

Hybridization and introgression between species

“Breakdown of isolating mechanisms”
according to Mayr

Long known in botany: hybrids in nature

Linnaeus believed that species were real things in nature, created by God.

However, in later life, Linnaeus discovered a number of species he thought might be hybrids. Maybe genera were the created kinds! He did the first crosses. This led to German “hybridizers” who investigated hybrid sterility and inviability in plants.

Mendel’s genetics discoveries were as a result of following in this tradition

HYBRIDIZATION AND NATURAL GENE-FLOW BETWEEN HIGHER PLANTS

By H. G. BAKER

Department of Botany, University of Leeds

(Received 28 November 1950)

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Baker (British botanist) 1951: By the 1950s, cytology was beginning to confirm natural hybridization

INTROGRESSIVE HYBRIDIZATION

BY EDGAR ANDERSON

Missouri Botanical Garden, St Louis, U.S.A.

(Received 10 October 1952)

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The importance of hybridization and introgression was well documented in plants: Anderson (American botanist, 1953)

“Introgressive hybridization is defined as the gradual infiltration of the germplasm of one species into that of another as a consequence of hybridization and repeated backcrossing”

Hybridization of Bird Species

Peter R. Grant and B. Rosemary Grant

Hybridization, the interbreeding of species, provides favorable conditions for major and rapid evolution to occur. In birds it is widespread. Approximately one in ten species is known to hybridize, and the true global incidence is likely to be much higher. A longitudinal study of Darwin's finch populations on a Galápagos island shows that hybrids exhibit higher fitness than the parental species over several years. Hybrids may be at an occasional disadvantage for ecological rather than genetic reasons in this climatically fluctuating environment. Hybridization presents challenges to the reconstruction of phylogenies, formulation of biological species concepts and definitions, and the practice of biological conservation.

Species of sexually reproducing organisms are "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups" (1). Periodically attempts have been made to improve on this definition by dealing *inter alia* with the awkward fact that for some populations the criterion of demarcation is not absolute (2–5). Some populations occasionally interbreed, and then the question becomes one of determining the fates of the offspring (1, 6). Therefore, hybridization, which strictly is the interbreeding of species, is of pivotal importance in two respects: in framing ideas about the nature of

hybridization have included the crossing of lines in the laboratory or greenhouse for genetical analysis, and the estimation of frequencies of phenotypic or genotypic classes in nature, their mating pattern, and their reproductive success. By themselves each is incomplete. In this article, we describe the desired but rarely achieved direct study of hybridization in nature through pedigree analysis. The study populations are birds. We present new information on the consequences of hybridization in populations of Darwin's finches over several generations.

The Broad Patterns

Grant & Grant 1992
Science

Big influence on me!

Reviewed world bird
hybridization records
by Russian, Panov.
Also their own studies
on Darwin's finches.

R.A. Fisher, Ernst Mayr, and hybridization

Fisher (1930): Hybridization may be “the grossest blunder in sexual preference which we can conceive of an animal making” (Fisher 1930), but it is nonetheless a regular event!

Mayr (1963): **Ch. 6. The Breakdown of Isolating Mechanisms (Hybridization)**

Hybridization: misleading to apply to interbreeding of conspecific populations; use gene exchange instead. But when, long isolated, term is ok to use; thus: hybridization is "the crossing of individuals belonging to two unlike natural populations that have secondarily come into contact"

- p.118. "In the majority of cases where introgressive hybridization in animals has been reported, two species are involved that had been conspecific until recently and are still largely allopatric. They are semispecies (in the emended definition of Lorkovic 1953), showing some of the characteristics of species and some of subspecies."
- p. 128: "By far the most frequent cause of hybridization in animals is the breakdown of habitat barriers, mostly as a result of human interference".

But:

- p.128: "Not all habitat disturbances that lead to hybridization are man-made".

How to measure “hybridization rate”

1) Many botanists have measured the “numbers of hybrids” pairwise:

For example if A, B and C and D are four species, and we know of AxB, AxC and BxC hybrids, we can say there are 3 hybrids, and we could estimate the prevalence as three out of six possible pairs, or 50% of pairs.

However, as the number of species, N , in the taxon (e.g. genus, or family) increases, this seems a strange measure, where $N(N-1)/2$ possible pairs exist.

As you increase the size of genus or family, this hugely increases the number of pairs. Given hybridization is normally between closely related pairs of species, it seems like hybridization becomes less and less prevalent in larger taxa!

2) I follow Panov and Grant in measuring the number of species that hybridize:

In the example, $N = 4$, and $3/4$ species hybridize (with at least one other species), so our prevalence measure is 75%.

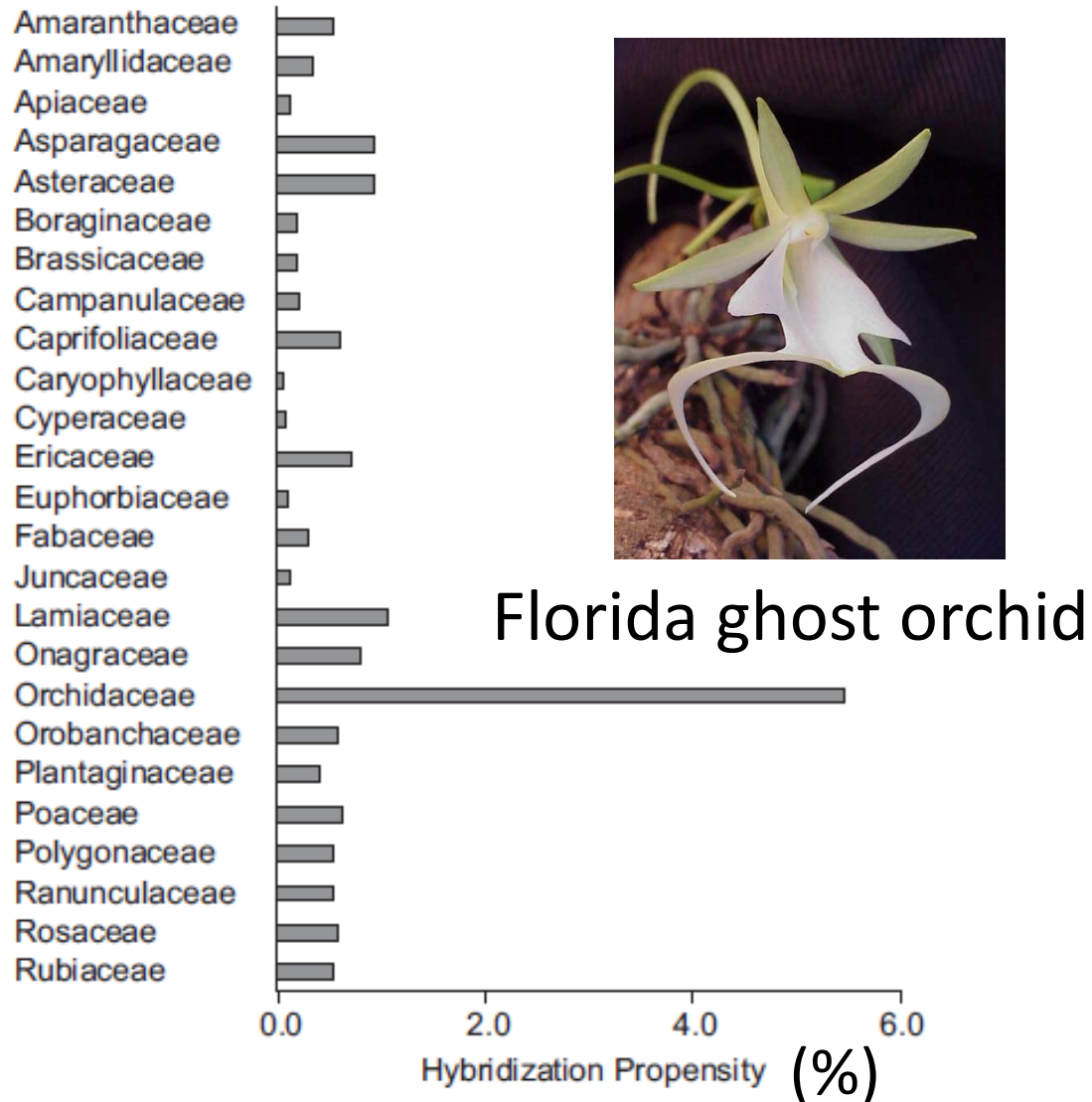


Fig. 2. Hybridization propensities in the 25 largest families surveyed. Hybridization propensities are weighted averages of the realized percentage of all possible hybrid combinations within the component genera.

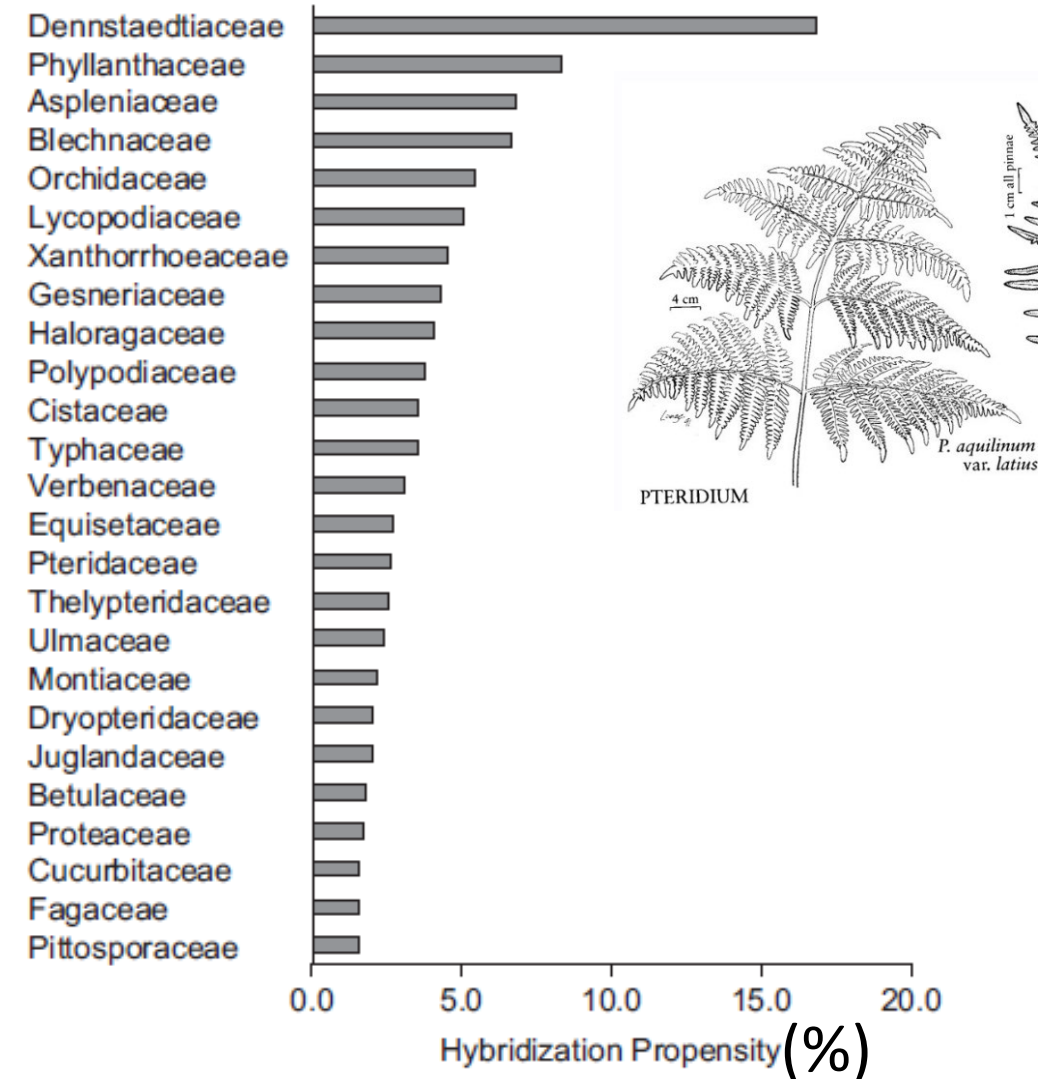


Fig. 3. The 25 most hybridization-prone families in our data set (families with < 10 species excluded from this figure). Hybridization propensities are weighted averages of the realized percentage of all possible hybrid combinations within the component genera.

Beware, Whitney et al. use the pairwise measure!

Whitney et al. 2010

Ghost orchid pollination



Hybridization in flowering plants of UK



Water avens
Geum rivale

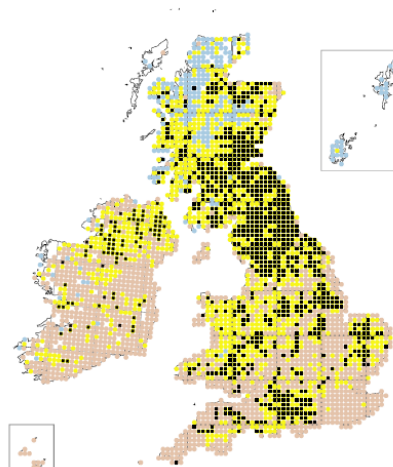


Hybrid



Wood avens
Geum urbanum

~ 25% of British flowering
plant species hybridize



Blue = *G. rivale*
Yellow = both
Black = hybrids

Stace 1975, 1997
as reviewed in Mallet 2005
Geum map: Preston & Pearman 2015

Hybridization

I.D.

birdandmoon.com



Closely related species often hybridize, as though even *they* don't know to which species they belong!

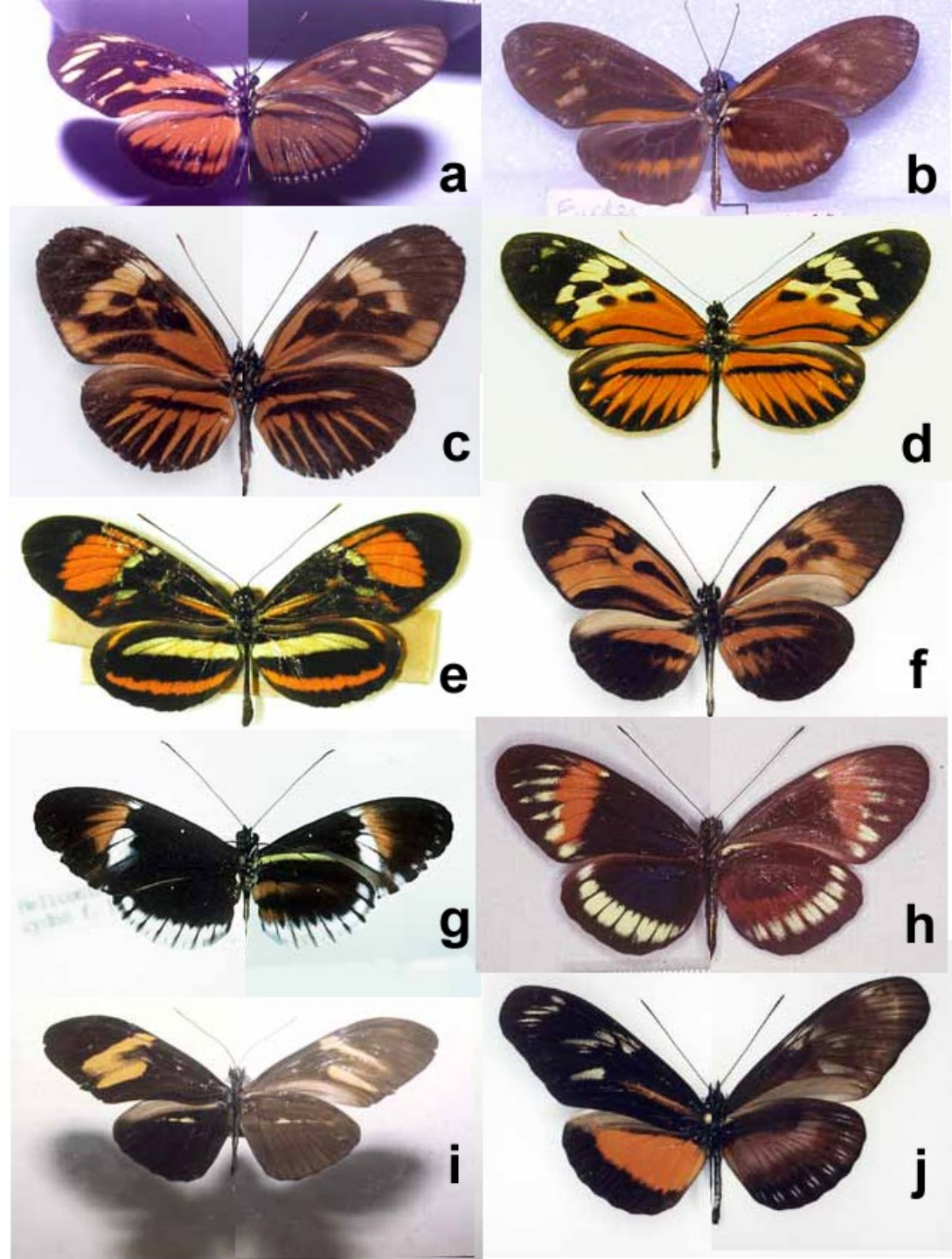


A *Heliconius melpomene* x *cydno* F1 hybrid from nature.
Hybrids were often named as separate species
(normally, < 1/1000 specimens are like this).

In *Heliconius*, hybrids between species are rare.

But occur regularly.

24% of the 73 species are involved;
~ ½ of these also known to backcross



Aware of these hybrids in Heliconius, in 1995 I began collecting photos and records of natural hybrids from museums and private collections around the world

By 2007 I had 161 putative hybrid *Heliconius* specimens

ucl.ac.uk/taxome/hyb/hybtabs.html

Jim's StuffHarvardLookupHenryTaxome ProjectGoogle MapsOEB 140: Speciation...Other bookmarks

Wild-caught hybrids among *Heliconius* and *Eueides* species

© James Mallet, Walter Neukirchen and Mauricio Linares 1997-2006

Click on hybrid number to see pictures

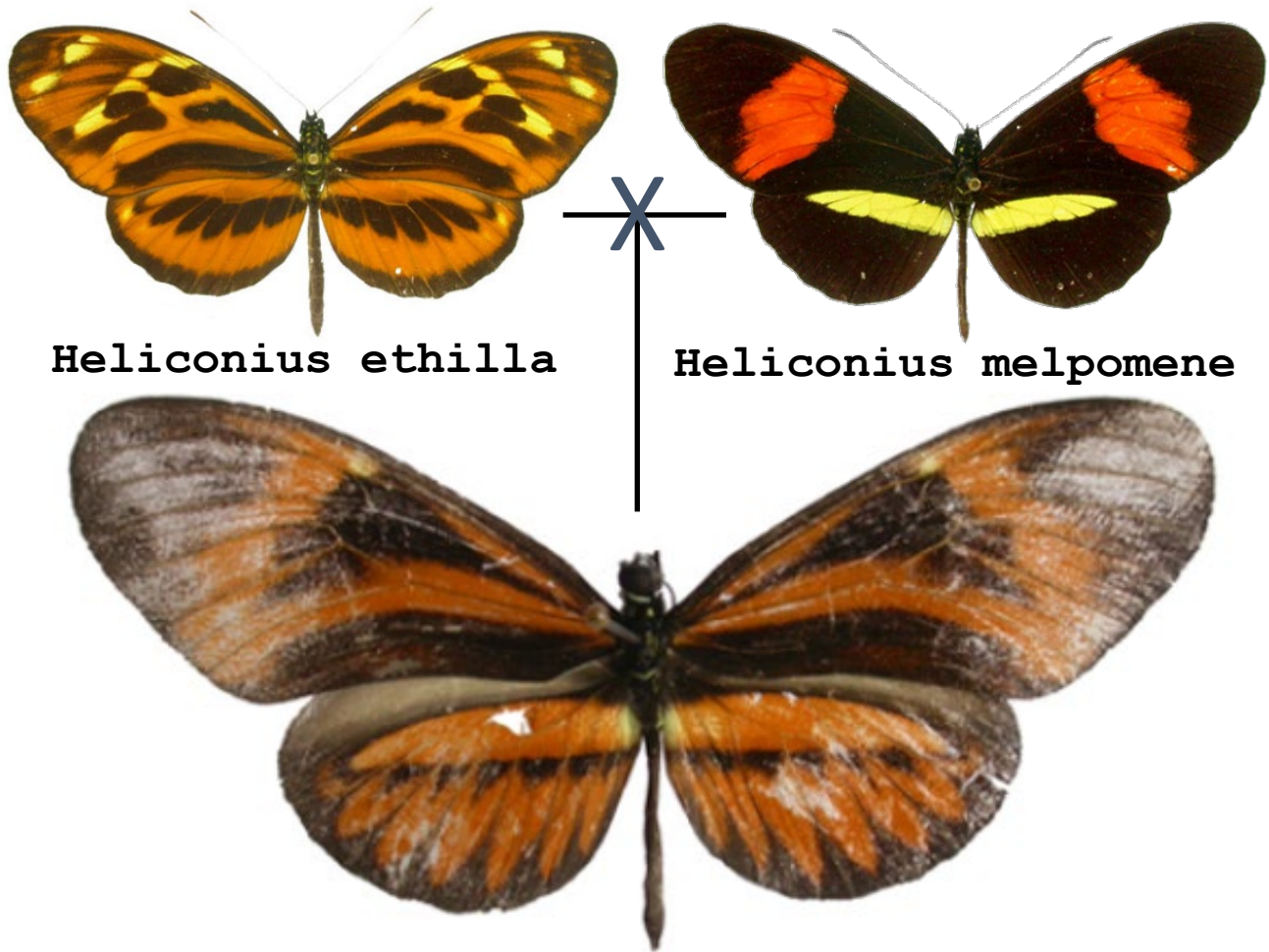
Back to hybridization document

J. Mallet home page

Last updated: Wednesday 30 July 2006

No	Species 1	Species 2	m/f	Country	Locality	Year	Collection	Author	Interpretation
1	E. lybia lybia	E. ?vibilia unifasciatus	m	Brazil	Benjamin Constant		MN/UFRJ		?F1
2	E. isabella eva	E. vibilia vialis	m	Mexico	Veracruz: Vigía	1978	UNAM		F1
3	E. isabella eva	E. vibilia vialis	f	Mexico	Oaxaca: Chiltepec	1976	UNAM		F1
4	E. isabella eva	E. vibilia vialis	m	Mexico	Oax: Sierra Juárez Metatos	1978	UNAM		F1
5	E. isabella eva	E. vibilia vialis	m	Mexico	Oaxaca: Chiltepec	1975	UNAM		F1
6	E. isabella eva	E. procula vulgiformis	m	Costa Rica	Cartago: Juan Viñas	1902	MCZ		F1
7	E. pavana	E. vibilia vibilia	m	Brazil	?Rio de Janeiro		MN/UFRJ		F1
8	H. numata superioris	H. melpomene melpomene	m	Brazil	Rio Arapiuns	1980	Wien	Holzinger & Holzinger 1994: 24,5c	F1
9	H. numata ?superioris	H. melpomene nr. meriana	m	Brazil	?Obidos		MN/UFRJ		F1?
10	H. numata ?superioris	H. melpomene nr. meriana	m	Brazil	Pará: Obidos	1985	Neukirchen		F1?
11	H. numata aurora	H. melpomene malleti	f	Peru	Loreto: Río Itaya	1997	Neukirchen		F1?
12	H. hecale vetustus	H. m. melpomene x thelxiopeia	m	Guyane	St. Laurent	<1932	BM	Ackery & Smiles 1976:123	F1
13	H. hecale fortunatus	H. m. melpomene melpomene	m	Brazil	?Obidos		MN/UFRJ		F1
14	H. ?hecale	H. elevatus zoelleri	f	Colombia	Guainia: Puerto Inírida	1974	Schmidt-M/IAvH	Velez & Salazar 1991: 132	BC->elevatus
15	H. hecale versicolor	H. elevatus pseudocupidineus	m	Peru	Loreto: Yurimaguas	1919	Wien	Holzinger & Holzinger 1994: 27,1b	BC->elevatus
16	H. hecale zeus	H. elevatus perchlorus	m	Bolivia	Chaparé: Todos Santos	1969	Wien		F1
17	H. ethilla nr. metalilis	H. melpomene melpomene	m	?Colombia		<1867	BM	Ackery & Smiles 1976:173	F1
18	H. ethilla nr. metalilis	H. melpomene melpomene	f	Colombia	Meta: Río Negro	1970	Schmidt-M/IAvH	Brown 1976: 15b	F1?
19	H. ethilla nr. metalilis	H. melpomene melpomene	m	Colombia	Meta: Cubarral	1979	Schmidt-M/IAvH		BC->ethilla
20	H. ethilla nr. metalilis	H. melpomene melpomene	f	Colombia	Meta: Cubarral	1979	Schmidt-M/IAvH		BC->ethilla
21	H. ethilla metalilis	H. numata peeblesi	m	Venezuela	Barinas: Barinitas	<1908	BM		F1?
22	H. ethilla narcaea	H. numata ethra	f	Brazil	Leopoldina	<1908	BM	Brown 1976: 15c	F1?
23	H. ethilla narcaea	H. besckei	m	Brazil	Sta. Cat.: R. Grande do Sul		Wien	Holzinger & Holzinger 1994: 18,5b	F1
24	H. ethilla narcaea	H. besckei	m	Brazil	Sta. Catarina: Joinville	1985	Neukirchen		F1
25	H. ethilla narcaea	H. besckei	m	Brazil	Sta. Catarina: Joinville	1981	Para		F1
26	H. ethilla narcaea	H. besckei	m	Brazil	Rio de Janeiro: Imbarie	1963	Para		F1
27	H. ethilla narcaea	H. besckei	f	Brazil	Sta. Catarina: Agrolandia	<1997	Para		F1
28	H. ethilla narcaea	H. besckei	f	Brazil	SP: Horto Forestal	1947	Wien		BC->besckei
29	H. melpomene rosina	H. cydno galanthus	m	Costa Rica	Río Sarapiquí 600m	1993	MNCR	Posla-Fuentes 1993	BC->cydno
30	H. melpomene rosina	H. cydno galanthus	f	Costa Rica	Río Sarapiquí	1993		Posla-Fuentes 1993	BC->cydno
31	H. melpomene rosina	H. cydno galanthus	f	Costa Rica	Limón: Guácimo, San Luis	1993	BM		F1
32	H. melpomene rosina	H. cydno chioneus	m	Panamá	Canal Zone: Pipeline Rd	1979	USNM		BC->cydno
33	H. melpomene cythera	H. cydno alithea	m	Ecuador	Balzapamba 800m	<1906	BM	Ackery & Smiles 1976:184	BC->melpomene
34	H. melpomene cythera	H. cydno alithea	m	Ecuador	Los Ríos: Río Palenque	1973	Allyn		F1
35	H. melpomene cythera	H. cydno alithea	m	Ecuador	Pichincha: Alluriquín	1989	MHN, Lima		F1
36	H. melpomene cythera	H. cydno alithea	m	Ecuador	Palmar 100m	~1905	BM		BC->melpomene

A hybrid my group caught in Peru



Lepbase *H. timareta* helico3 scaffold 13388

ACTAATAGCAATTGGACATGA

AM709679 *H. melpomene* *amaryllis* 02-1882

ACTAATAGCAATTGRMCATGA

AM709680 *H. melpomene* *amaryllis* 02-1850

ACTAATAGCAATTGGACATGA

AM709681 *H. melpomene* *amaryllis* 02-944

ACCAATAGCGATTGGACAYAA

AM709682 *H. melpomene* *aglaope* 02-2060

ACYAATAGCRATTGGACATGA

AM709683 *H. melpomene* *aglaope* 02-1894

ACTAATAGCAATTGRCCATGA

AM709684 *H. melpomene* *aglaope* 02-366

ACTAATAGCAATTGGACATGA

AM709685 *H. melpomene* *aglaope* 02-288

MCYWATAGTRATTGGACATGA

AM709686 *H. melpomene* *aglaope* 02-286

ACTAATAGCAATTGGACRTGA

AM709690 *H. ethilla* x *H. melpomene* 06-921

AYTARYRKYARYYRGAYATGR

AM709687 *H. ethilla* *aerotome* 02-3

AYTAGCGTTAGCCRGATATGG

AM709688 *H. ethilla* *aerotome* 02-975

AYTAGCGTTAGCCRGATATGG

AM709689 *H. ethilla* *aerotome* 02-1483

ACTAGCGTTAGCCGGATATGG

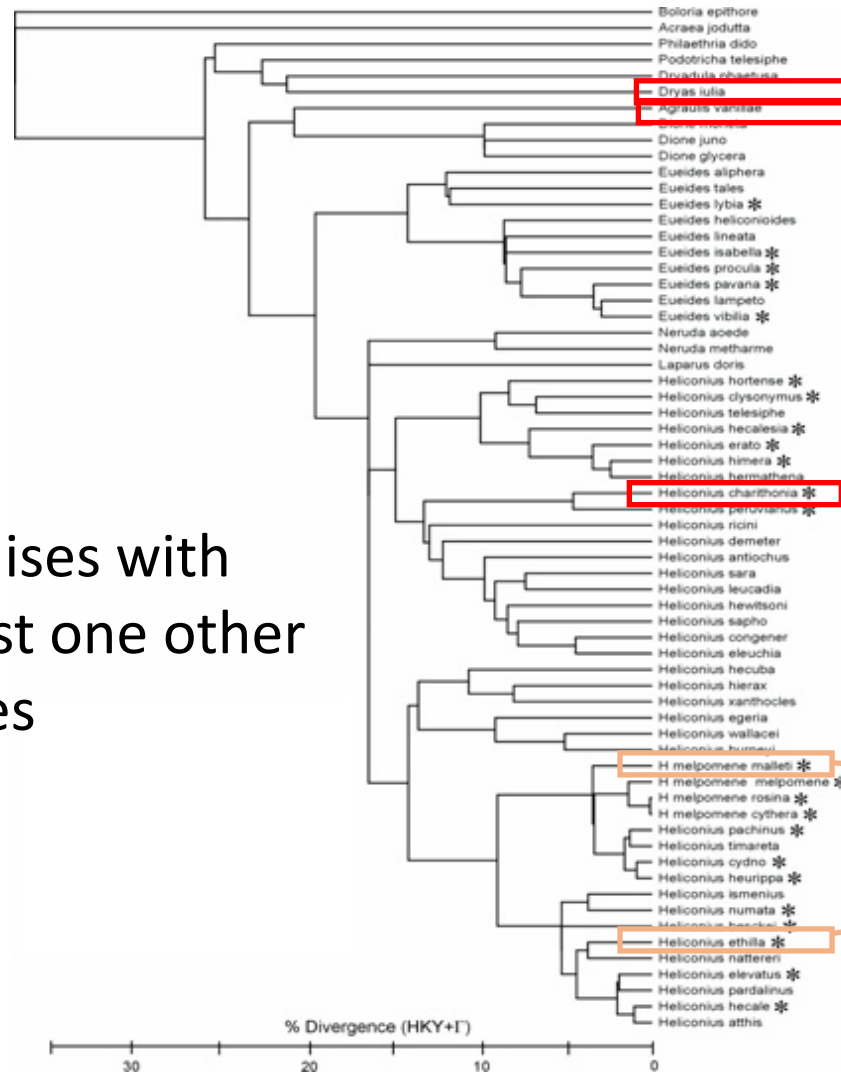
Lepbase *H. pardalinus* helico3 scaffold 6955

ACTAGCATTAGCCGGACATGG

Natural hybridization in *Heliconius*:

Especially in rapidly radiating, recent lineages

* = hybridises with
at least one other
species



Julia Longwing



Gulf Fritillary



Zebra Longwing



H. melpomene x
H. ethilla hybrid

Eueides

Heliconius:

erato
group

melpomene
-*silvaniform*
group



Swallowtails,
Papilio butterflies,
7-15% of species
hybridize
(47% of North
American *Papilio*)



(©NHM & Henri Descimon)

Sperling 1990. Canad. J. Zool. 68:1790-1799
reviewed in J Mallet. 2005. TREE 20: 229-237

16 • Bad species

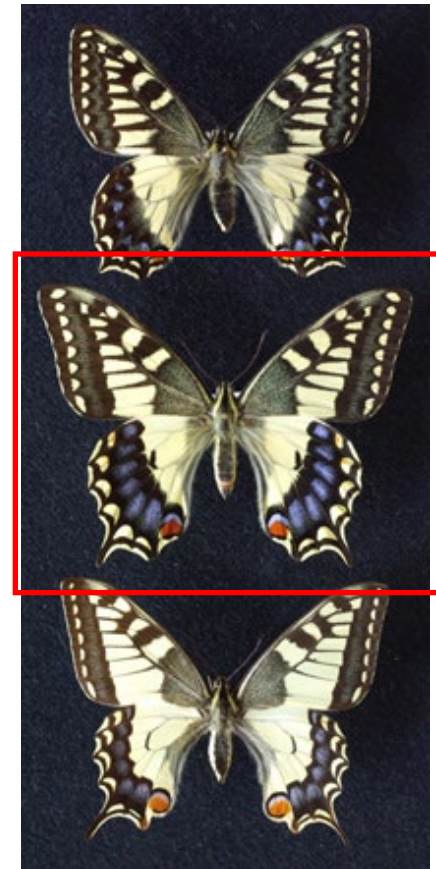
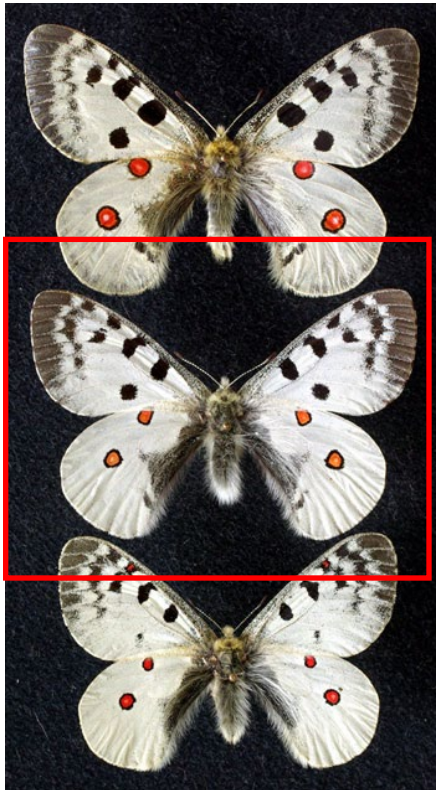
HENRI DESCIMON AND JAMES MALLET

Parnassius apollo
x phoebus

Zerynthia polyxena
x rumina

Papilio hospiton x machaon

Ecology of Butterflies in Europe, eds. J. Settele, T. G. Shreeve, M. Konvička and H. Van Dyck.
Cambridge University Press. © Cambridge University Press 2009.



H. Descimon & J. Mallet 2009 "Bad species"

Species 1	Species 2	Location	Hybrid frequency ^a	Characters, except morphology ^b	Taxonomic interpretation	Source
<i>Papilio machaon</i>	<i>P. hospiton</i>	Corsica, Sardinia	F	D, A, M, E, H(I), P!	Sibling species	See text
<i>Iphiclides p. podalirius</i>	<i>I. p. feisthamelii</i>	Languedoc	F	A, M	Parapatric sibling species	See text
<i>Zerynthia polyxena</i>	<i>Z. rumina</i>	Provence	R/E		atric species	See text
<i>Parnassius apollo</i>	<i>P. phoebus</i>				lly sympatric species	See text
<i>Artogeia napi</i>	<i>A. bryonia</i>		F		atric sibling species	Bowden, 1992; I
<i>Artogeia napi</i>	<i>A. balcanica</i>				patric subspecies	Tolman &
<i>Artogeia napi</i>	<i>A. rapae</i>				atric species	Klemann 0000
<i>Pontia daplidice</i>	<i>P. edusa</i>				atric sibling species (row overlap)	Geiger <i>et</i> Wenge [“semi: 1997 [1
<i>Euchloe crameri</i>	<i>E. simplon</i>		kc		atric, ecologically divergent forms	Lux, 198
<i>Anthocaris belia euphenoides</i>	<i>A. cardamines</i>		E		lly sympatric species	Legras in

Anthocaris

Erebia

belia

epiphron

hybrid

“Descimon’s ringlet”

“serotina”

cardamines

pronoe

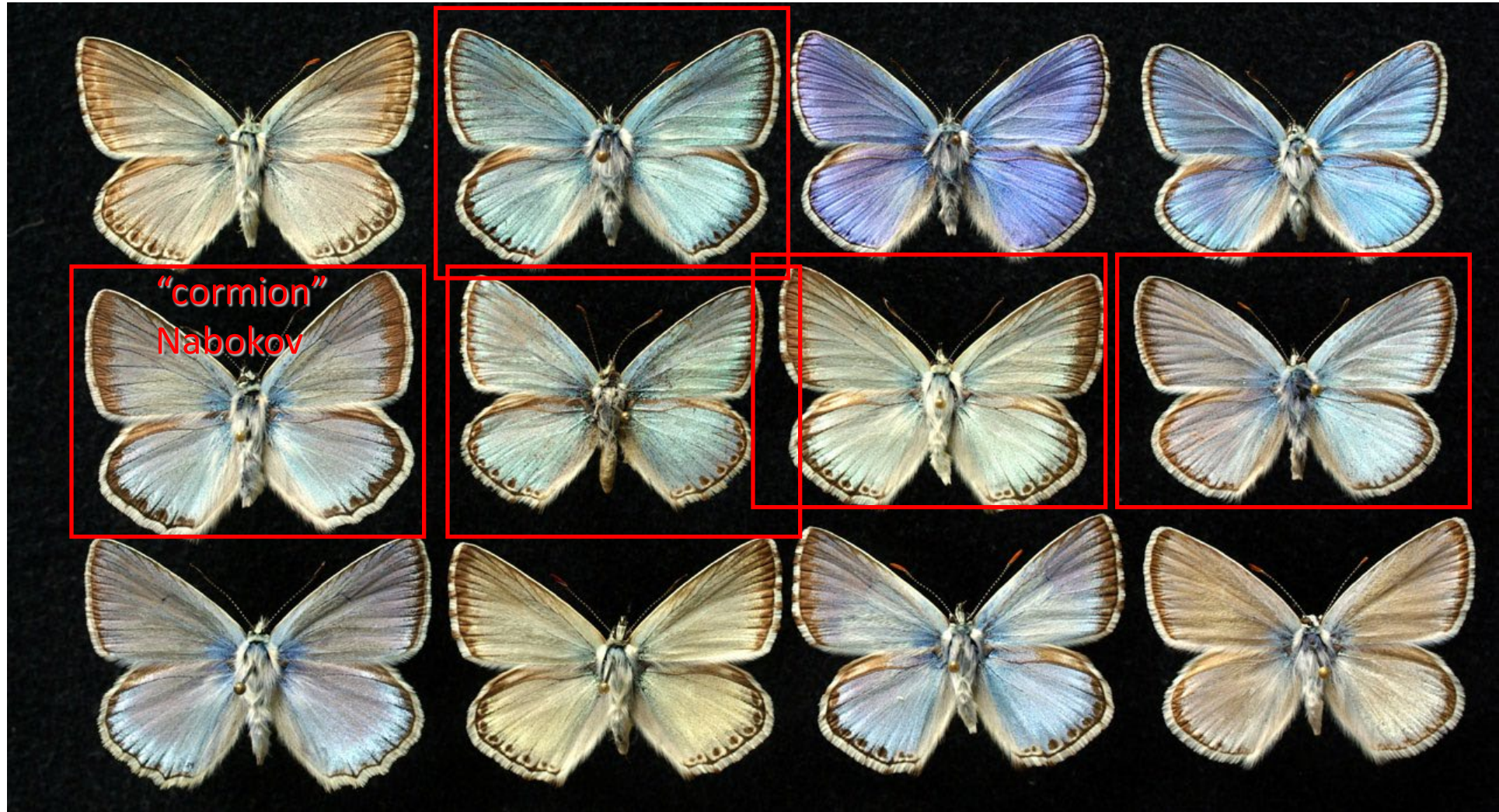
Polyommatus (s.l.) spp. and hybrids

L. coridon

"polonus"

L. bellargus

Plebicula dorylas



"cormion"
Nabokov

Meleageria daphnis

L. hispana

L. caelestissima

P. nivescens

Overall, 16% of European butterfly species hybridize

H. Descimon & J. Mallet 2009 "Bad species"



World birds:

9% of species
hybridize
(Panov, in Grant &
Grant 1992)

Tits of the world
(Paridae):
29% of species
hybridize

Blue Tit *Parus caeruleus* and Long-tailed
Tit *Aegithalps caudatus*.

S. Harrap & D. Quinn 1996. Tits,
Nuthatches & Treecreepers.

*Panov 1989; reviewed by Grant & Grant 1992;
reviewed in J Mallet. 2005. TREE 20: 229-237*



American warblers
(Parulidae):

24% of species
hybridize

Cape May warbler *Dendroica tigrina*
and golden-winged warbler
Vermivora chrysoptera.

JJ Audubon. 1835-8. Birds of America

reviewed in J Mallet. 2005. TREE 20: 229-237



Eurasian warblers
(Sylviidae):

hardly any species
known to hybridize

Willow warbler, wood warbler, and chiff-chaff. 1925.

British Birds.

Plate 17, Volume 1. Archibald Thorburn.



British ducks: 75% of species hybridize

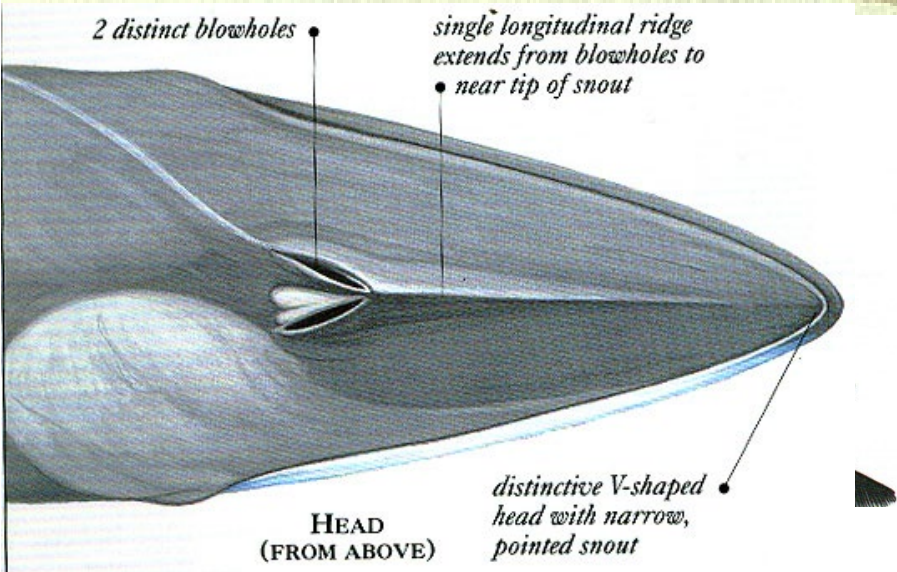
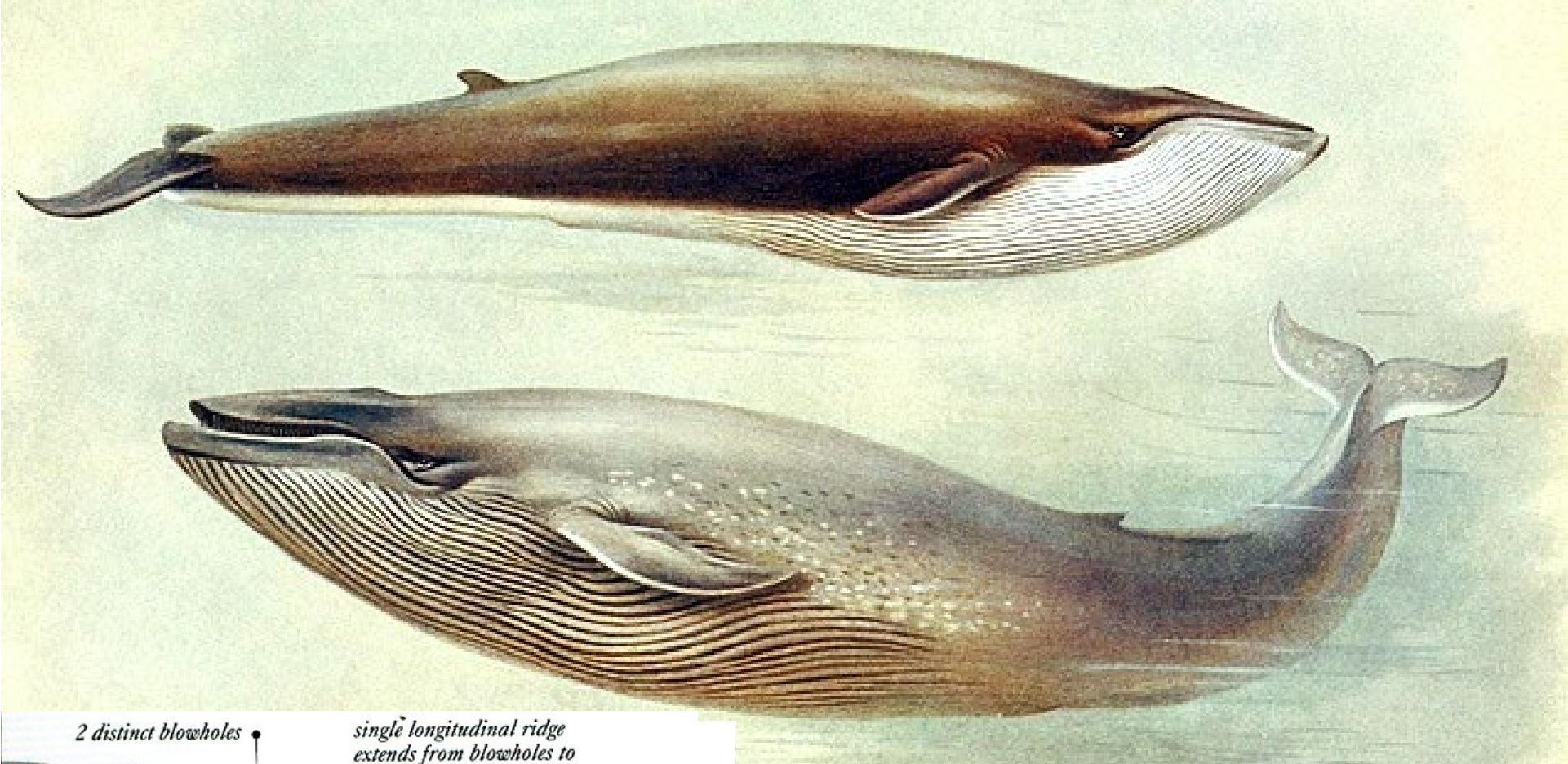
Shoveler *Anas clypeata* and Garganey *Anas querquedula*.

Archibold Thorburn 1926 British Birds.



British grouse (Tetraonidae)
100% of 4 spp. hybridize

Ptarmigan *Lagopus mutus*. John Gould 1873.



These two species, the biggest animals on the planet (ever) hybridize, & backcross – fin whale and blue whale

In mammals:

6% of European species hybridize

Hybridization

e.g. American warblers (Parulidae):

- 24% of species hybridize

~10% of all animal species, and
~25% of flowering plants hybridize
in nature

Hybrids usually rare,
< 1/1000 individuals

Hybrids may be sterile, show
Haldane's Rule, or may be fertile

But *introgression* (gene flow) does
occur between species



Cape May warbler *Dendroica tigrina*
and golden-winged warbler
Vermivora chrysoptera.

JJ Audubon. 1835-8. Birds of America

What about introgression?

“Introgressive hybridization is defined as the gradual infiltration of the germplasm of one species into that of another as a consequence of hybridization and repeated backcrossing”

Can we find evidence? Molecular genetics and genomics.

Is introgression ever “adaptive”? “Adaptive introgression” has become a buzzword (or buzz phrase). It doesn’t mean that introgression is always adaptive, and it is probably mostly deleterious. But occasionally, there is evidence that introgressed regions of the genome are exploited in adaptive evolution. Some examples follow.

Mayr 1942 view: hybridization doesn't have any important effects in animals

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BIOLOGY OF SPECIATION

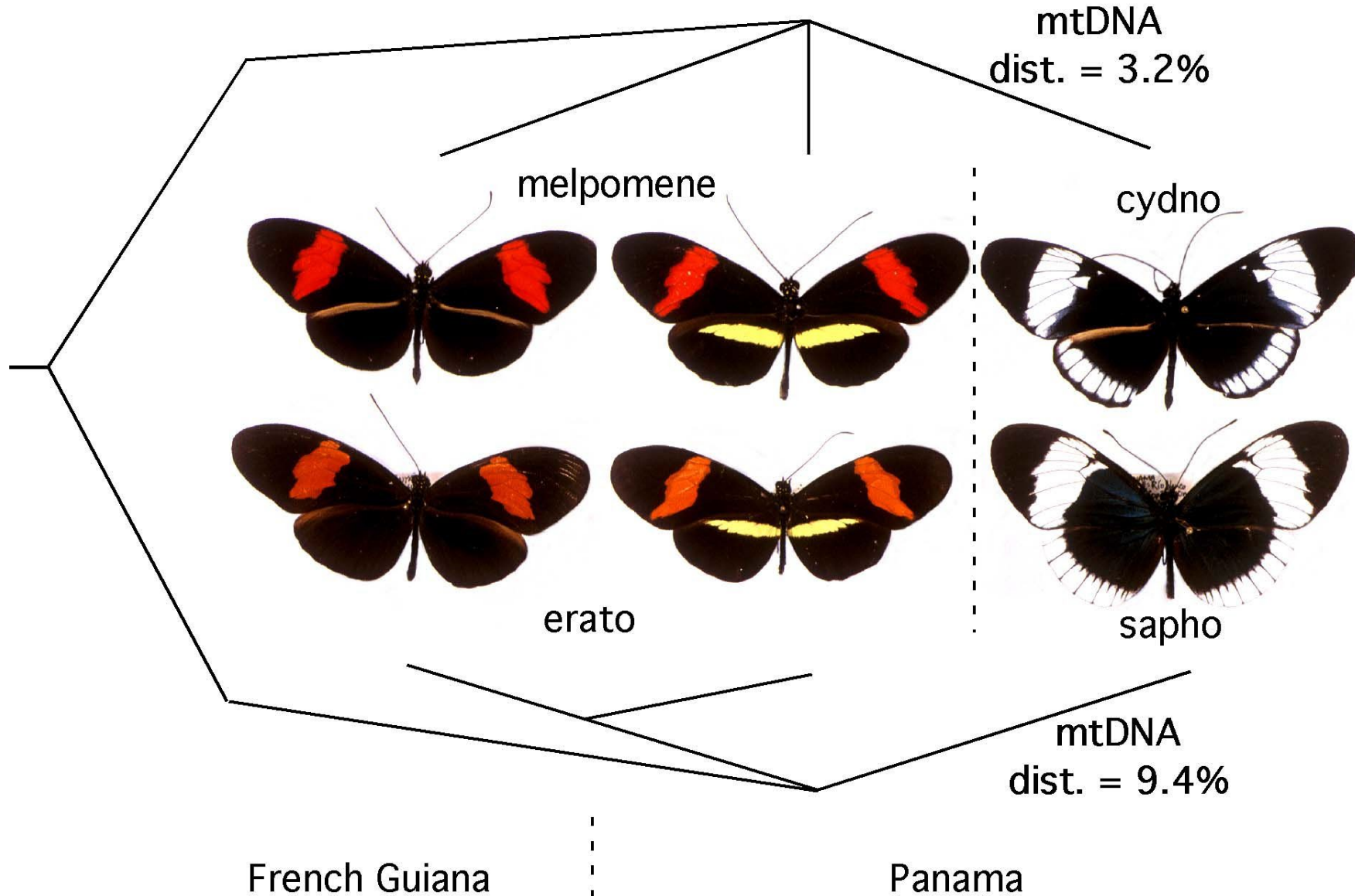
THE BREAKDOWN OF ISOLATING MECHANISMS AND ITS CONSEQUENCES

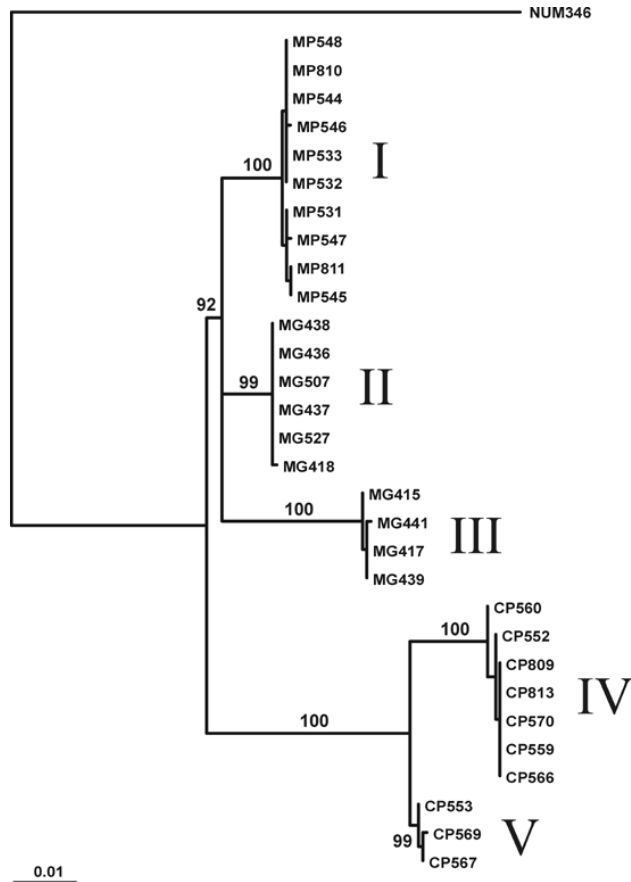
260

OCCASIONAL HYBRIDS BETWEEN SYMPATRIC SPECIES

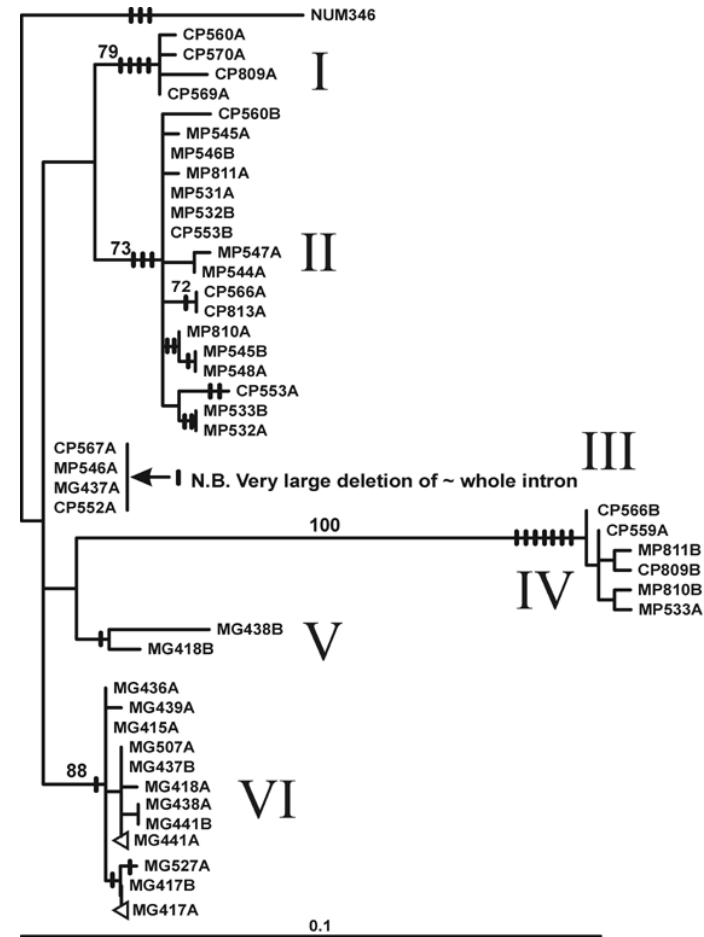
and it is probable that the hybridization is of recent date and caused by man-made habitat disturbances. Hybrids form only a very minute percentage of the individuals in all the species mentioned, and I know of no case in which the occurrence of hybrids has resulted in a blurring of the border line between these species.

Closely related species *Heliconius melpomene* and *Heliconius cydno*





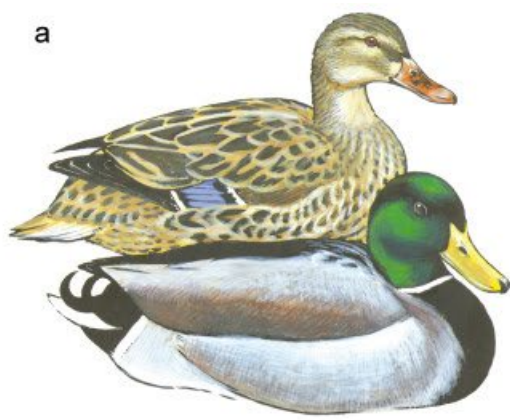
mtDNA
(*Col* & *Coll*)



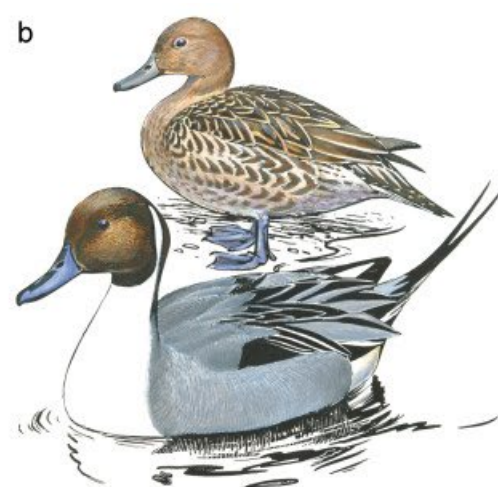
nuclear gene
(*Mpi*)

This gene flows between species!!

Vanessa Bull et al., 2006, BMC Biology 4:11



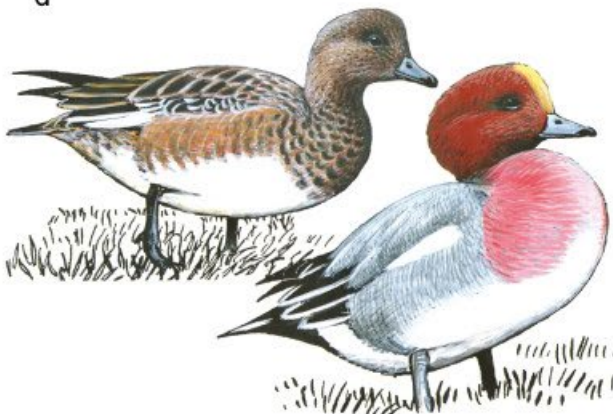
Anas platyrhynchos (Mallard)



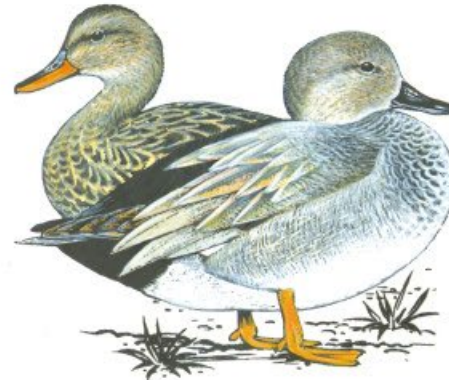
Anas acuta (Northern pintail)



Anas crecca (Teal)



Anas penelope (Eurasian wigeon)

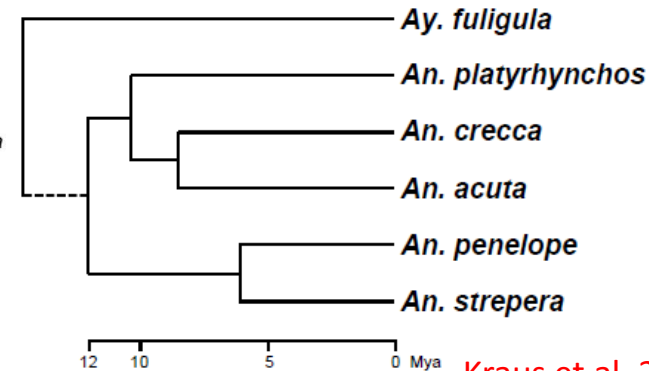
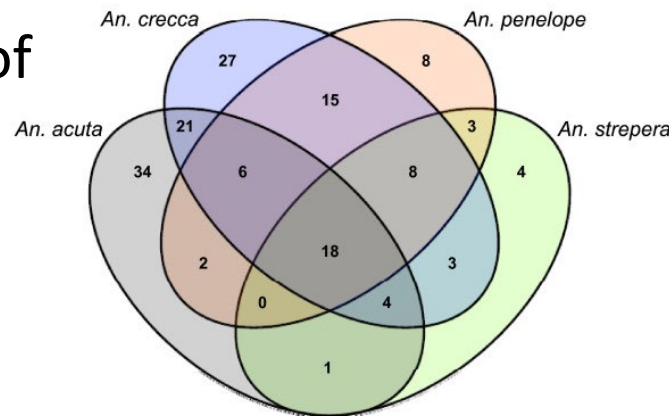


Anas strepera (Gadwall)



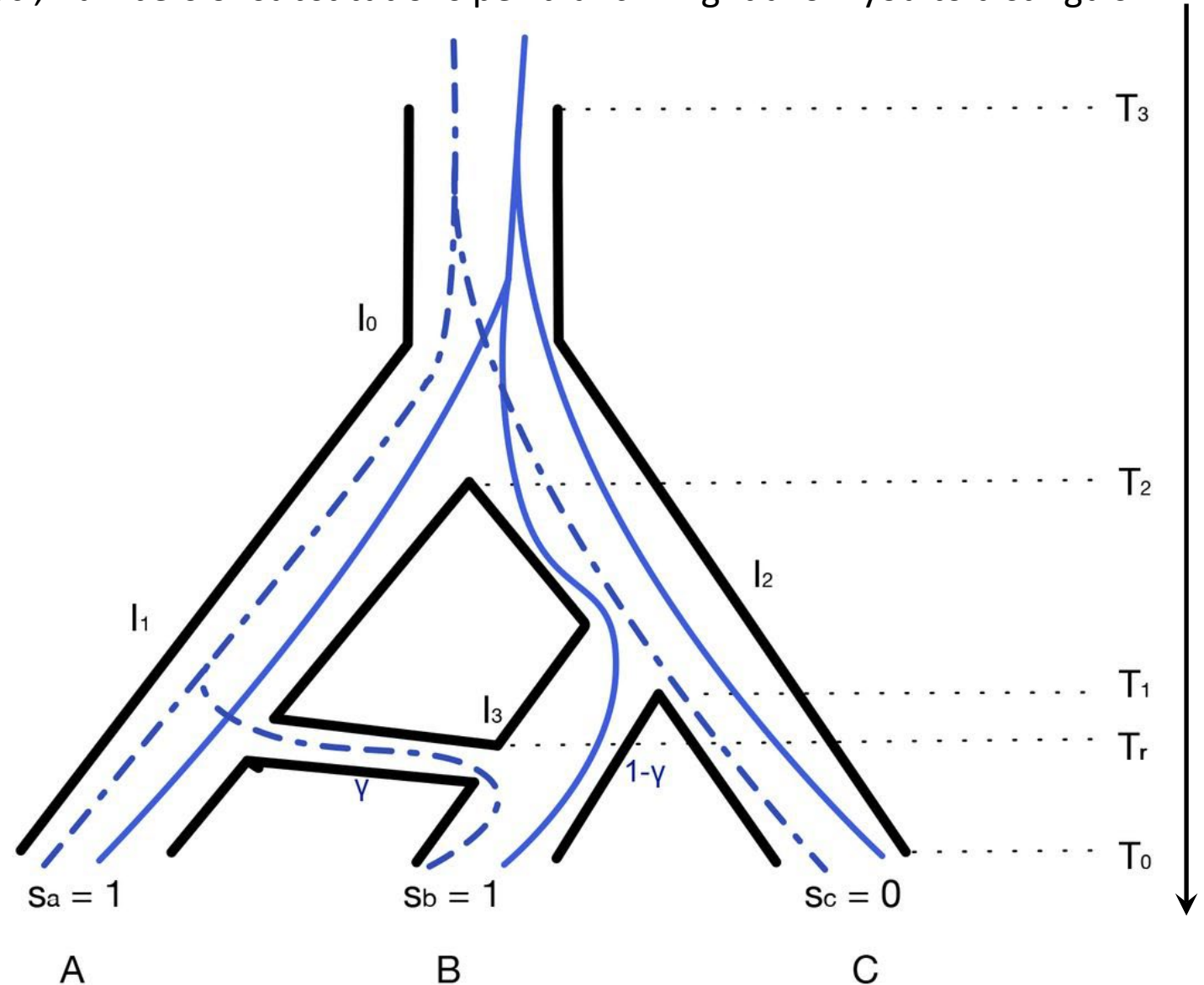
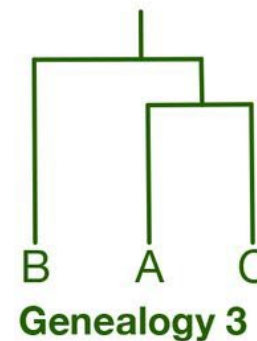
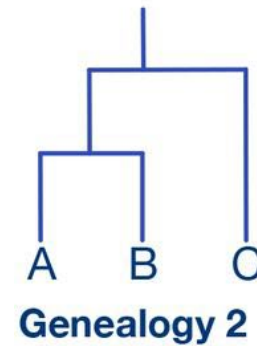
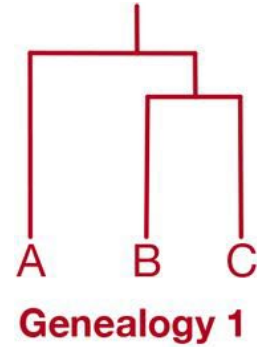
Aythya fuligula (Tufted Duck)

Very high fractions of shared polymorphisms among these duck species



Introgression? Or incomplete lineage sorting?

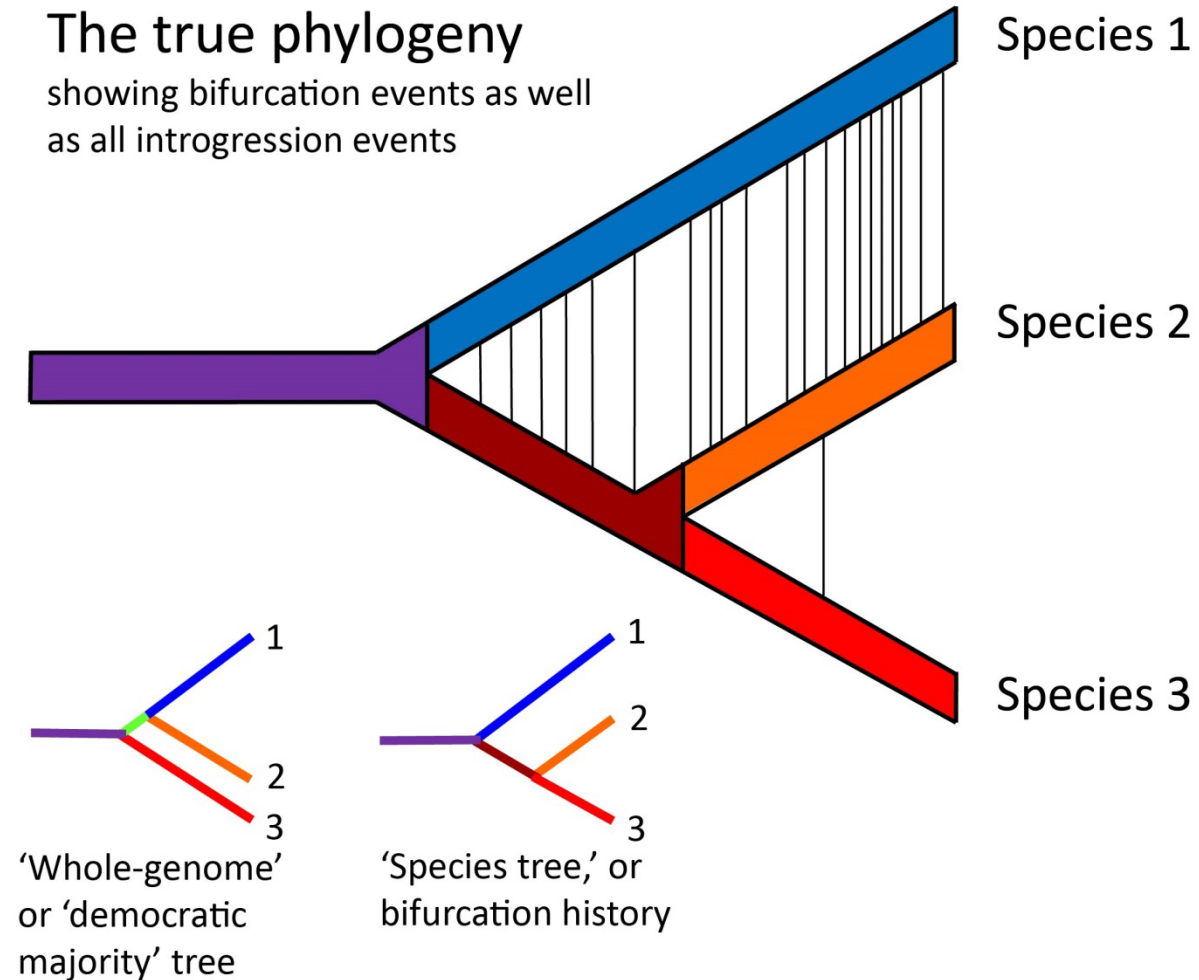
Both incomplete lineage sorting and gene flow will produce gene trees like genealogy 2. But if you have enough loci, numbers of substitutions per branch might allow you to distinguish.



Genomics!!

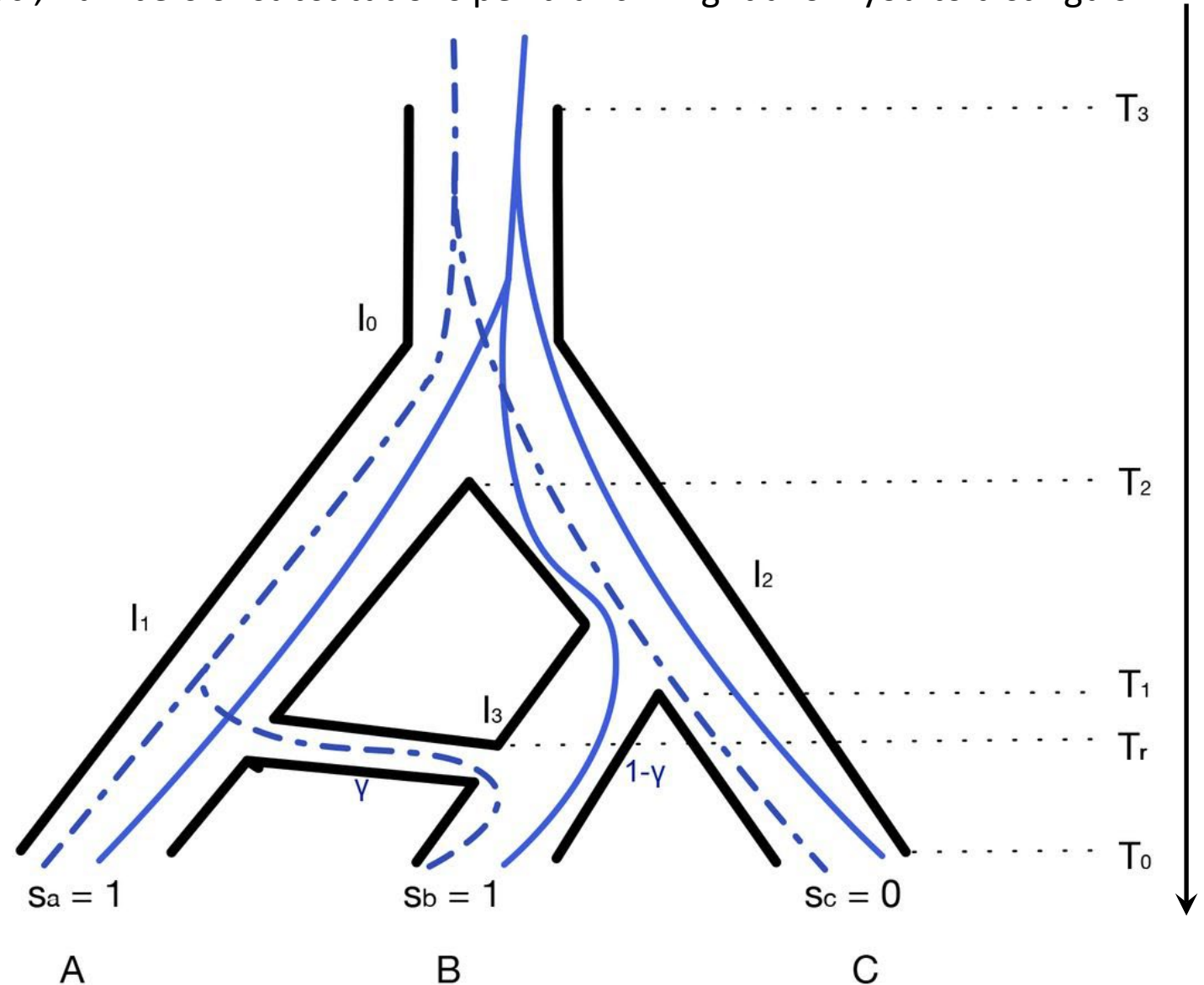
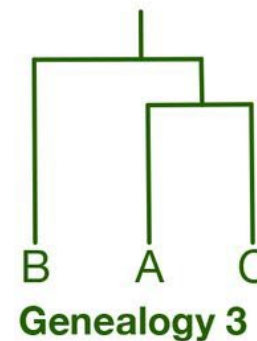
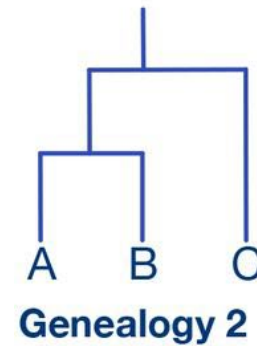
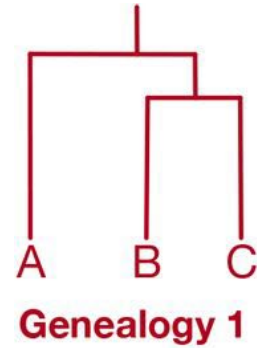
- Has revolutionized understanding of gene flow
- Especially whole genome resequencing now used

What are species? Not what we thought



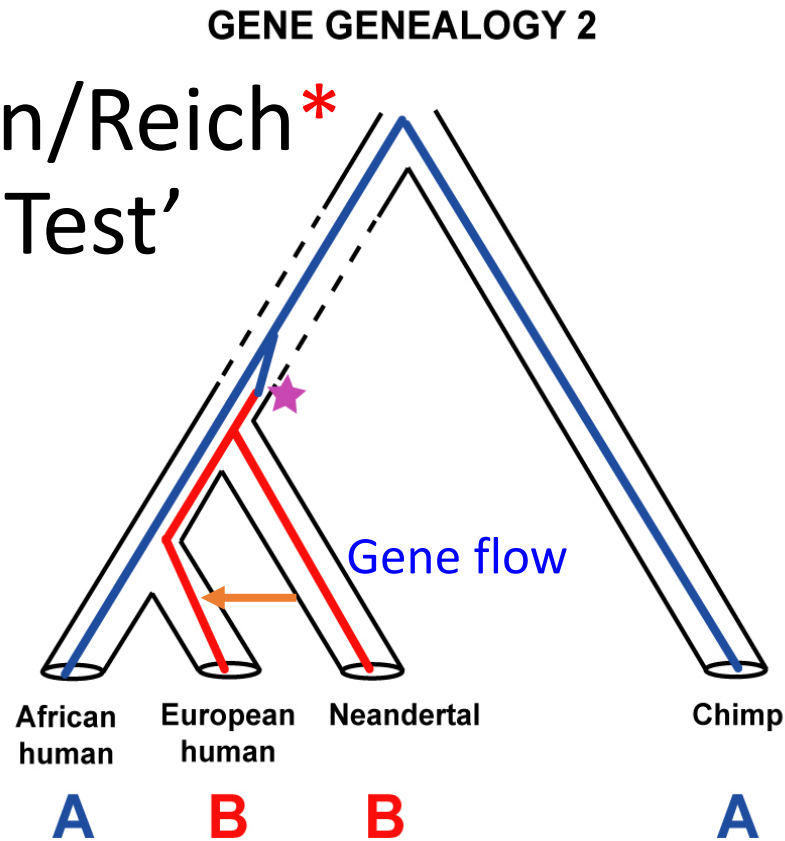
Introgression? Or incomplete lineage sorting?

Both incomplete lineage sorting and gene flow will produce gene trees like genealogy 2. But if you have enough loci, numbers of substitutions per branch might allow you to distinguish

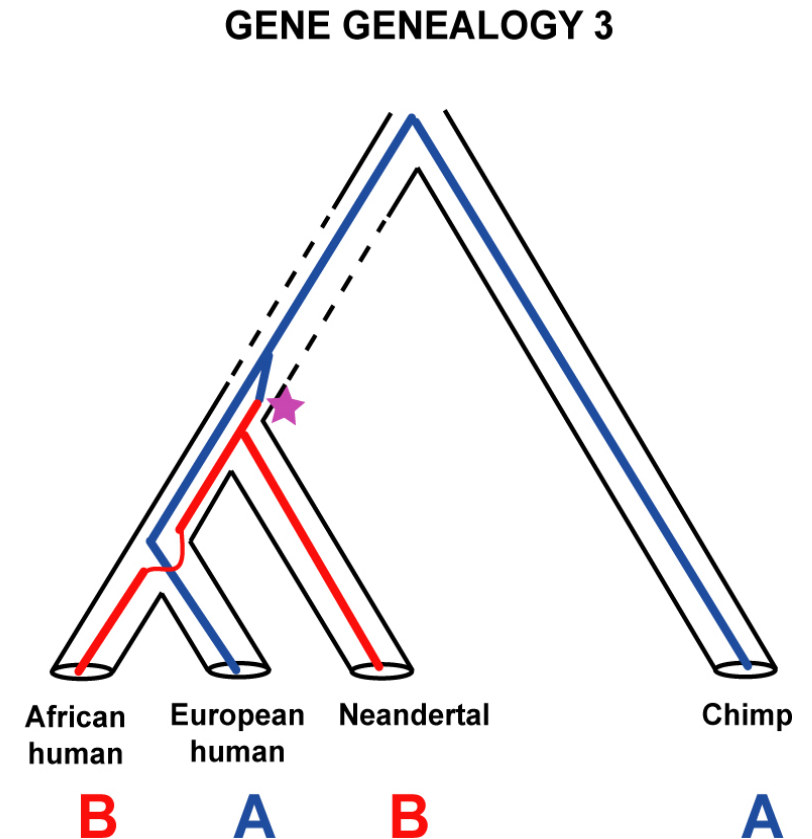


Introgression or “incomplete lineage sorting?”

The Patterson/Reich* ‘ABBA-BABA Test’



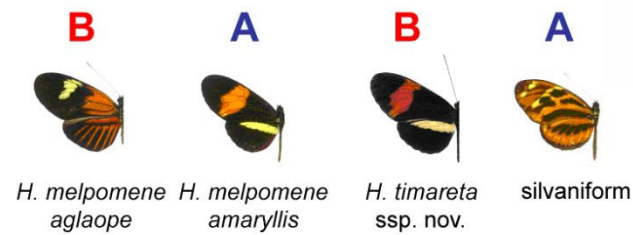
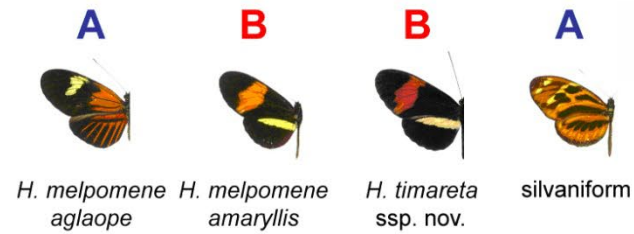
EXPECT:
50% ABBA nucleotide sites
50% BABA sites



OBSERVE:
103612 ABBA sites
94029 BABA sites

* Kulathinal RJ, Stevison LS, Noor MAF. 2009. PLoS Genetics
Green et al. 2010 Science 328:710-722

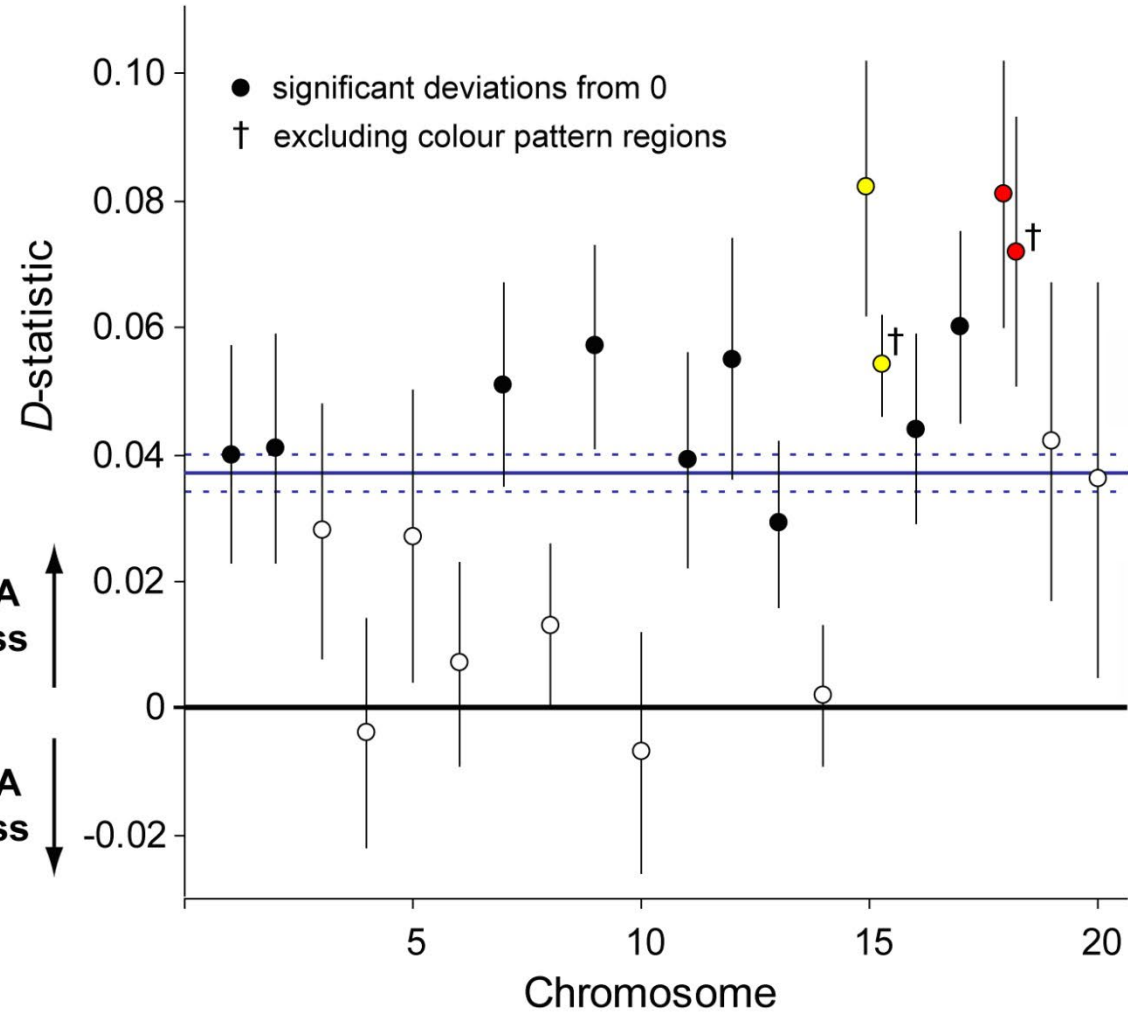
ABBA-BABA test on RAD data across genome



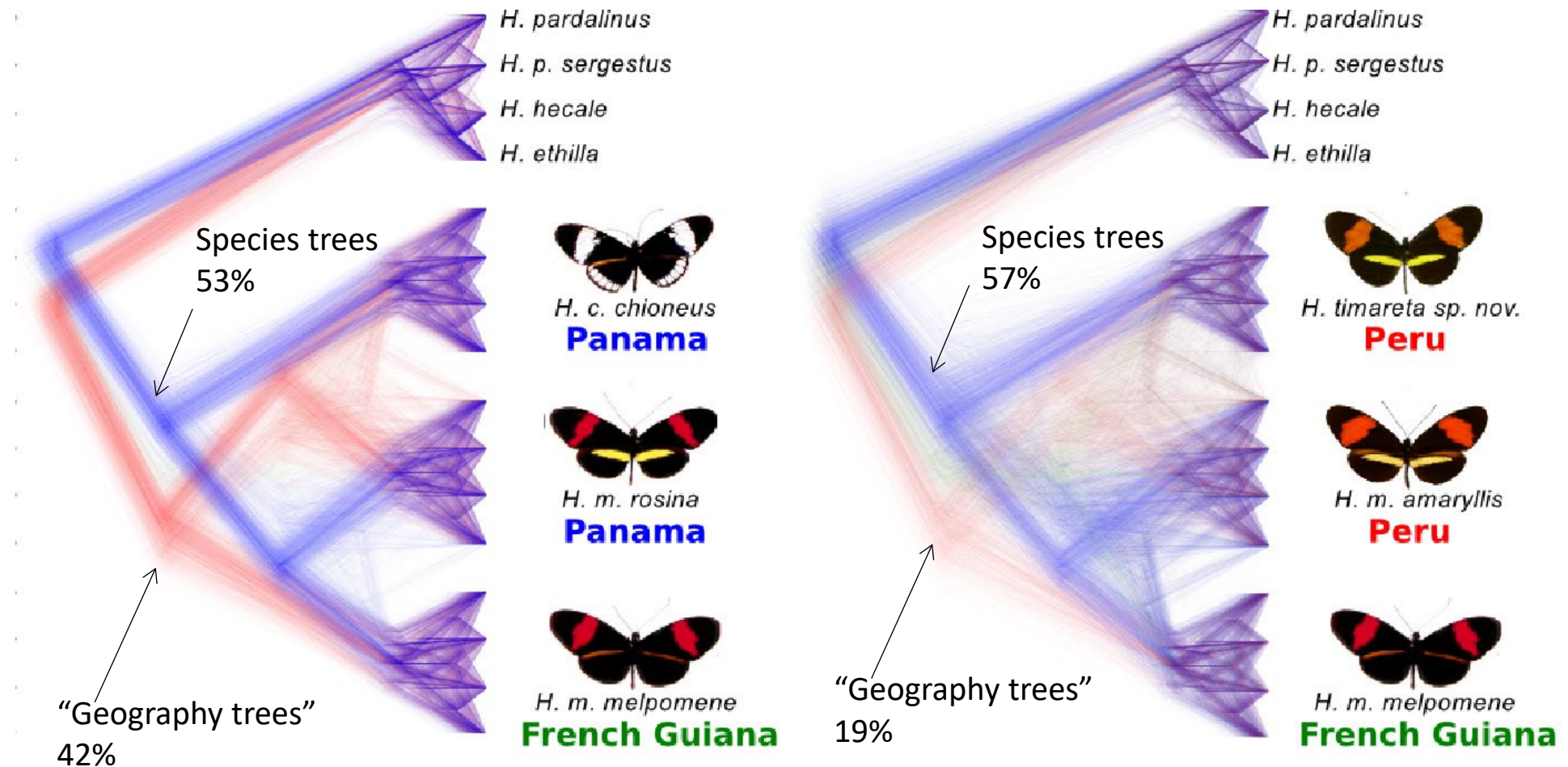
ABBA
excess ↑

BABA
excess ↓

$$D\text{-statistic} = (\#ABBA - \#BABA) / (\#ABBA + \#BABA)$$

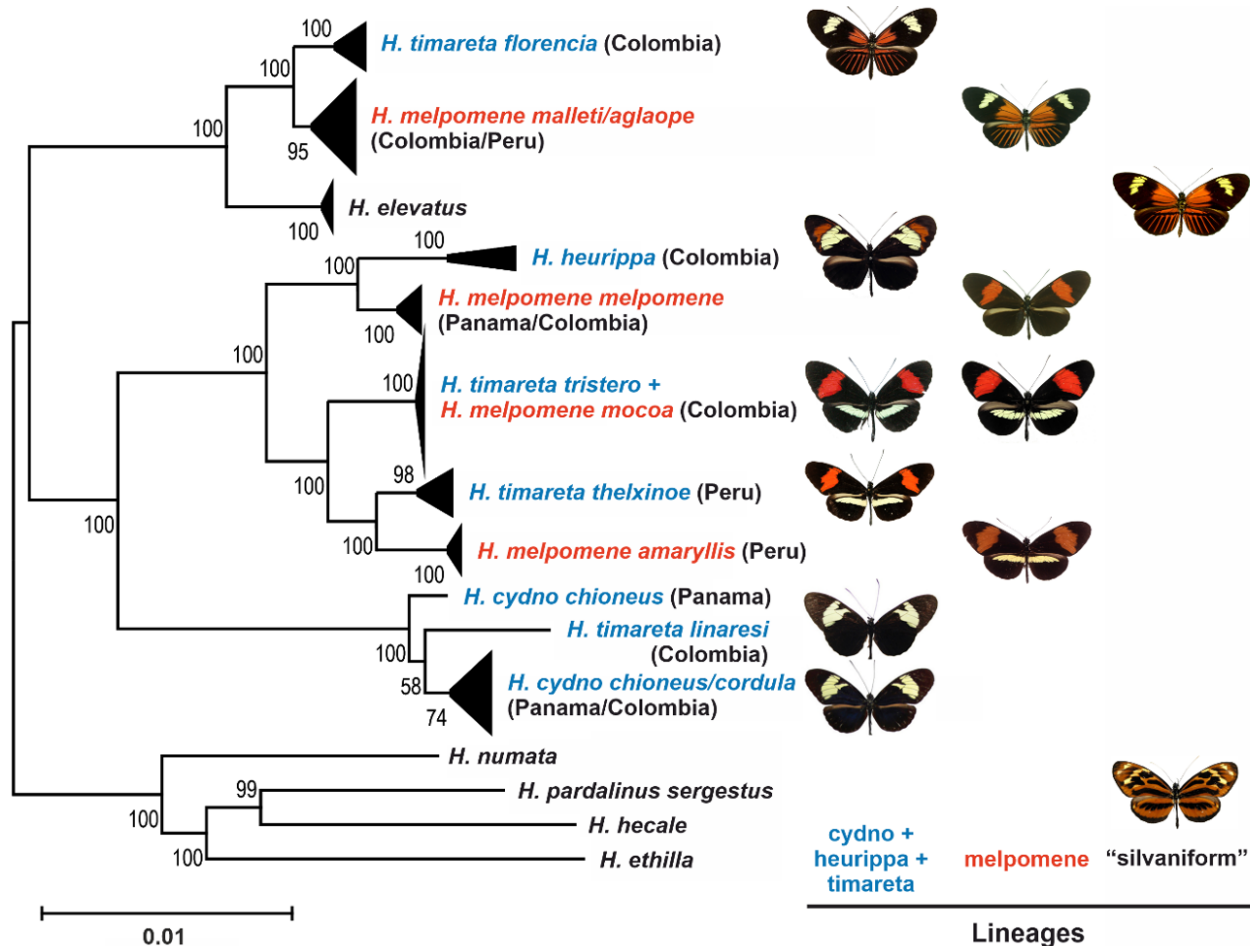


Whole genome sequencing “geography gene trees” vs. “species tree gene trees”



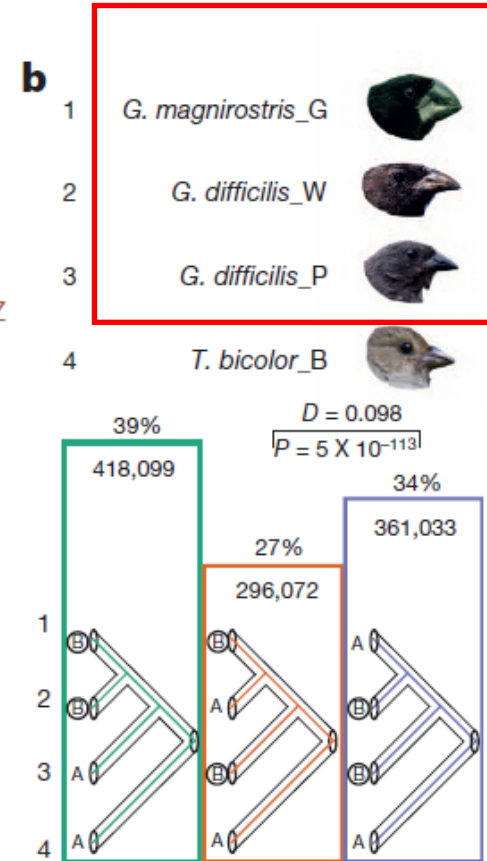
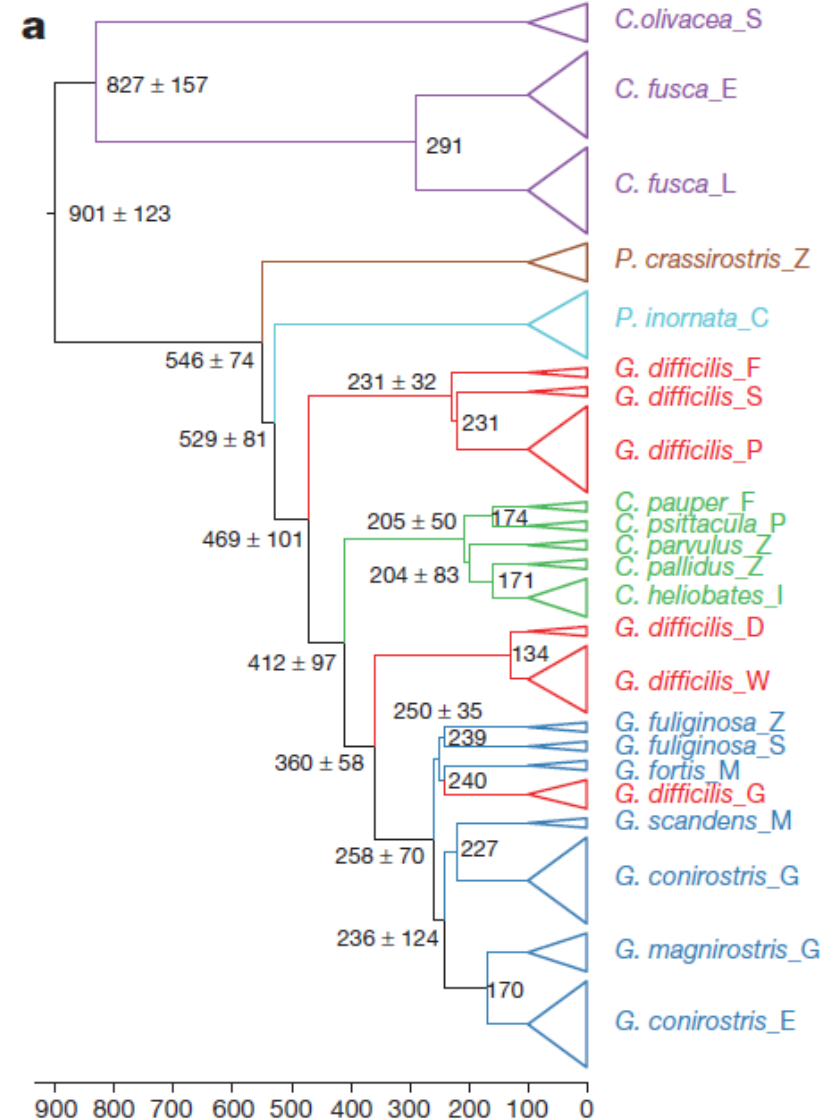
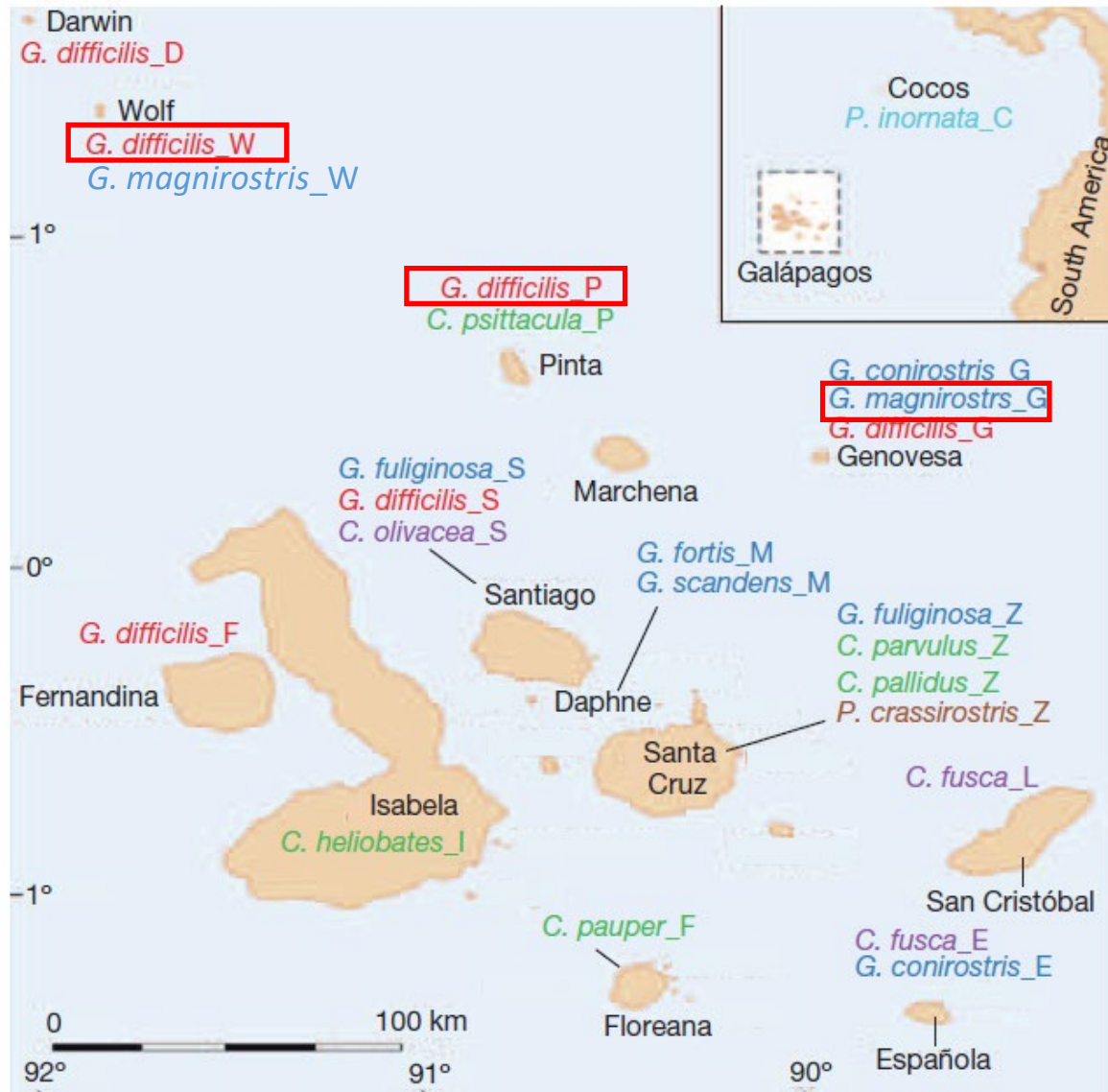
‘Control tree:’ (*timareta* or *cydno* with *melpomene* French Guiana) rare in both cases

Multiple local introgression events at a color pattern locus in *Heliconius melpomene* and *H. timareta*

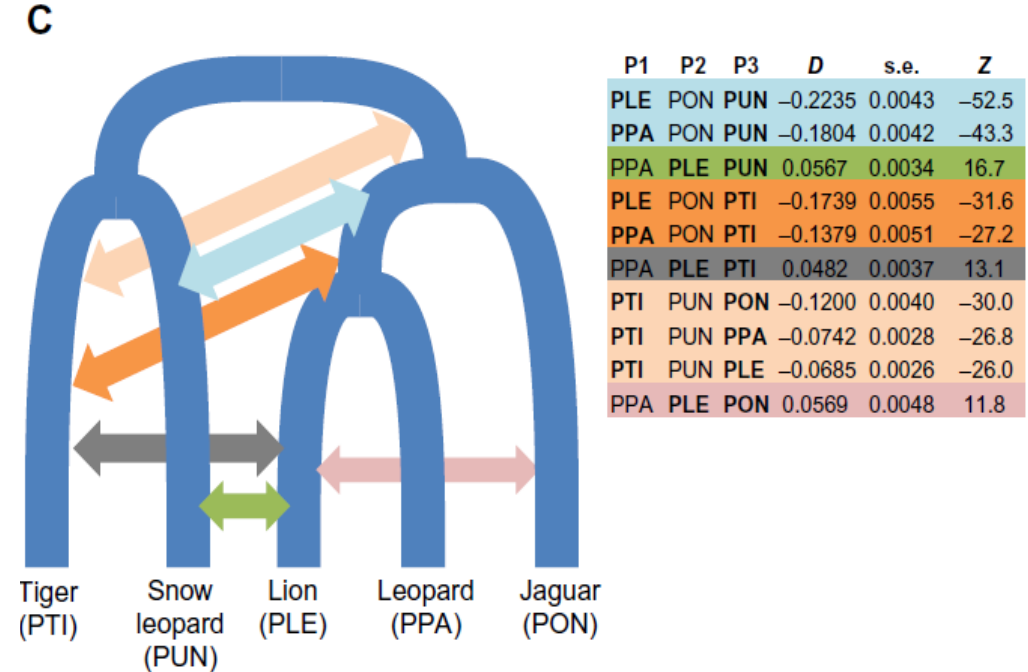
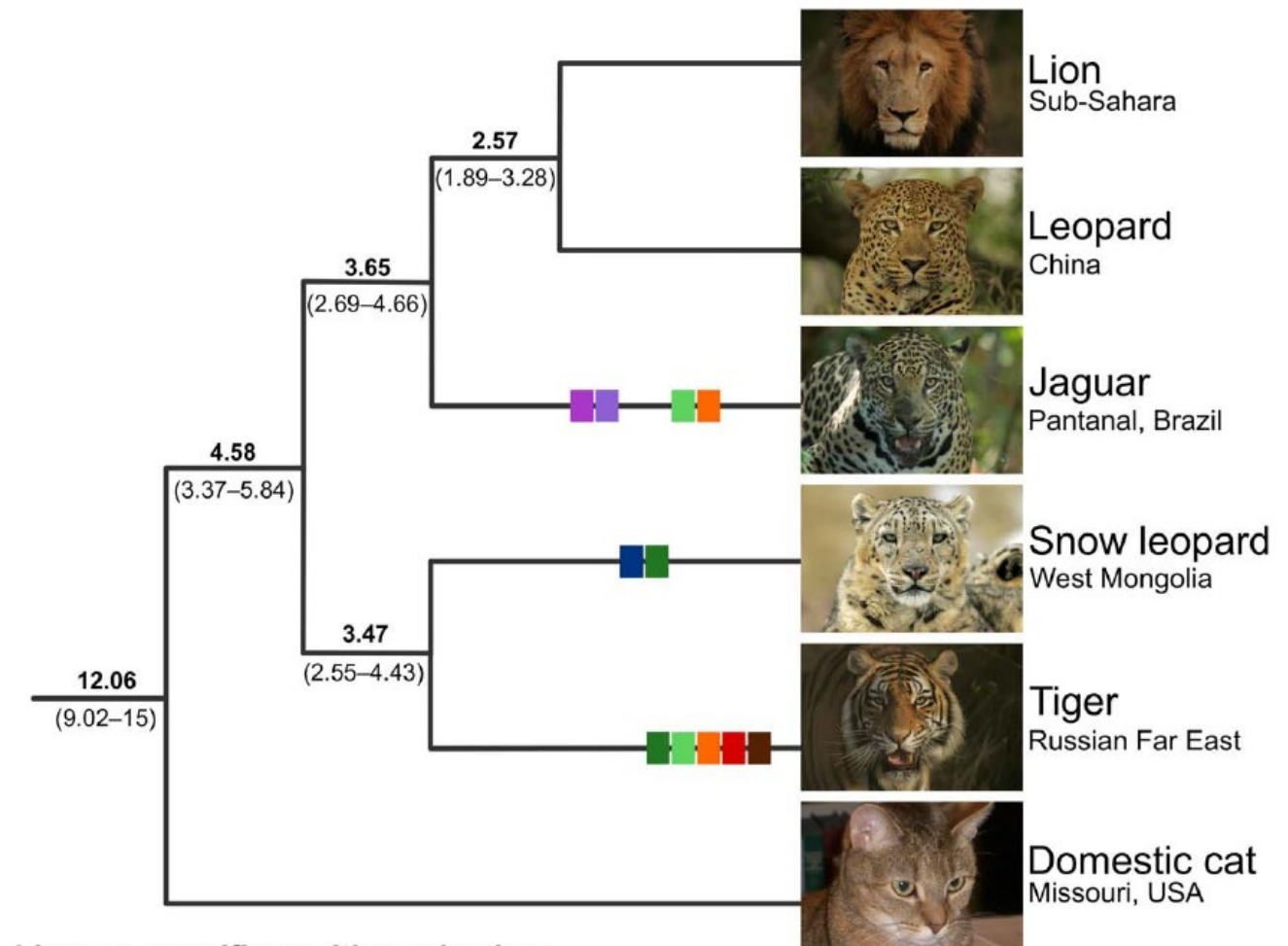


Tree is estimated based on 21 kb section of the ~50 kb *cis*-regulatory region of *optix*, a known region of mimicry colour pattern regulation

ABBA-BABA tests on Darwin's finches: much gene flow

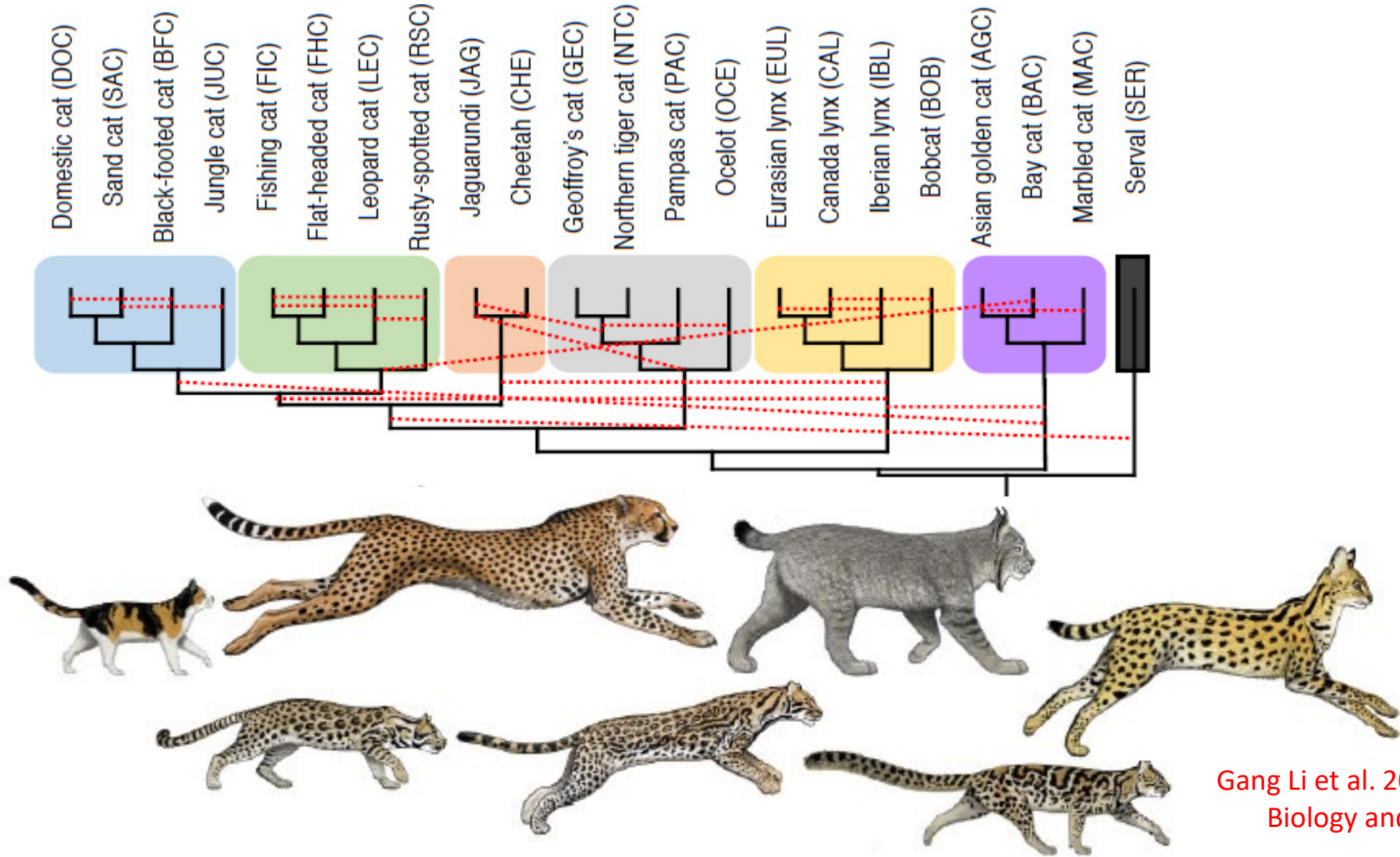


Genomic tree of big cats, and ABBA-BABA tests



Figueiró et al. 2017 PNAS

Felidae, the cat family



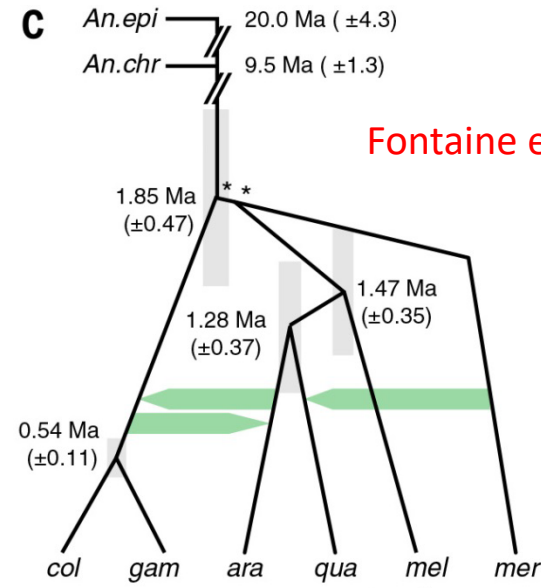
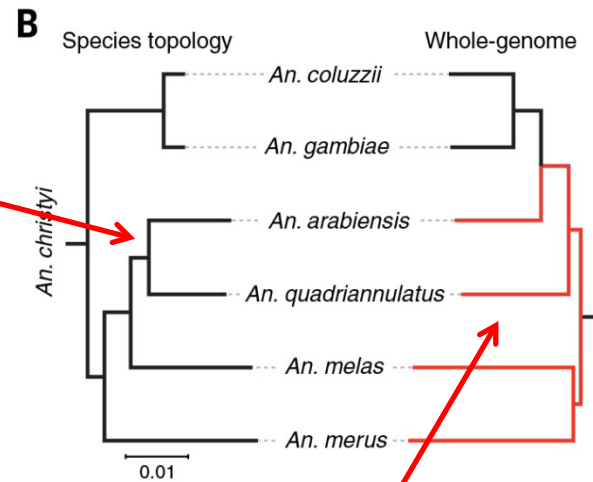
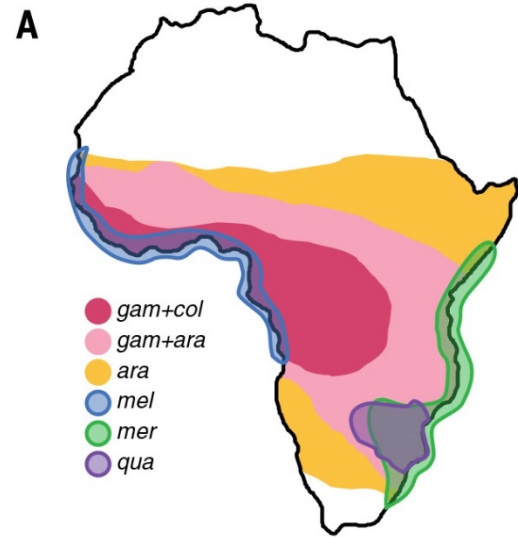
Gang Li et al. 2019. Molecular Biology and Evolution

Anopheles gambiae group, Africa

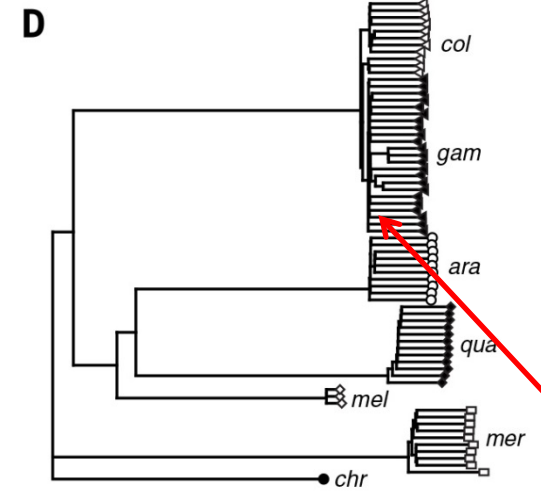


Only 2% of the genome shows this topology!

Introgression over 98% of the genome led to “whole genome tree”

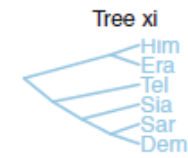
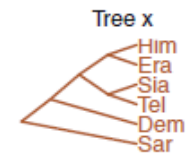
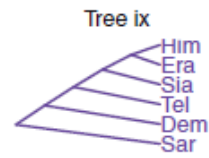
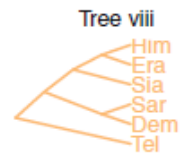
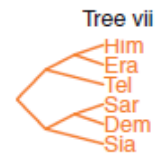
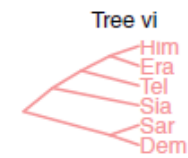
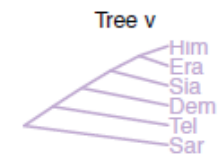
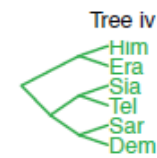
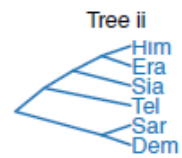
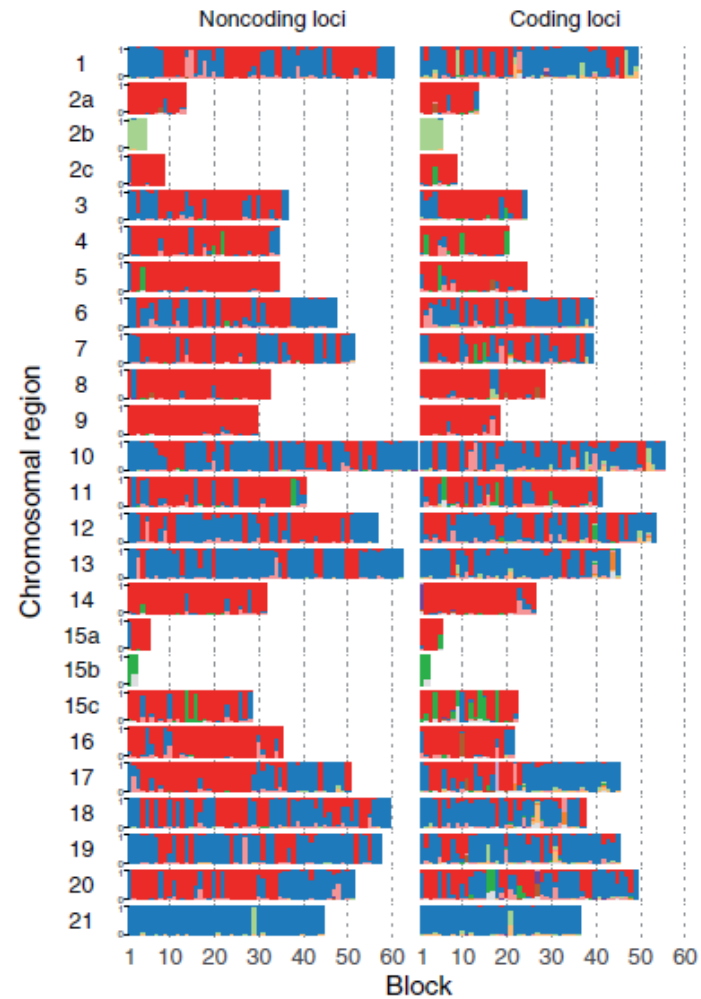


Fontaine et al. 2014 Science



X chromosome shows the “species topology”

a) Blocks of 100 loci



Heliconius species



erato



himera



hecalesia



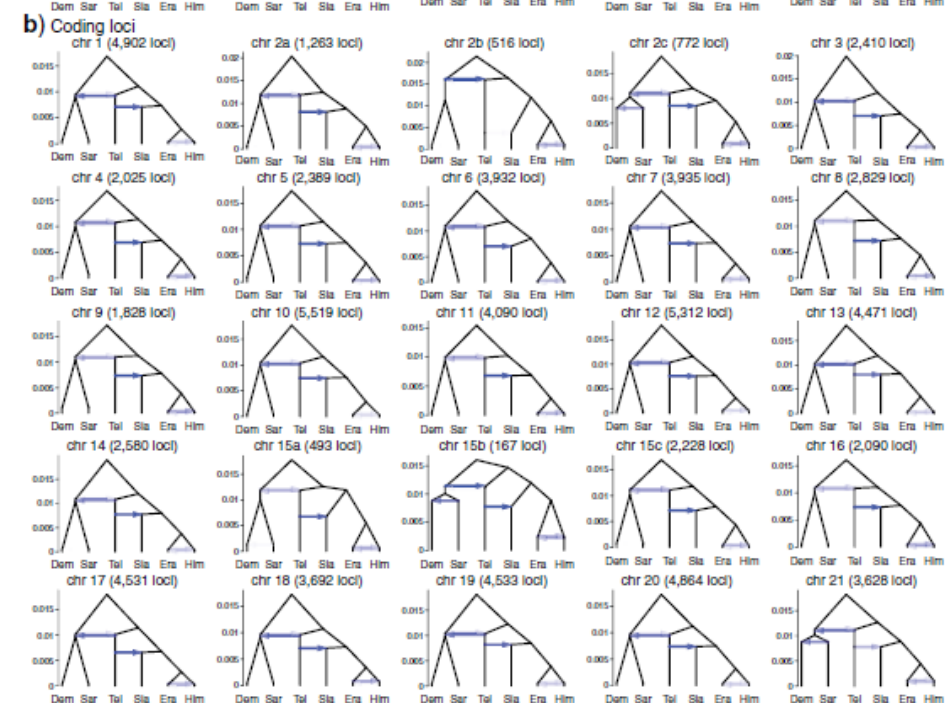
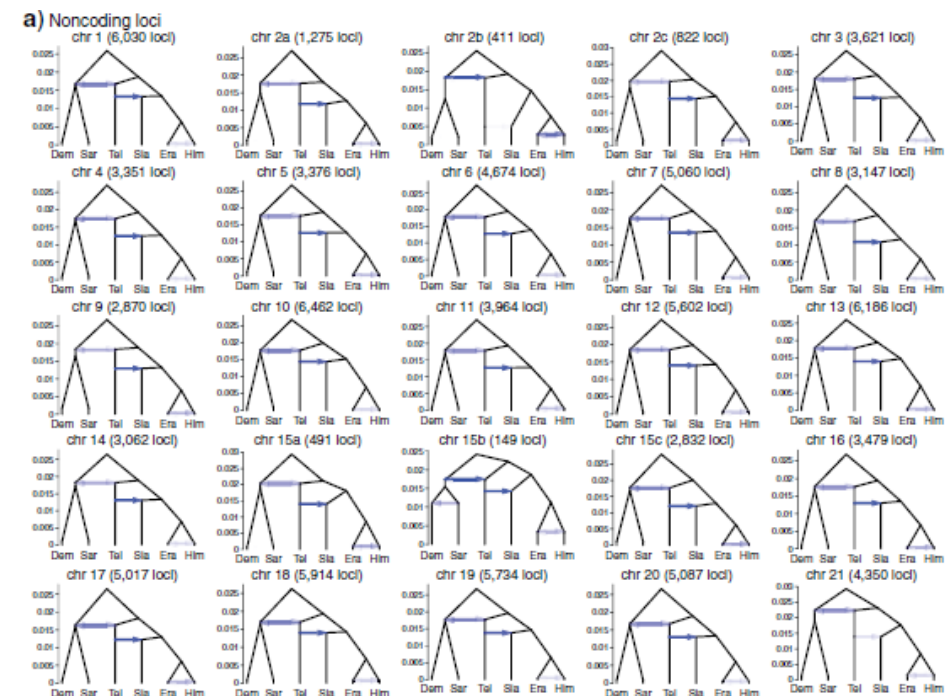
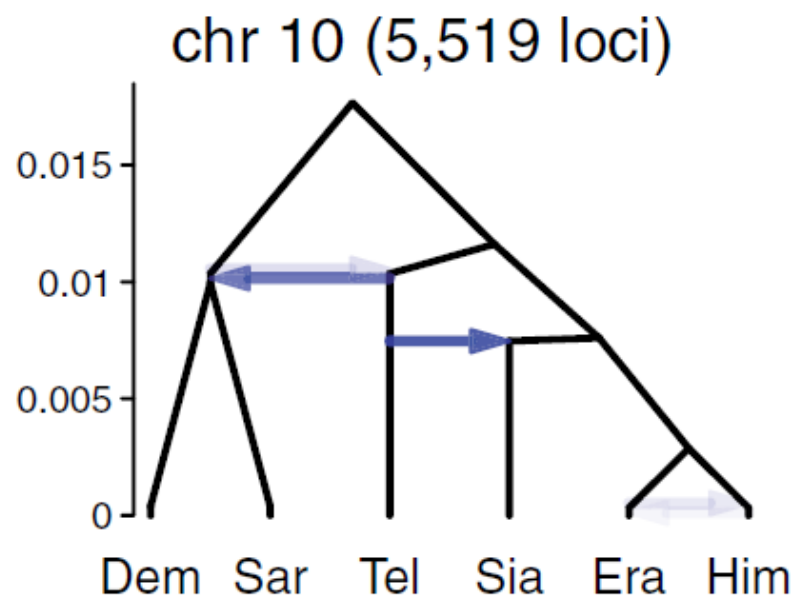
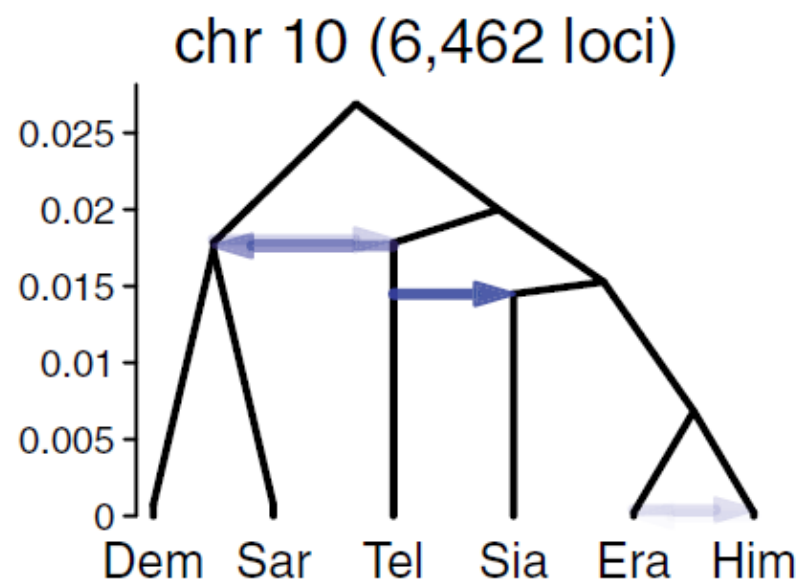
telesiphe



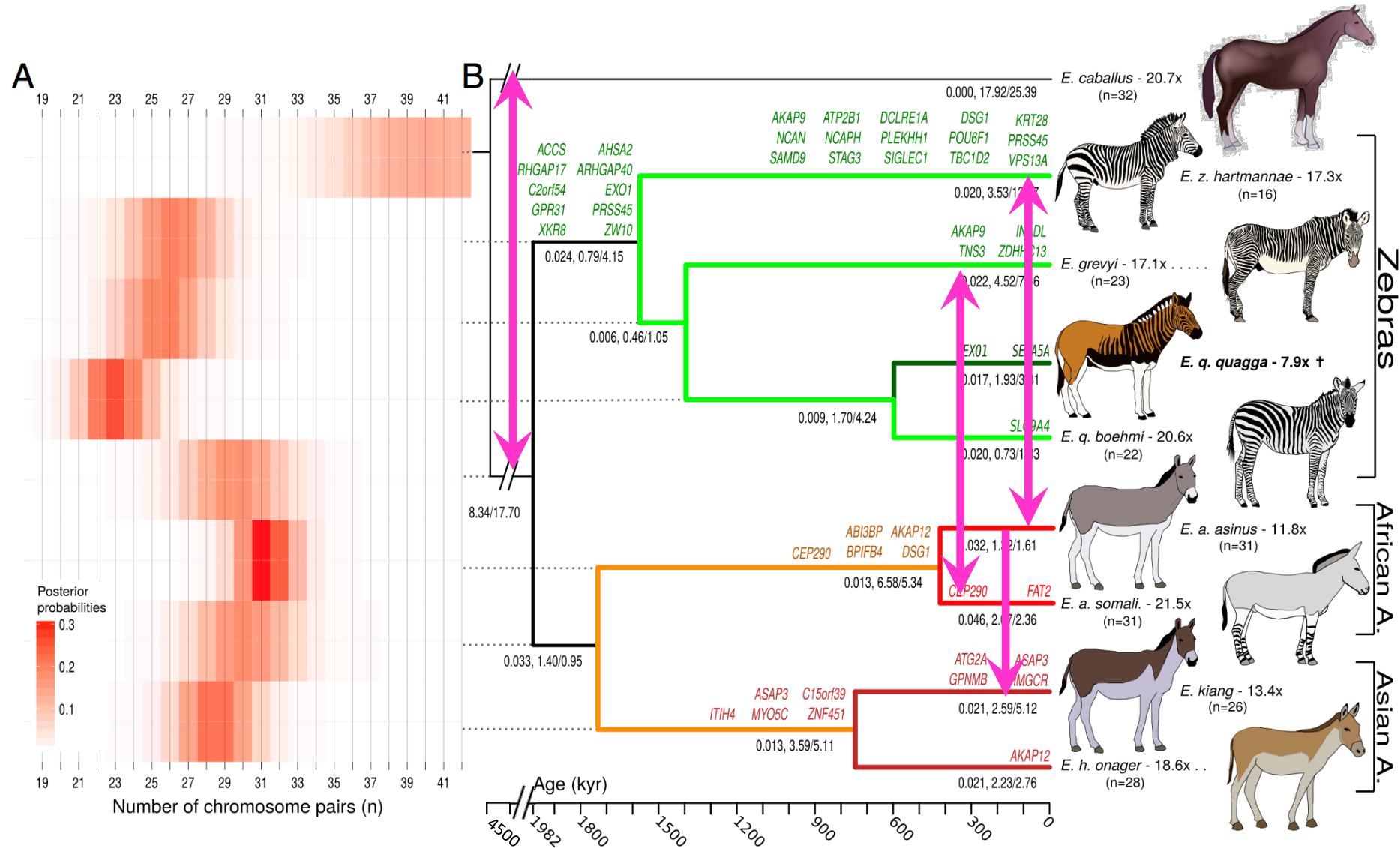
demeter



sara

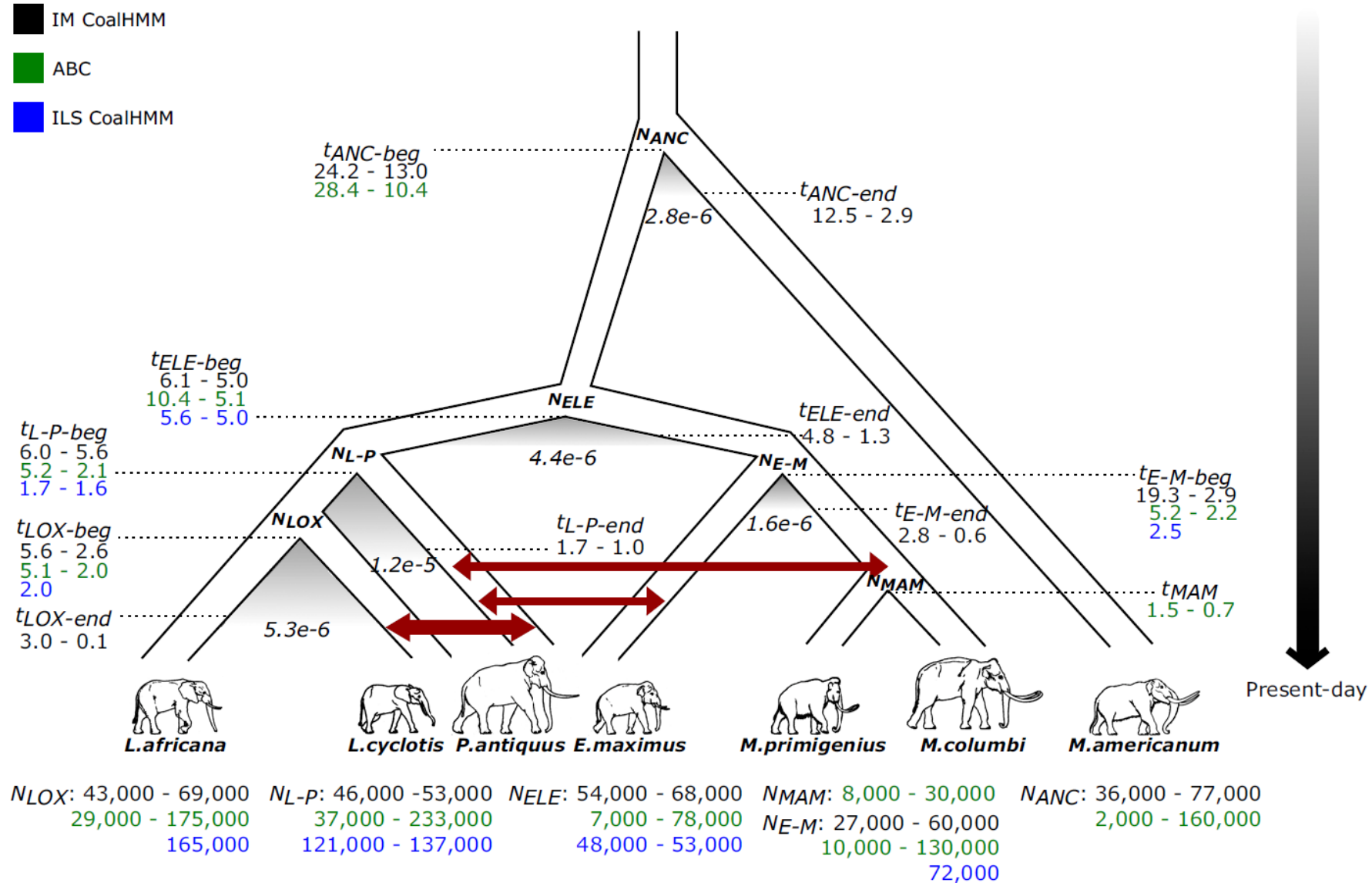


Equid genomes – introgression evidence



Jónsson et al. 2014 PNAS

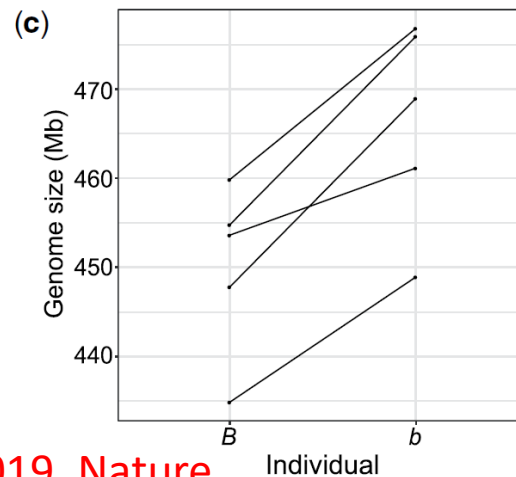
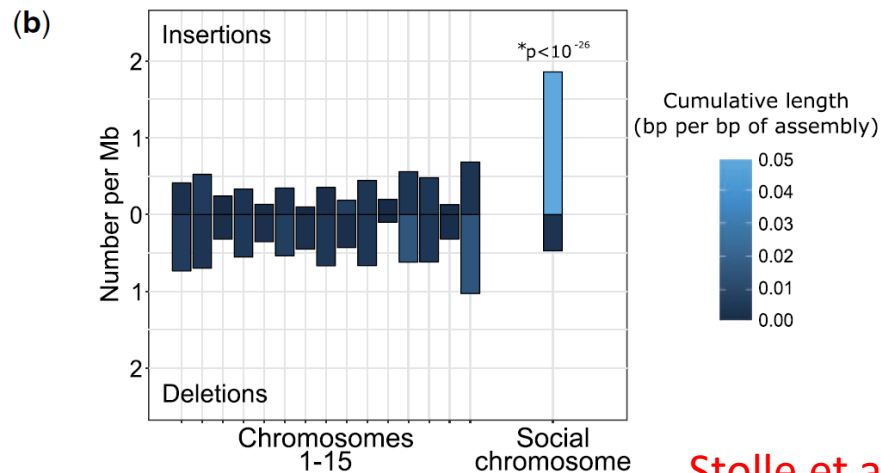
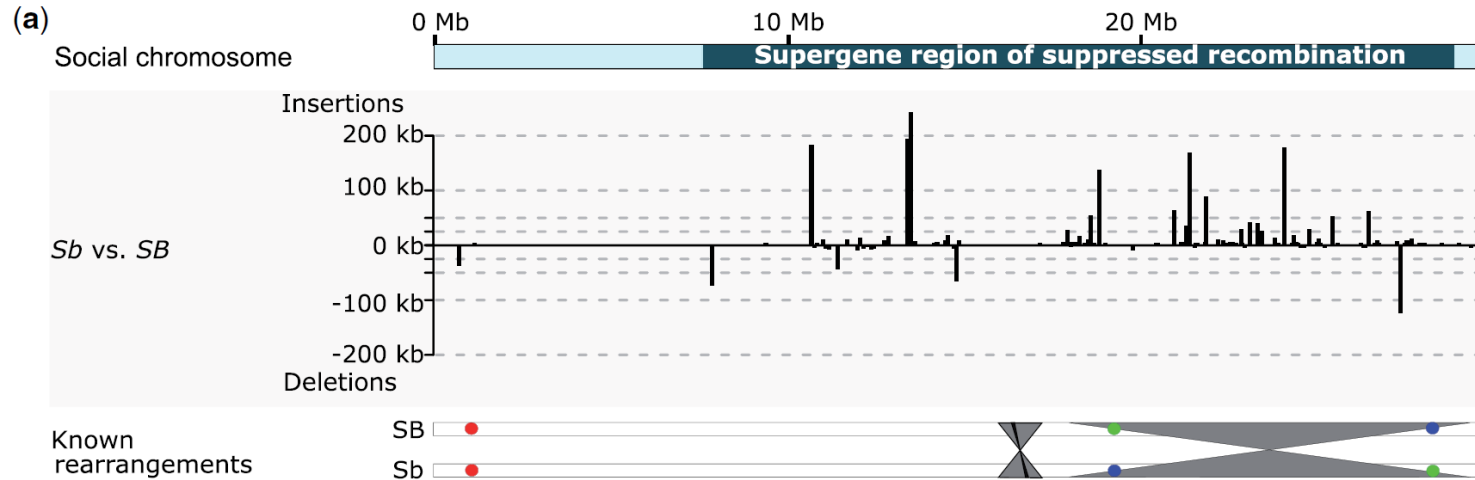
Elephants! Including mammoths and mastodon



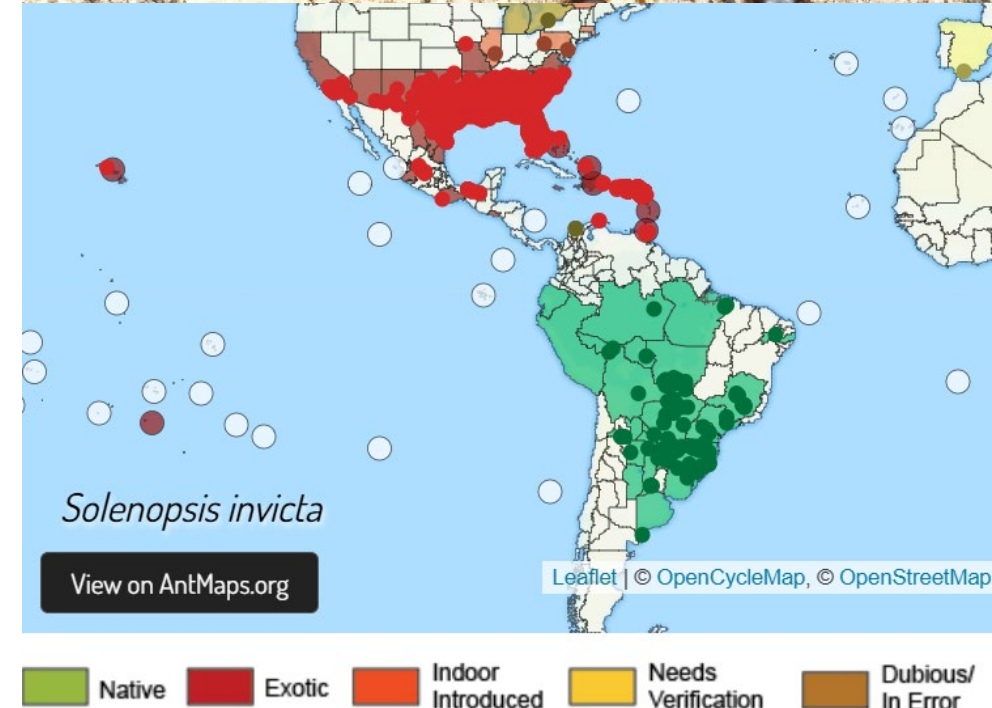
Fire ants: invasive in N. America

The “social supergene” *Sb* causes multiple queen colonies in the invasive species.

Recombination rate ~ 0



Stolle et al. 2019. Nature



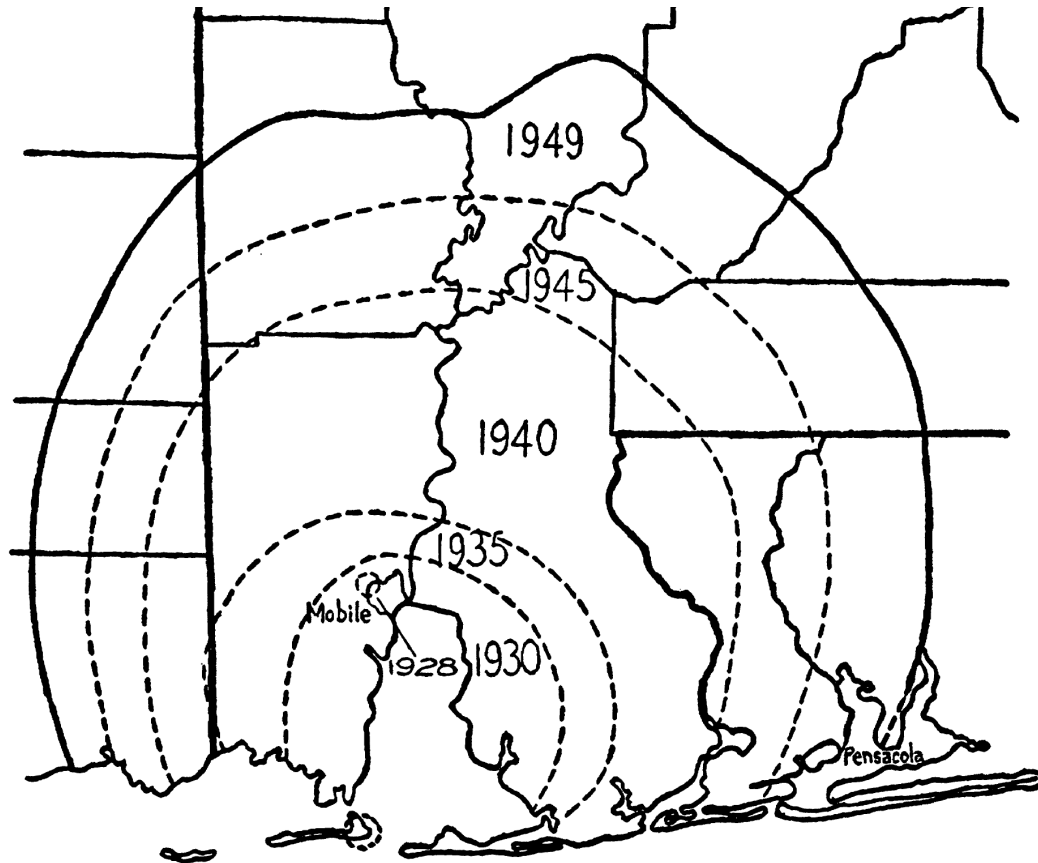


FIG. 6. ESTIMATED RATE AND DIRECTION OF SPREAD OF THE MAIN AREA OF SPREAD OF THE IMPORTED FIRE ANT, *SOLENOPSIS SAEVISSIMA*, IN THE CENTRAL GULF COAST REGION OF THE UNITED STATES, AS OF 1949

Brown 1957

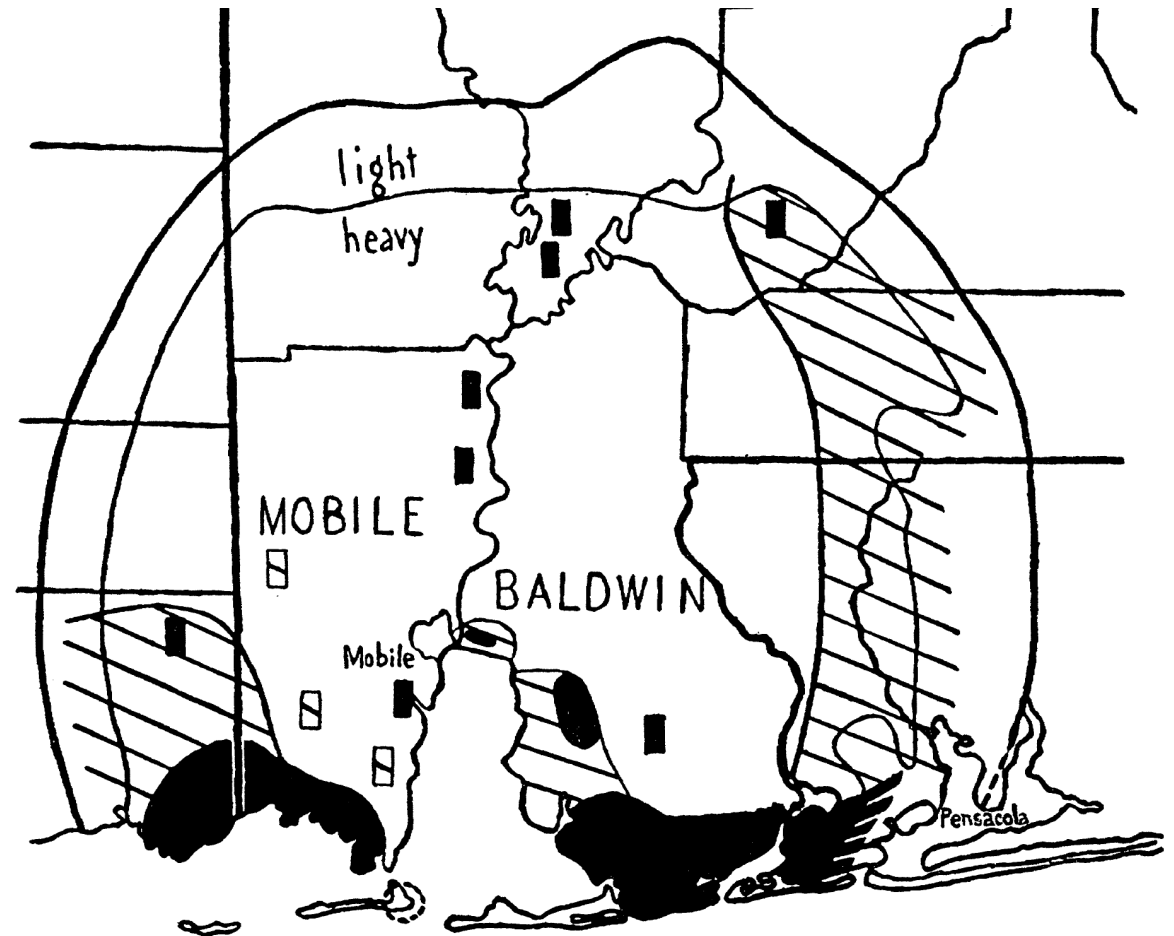
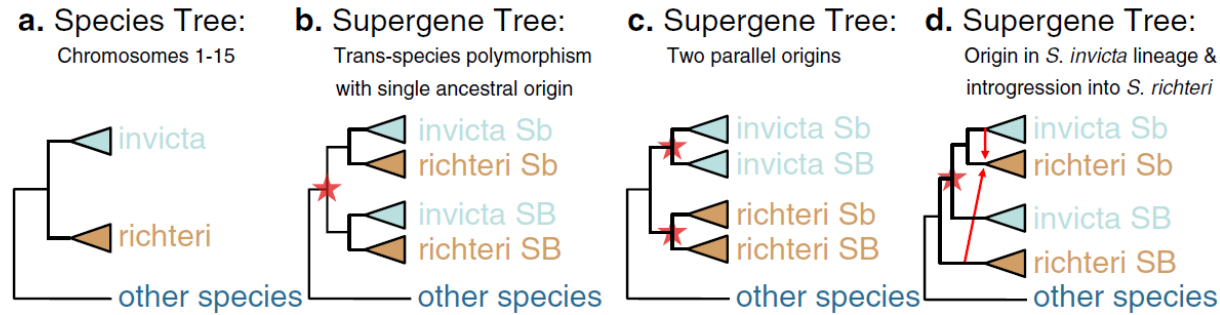


FIG. 7. DISTRIBUTION OF THE COLOR PHASES OF THE IMPORTED FIRE ANT IN THE MAIN AREA OF INFESTATION, AS OF 1949

Solid black represents areas with incidence of dark and intermediate phases of greater than 20 per cent; hatching represents areas with incidence of these phases of 5–20 per cent. Small black rectangles represent minor isolated dark-phase populations. In the centers of infestation outside the area shown in 1949, some populations were dark, others light; the present status of these is unknown. (After Wilson, 1951.)

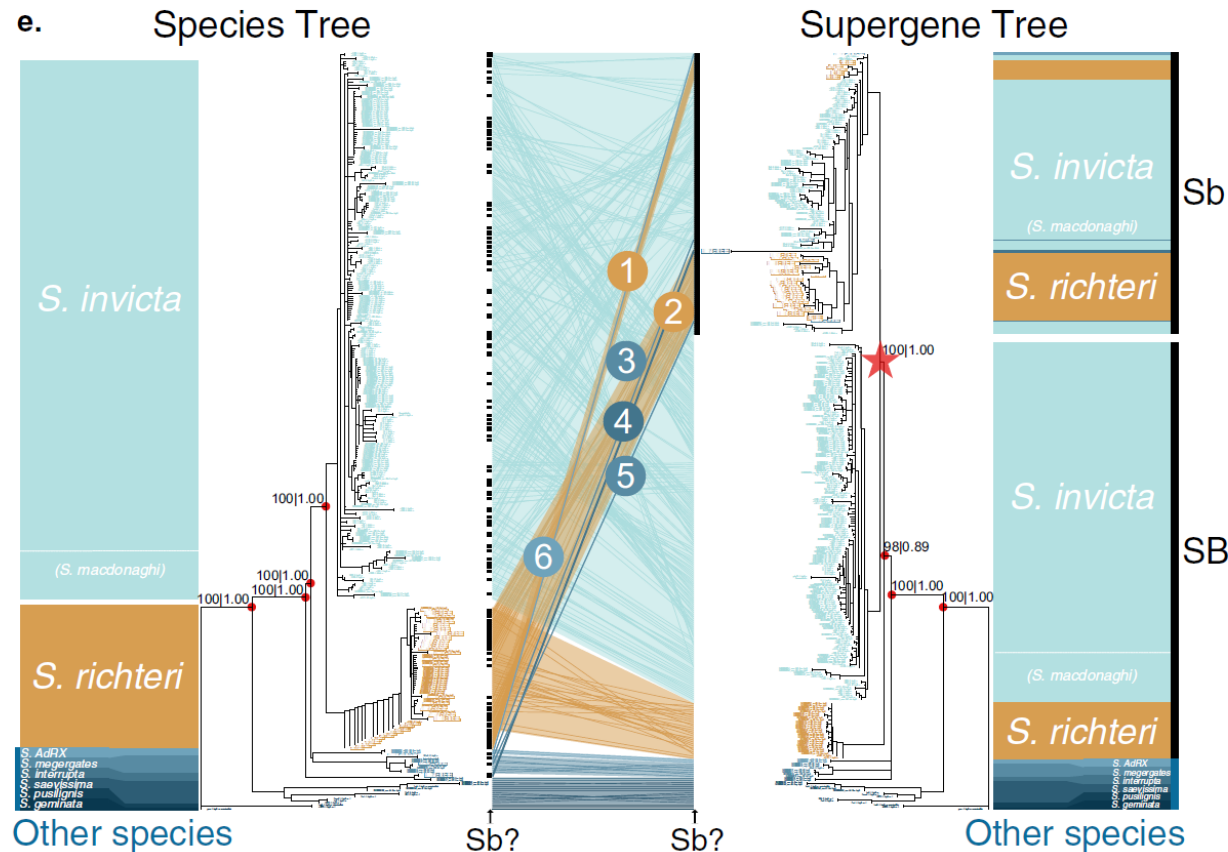
Fire ants: “adaptive introgression” of supergene



Both *Solenopsis richteri* and *Solenopsis invicta* have the same *Sb* social supergene.

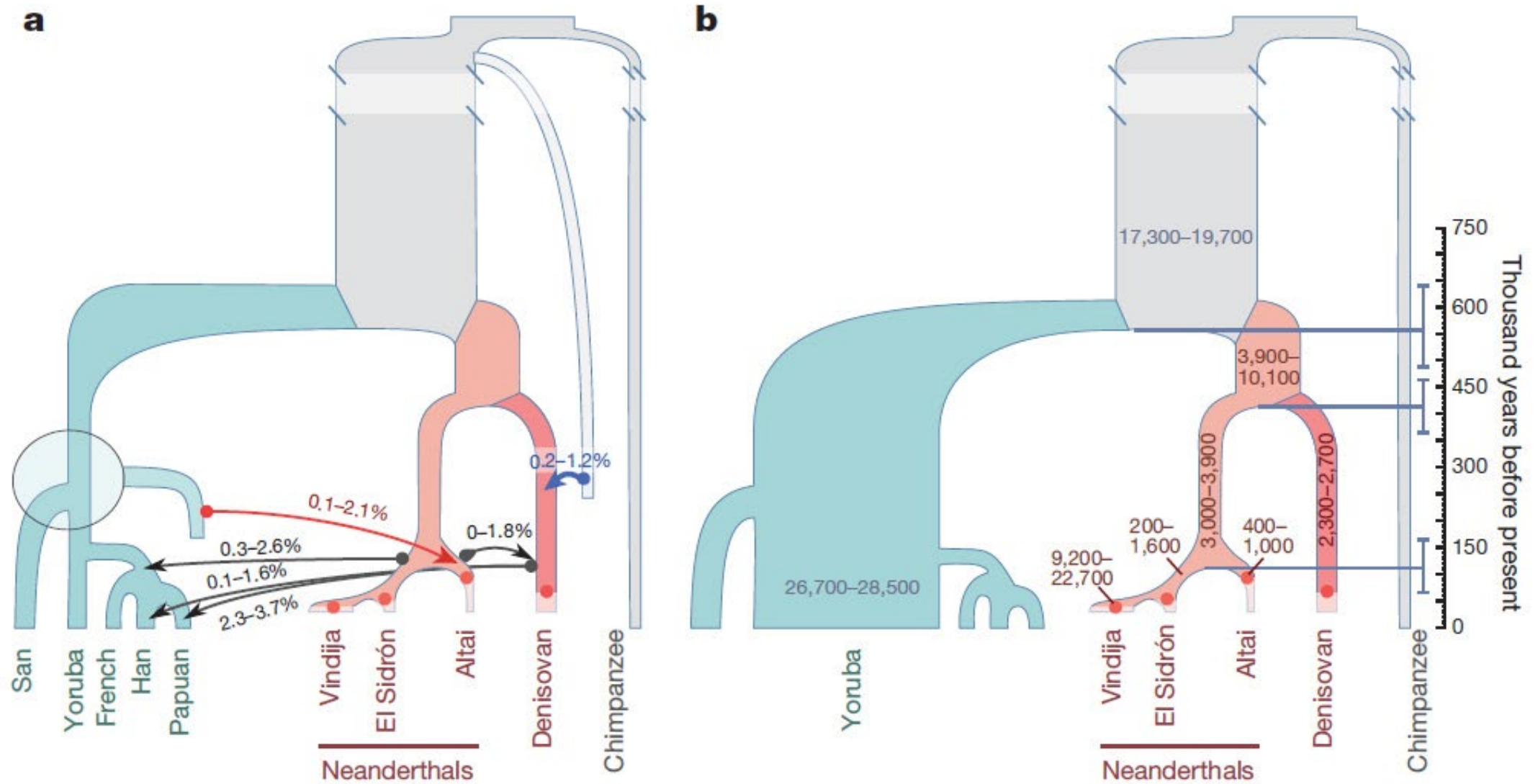
Phylogenetic discordance at the supergene: ancestral polymorphism? Or introgression?

Authors conclude: “the supergene variant responsible for multiple-queen colonies evolved in one species and repeatedly spread to other species through introgressive hybridization.”



Stolle et al. 2022. Nature Commun.

Archaic humans

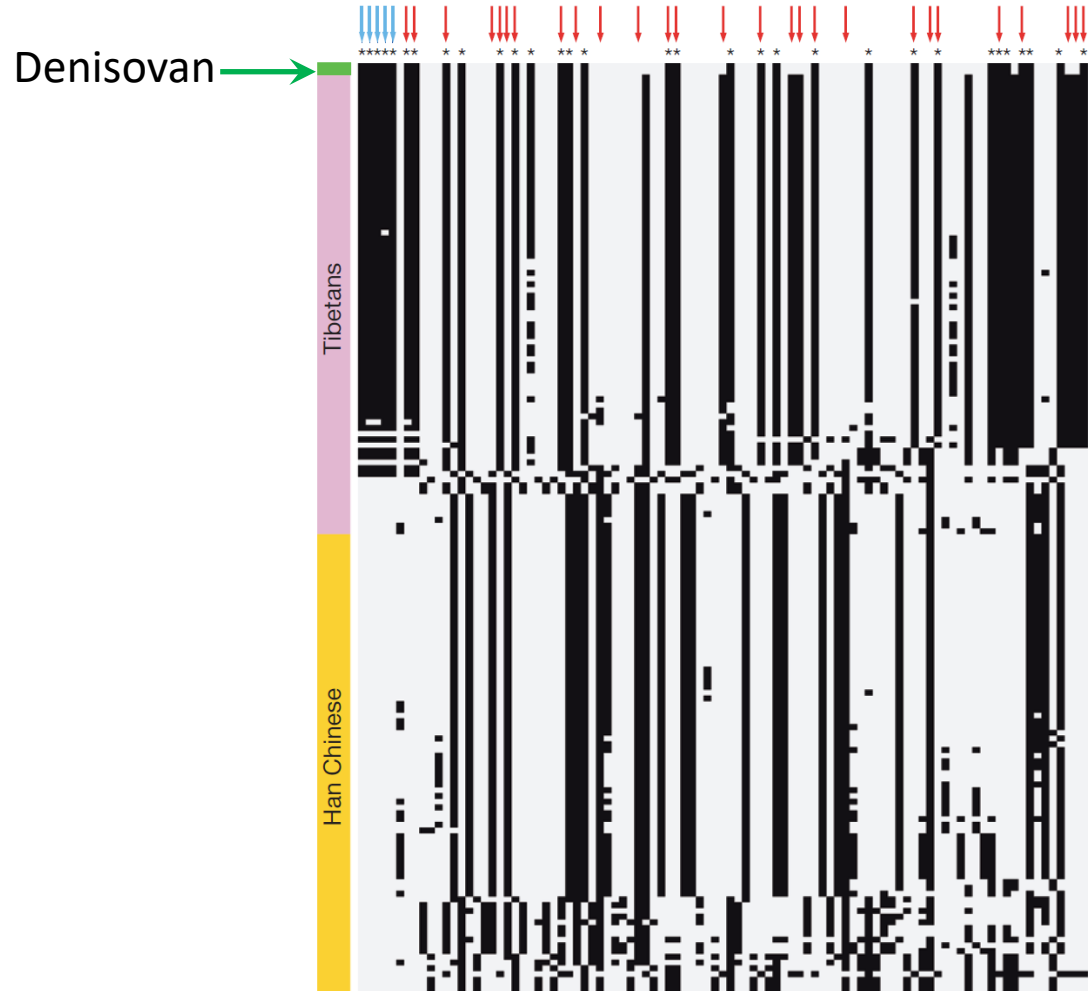


Kuhlwilm et al. 2016

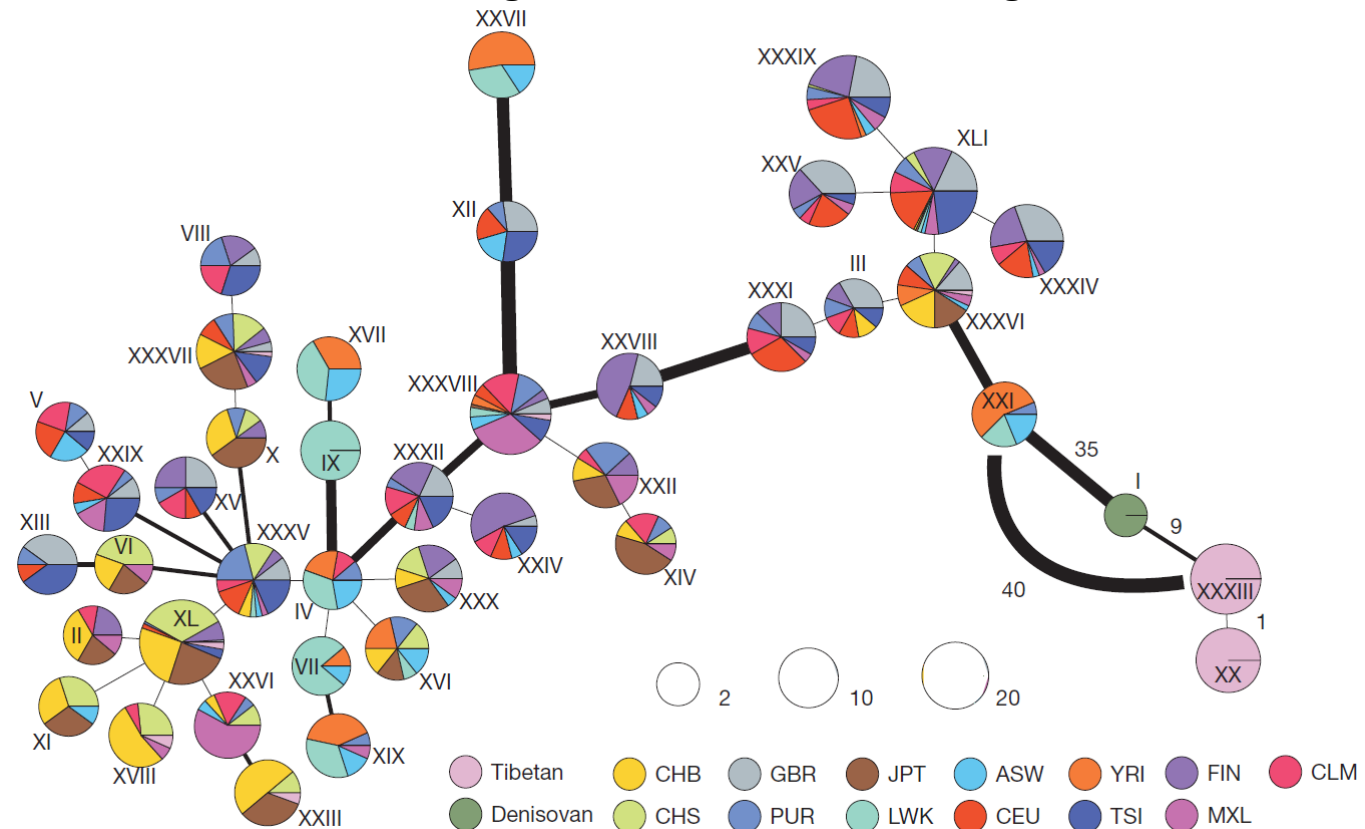
High altitude adaptation in Tibetans

EPAS1 gene, introgressed from Denisovans, Neanderthal-related lineage

A hypoxia pathway gene, *EPAS1*, has the most extreme signature of positive selection in Tibetans, and is associated with differences in haemoglobin concentration at high altitude.



Black = derived variant along sequence relative to chimp



Haplotype tree of 515 polymorphic SNPs in the 32.7 kb *EPAS1* region

Huerta-Sánchez et al. 2014 Nature

Hybridization and introgression: conclusions

- Natural hybridization between species: known to be common in plants (~25% of species?). Now appears to be common among animals too (>10% of species). More common in closely-related species.
- Hybridization is rare per individual, with estimates usually ~0.1% or less in animals, but sometimes up to ~5% (Darwin's finches, Apple maggots)
- Hybrids often less fit (hybrid inviability, sterility; Haldane's Rule)
- So, could introgression be important? In plants, yes (Anderson 1940s)
- In animals, as well as plants, recent genomic data confirms the importance and adaptive uses of introgression in many groups of species
- a) Species concepts, b) phylogeny estimation, c) comparative biology
 - All much more difficult than we had thought in pre-genomic days!

ABBA-BABA test in mimicry gene contig

