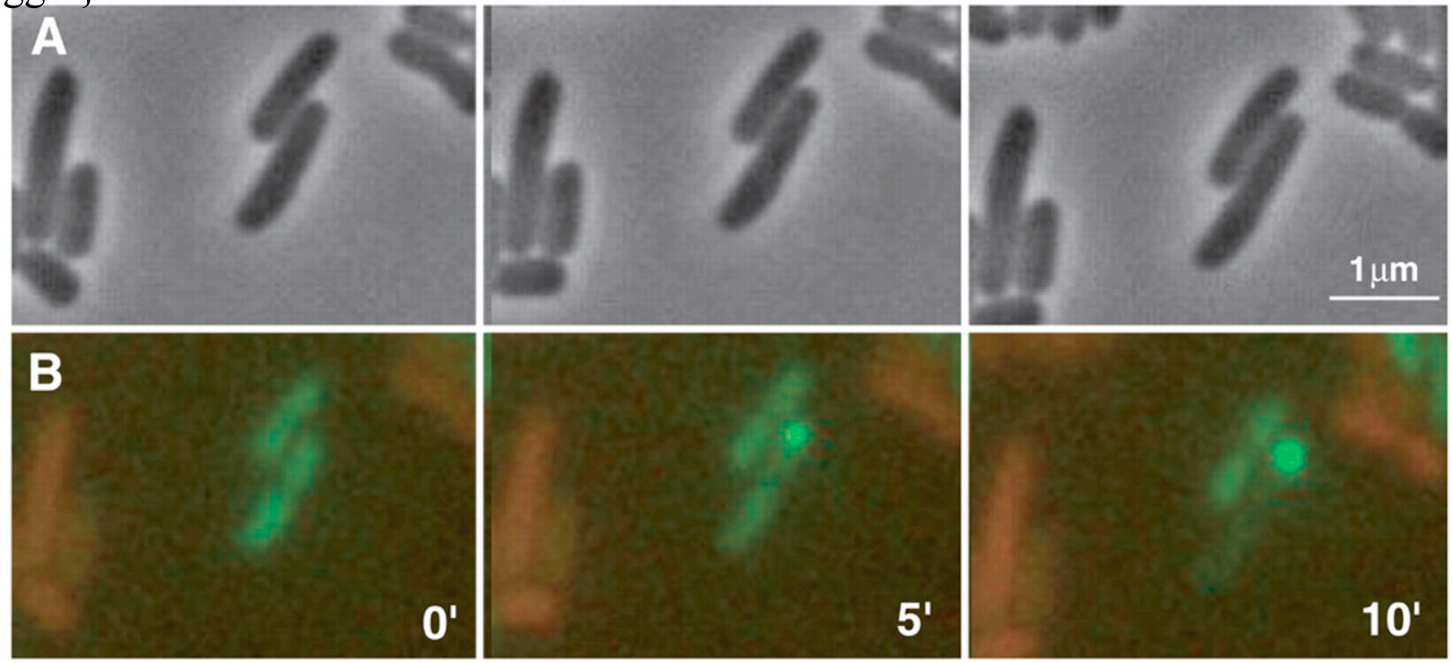


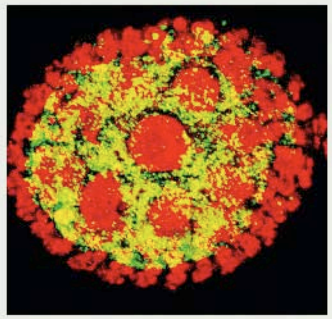
Fig. 2. Representative example of conjugational DNA transfer without visible cell contact between donors and recipients. Recipients and donors were plated on the nutrient-agarose slab without previously being in contact and were observed by time-lapse fluorescence microscopy. (A) Phase contrast images. (B) Overlay of fluorescence images of recipients (green cells) and donors (red cells) at 0, 5, and 10 min after plating on LB-agarose in a cavity slide.

Horizontal Gene Transfer

Genomes within genomes

Another team of genome researchers at the J. Craig Venter Institute in Rockville, Maryland, which has been investigating the DNA of a rather less salubrious organism, this week reports a surprise discovery: the DNA of fruitfly *Drosophila ananassae* contains the entire genome of a parasitic bacterium of the *Wolbachia* genus. Smaller parts of the parasite's genetic material also turned up in worms and wasps.

Bacteria commonly swap DNA with each other. But transfer of bacterial genes into animals was thought to be rare. The new work, published in *Science* (J. C. Dunning Hotopp *et al. Science* doi:10.1126/science.1142490; 2007), suggests that gene flow from bacteria to animal hosts happens on a larger scale and more commonly than suspected. And it hints that the bacterial genome may have provided some sort of evolutionary advantage to its host. "You're talking about a significant portion of [the fruitfly] DNA that is now from *Wolbachia*," says Julie Dunning Hotopp, who led the study. "There has to be some sort of selection to carry around that much extra DNA."



SCIENCE

Invader: *Wolbachia* bacteria (yellow) inside a developing fruitfly egg (red).

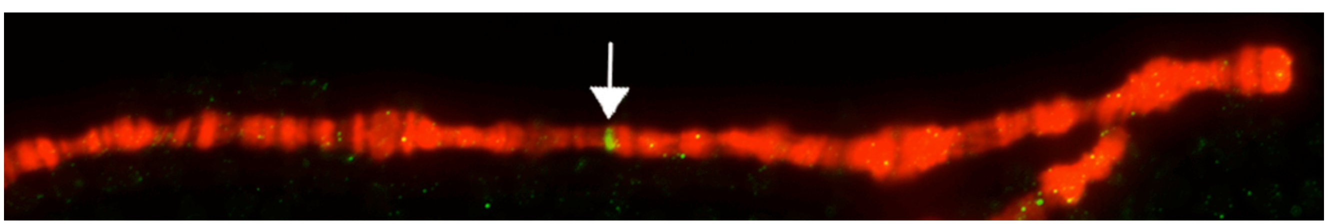
But Dunning Hotopp's former colleague Jonathan Eisen of the University of California, Davis, contests this. "One cannot conclude that some DNA is advantageous simply because it is there," he says.

Up to 75% of insect species are plagued by *Wolbachia*, which lives inside testes and ovaries and passes from one female generation to another through infected ova. To ensure its spread, *Wolbachia* can skew insect birth ratios towards females and even prevent infected males from successfully mating with disease-free females. The bacterium's close association with egg cells means there's ample opportunity for bacterial DNA to get permanently sewn into a host's nuclear genome, says Dunning Hotopp.

When Dunning Hotopp and her colleagues analysed the DNA of *D. ananassae* uninfected by *Wolbachia*, they found 44 of the 45 *Wolbachia* genes they searched for. Because these selected genes are so widely spread throughout *Wolbachia* DNA, this suggests that the rest of its more than 1-million-base-pair genome is also likely to be found in fruitflies.

Many of the *Wolbachia* genes were infiltrated by strands of insect DNA that jump around the genome, and so are unlikely to be functional. But the researchers showed that at least 28 of the bacteria's 1,206 genes are active in the flies. More genes that have seeped from bacteria into animals are certain to be found, the researchers say, particularly in reptiles and amphibians. But finding bacterial genes in mammals is unlikely because no bacteria are known to infect their sperm and egg cells. ■

Ewen Callaway



Insights Into Human Evolution

Key lesson: Darwin hesitated on this most delicate and ultimate of questions. In the time since, advances on all of the important quarters for determining evidence for evolution have painted an enlightening picture of human evolution that is consonant with everything else we know about the subject.

Chromosome Structure

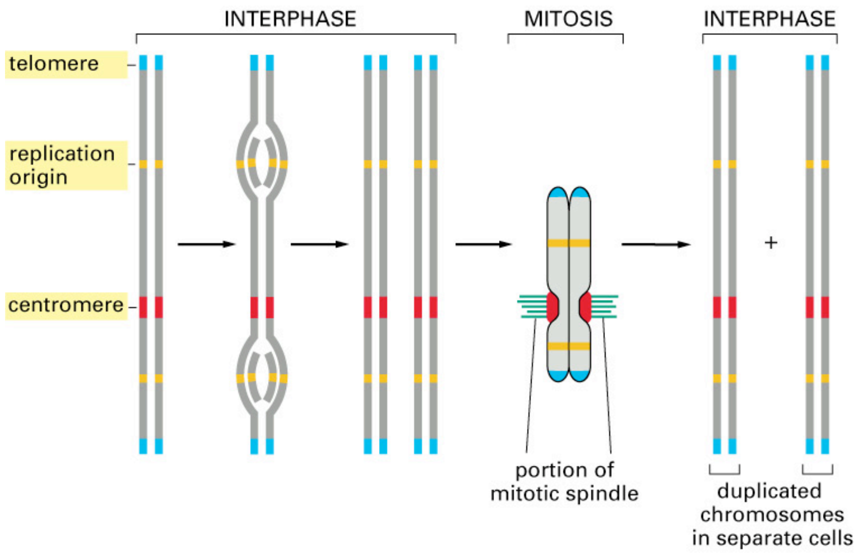


Figure 4–22. Molecular Biology of the Cell, 4th Edition.

- ***Our last example will center on the interesting properties of human chromosome 2.***
- ***This slide shows some of the key landmarks on chromosomes such as telomeres and centromeres.***

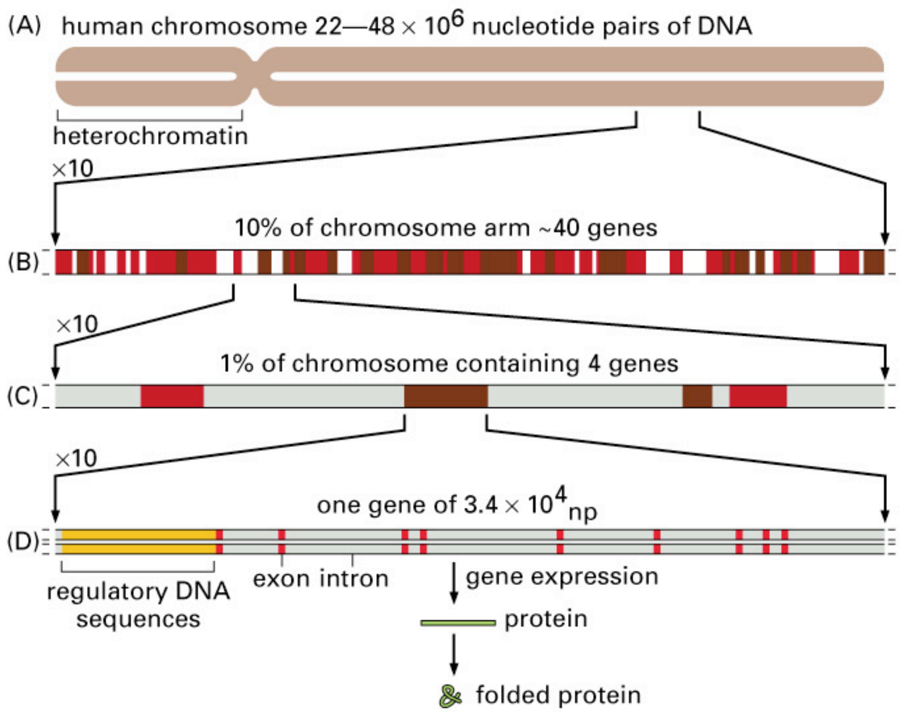
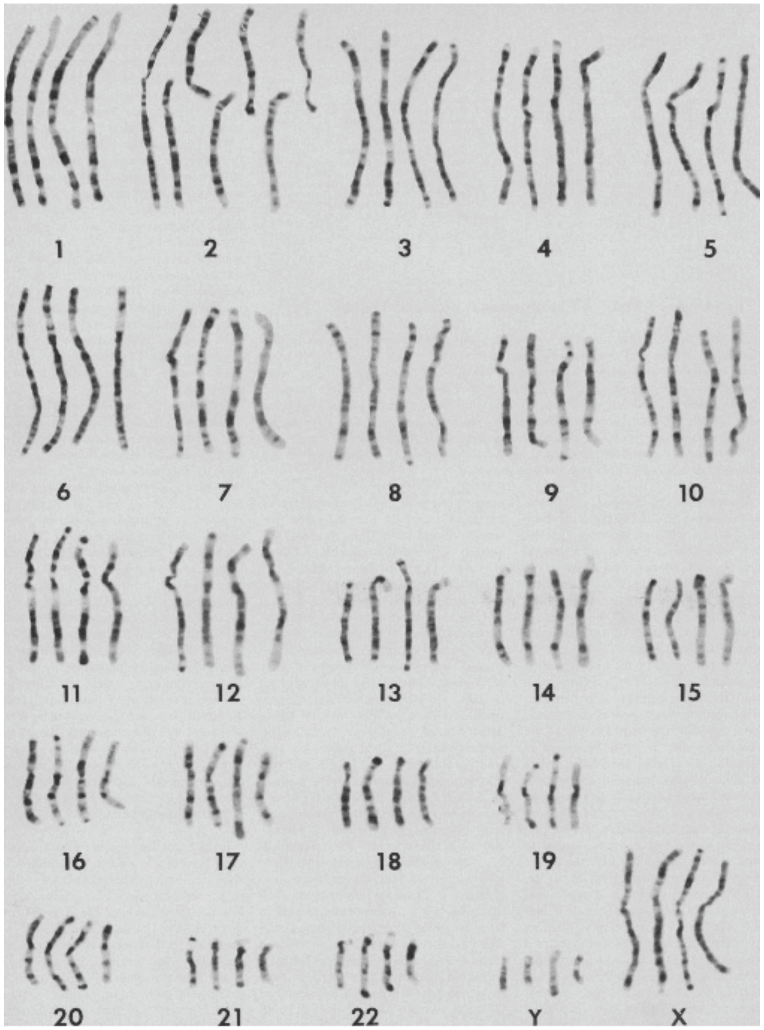


Figure 4–15. Molecular Biology of the Cell, 4th Edition.

Genes and DNA: What Have We Learned?

- *Chromosome geography revealed by banding patterns.*
- *These patterns reveal similarities between human and primate DNA.*

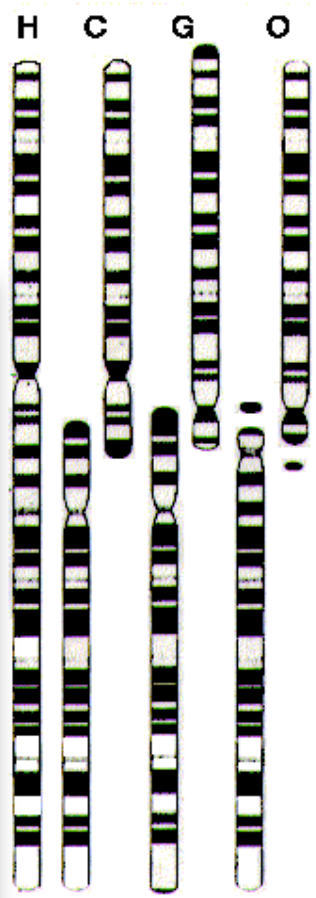


``The origin of man: a chromosomal pictorial legacy'' Science, 215, 1525 (1982).

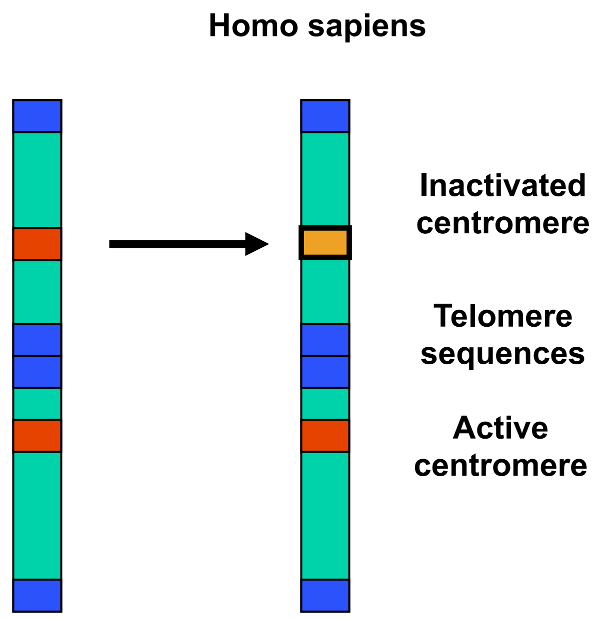
What We Have Learned From Whole Genome Sequences

- *Human chromosome number 2 has the stamp of a fusion of an earlier two chromosomes.*

"Chromosome 2 is unique to the human lineage of evolution, having emerged as a result of head-to-head fusion of two acrocentric chromosomes that remained separate in other primates. The precise fusion site has been located in 2q13–2q14.1 (ref. 2; hg 16:114455823 – 114455838), where our analysis confirmed the presence of multiple subtelomeric duplications to chromosomes 1, 5, 8, 9, 10, 12, 19, 21 and 22 (Fig. 3; Supplementary Fig. 3a, region A). During the formation of human chromosome 2, one of the two centromeres became inactivated (2q21, which corresponds to the centromere from chimp chromosome 13) and the centromeric structure quickly deterioriated (42)."



``The origin of man: a chromosomal pictorial legacy'' Science, 215, 1525 (1982).



``Generation and annotation of the DNA sequences of human chromosomes 2 and 4'', Nature, 2005, Hillier et al.