What are species? Concepts of species

Today:

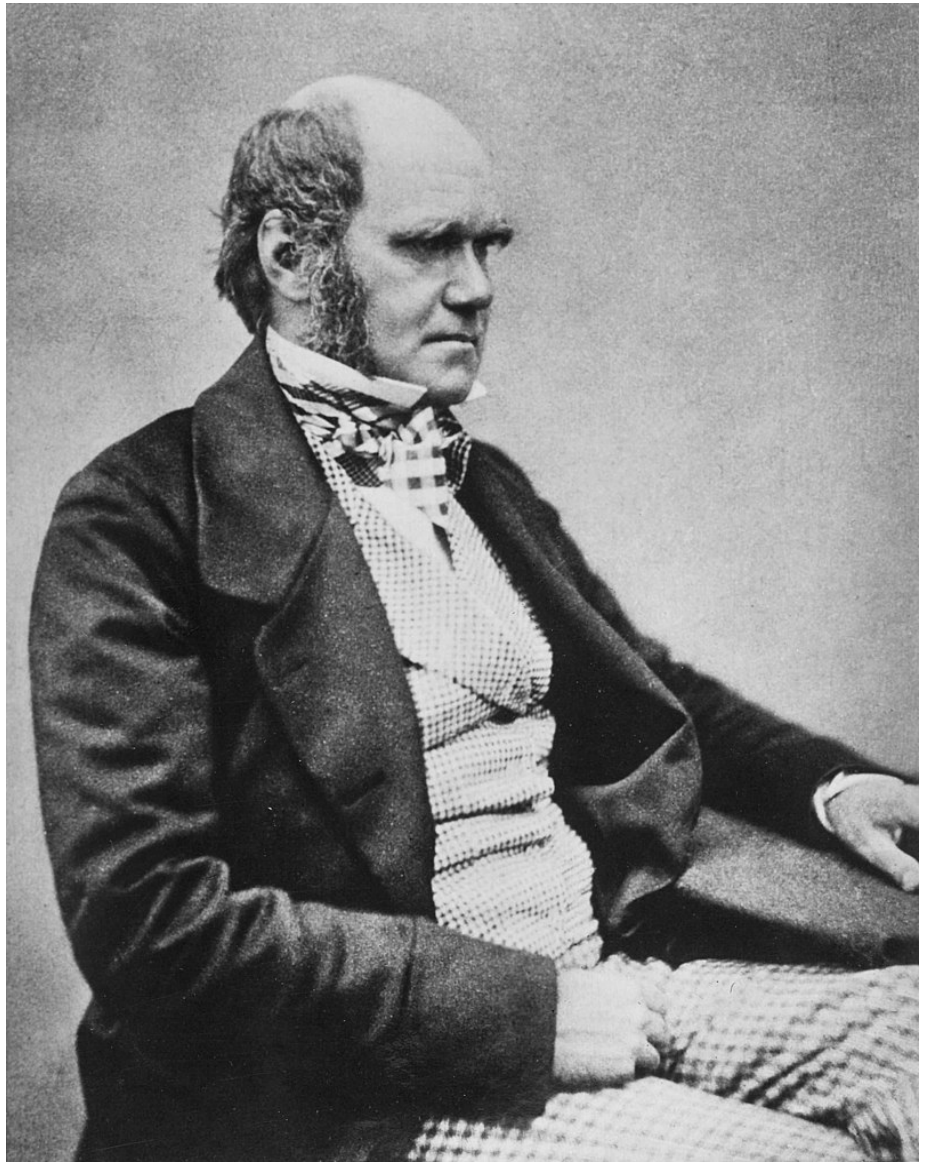
Finish up on natural selection and the "Modern Synthesis"

What do we mean by species?

- "Species concepts"

Before I forget: volunteers to lead discussion of Darwin's "On the Origin of Species..." readings!

Sign up here!!



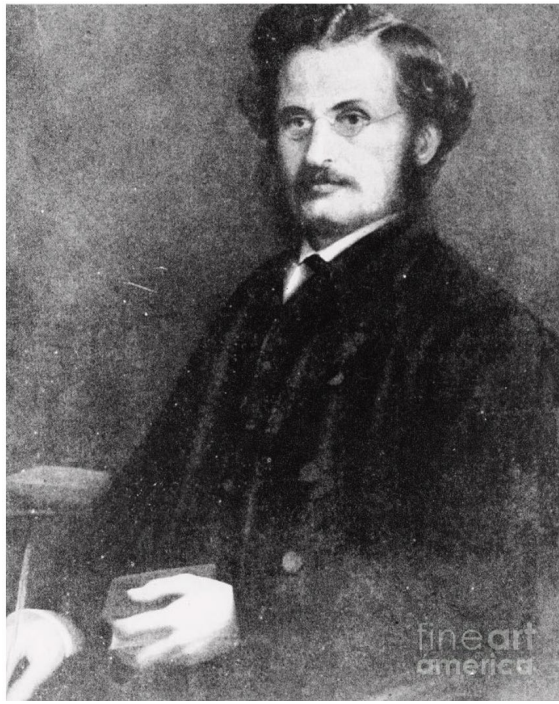
Charles Darwin 1859

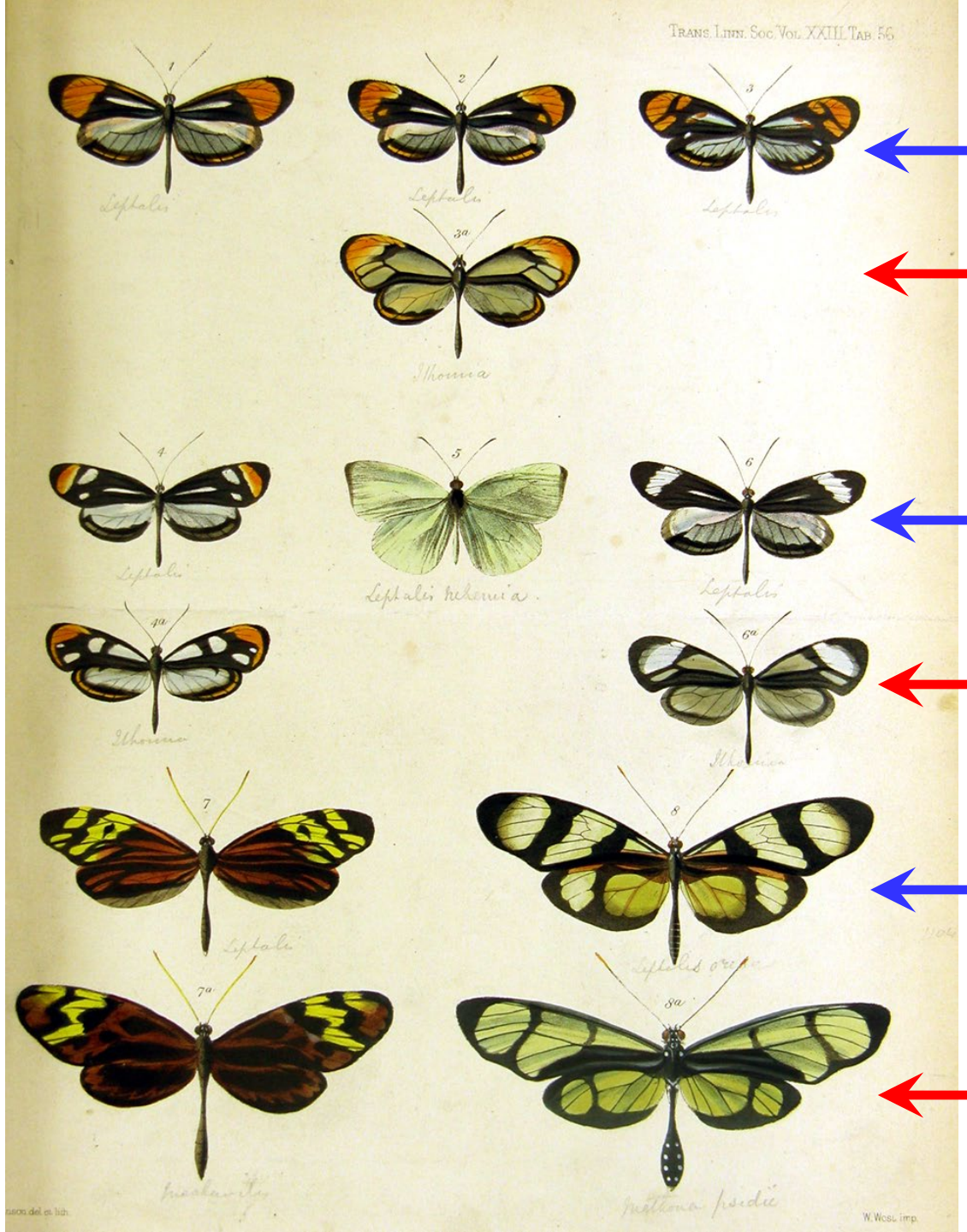
1859 On the Origin of Species...

Explains the clear logic behind natural selection. But this whole book has *NO EXAMPLES OF NATURAL SELECTION.*

It was *ALL THEORETICAL!*

1859 Henry Walter Bates arrives back from the Amazon after 12 years





Henry Walter Bates in the Brazilian Amazon:

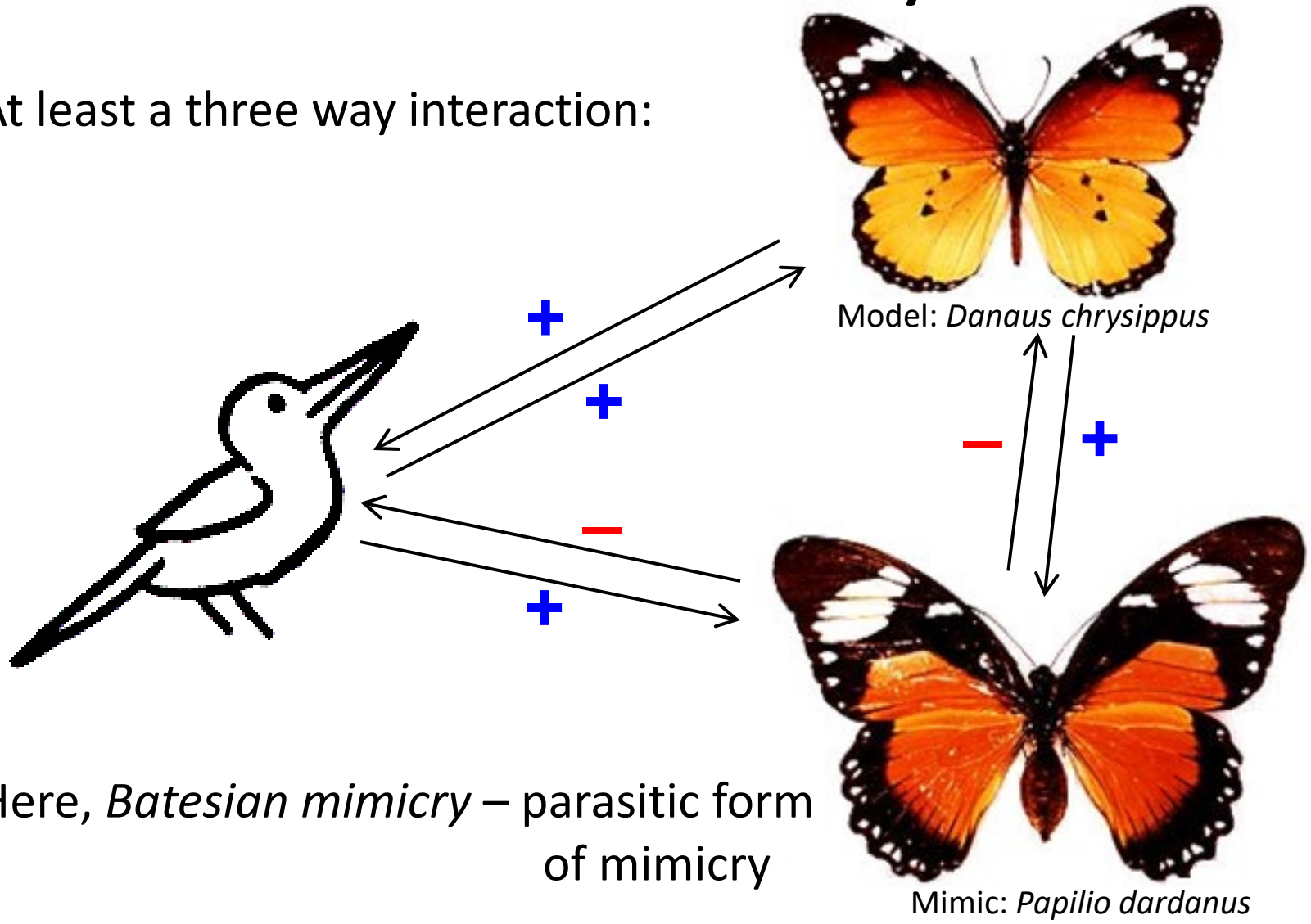
Ithomiinae (related to monarchs) distasteful **models**

Dismorphiinae (related to “cabbage white”) edible **mimics**

H.W. Bates 1862. Trans Linn Soc

Batesian mimicry

At least a three way interaction:



Here, *Batesian mimicry* – parasitic form of mimicry

Batesian mimicry

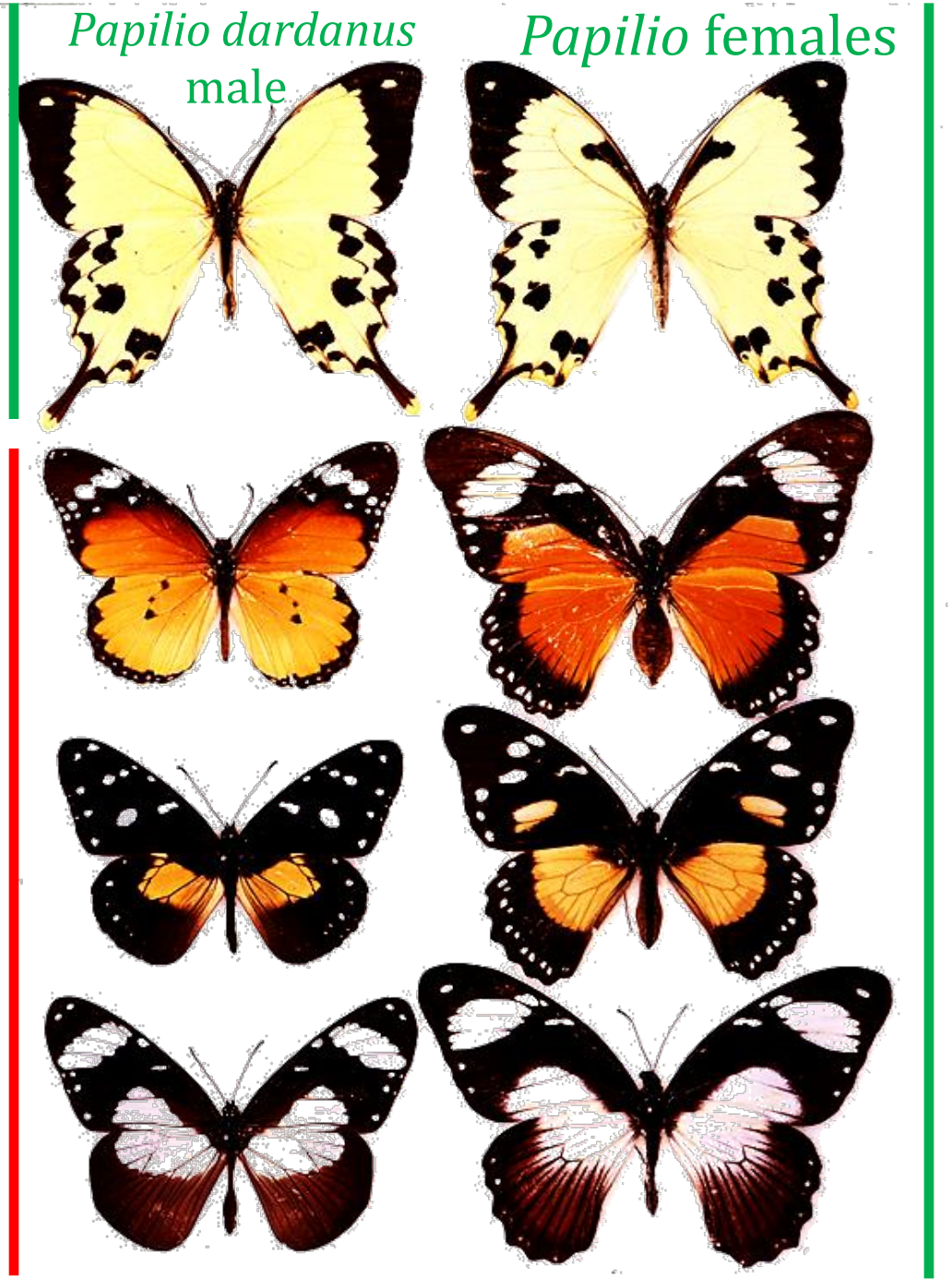
(Bates 1862)

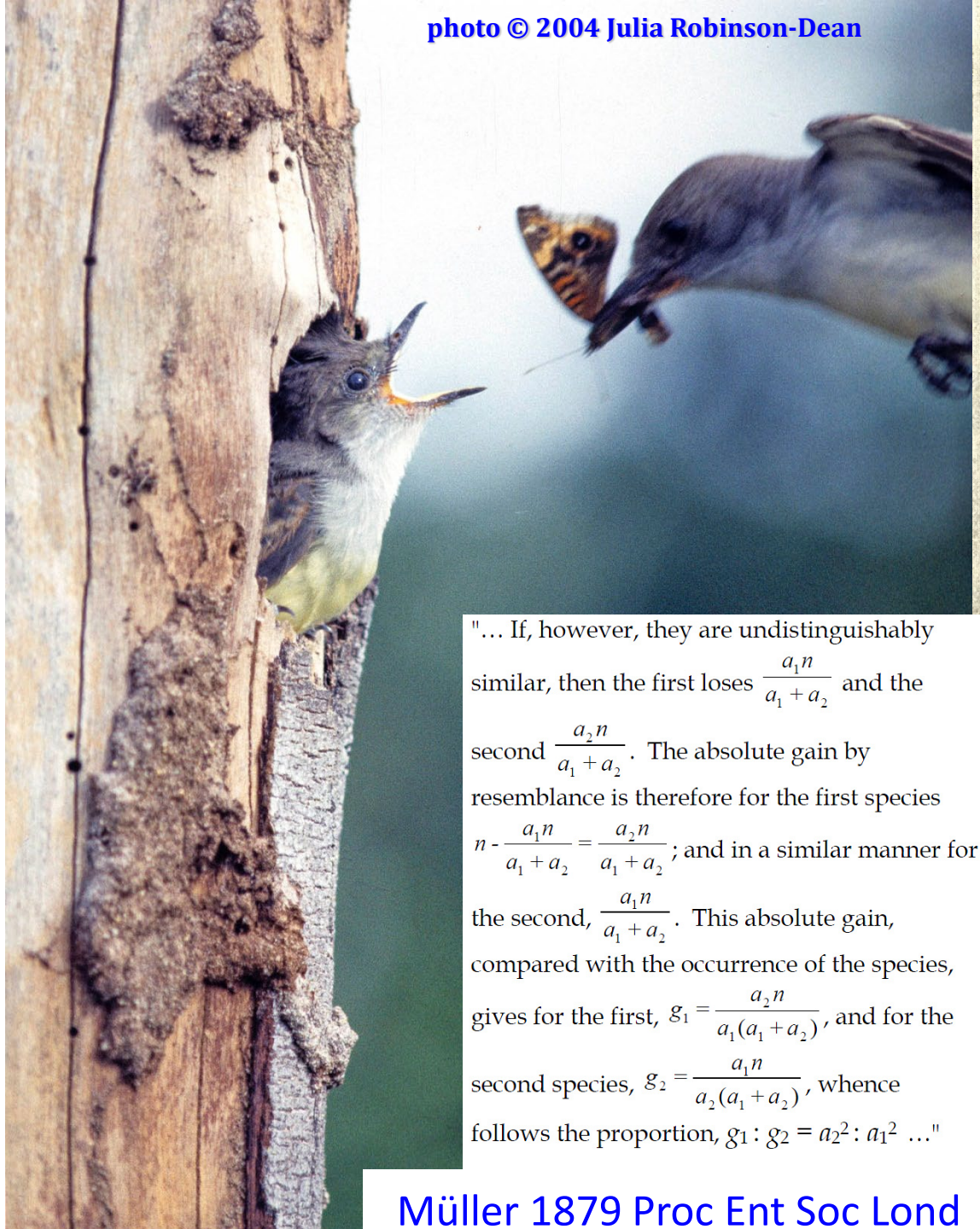
+ / –

a form of parasitism!!

(e.g. *Papilio dardanus* female forms, mimic Danaidae in Africa)

Leads to diversifying (negative) frequency dependent selection, and polymorphism





"… If, however, they are undistinguishably similar, then the first loses $\frac{a_1 n}{a_1 + a_2}$ and the second $\frac{a_2 n}{a_1 + a_2}$. The absolute gain by resemblance is therefore for the first species $n - \frac{a_1 n}{a_1 + a_2} = \frac{a_2 n}{a_1 + a_2}$; and in a similar manner for the second, $\frac{a_1 n}{a_1 + a_2}$. This absolute gain, compared with the occurrence of the species, gives for the first, $g_1 = \frac{a_2 n}{a_1(a_1 + a_2)}$, and for the second species, $g_2 = \frac{a_1 n}{a_2(a_1 + a_2)}$, whence follows the proportion, $g_1 : g_2 = a_2^2 : a_1^2$ …"

Müller 1879 Proc Ent Soc Lond

Fritz Müller

Müllerian mimicry

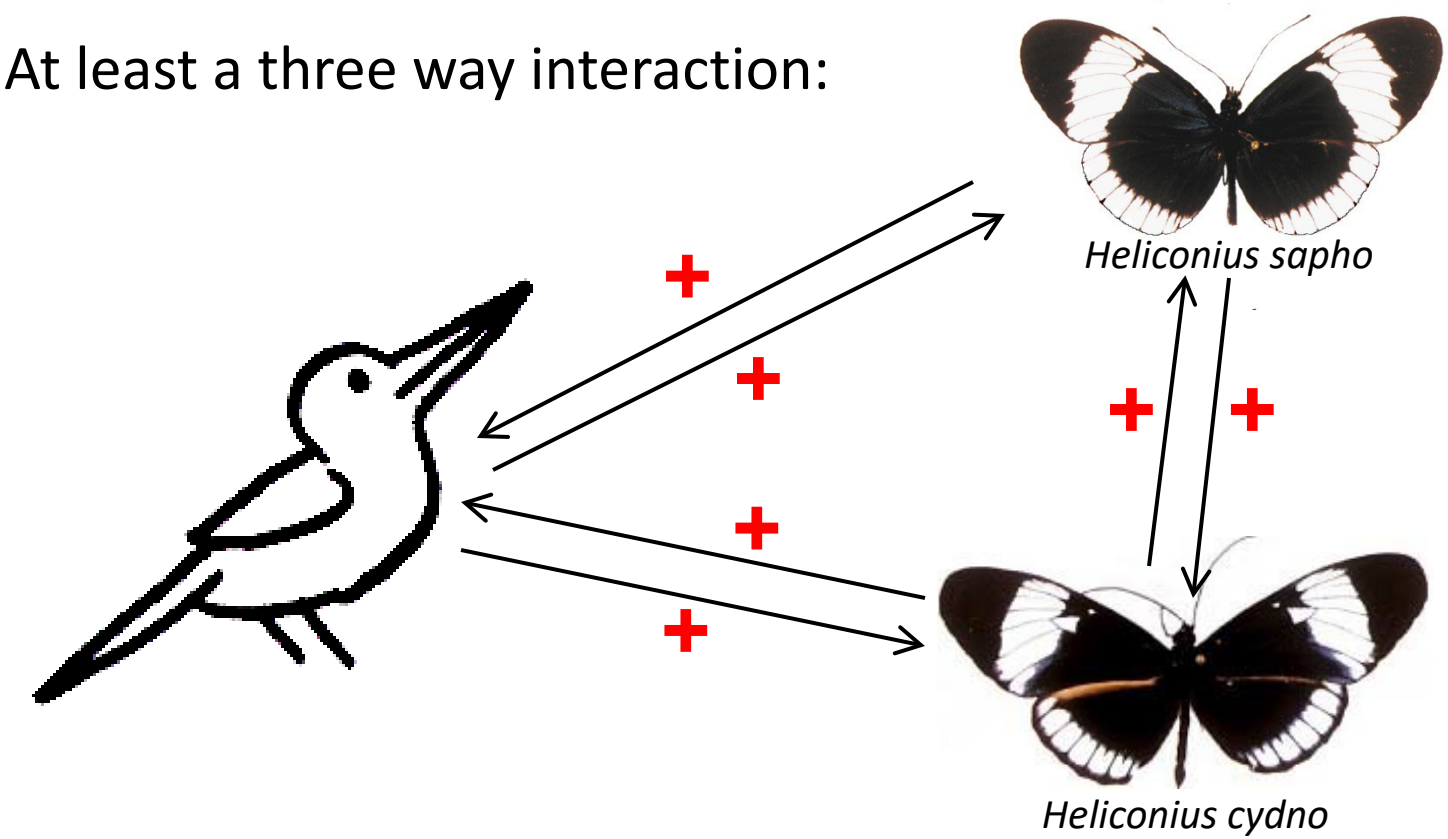
(Müller 1879)
+ / +
a mutualism

(e.g. *Heliconius*
and Ithomiini
species in South America)

Leads to purifying (positive)
frequency dependent selection,
lack of polymorphism

Müllerian mimicry

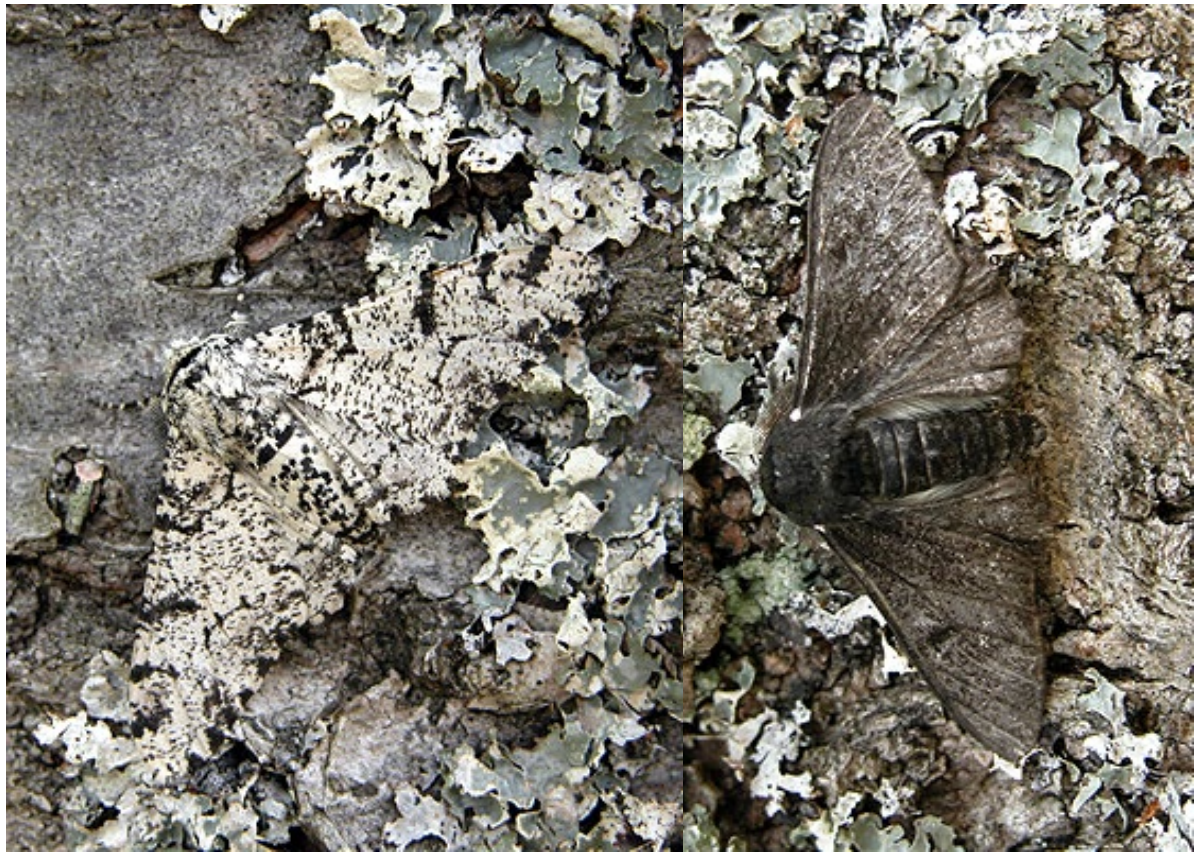
At least a three way interaction:



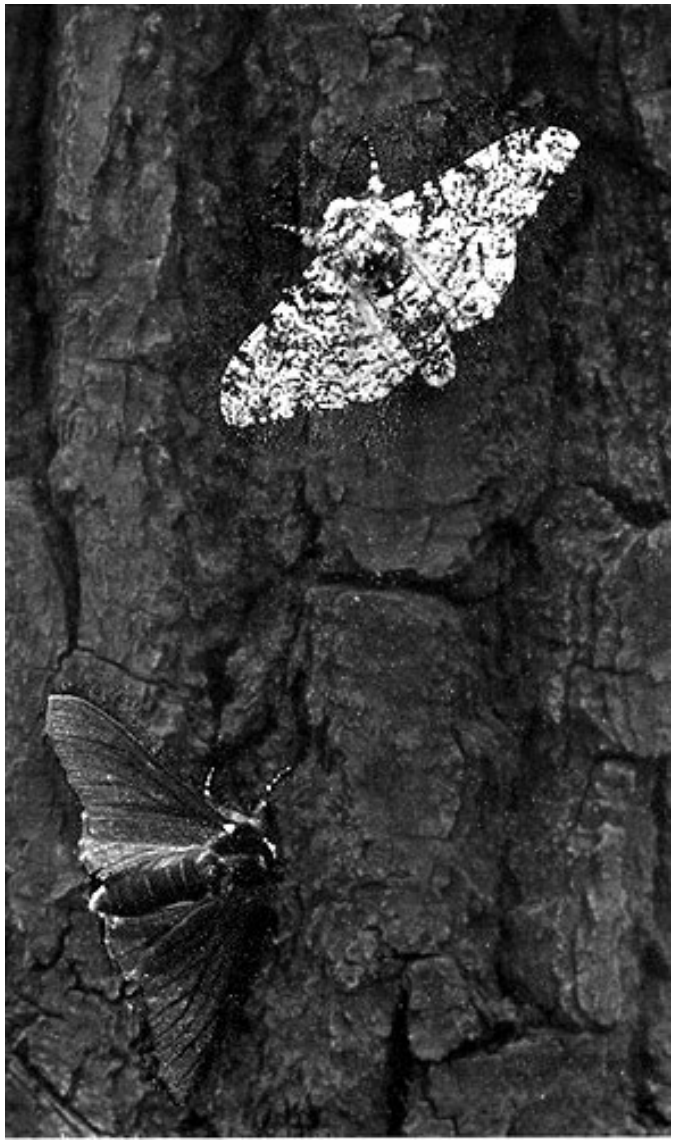
Here, *Müllerian mimicry* – benefits for all!

Heliconius erato (above), and *H. melpomene* (below), a pair of Müllerian co-mimics from different sites in Ecuador and Northern Peru. Each species gains protection from the other's unpalatability. Within any site, the two species are excellent co-mimics, but major geographic differences in colour pattern have evolved within each species. This geographic diversity is extraordinary by temperate zone standards: the region (about 600km x 300km) of the Andean foothills from which all these forms within each species can be found is less extensive than New England or Great Britain.

The peppered moth *Biston betularia*



Left: color photo of form *typica* (left), and melanic *carbonaria* (right) on lichen-covered trunk in my parents' garden in rural Kent



Right: black and white photo on soot-covered tree near Birmingham in the 1950s

Evolution as a change in gene frequency: The usual model in textbooks

Simplest discrete generation model, of Sewall Wright:

Genotypes	A_1A_1	A_1A_2	A_2A_2
Relative fitness, W_{ij}	W_{11}	W_{12}	W_{22}
Per generation selection, s	1	1- hs ($0 < h < 1$, *dominance*)	1- s

Wright from 1921

However, continuous time approximation (Fisher-Haldane) generally makes math simpler!

$(s = r_1 - r_2)$

Haldane from 1922

Fisher from 1918

What is “fitness”?

In *ecology*, absolute fitness is important (per capita population growth rates, r_1, r_2, where e.g. $r_1 = b_1 - d_1$)

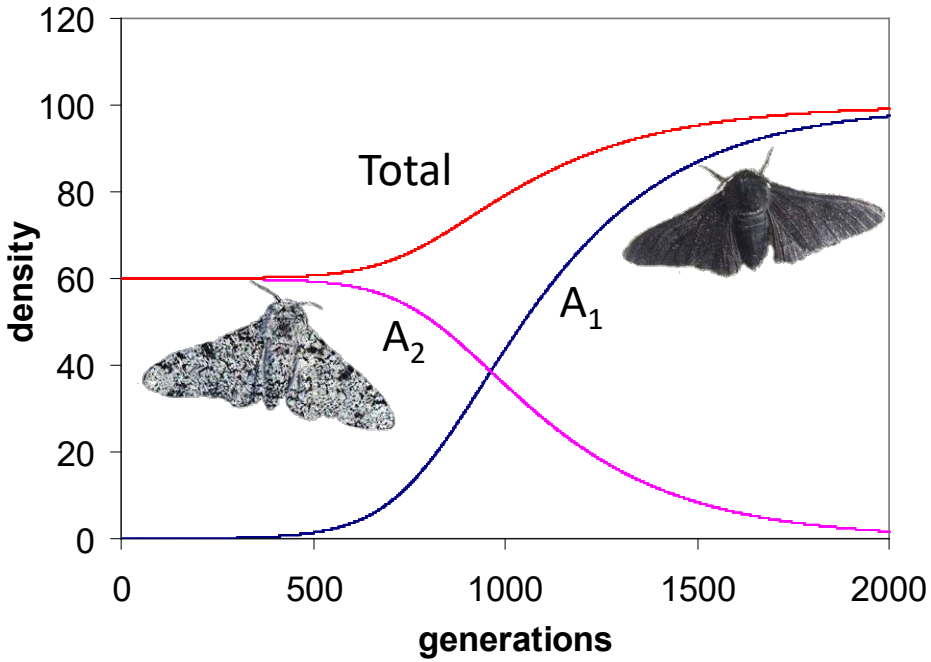
In *evolution*, only *relative fitness* ($s = r_1 - r_2$) matters! s is the “selective coefficient”

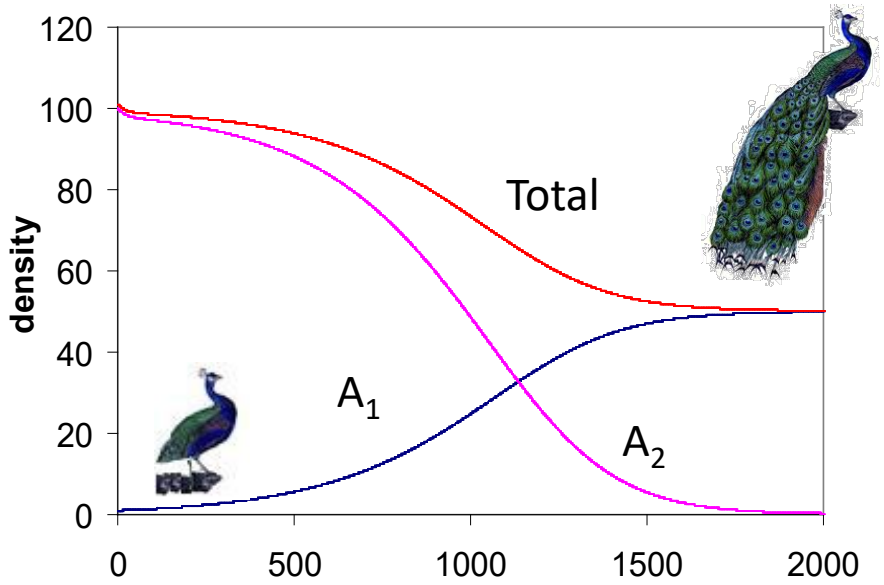
Per capita density-dependent population growth:

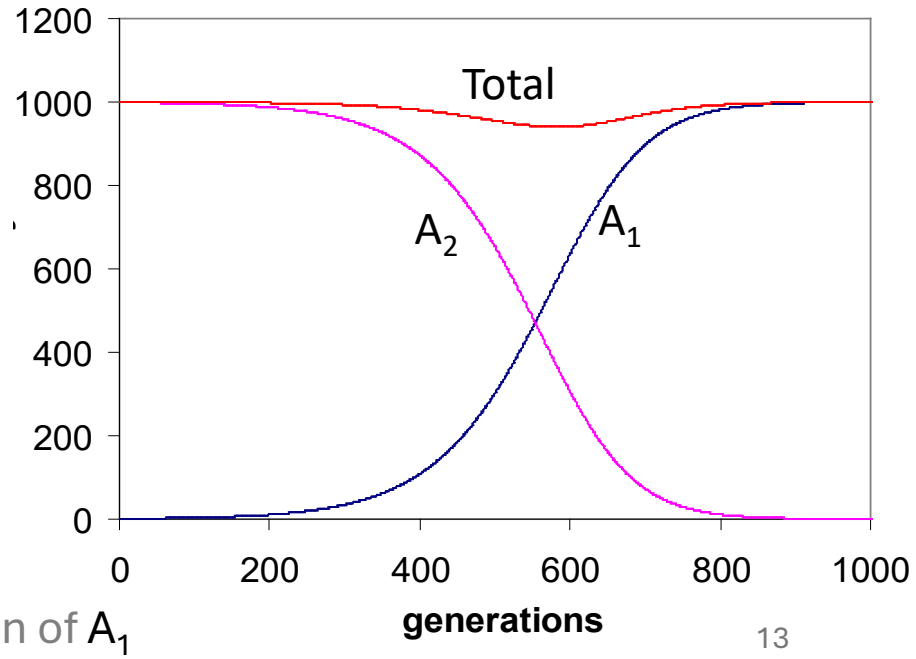
$$\left(\frac{1}{N}\right)\frac{dN}{dt} = r - \alpha N$$

Equilibrium density is:

$$\widehat{N} = r/\alpha$$

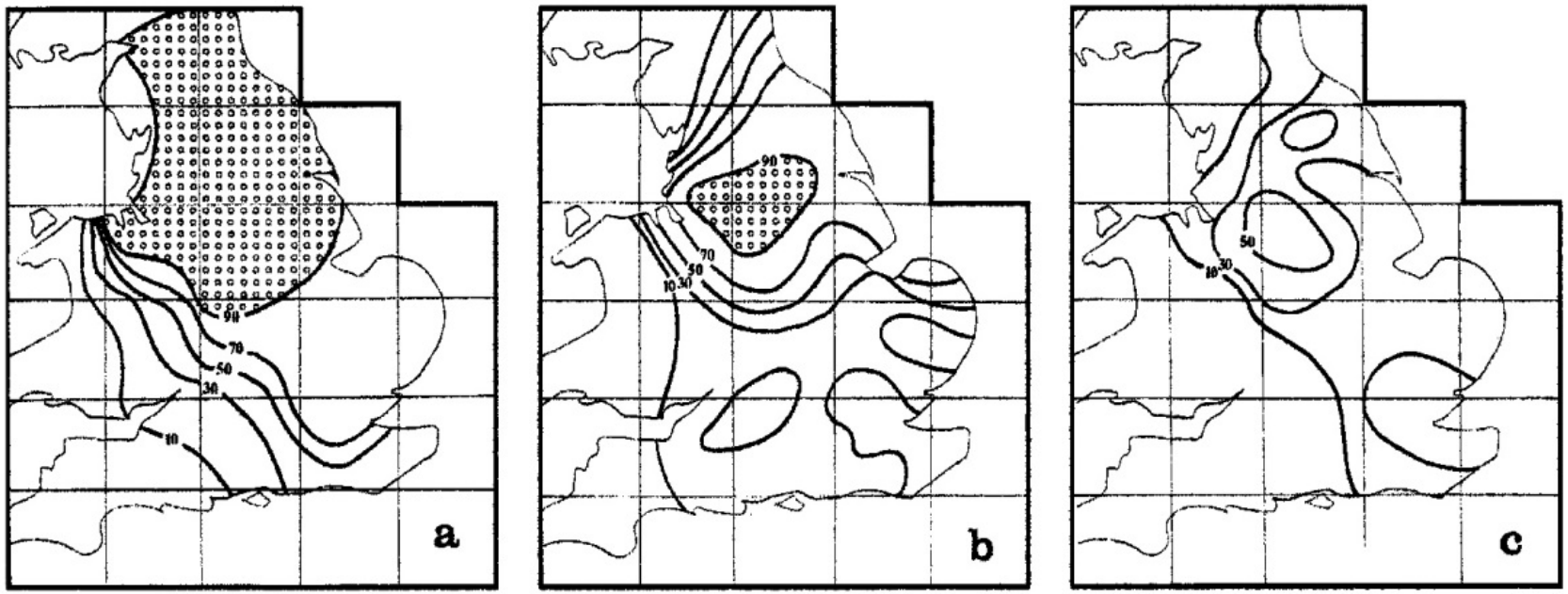






All lead to fixation of A_1

Melanic form now disappearing in UK!



1950-early 1970s 1983-4 1987-1999

... due to the Clean Air Act of the 1960s that banned burning of coal or wood in cities

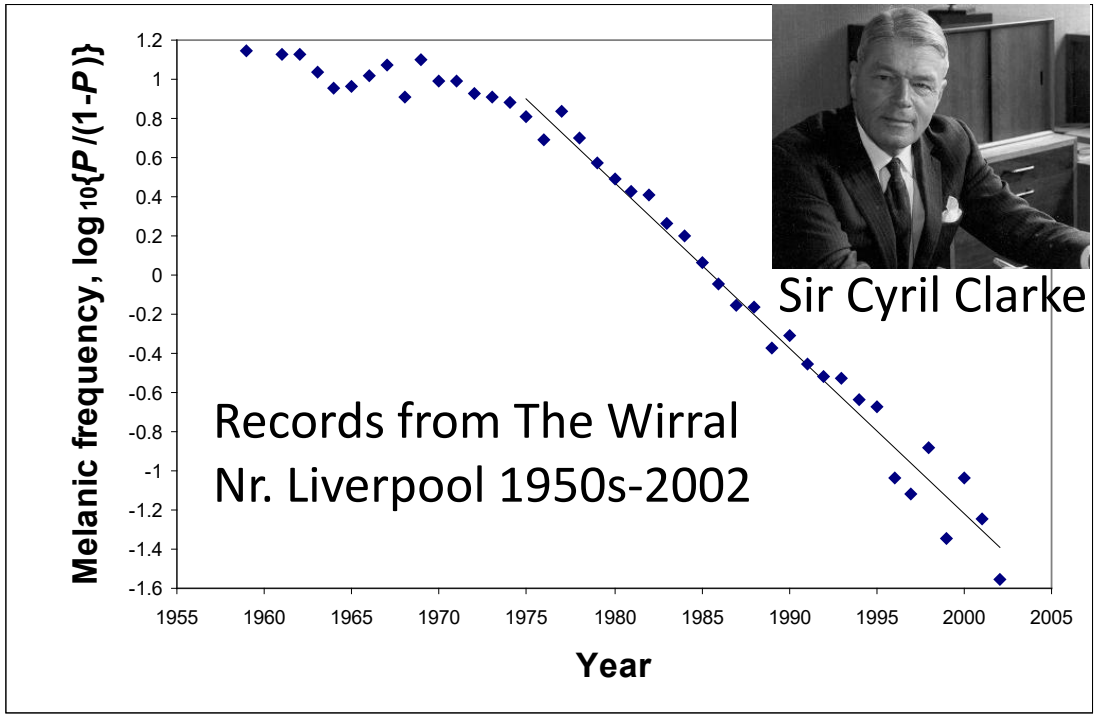
Can we measure selection in nature? The peppered moth:

$r = b - d$ – Birth rate, b; death rate, d

Selection coefficient = $r_1 - r_2 = (b_1 - d_1) - (b_2 - d_2)$

Selection well approximated by difference in constant death rates (assume $b_1 = b_2$)

$$d_{typ} - d_{mel} = s \approx 0.179 \pm 0.005$$



“Selective bird predation on the peppered moth: the last experiment of Michael Majerus”

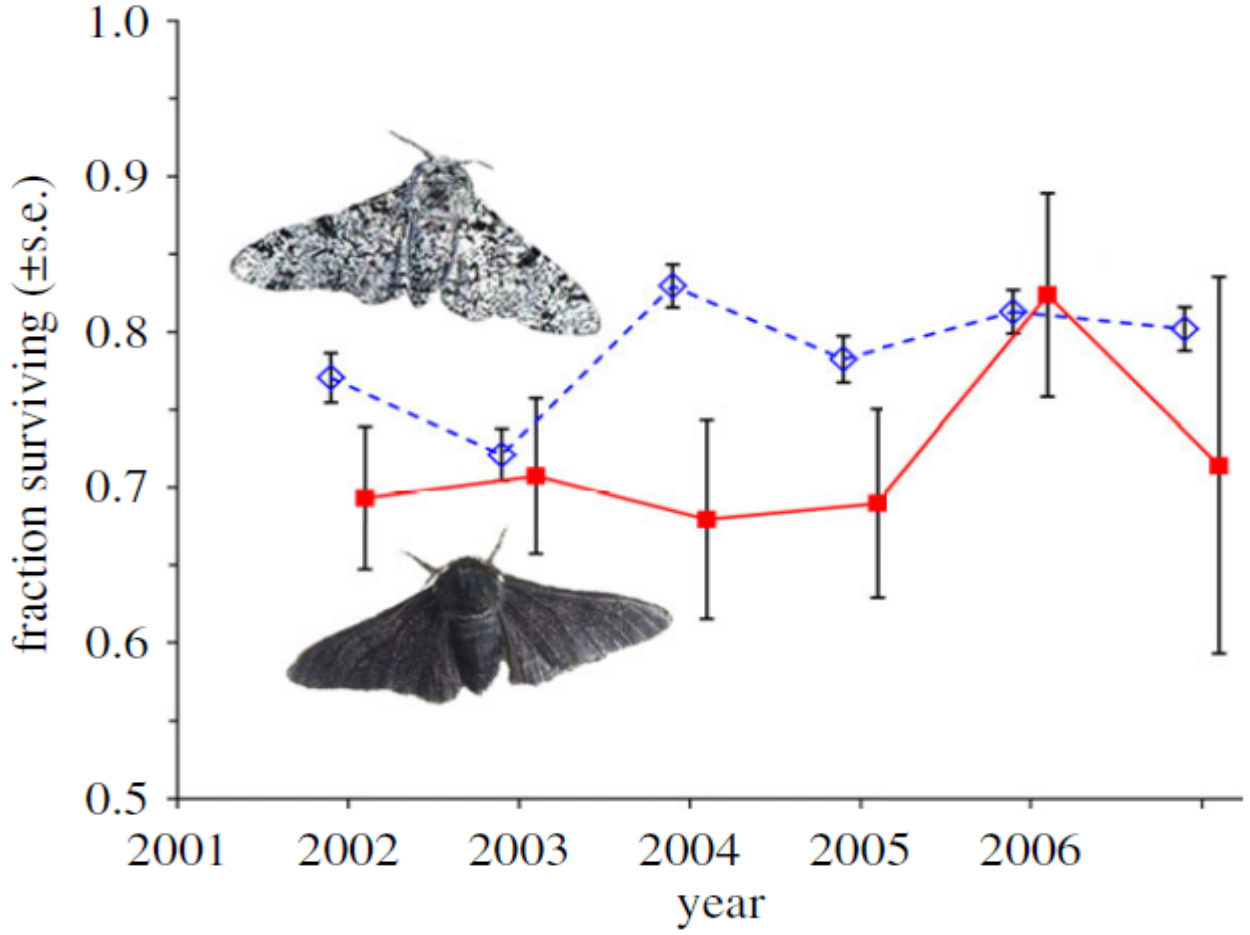


Figure 1. Survival of moths (±s.e.) over the course of the predation experiment. Unfilled diamonds with dashed lines, non-melanic; filled squares with solid lines, melanic.

Melanic and typical moths were released on trees at night and monitored until 4 hours after sunrise in a rural garden outside Cambridge, England, and any losses were noted.

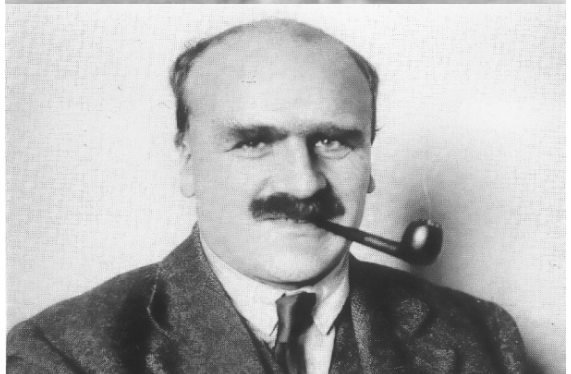
There was an approximately s = 9% *per day* advantage of “typical” (white-and-black) peppered moths over “melanic” (black) moths.

Agrees closely with selection pressure *per generation* est. from decline in frequency near Liverpool (s = 18%).

Modern Synthesis. Part I

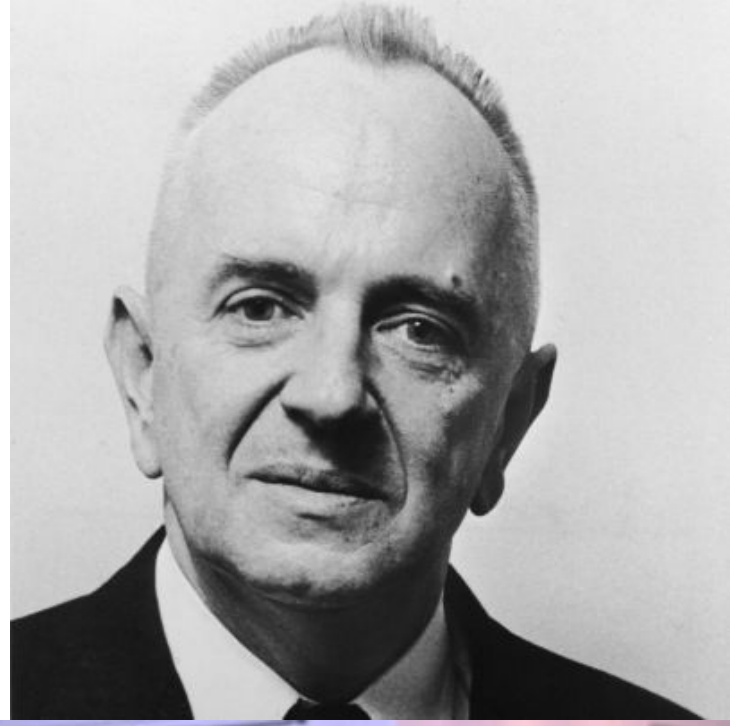
1930 Ronald A. Fisher: The Genetical Theory of Natural Selection. Book
1931 Sewall Wright: Evolution in Mendelian populations. Paper
1932 JBS Haldane: The Causes of Natural Selection. Book

- Mendelian genetics worked just great with evolution by natural selection.
- Didn’t discuss origin of species much. Agreed with Darwin: species were just “varieties” that had diverged a bit more



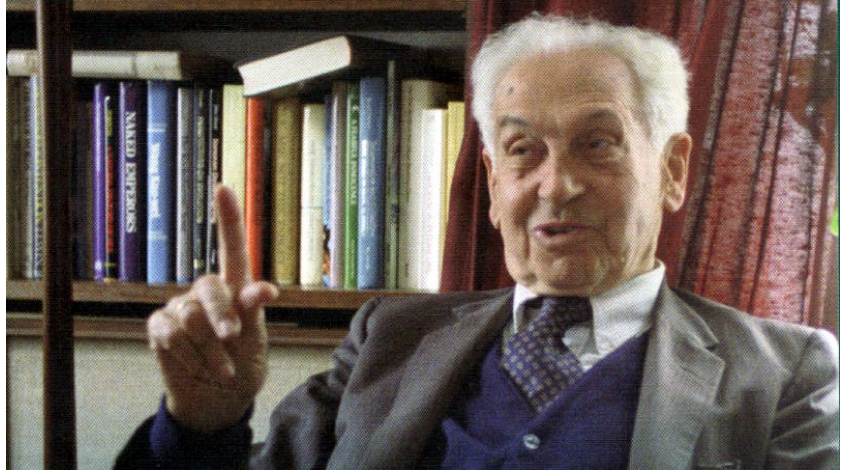
Modern Synthesis. Part II. Species

1937 Theodosius Dobzhansky: Genetics
and the Origin of Species. Book
1942 Ernst Mayr: Systematics
and the Origin of Species. Book



- They argued Darwin was wrong about species and speciation. D. didn't understand species!
- Species are "reproductively isolated"
- Species are special. Speciation is difficult.
- Speciation requires special mechanisms, like separation of populations by geography

Crazy: I actually met Ernst Mayr, here in Cambridge MA, in 1999!



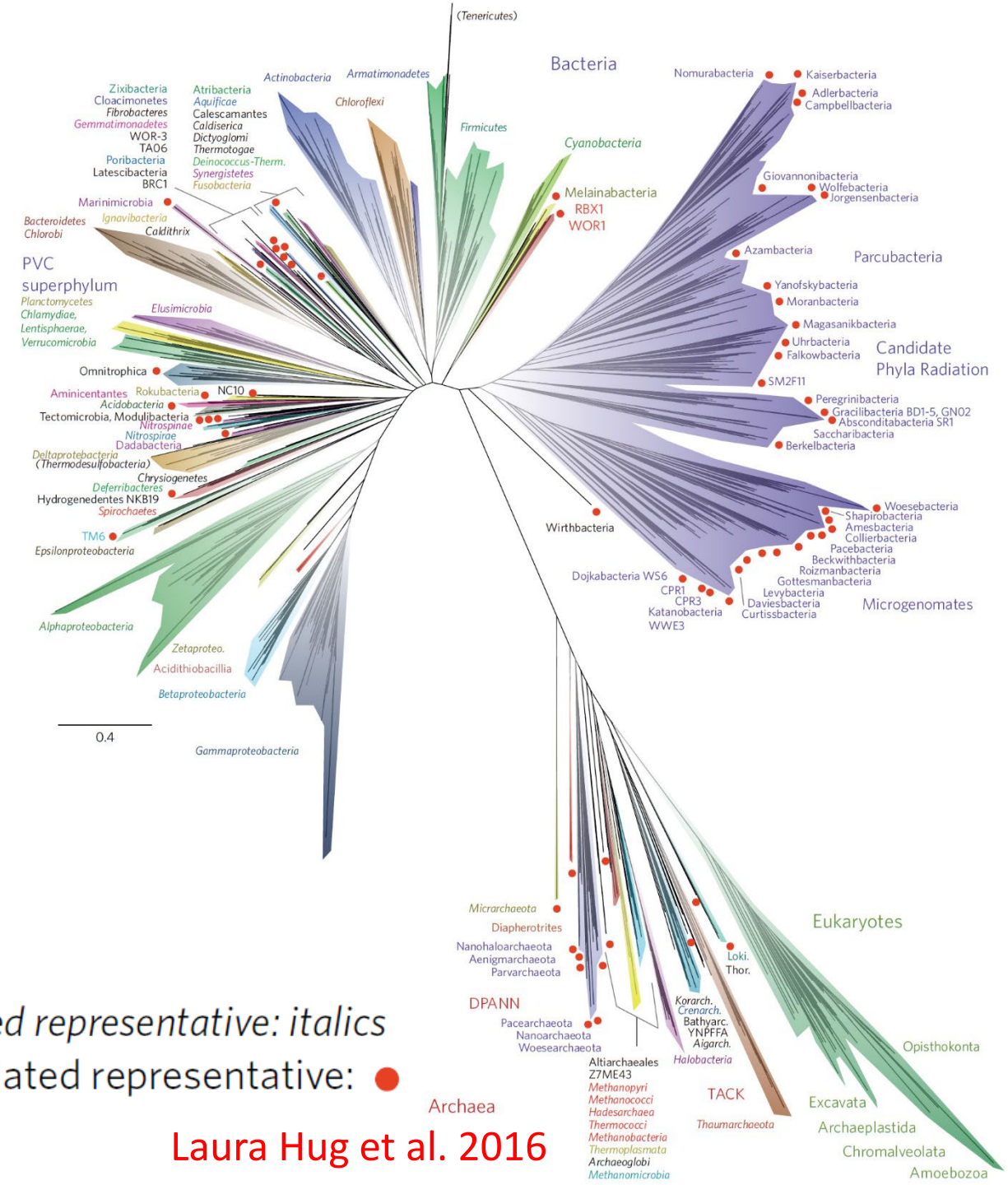
Ernst Mayr's career

Harvard prof: 1953-2005
Director, MCZ: 1961-1970

career:	Ernst Mayr	James Mallet
lifespan	100 yrs	~70 yrs so far
books	21	0.05
papers	863	~250
prizes & awards	35	1
honorary degrees	17	0

Speciation: by 2020s

- Fossil fuels
- Genetic drift & stochastic processes in evolution
- Nuclear power & nuclear weapons
- Levels of selection: gene, individual, population
- Phylogenetic methods
- Climate change
- The internet
- Molecular genetics: DNA sequencing, genomics



Major lineages with isolated representative: italics

Major lineage lacking isolated representative: ●

Laura Hug et al. 2016

Were Neanderthals and Humans different species?

Can you tell which is which?

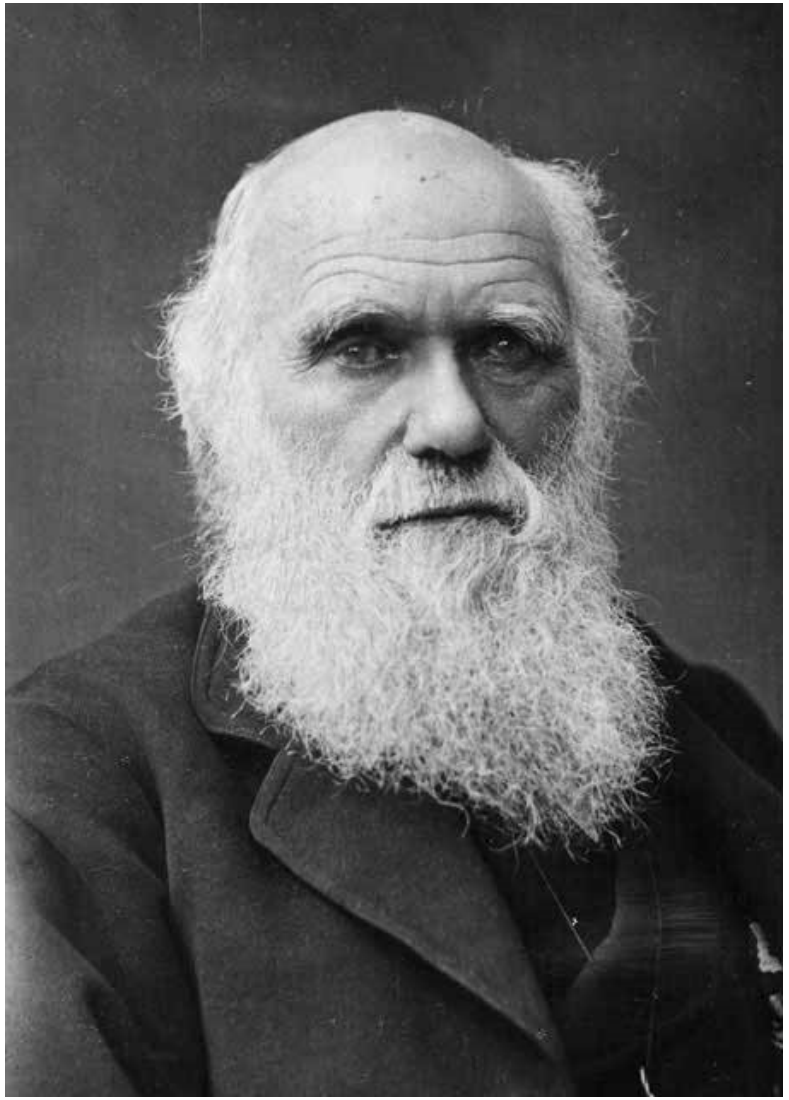
Reconstructions are based on skulls and fossil genetic data

Species "concepts" – What do we mean by species?

Darwin proved species evolved

Species weren't created kinds, with an *essence*. They gradually evolved from each other.

Darwin proved: *species aren't "real"* least in the "created kind" sense. This means that *we humans* must decide where to draw the line between species and varieties



Darwin 1859, p. 485:

"Hereafter, we shall be compelled to acknowledge that the only distinction between species and well-marked varieties is, that the latter are known, or believed, to be connected at the present day by intermediate gradations, whereas species were formerly thus connected."

Darwin 1871. The Descent of Man..., pp. 214 - 215:

"Independently of blending from intercrossing, the complete absence, in a well-investigated region, of varieties linking together any two closely-allied forms, is probably the most important of all the criterions of their specific distinctness."

AR Wallace, 29 Nov 1900, letter to H.M. Bernard:

"Definition of a Species: A species is a group of individuals which reproduce their like within definite limits of variation, and which are not connected with their nearest allied species by insensible variations."

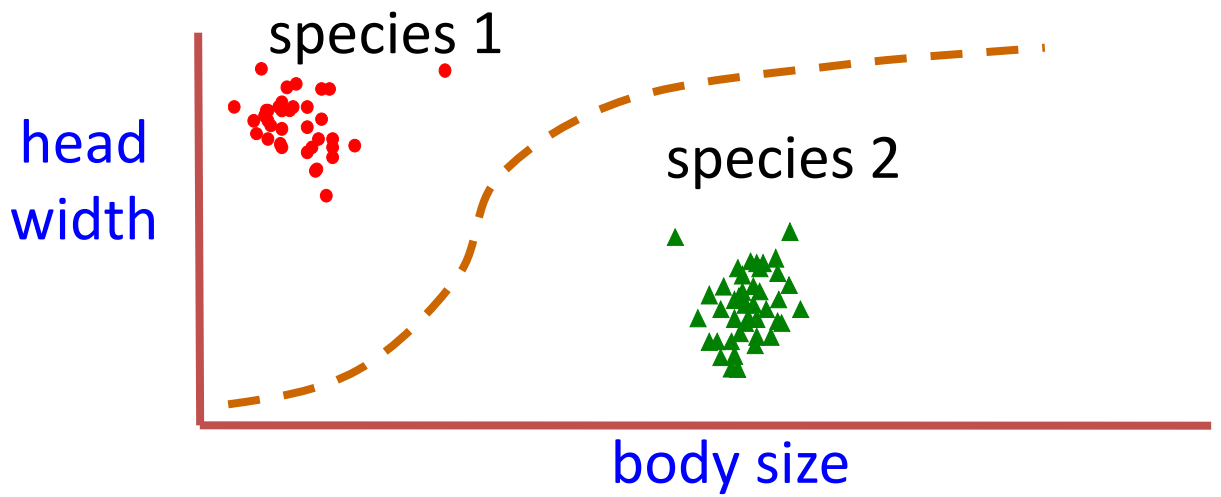
(1) Diagram of a species in process of development into 3 new species

(2) Here one var. has become completely isolated by extinction of intermediate forms, and is a new sp. When the intermediates between the other two var. have been exterminated in the struggle for life we shall have 3 new species.

from Cock, A.G. 1977. Biol J Linn Soc 9:1-30.

Species concepts

1. *Darwin/Wallace idea of species*. Darwin's pragmatic solution: species are delimited by gaps in morphology



Later called by Mayr: "Darwin's morphological species concept"

Primula vulgaris (primrose, top left), *Primula elatior* (oxslip, top right), and *Primula veris* (cowslip, left) hybridize & produce rare intermediates.

Darwin: different species, OK, but there are intermediates!

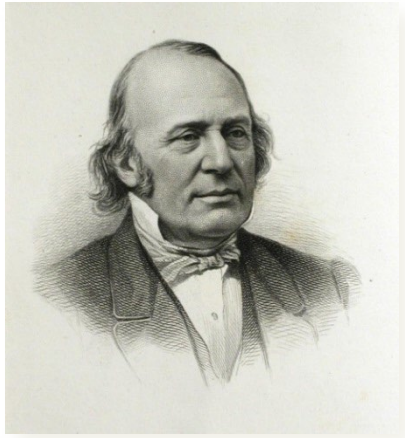
Darwin's concept of species

As an example, according to Darwin:

(i) *Primula vulgaris* (primrose), *Primula elatior* (oxslip), and *Primula veris* (cowslip) are different species, even though hybrids exist (rare, and partially sterile). Evidence for continuity of species and "varieties"

(ii) In contrast, Darwin also argued that the races of humans were all the same species. In this case, there were *no good dividing lines* between races.

Louis Agassiz, of Harvard University, founder of the Harvard Natural History Museum on Oxford Street, a creationist, argued the opposite:

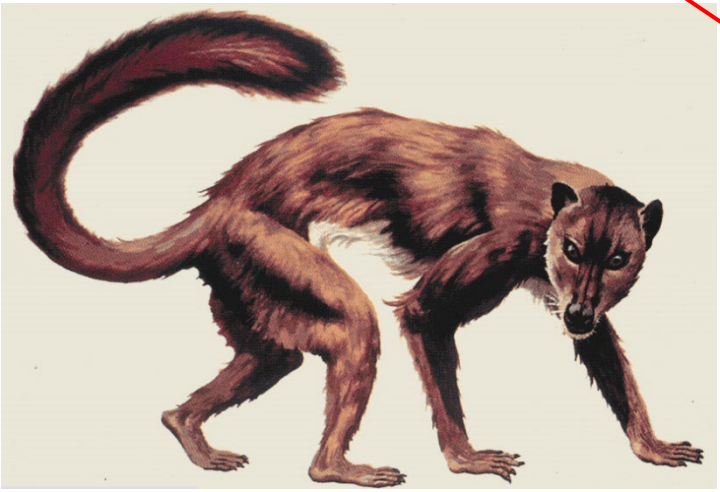


"… The differences between distinct [human] races are often greater than those distinguishing species of animals one from the other."

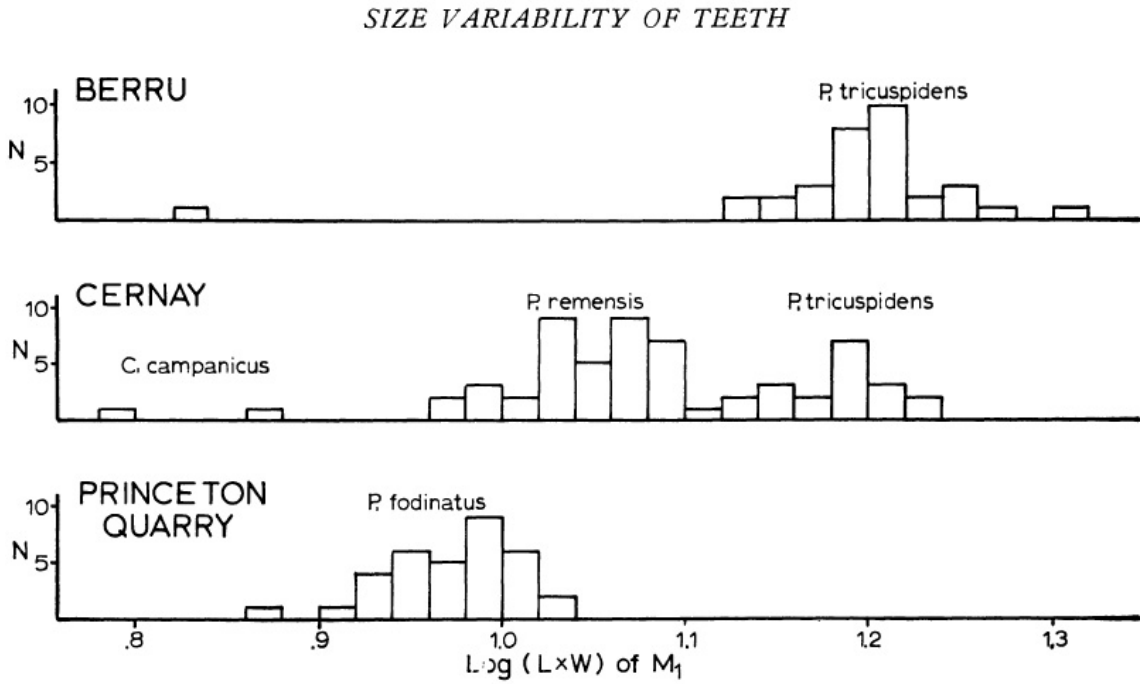
(Asa Gray sided with Darwin on this!)

1960s-1970s, Phenetic species concept

A statistical restatement of Darwin's ideas based purely on phenotypic distance (in fossils, what else?!):



Paleocene mammal, *Plesiadapis* sp.



TEXT-FIG. 3—Histograms of the logarithm of length multiplied by width for M_1 of all plesiadapids from Berru, Cernay, and Princeton Quarry. Note that the variability of *Plesiadapis remensis* and the variability of *P. tricuspidens* from Cernay compare closely with the variability of *P. tricuspidens* from Berru and *P. fodinatus* from the Princeton Quarry.

Also:

- *Chromosome number*
- *Immunological differences*
- *DNA divergence*
- *Any other "genetic markers"*

1960s-1970s, *Phenetic species concept*
A multivariate statistical restatement of Darwin's ideas:
based on *distance*

Phenetic differences can apply to *genetic variation*, as well as *morphological variation*

- e.g. enzyme differences in *Drosophila*

Also:

- *Chromosome number*
- *Immunological differences*
- *DNA divergence*
- *Any other "genetic markers"*

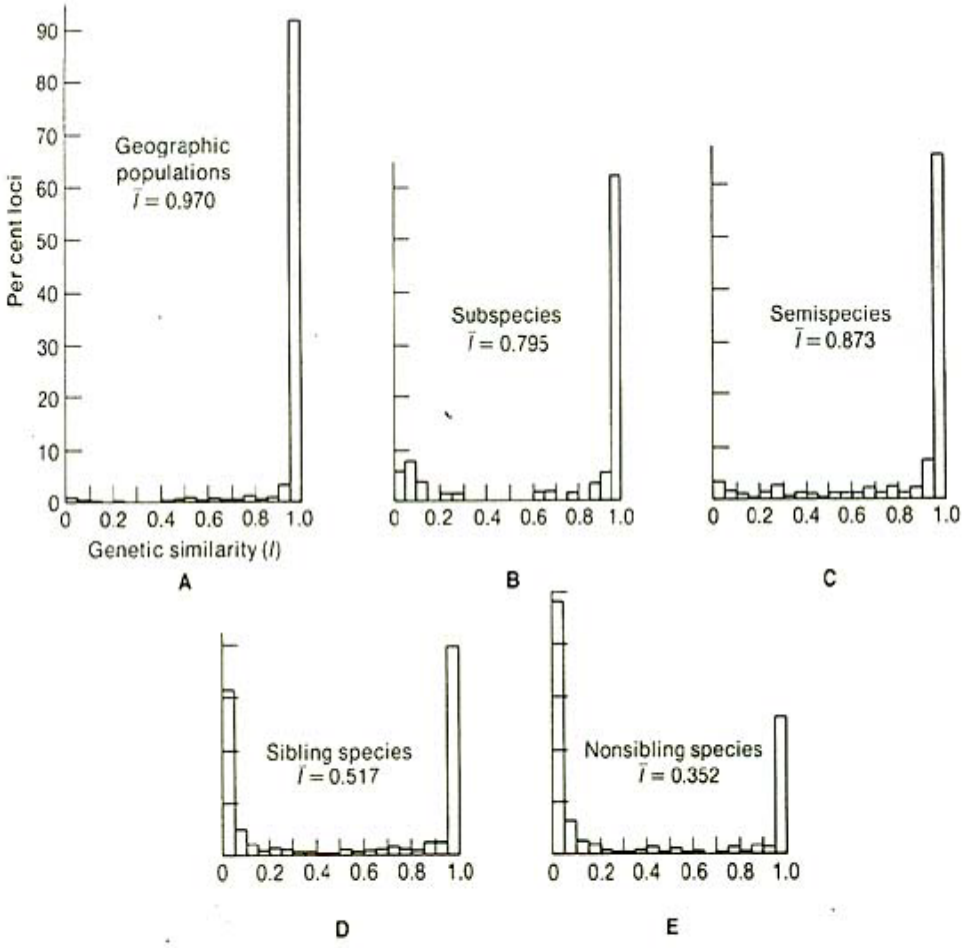


FIGURE 1
The percentage of electrophoretic loci that exhibit various levels of gene frequency similarity among (A) geographic populations, (B) named subspecies, (C) semispecies, (D) sibling species, and (E) nonsibling species in the *Drosophila willistoni* complex. (From Ayala et al. 1974)

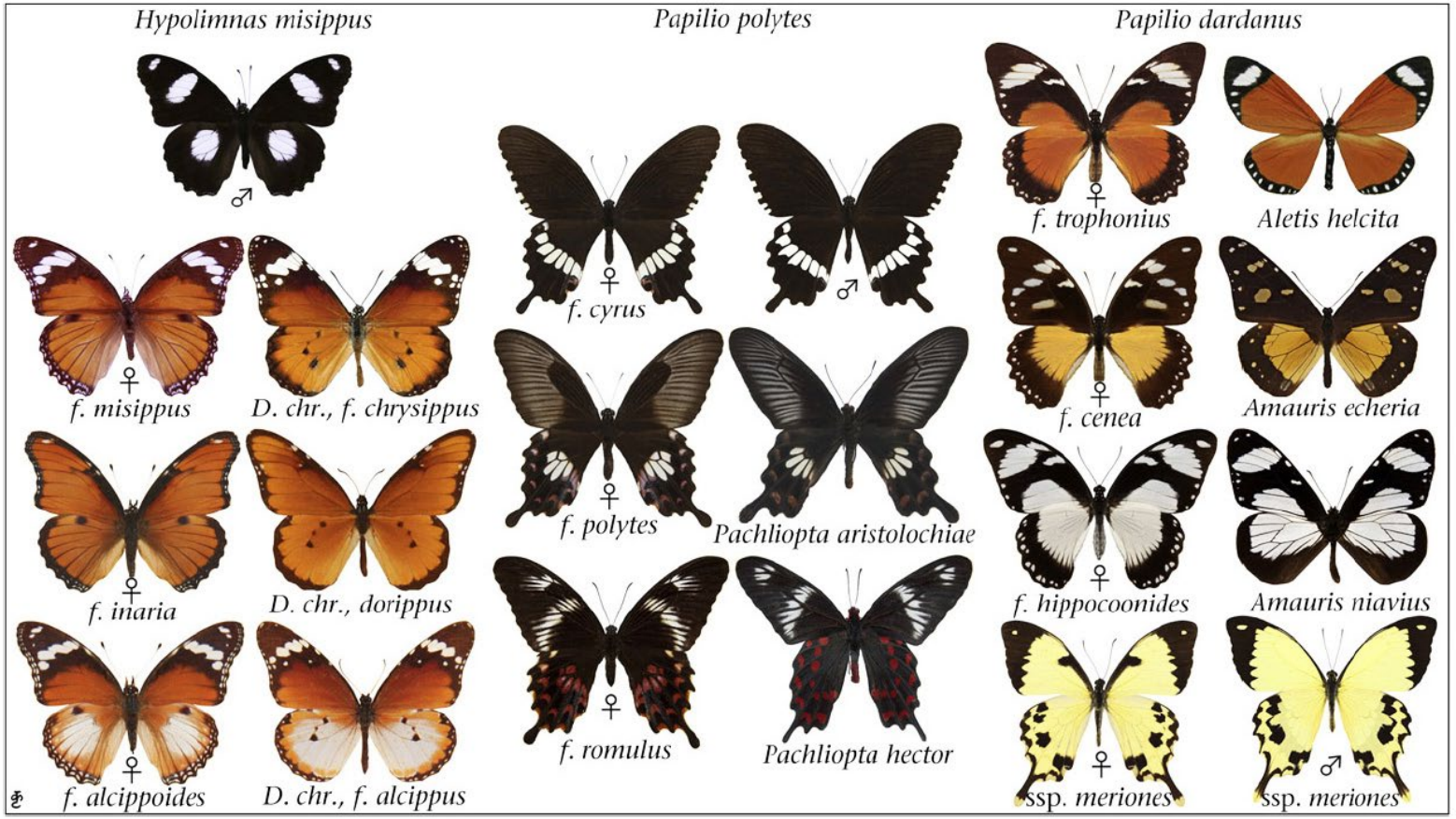
Arguments against Darwin's species concept

By the 1940s, two major criticisms
of Darwin's ideas on species:

a. Plenty of morphological gaps within species

e.g. Major effects of some Mendelian alleles:

Peppered moths
Mimetic butterflies like *Hypolimnas* and *Papilio* butterflies



Arguments against Darwin's species concept

b. *Few or no morphological differences between some "good" species*: "*Sibling species*" which are:

(i) *morphologically similar*, though they differ genetically
(ii) *evolve more or less separately*
(iii) *little or no hybridisation/gene fl*

e.g. *Drosophila pseudoobscura* vs.
D. persimilis: chromosomal differences
sterility of hybrids

Anopheles mosquitoes: habitat, biting, malaria transmission

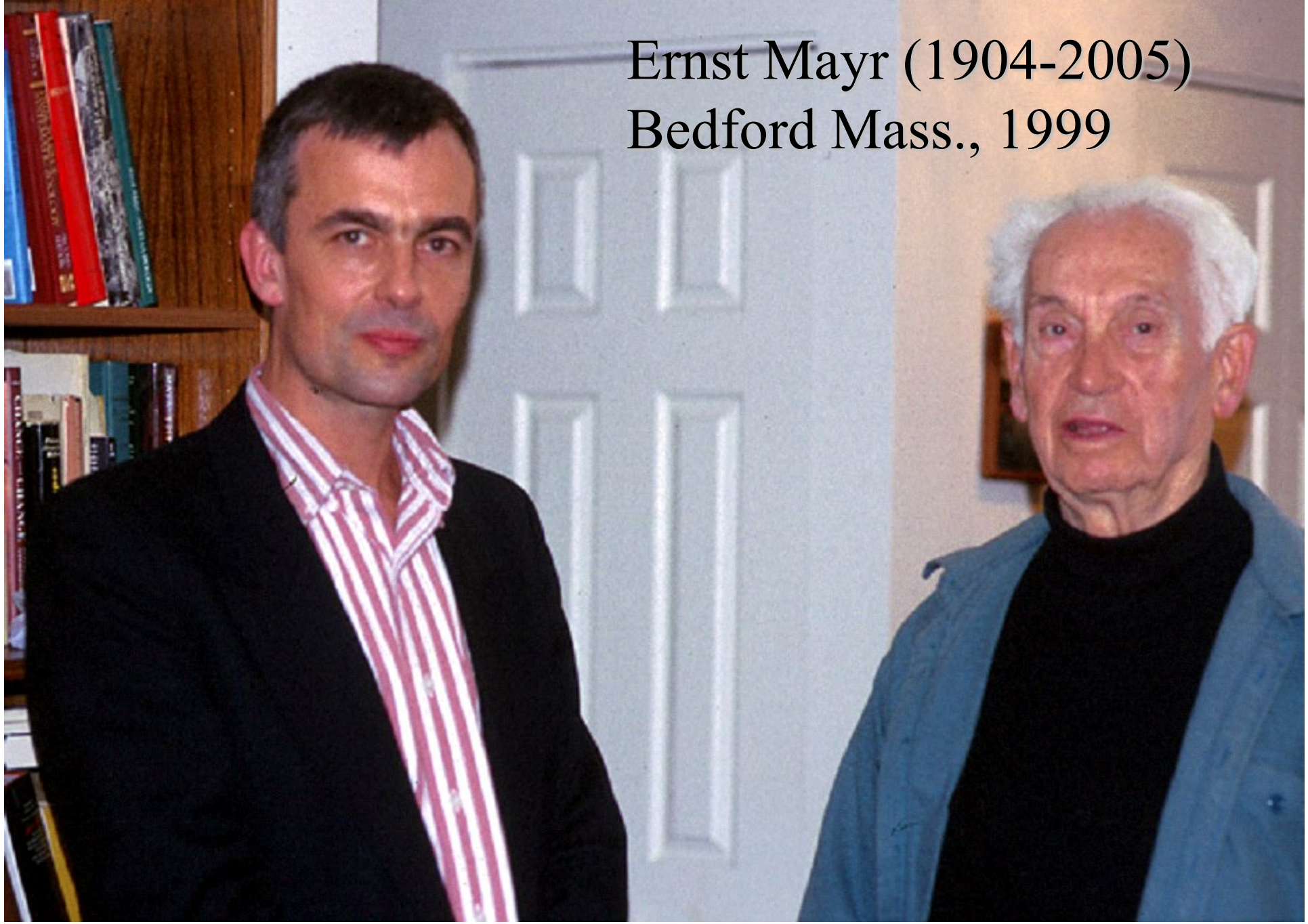
Also in many bird species

Sibling species of flies

	Drosophila pseudoobscura	*Drosophila persimilis*
male		
female		

Rarely hybridize in nature. When they do, testes of male hybrids develop poorly. Male hybrids are sterile.

Theodosius Dobzhansky (1937) recognized these forms (then called “Race A” and “Race B” of *D. pseudoobscura*) as separate species. Dobzhansky argued that “reproductive isolation” was the definition of species.


Ernst Mayr (1904-2005)
Bedford Mass., 1999

Jerry Coyne & H Allen Orr 2004
Speciation

"Darwin's magnum opus remains largely silent on the '*mystery of mysteries*' [i.e. origin of species]

… and
the little it does say about this mystery is seen by most modern evolutionists as muddled or wrong"

Andrew Berry & Hopi Hoekstra (Harvard biologists) 2009 in "Rereading *The Origin*"

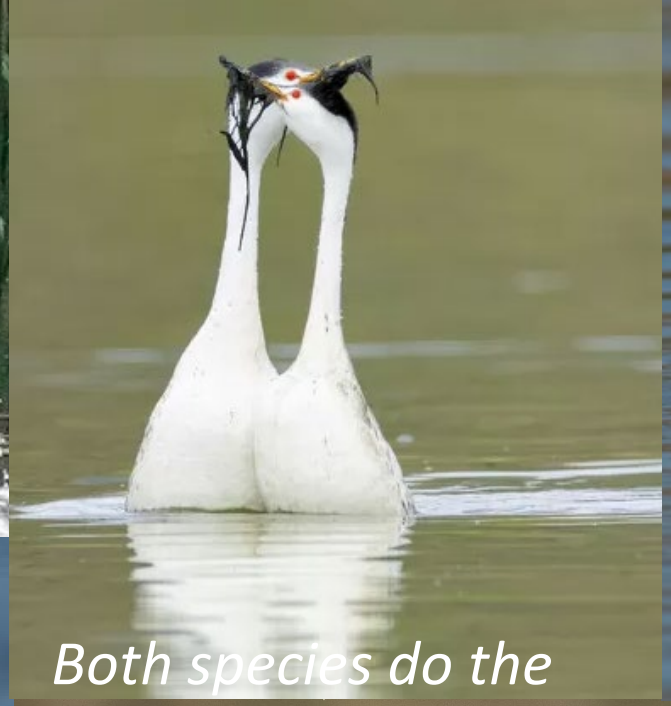
"… speciation, arguably the lynchpin of the evolutionary process, was *terra incognita* for Darwin."

Berry, A. & Hoekstra, H. 2009. Current Biology Jan 2009: R9

Why was Darwin (thought) wrong?

"Darwin succeeded in convincing the world of the occurrence of evolution and ... he found (in natural selection) the mechanism that is responsible for evolutionary change and adaptation. It is not nearly so widely recognized that Darwin failed to solve the problem indicated by the title of his work. … He never seriously attempted a rigorous analysis of the problem of the multiplication of species, the splitting of one species into two. I have examined the reasons for this failure (Mayr 1959a) and found that among them Darwin's lack of understanding of the nature of species was foremost."

Mayr 1963: 12



Both species do the
"weed ceremony"

Clark's Grebe
Aechmophorus clarkii
Dance: top left. Close-up: top right

Sibling species of birds

Western Grebe
Aechmophorus occidentalis

Close-up: bottom left. Dance: bottom right

2. The biological species concept (BSC)

Species defined by interbreeding within species and reproductive isolation between species (Poulton 1903, Dobzhansky 1937, Mayr 1942).

Simple idea:

1) Gene flow homogenizes variation within each species

2) Lack of hybridization or gene flow between species, which can diverge indefinitely

Lack of gene flow is due to "*reproductive isolating mechanisms*", today often called "*barriers*"

Among evolutionary biologists, biological species concept is generally preferred (as in Coyne & Orr 2004) – but not by me! Some problems:

a) *Does not easily apply in allopatry, or in the fossil record*. Species become less clear over large spans of space (in geography) or time (in the fossil record)

b) *Does not apply in asexual species.*
Prokaryotes and many protists. Bdelloid rotifers. Lichens! Bacteria! Viruses!

c) *Natural hybridisation*/introgression in nature
10% of animal spp., 25% of plant spp. hybridize in the wild (later lecture…)

- *Introgression* (successful flow of genes between species) occurs
- *Hybrid speciation* (introgression leads to new species) occurs

“Relaxed” biological species concept

“In our view distinct species are characterized by substantial but not necessarily complete reproductive isolation. …. the process of speciation involves acquiring reproductive barriers, and … this process yields intermediate stages when species status is more or less irresolvable.”

Jerry Coyne & H. Allen Orr (2004)

The so-called phenetic species concept

In 1970, the famous statistician R.R. Sokal and a botanical colleague, T. J. Crovello wrote a paper which logically dismantled the Biological Species Concept.

It was read, but perhaps was generally rejected by evolutionary biologists.

Especially as they increasingly became enamored of the new “Cladistics” movement

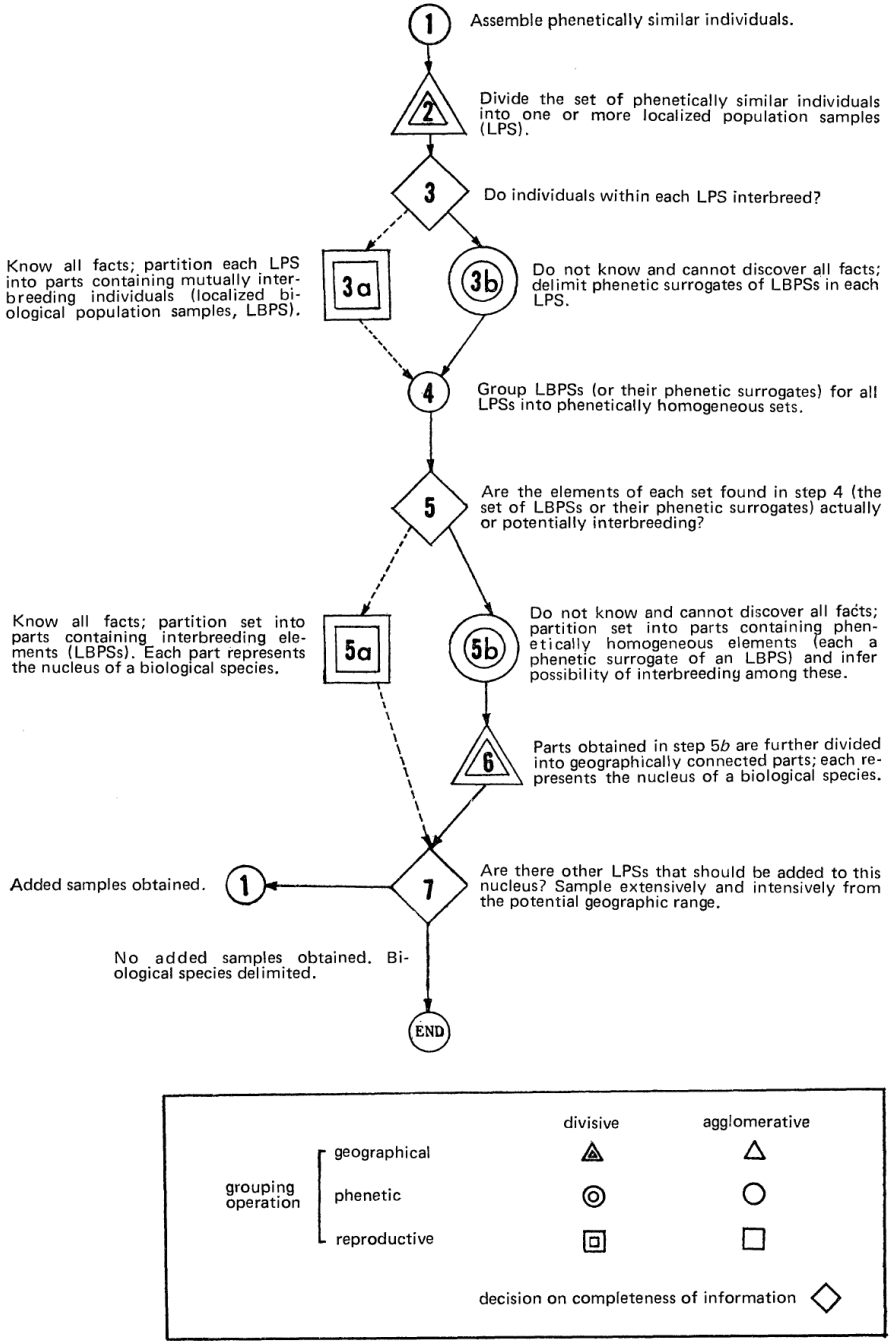
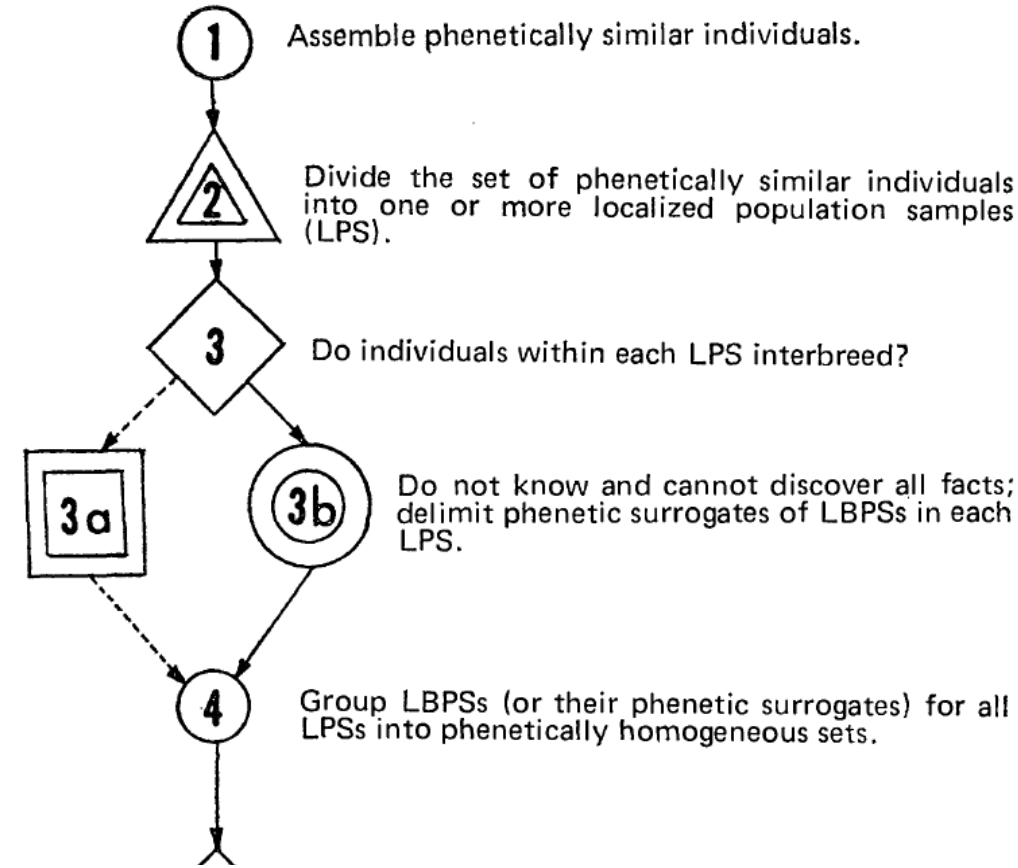


FIG. 1.—Flow chart for determining biological species. For explanation, see text.

Know all facts; partition each LPS into parts containing mutually interbreeding individuals (localized biological population samples, LBPS).



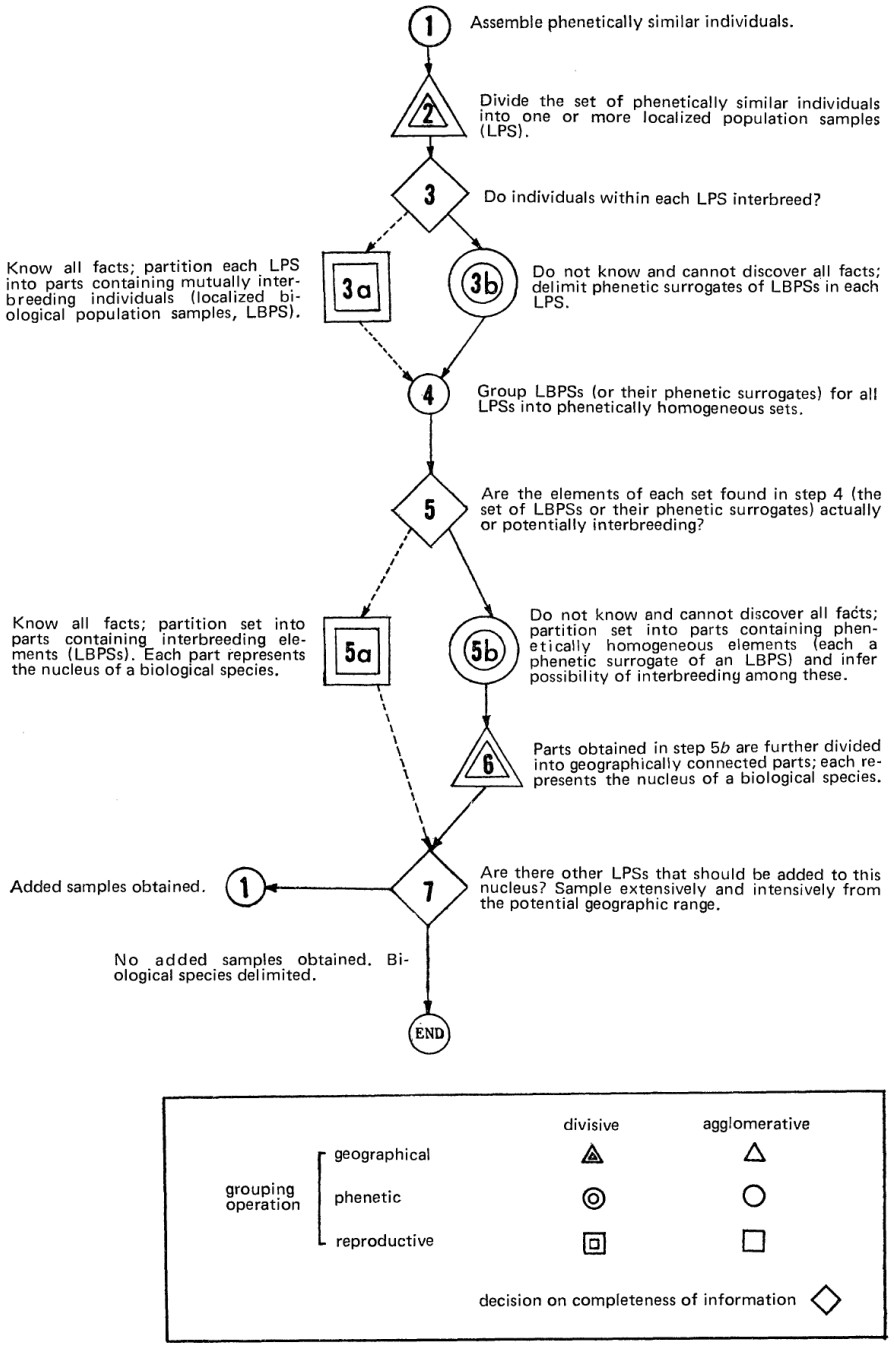
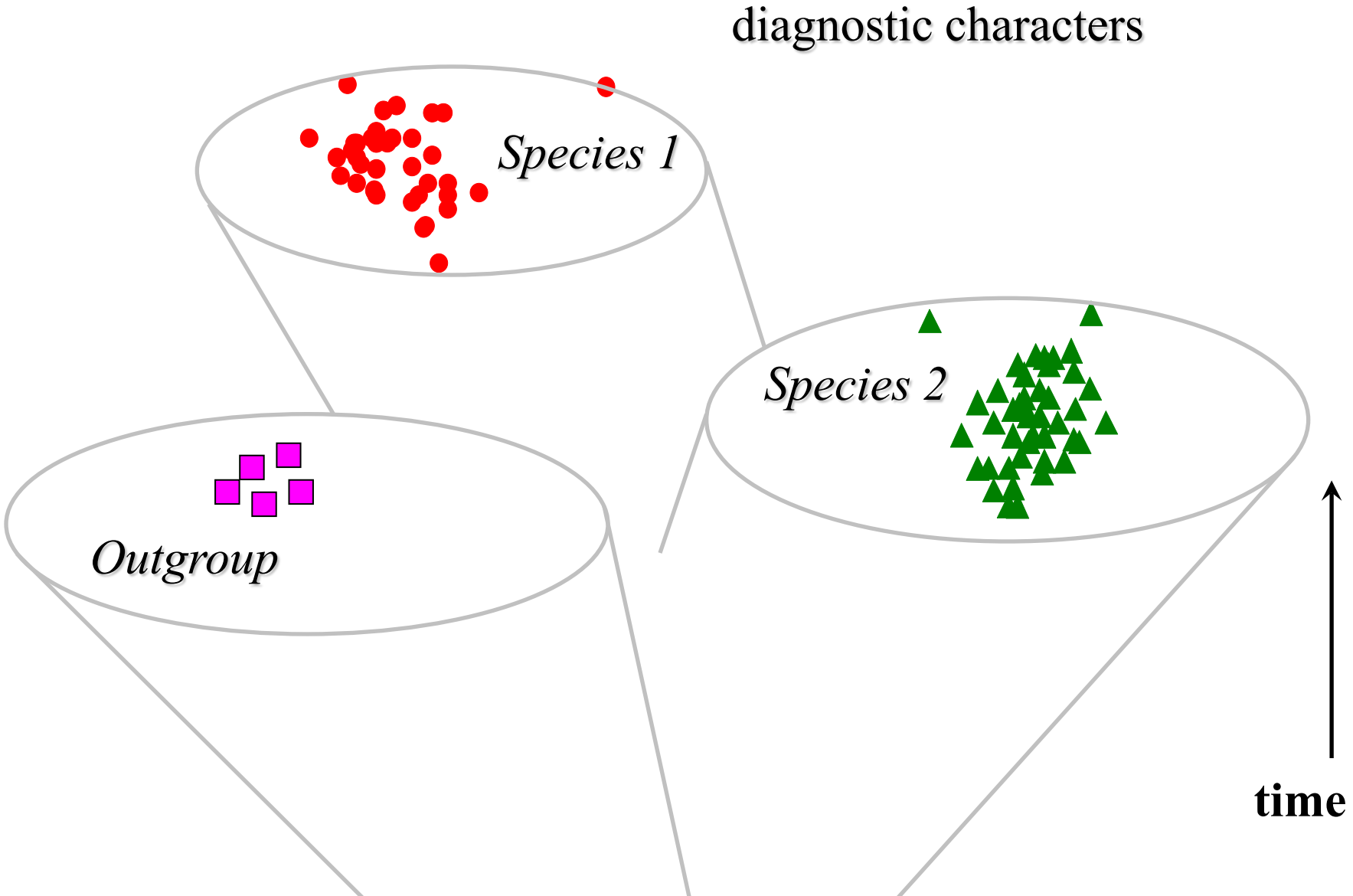


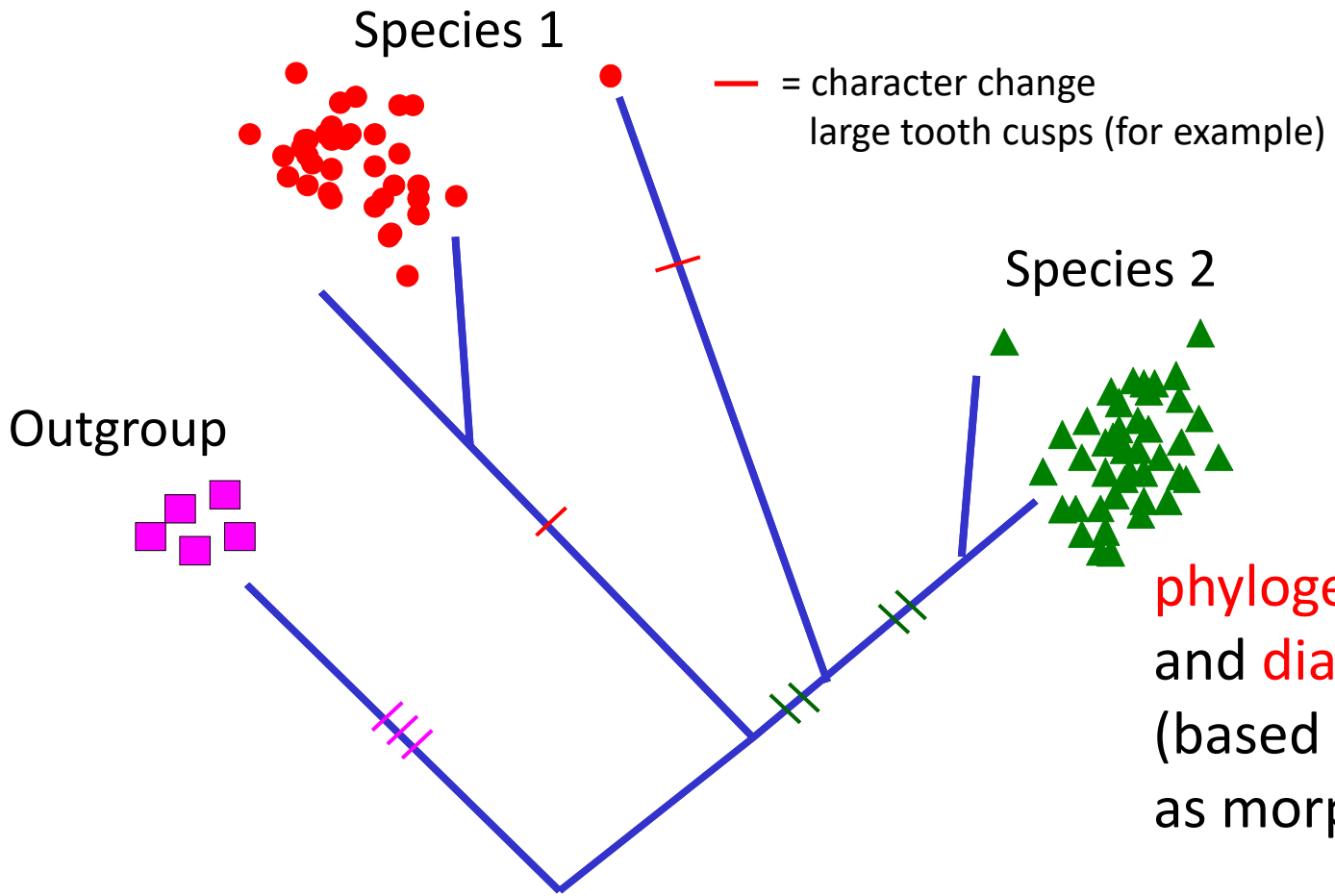
FIG. 1.—Flow chart for determining biological species. For explanation, see text.

Phylogeny - relationships



3. Phylogenetic species concepts

Cladistic movement founded by Willi Hennig in the 1950s.
If higher taxa are defined by means of phylogeny, then so should species, reasoned *cladists.*



Tree-building Methods:

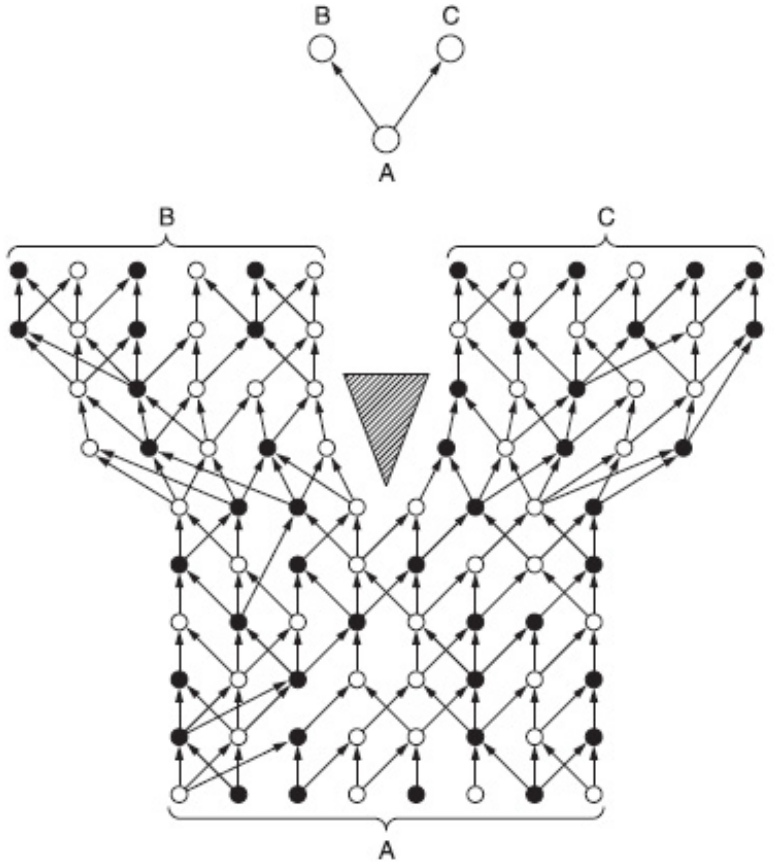
- Parsimony
- Distance
- Likelihood - Bayesian

phylogenetic (based on monophyly) and diagnostic species concepts (based on diagnostic characters, such as morphology or mtDNA bases).

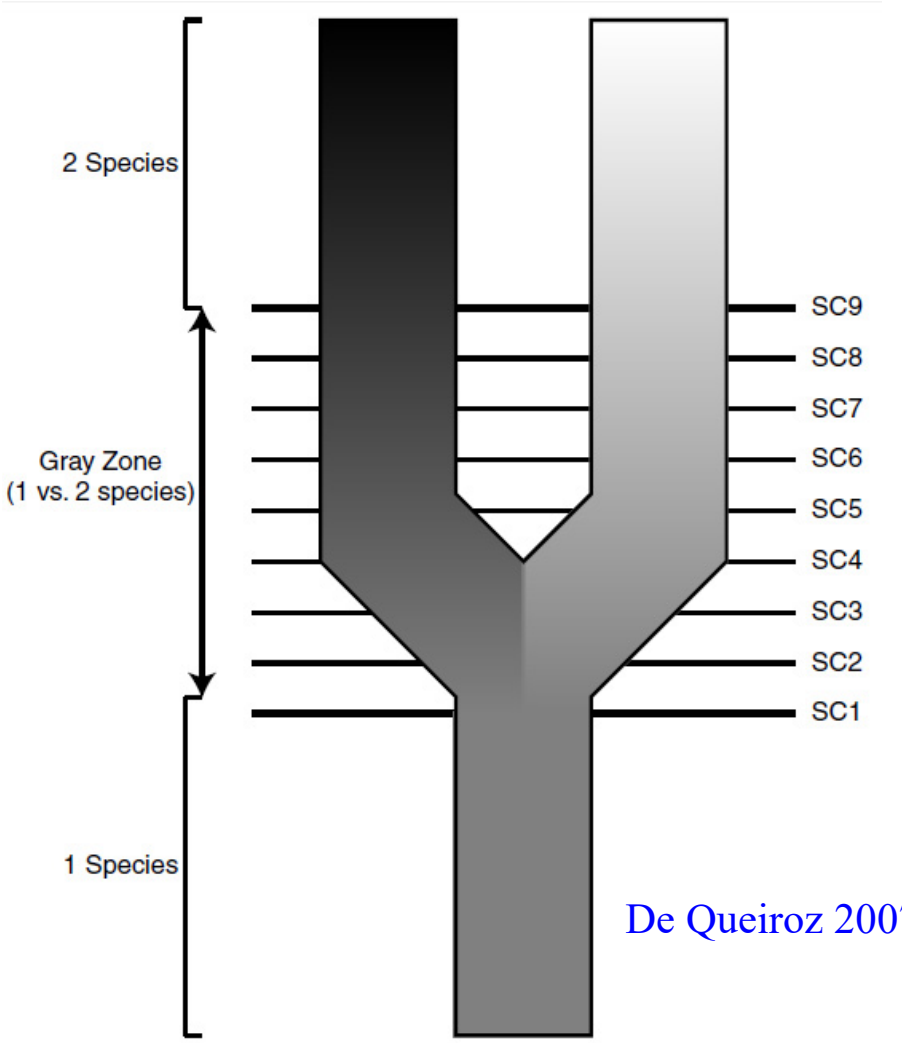
Phylogenetic species concept: Joel Cracraft 1989

"A phylogenetic species is an irreducible (basal) cluster of organisms, diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent"

Phylogenetic species concepts



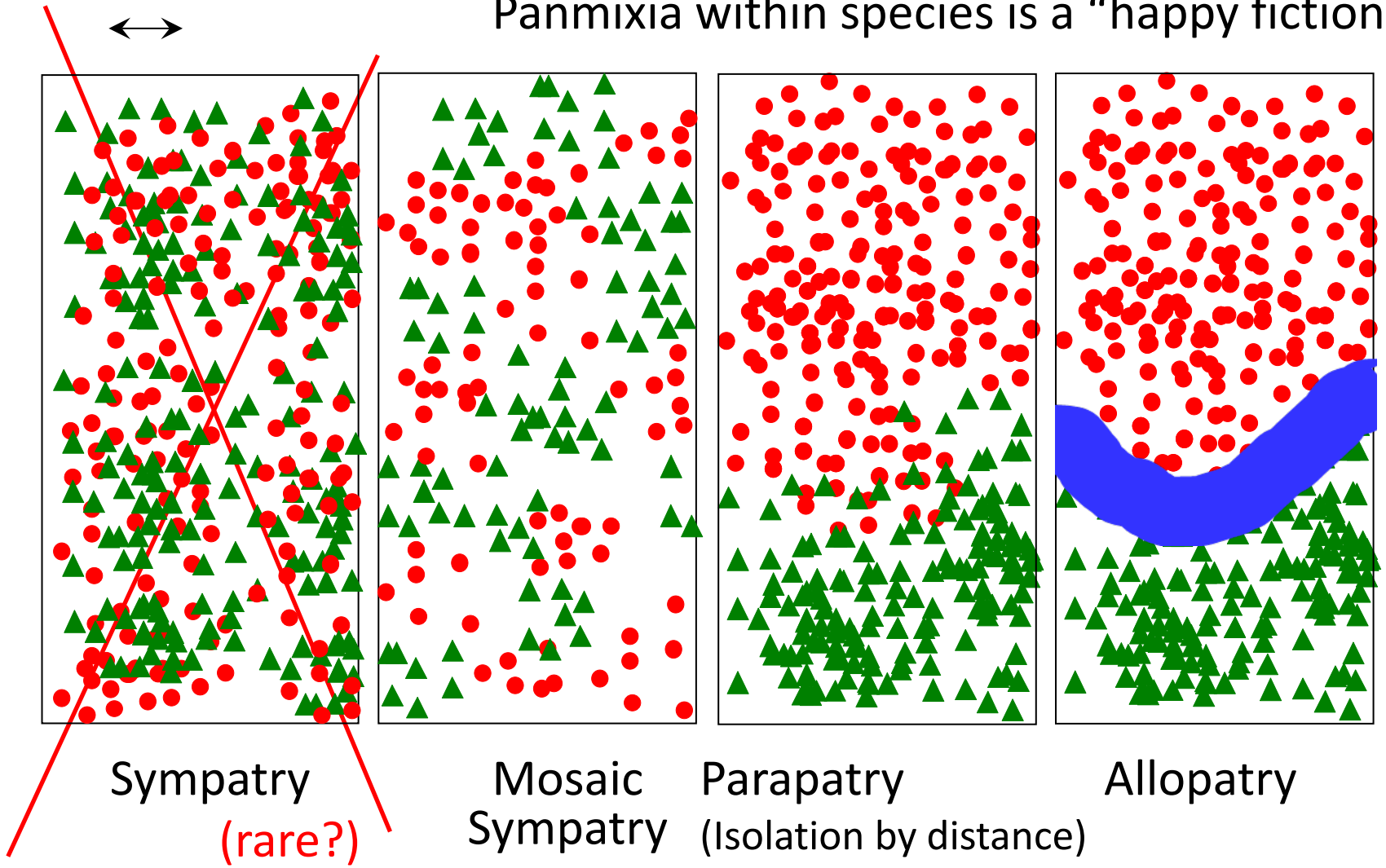
Hennig 1968



De Queiroz 2007

But species trees branch in space...

scale of dispersal distance
+ habitat choice



Panmixia within species is a “happy fiction”

Sympatry (rare?)

Mosaic Sympatry

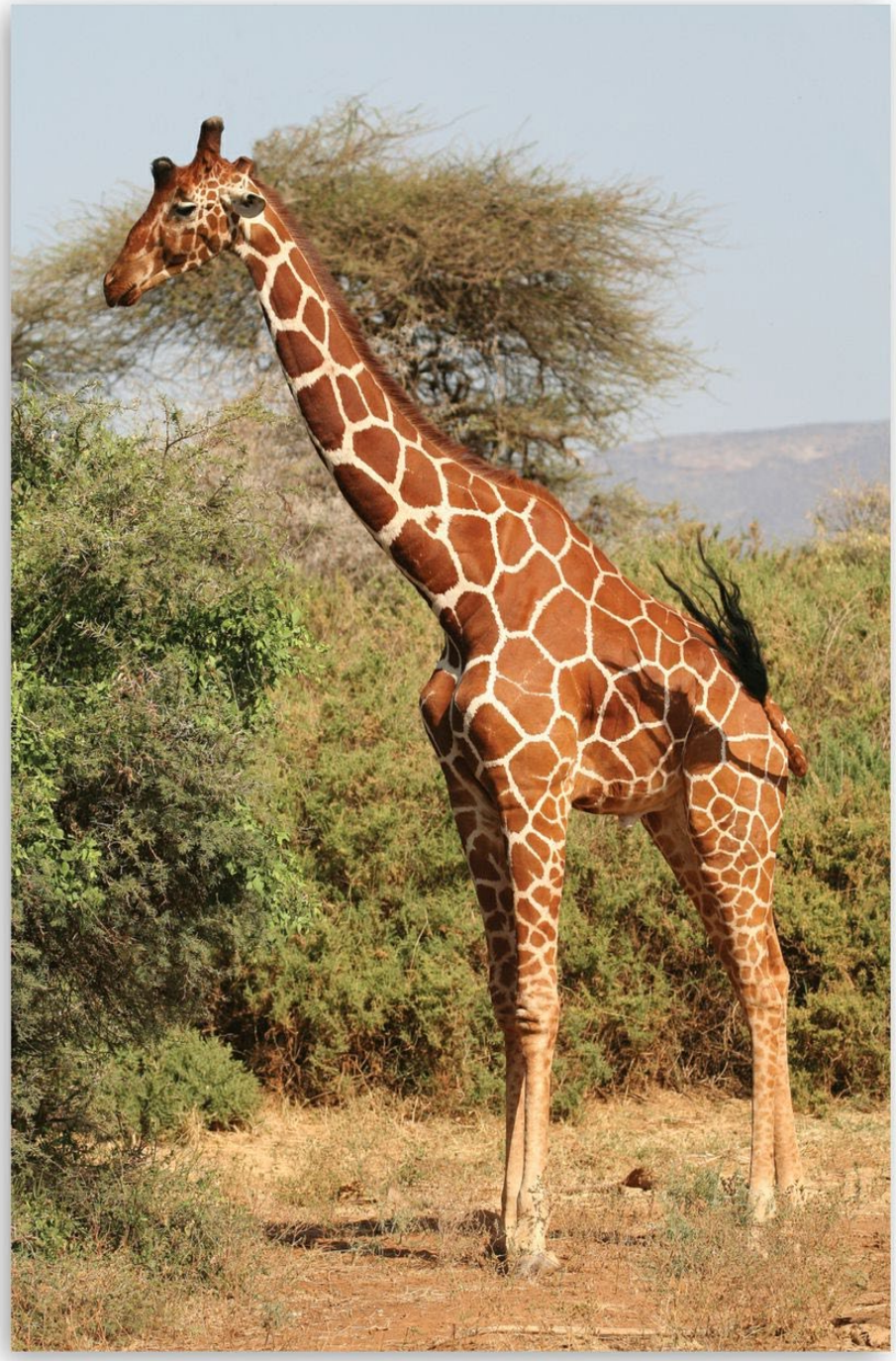
Parapatry (Isolation by distance)

Allopatry

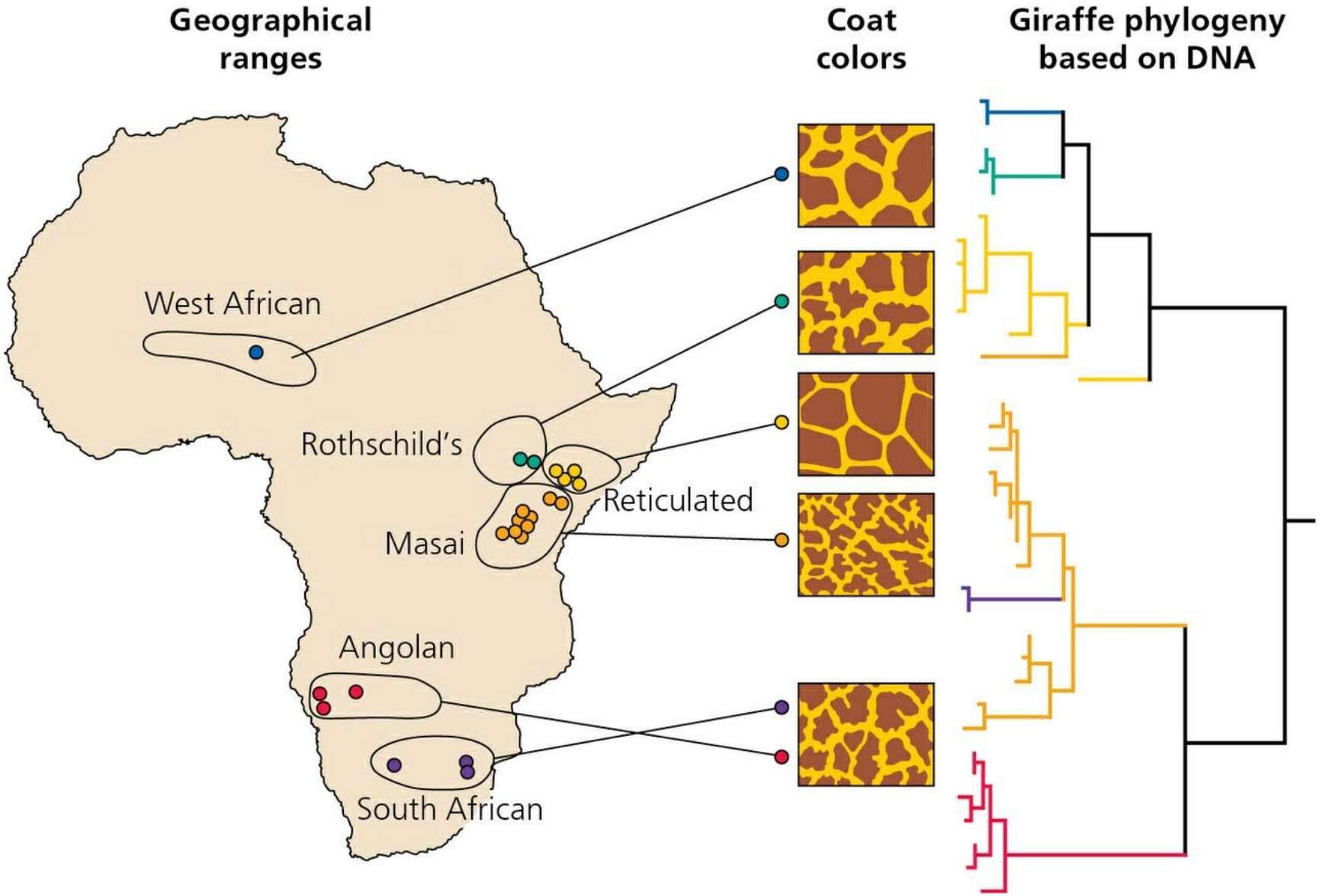
Mallet, J., Meyer, A., Nosil, P., & Feder, J.L. 2009

“Splitting” vs. “Lumping”

Fashion in species concepts changes. With the phylogenetic species concept and DNA methods, we’re now in a phase of “splitting.” e.g. giraffes

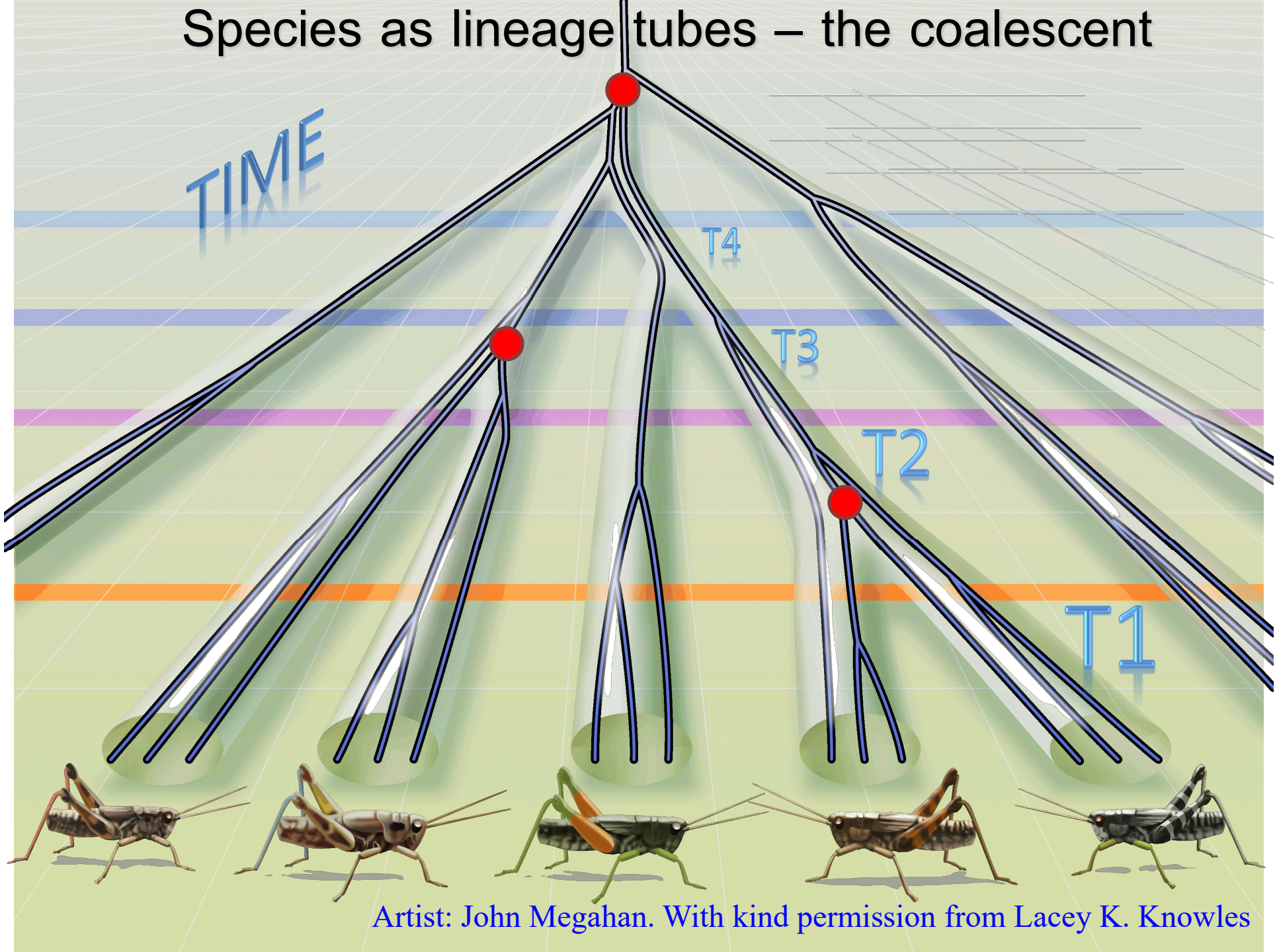


“Splitting” giraffes on basis of PSC (Rick Brenneman et al.)



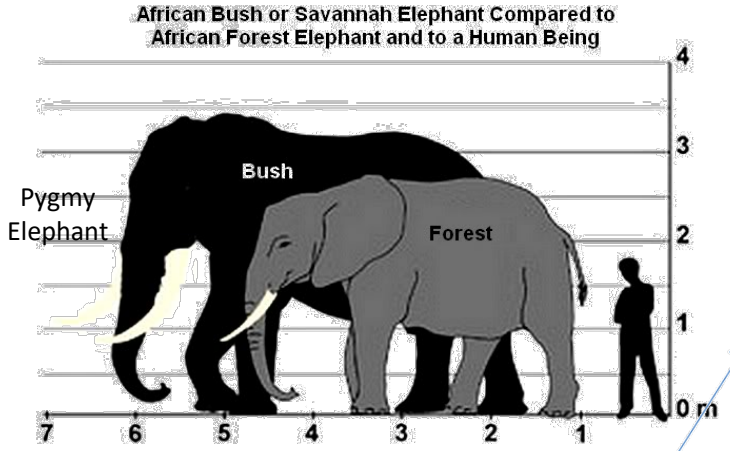
These “species” are not reproductively isolated!

Species as lineage tubes – the coalescent



Artist: John Megahan. With kind permission from Lacey K. Knowles

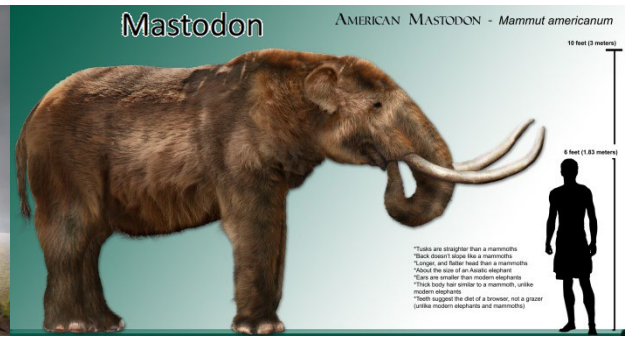
Splitting the elephants



In 2010, Rohland et al. argued that forest and savanna (or bush) forms of the African elephant were separate species, though still hybridizing

Mammoth

Mastodon



Problems with "phylogenetic" concept of species

Clarkia speciosa

e.g. *Clarkia reticulate Phylogeny* due to *polyploidy*

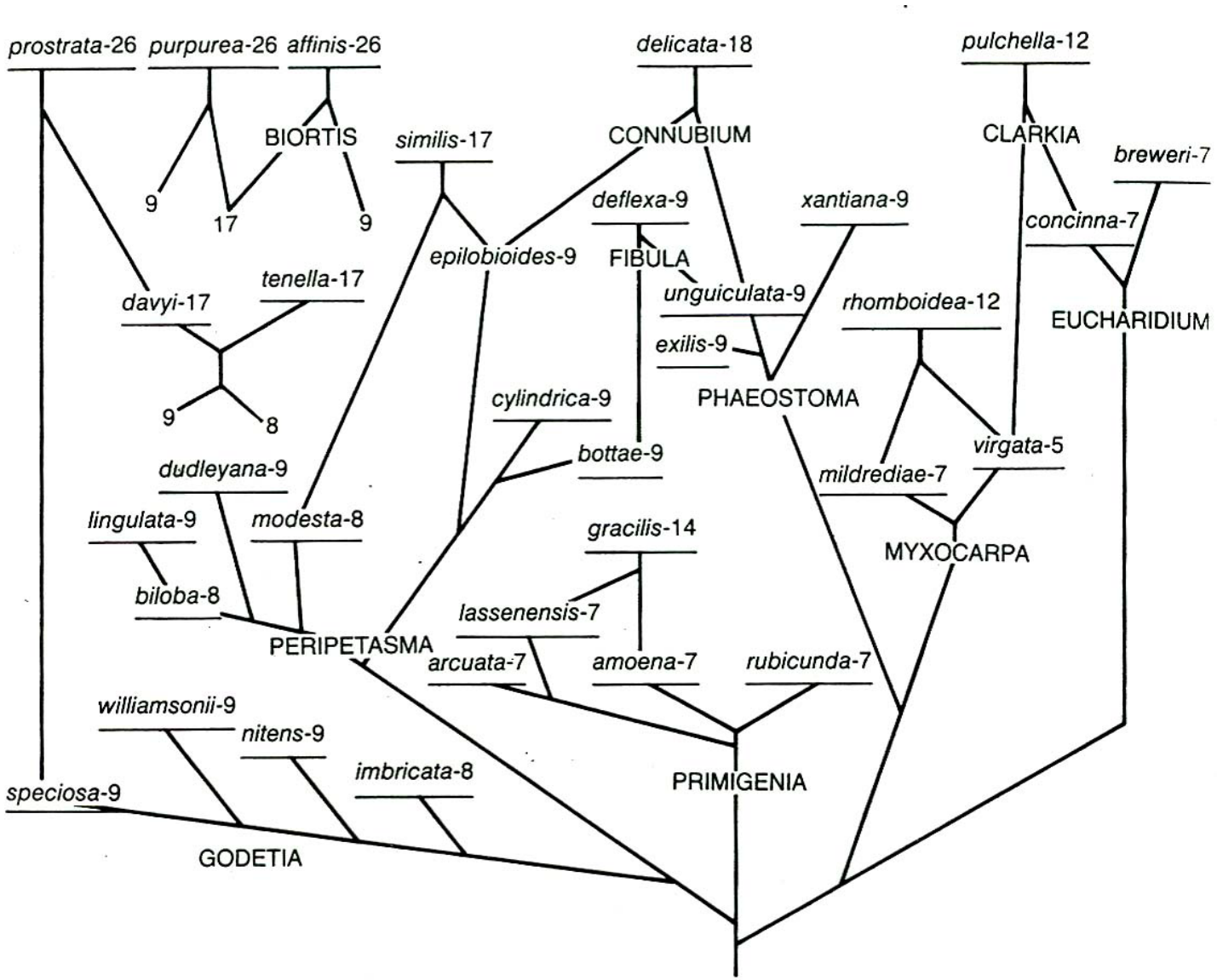


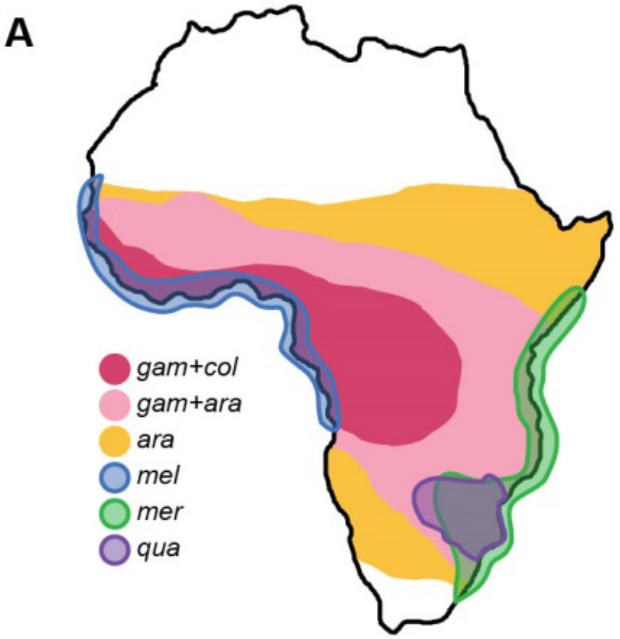
FIGURE 4

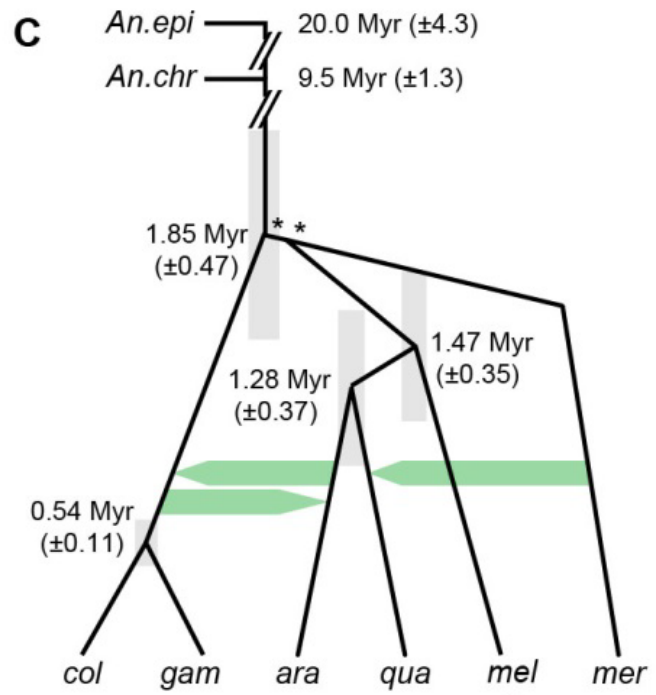
Inferred phylogenetic relationships among polyploid forms in the plant genus *Clarkia*. The names in upper case letters are sections of the genus; those in lower case are species, with their usual gametic chromosome numbers indicated. Chromosome numbers without associated names represent hypothetical ancestors. Note that polyploid forms have arisen from hybridization between species. (After Lewis and Lewis 1955)

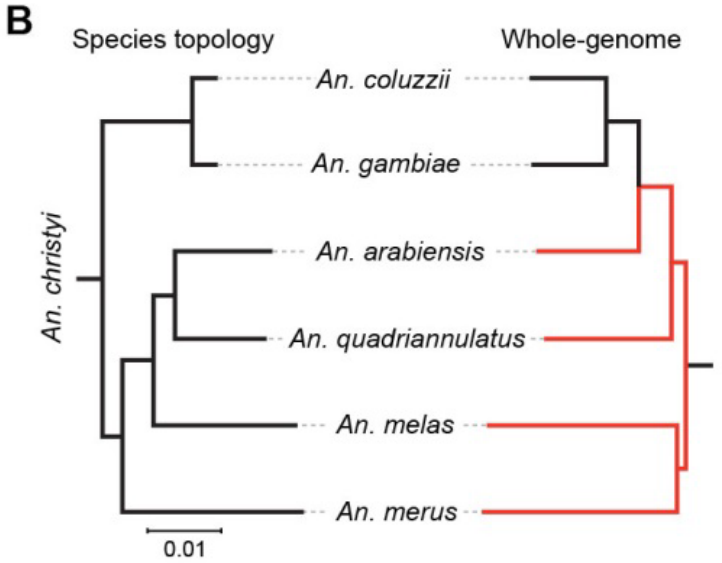
Anopheles gambiae complex: African malaria mosquitoes

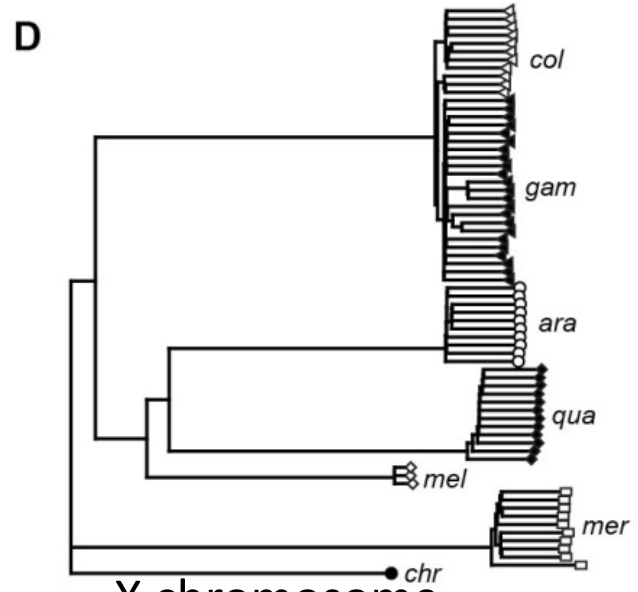
“True” species tree present in only 2% of genome

“Whole genome” tree is different



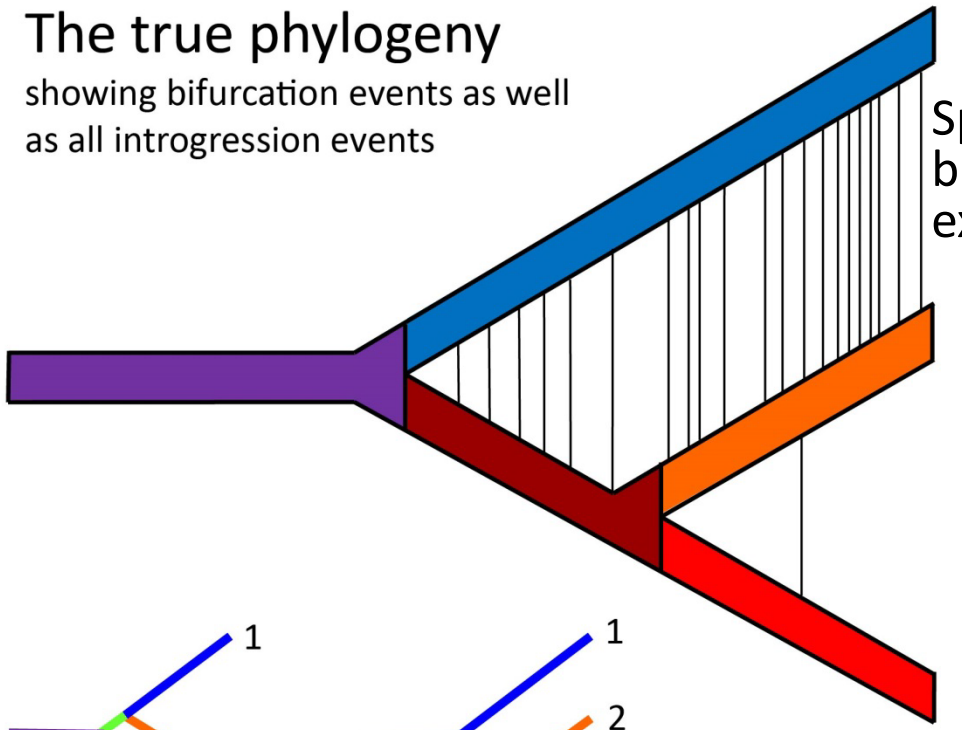


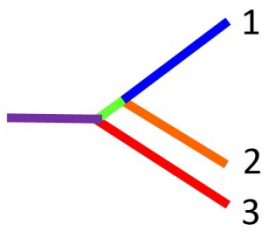




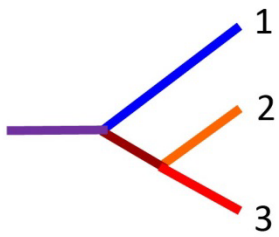
X chromosome

What is a species? What is phylogeny?





'Whole-genome' or 'democratic majority' tree



'Species tree,' or bifurcation history

Can species 1 & 2 really be described as "reproductively isolated?"


ERIC LE BRUN

Were Neanderthals and Humans different species?

David Reich: it doesn’t matter. We decided not to discuss it in 2010
Me: I think so… (even though it looks like there were hybrids)

AR Wallace, 29 Nov 1900, letter to H.M. Bernard:

"Definition of a Species: A species is a group of individuals which reproduce their like within definite limits of variation, and which are not connected with their nearest allied species by insensible variations."

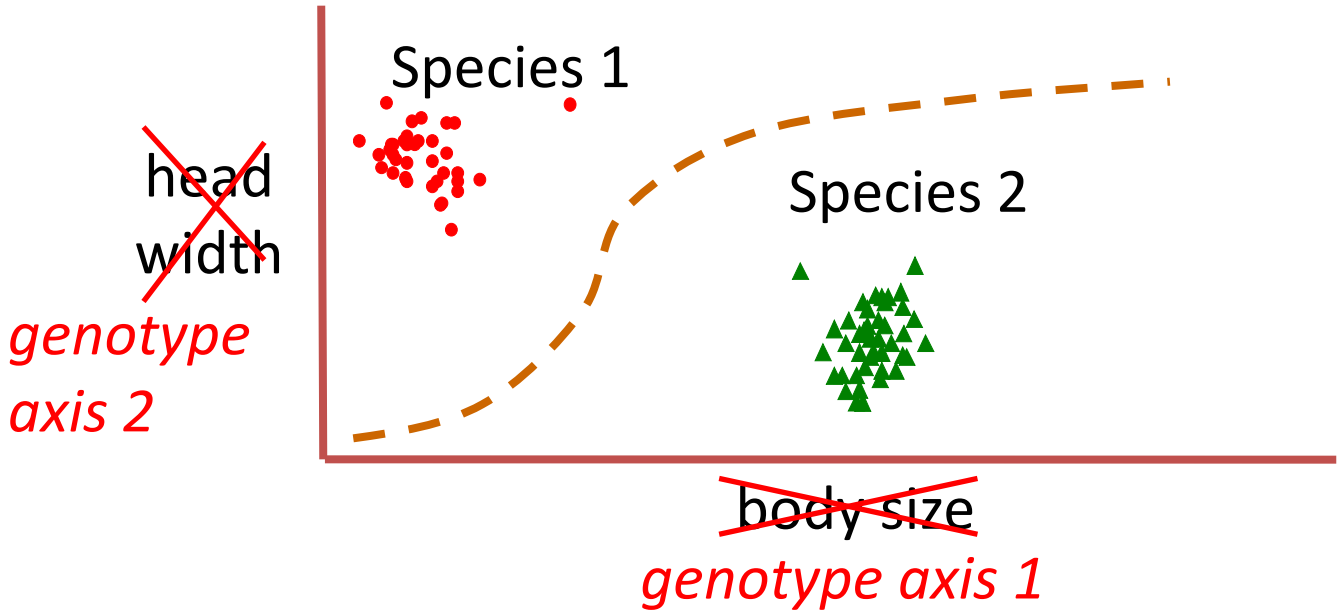
(1) Diagram of a species in process of development into 3 new species

(2) Here one var. has become completely isolated by extinction of intermediate forms, and is a new sp. When the intermediates between the other two var. have been exterminated in the struggle for life we shall have 3 new species.

from Cock, A.G. 1977. Biol J Linn Soc 9:1-30.

Genetics and the definition of species

Updating *Darwin's view of species* with genetics (which Darwin did not know about). Darwin's view:



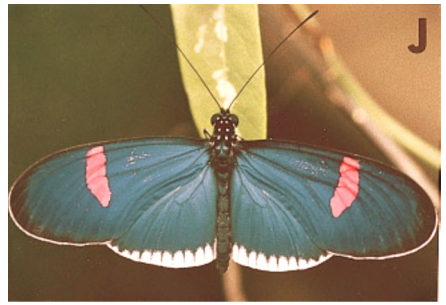
Species are detectable groups of genotypes or *genotypic clusters* with discontinuities or gaps separating them **– in sympatry**

Two *Heliconius* species hybridize in a narrow hybrid zone

Bimodal distribution of phenotypes/genotypes

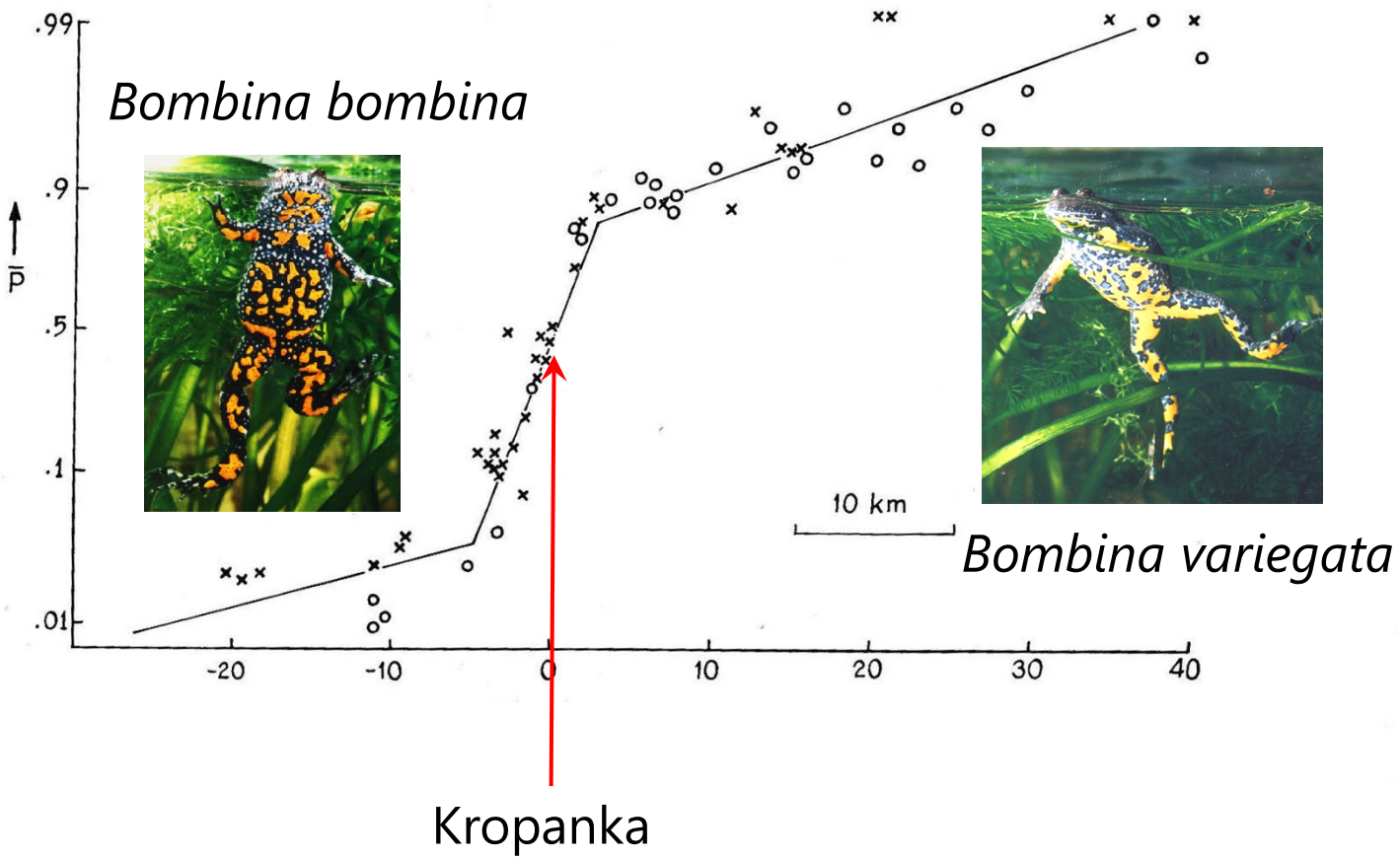
Heliconius himera

Heliconius erato

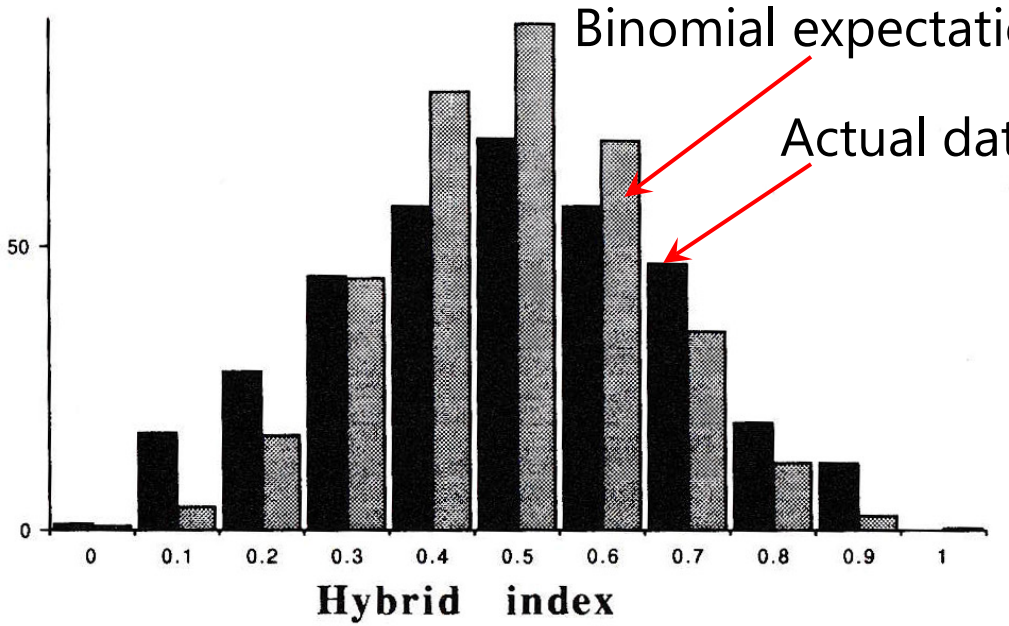


These two European *Bombina* toads from a hybrid zone

…are NOT separate species (according to Mallet!)

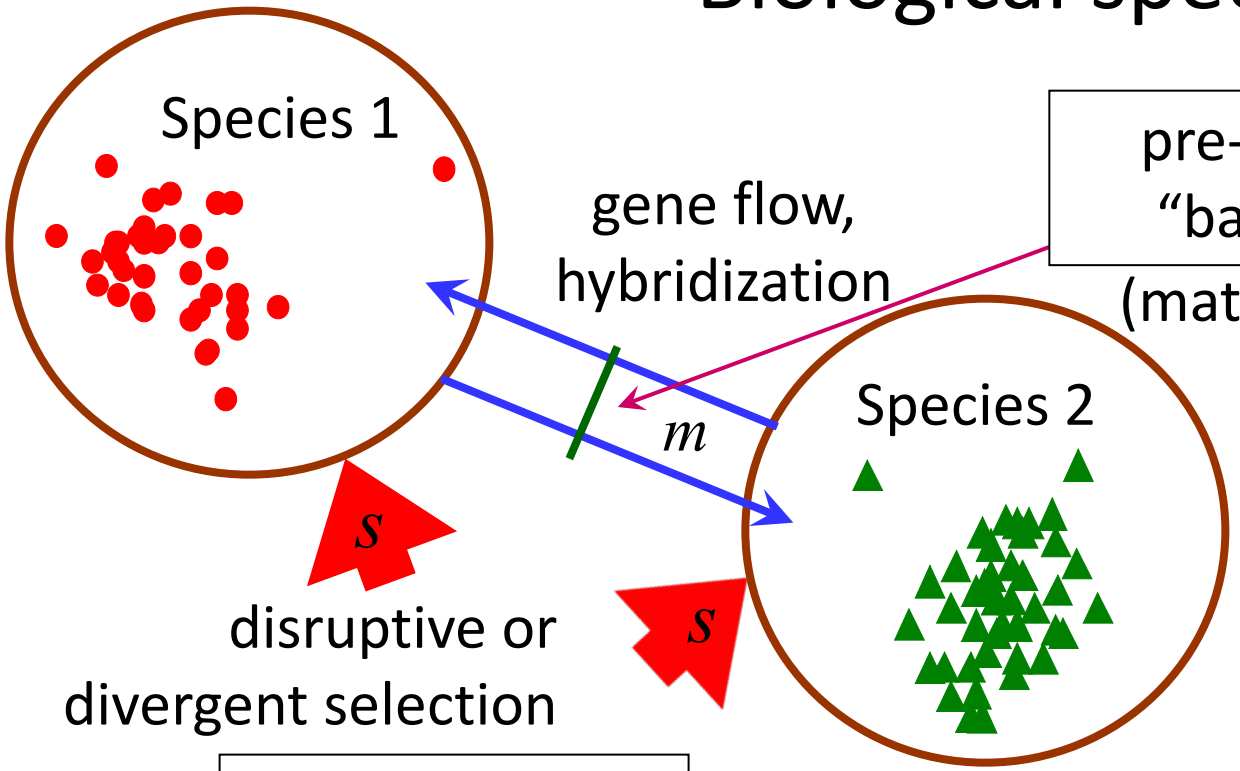


Hybrid index at Kropanka



Barton, N.H., & Gale, K.S. 1993. Genetic analysis of hybrid zones, in R.G. Harrison, ed. Hybrid Zones and the Evolutionary Process. New York, Oxford University Press

Biological species concept



Darwin’s cluster species concept

underlies most other species concepts

(e.g. ecological, or Dobzhansky-Muller)

Gene flow, if present, can be balanced by *disruptive selection*

A form of *migration-selection balance, so* $m << s$ *. Selection can be:*

- intrinsic (*post-mating isolating barriers*)
- extrinsic (*ecological effects*)

Species are reasonable *approximate* units of *local* diversity

Most biologists agree that forms that **overlap (sympatry)**, yet maintain multiple genetic differences, are different species

sympatry

If these forms merge together, or have too many "intermediate gradations" (in Darwin's terms), then we call them variants in the same species, or ecological or geographic "races"

Species are not necessarily "reproductively isolated," but they are *stable* to any potential hybridization

So field guides are of course useful!

We can (hope to) get an approximate estimate of biodiversity by counting species. At least in a local area.

Today: Species and varieties

Natural selection and the modern synthesis I and II

What we mean by species. Species "concepts."

Darwin’s “gap” idea, genotypic clusters
Biological Species Concept
Phylogenetic Species Concept

& how they are all related