

# GEOGRAPHIC SUBSPECIFIC VARIATION



# Subspecies concept

- Darwin showed that there was no essential difference between species and “varieties”; species were simply varieties which had diverged more, and which could coexist without intermediates being common.
- However, with his term “varieties” Darwin did not clearly distinguish between polymorphic variants within populations and the identifiable geographic populations normally today considered as geographic “races” or “subspecies.”
- To Darwin the distinction was unimportant, because polymorphic variants, clinal variation, geographic races or subspecies, and “good” species formed a continuum. Darwin demonstrated that this continuum was excellent evidence for an evolutionary origin of the taxa we call species.
- Geographic replacement forms, subspecies and semispecies, would be incipient species,

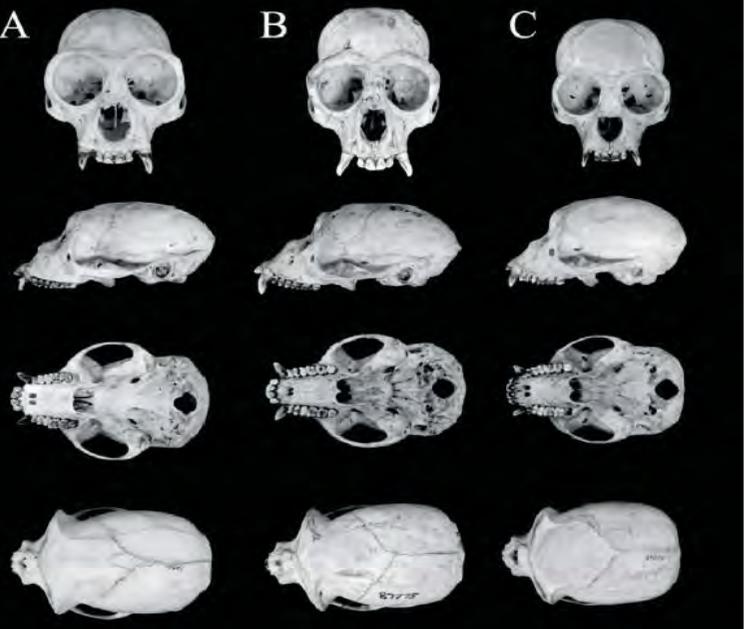
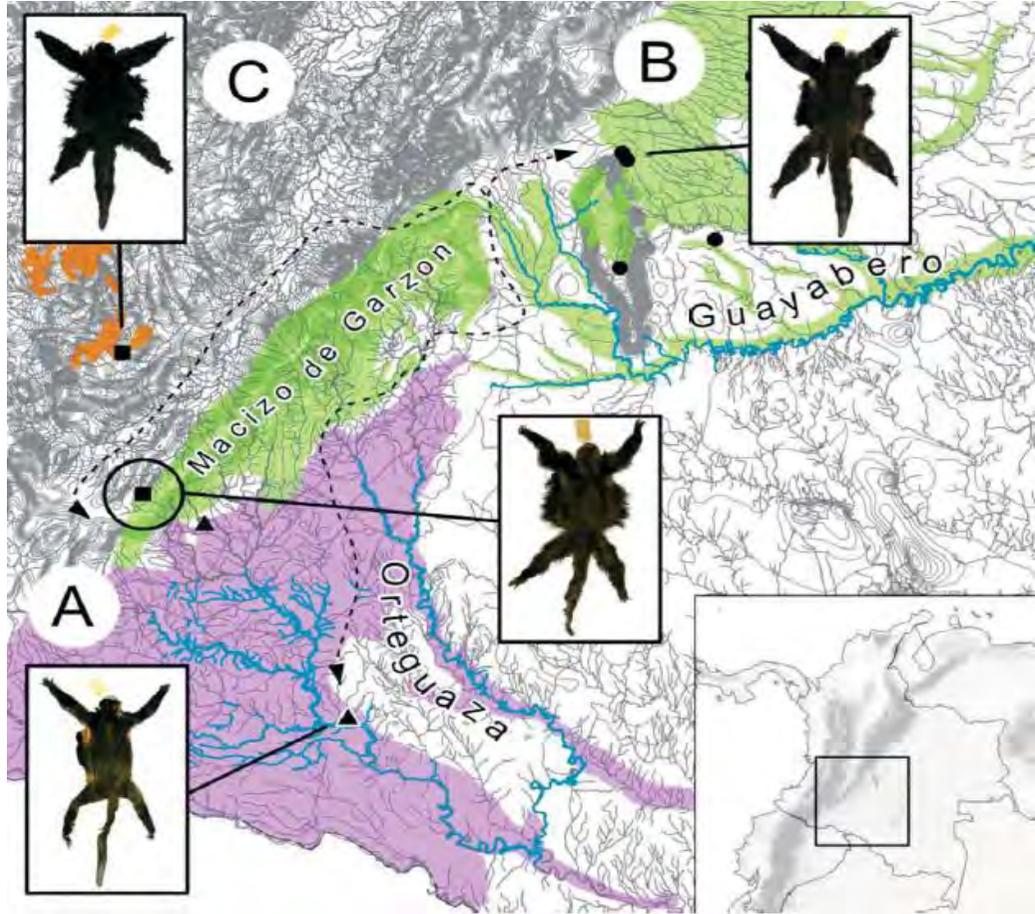
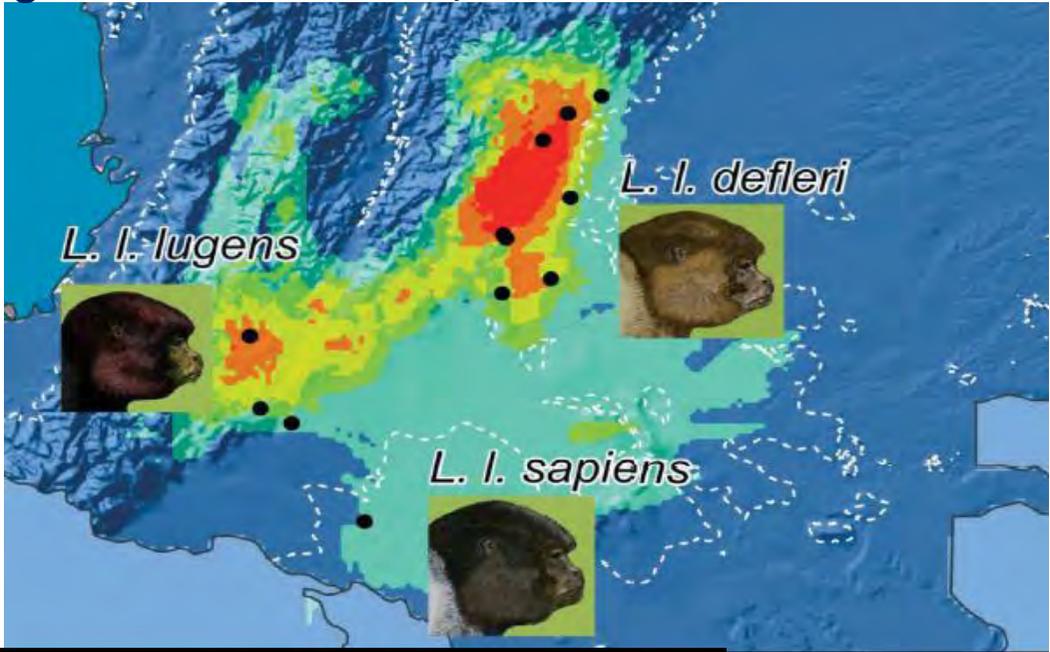
# Geographic variation

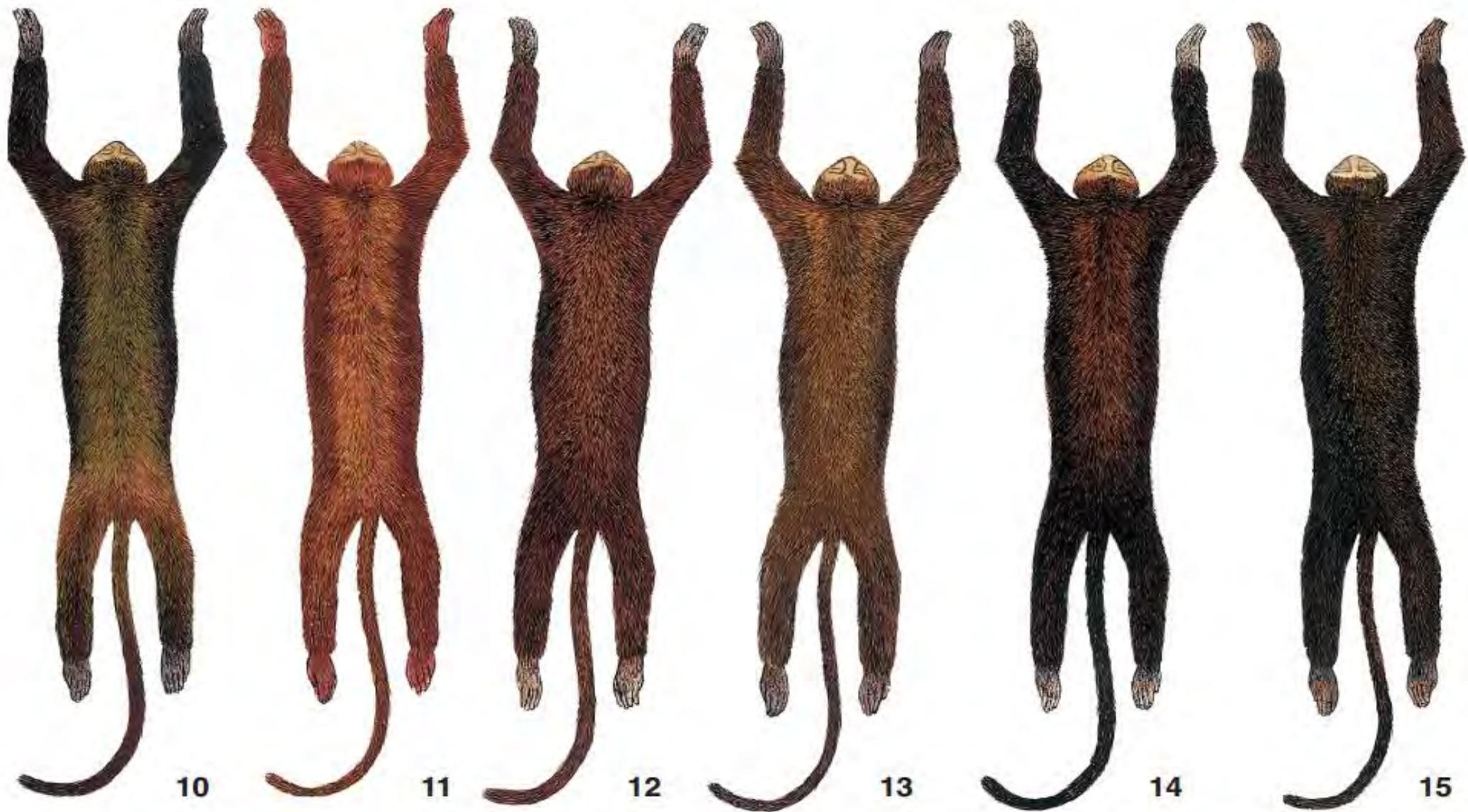
- Darwin showed that there was no essential difference between species and “varieties”; species were simply varieties which had diverged more, and which could coexist without intermediates being common.
- In progress allopatric speciation may be a good example of the subspecific variation due to geographical migration/separation.
- *Lagothrix lugens* (Primates: Atelidae) demonstrate that geographical variation (allopatric speciation) may lead to the rise of different morphotypes, variants or subspecies.

## Bibliography:

- Gregorin R. 2006.** Taxonomia e variacao geografica das especies do genero Alouatta Lacepede (Primates, Atelidae) no Brasil. Rev. Bras. Zool. 21(3): 64-144.
- Mantilla-Meluk, H. 2013.** Subspecific Variation: An Alternative Biogeographic Hypothesis Explaining Variation in Coat Color and Cranial Morphology in *Lagothrix lugens* (Primates: Atelidae). : Primate Conservation, 26(1):33-48.
- Mallet, J. 2001.** Subspecies, semispecies, superspecies. - pp. 523-526, in: Levin, S. A.: Encyclopedia of biodiversity. Volume 5. R-Z. -- pp. i-xxxii [= 1-31], 1-1103. Amsterdam. (Elsevier).

Figures: Mantilla-Meluk, H. 2013.





Gregorin 2006

# Wilson and Brown's (1953): critique of currently named subspecific taxa

- \* much discordance among character sets
- \* polytopy
- \* microgeographic variation
- \* arbitrariness in delimitation
- \* rapid subspeciation

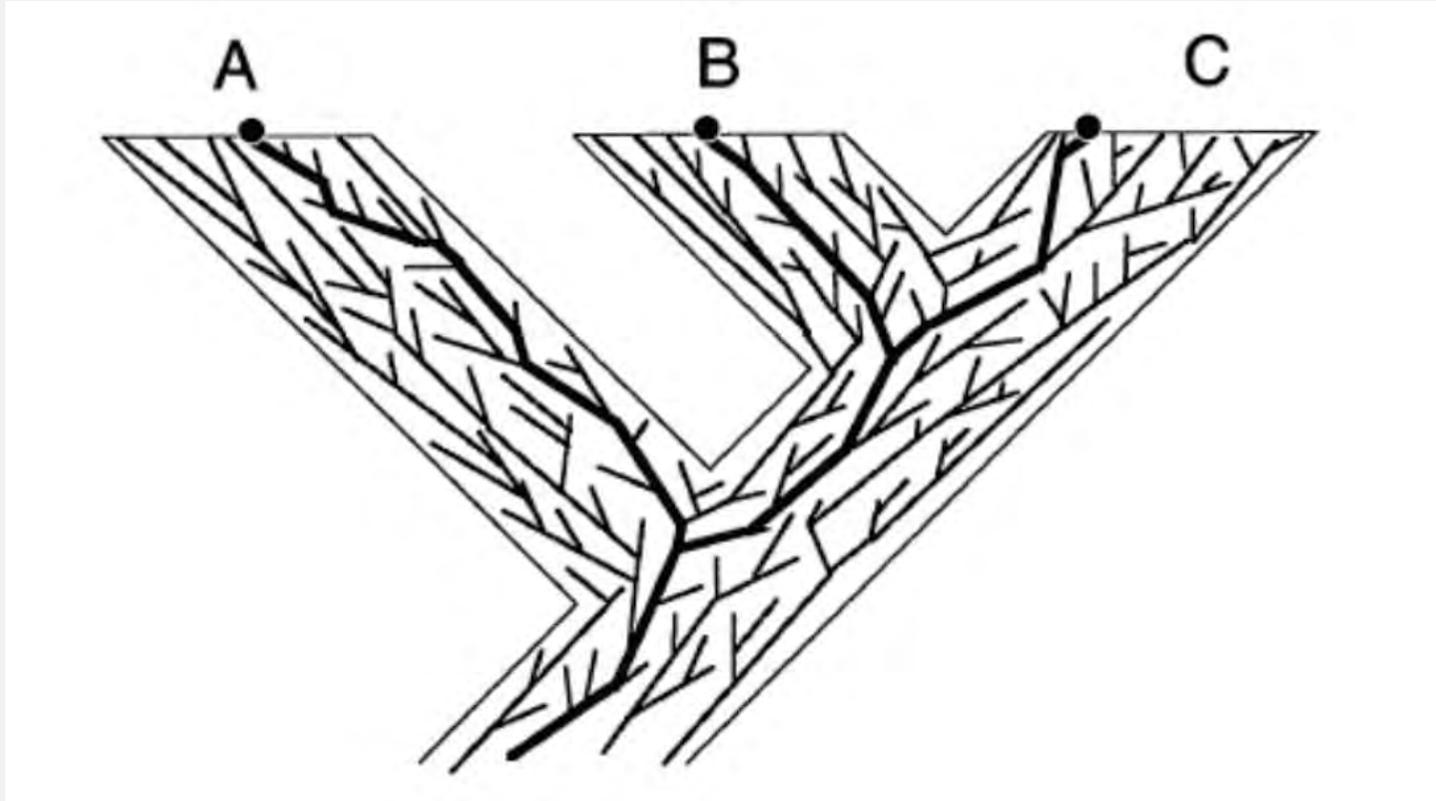


# Recommendations

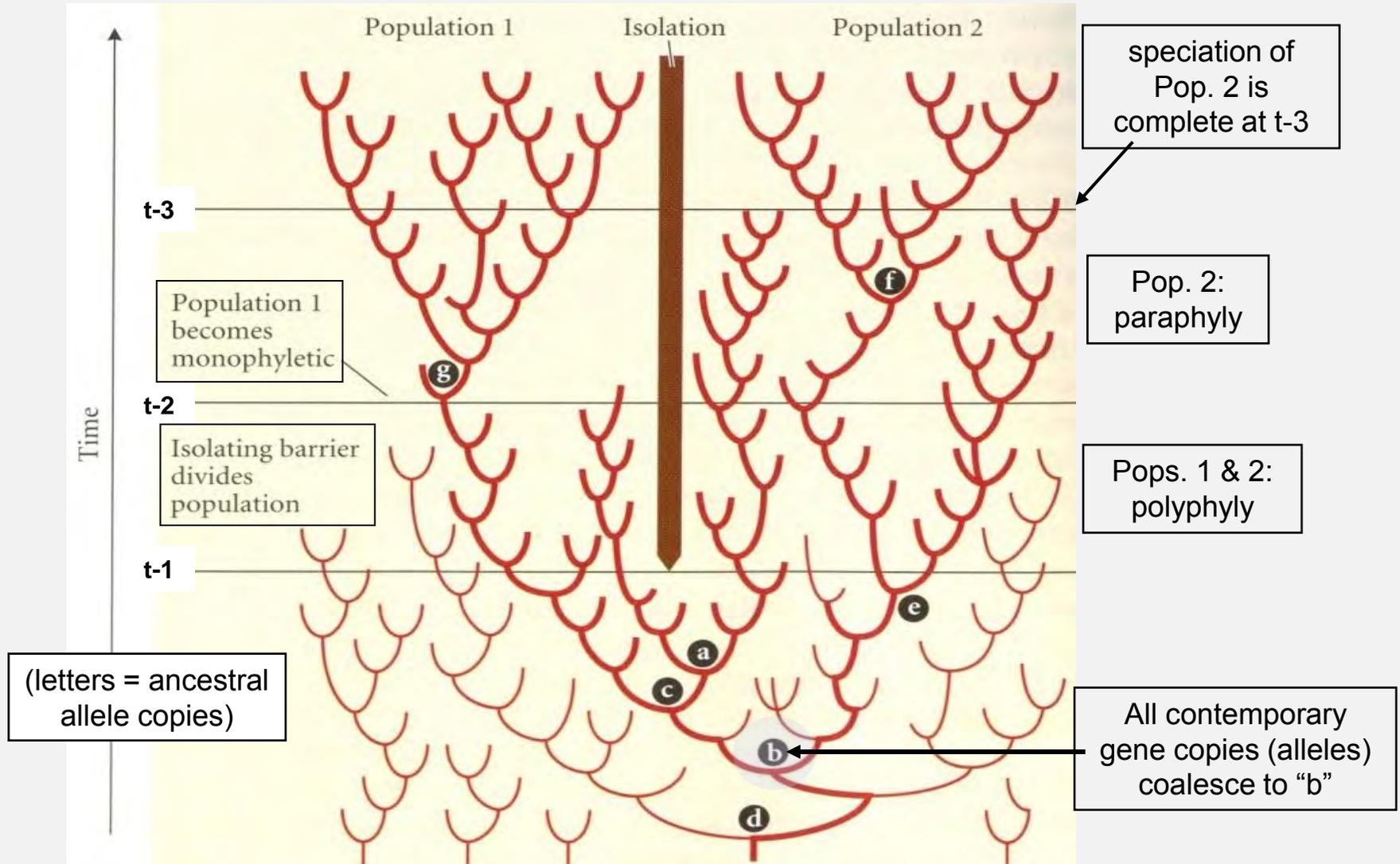
1. Consider biogeographic history of the area and species that are under study then
2. Sample thoroughly within and between populations
3. Employ multiple characters, avoid according much weight to one or a few characters, esp. those under obvious selection
4. Employ (selectively neutral) molecular characters where possible

Bottom line: focus on identifying meaningful **evolutionarily significant units**

# Gene Trees versus Species Trees



Lineages of haplotypes (allele polymorphisms) at a single locus: transition from polyphyly to paraphyly to monophyly during speciation (Avisé & Ball 1990)

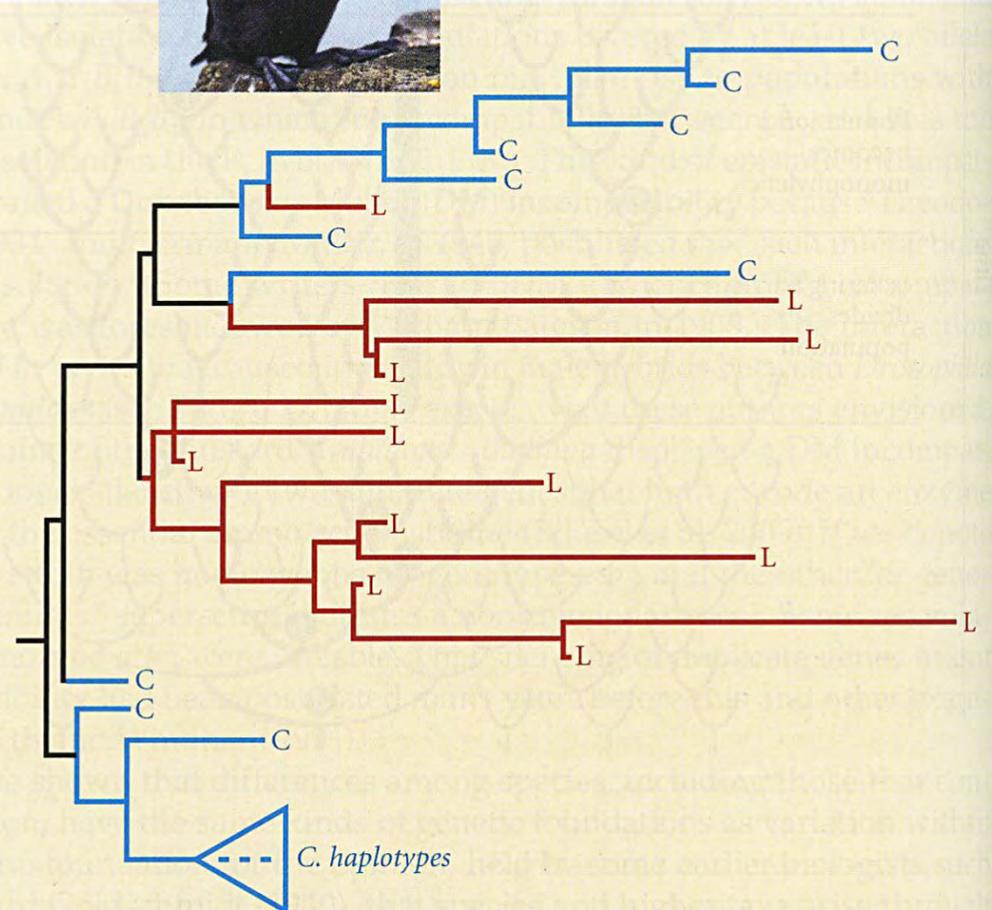


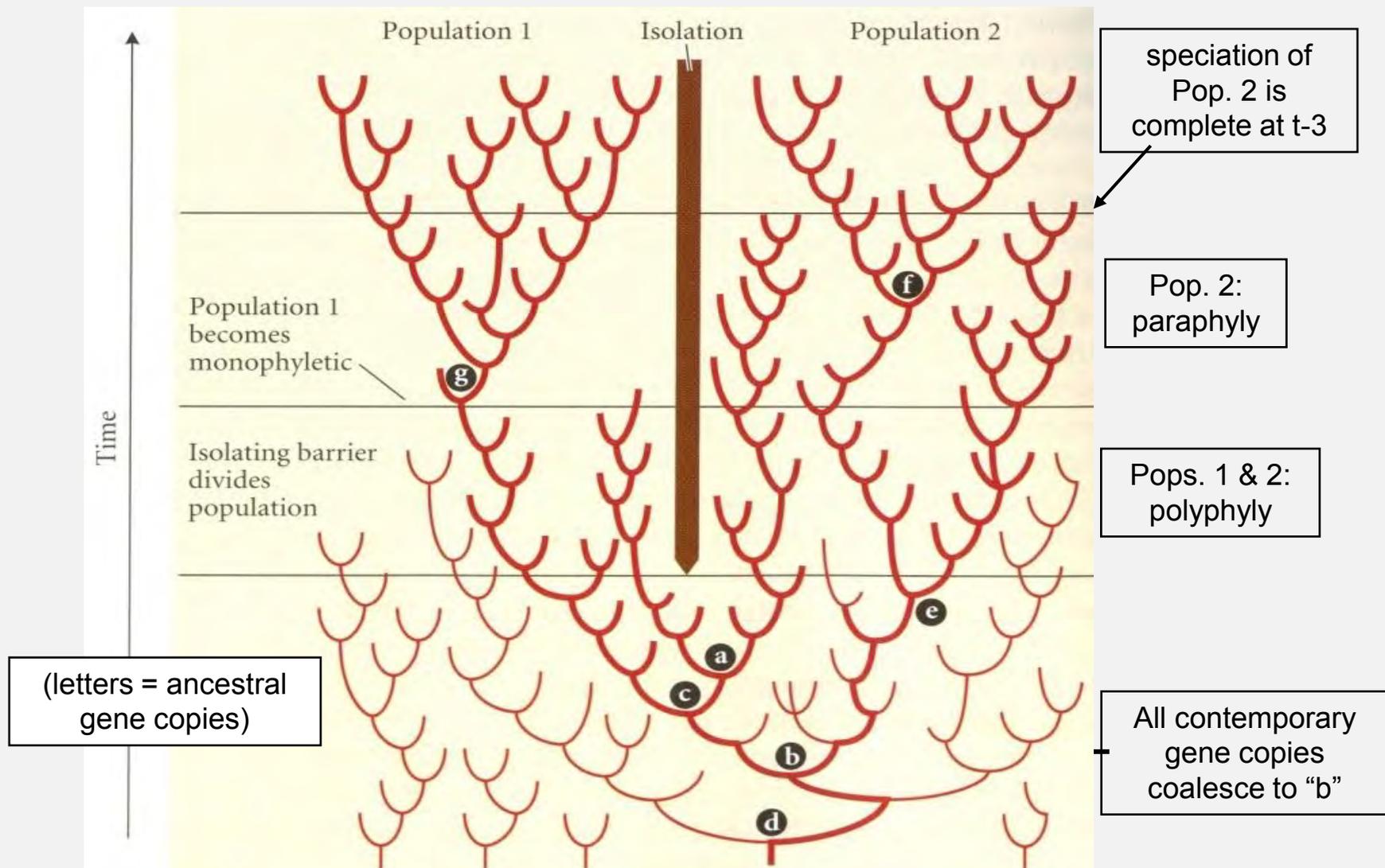
**FIGURE 17.16** Incomplete lineage sorting results in a polyphyletic gene tree for the  $\alpha$ -enolase locus in two closely related seabird species. Blue (C) and red (L) branches mark haplotype lineages found in the crested auklet (*Aethia cristatella*) and the least auklet (*A. pusilla*), respectively. (After Walsh et al. 2005; *A. cristatella* photo courtesy of Art SOWls, U.S. Fish and Wildlife Service.)

Crested Auklet

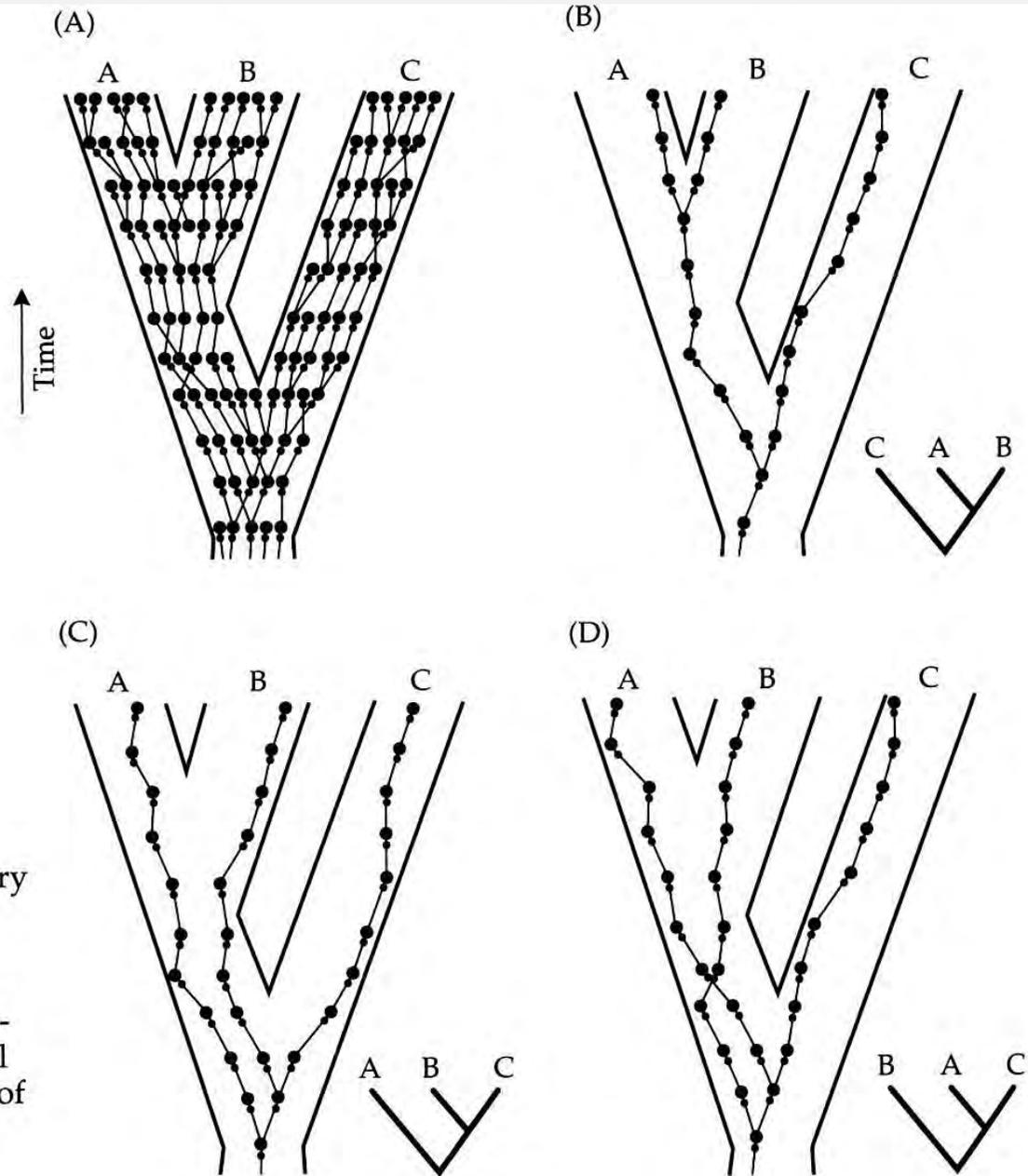


Least Auklet





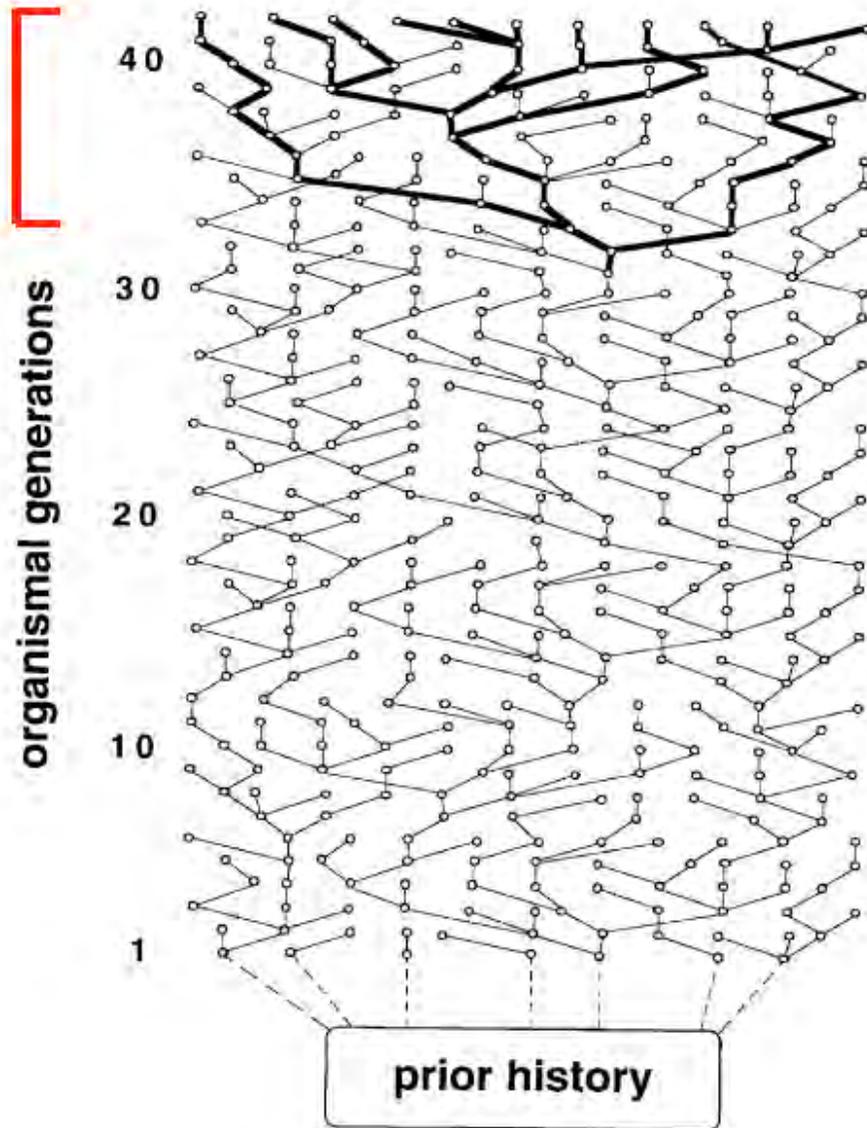
Once two populations become separated (by a barrier to gene flow) their genes will go from being polyphyletic to paraphyletic to reciprocally monophyletic (through drift and selection). Reciprocally monophyletic = when all copies of a gene within one lineage are all more closely related to one another than any outside (= exclusivity)...when gene and species trees become identical (again).

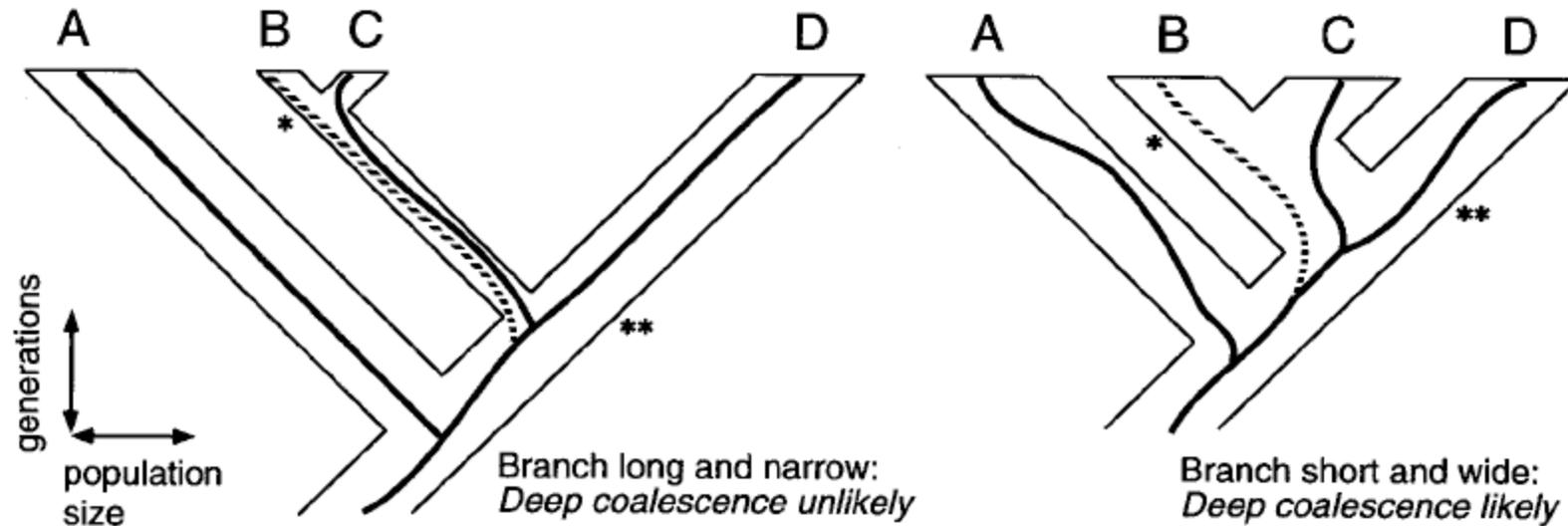


**Figure A.2** Gene sorting occurring in a phylogeny whose true population history is shown in (A). Depending on which gene copies are picked for analysis, one can derive all three possible phylogenies, shown by the small diagrams to the lower right of diagrams (B), (C), and (D). (After Hey 1994.)

Time to  
monophyly

Time to monophyly  
depends on the  
population size and  
the number of  
generations, and is  
 $\sim N_e$  generations





- \* As a result of an ancestral polymorphism, in both trees, the gene tree does not equal species tree (because C and D appear to be more closely related than either is to B)
- \* Gene tree/species tree conflict (aka deep coalescence, lineage sorting, etc.) less likely when branches long, narrow, and well spaced (because allele extinctions eliminate the problem)
- \* Gene tree/species tree conflict likely when branches short, thick, approximate

Expected time to monophyly for neutral mitochondrial and nuclear genes  
(values are times in units of  $N_e$  generations)

Number and location of loci	Probability reciprocal monophyly			Probability monophyly		
	0.05	0.50	0.95	0.05	0.50	0.95
1 mitochondrial	0.38	0.94	2.20	0.29	0.71	1.80
1 nuclear	1.50	3.80	8.70	1.20	2.80	7.30
5 nuclear	4.00	6.70	11.80	3.00	5.50	10.50
15 nuclear	6.00	8.90	14.10	4.80	7.60	12.80
25 nuclear	7.00	9.90	15.20	5.70	8.60	13.90
11,500 nuclear	19.10	22.1	—	17.90	20.80	26.30

Source: Hudson and Coyne, 2002

- \* mitochondrial genes coalesce 4x more quickly because only female gametes carry mitochondrial and only a single haplotype is represented in gametes
- \* for nuclear genes need about 8-24  $N_e$  generations for monophyly, i.e., for expectation that any set of genes will recover the species tree

# Infrasubspecific variation :

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Photo: Anders Forsman

- \* Good systematics depends on the proper recognition and understanding of variation over many evolutionary levels the species---> subspecies---> population---> individual
- \* today focus on **outwardly detectable phenotypic differences** below the subspecies level (i.e., within a population)
- \* emphasize examples of a nature that could complicate systematic studies...especially in unfamiliar area or if you have limited samples

# Infrasubspecific variation

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## **Population Variation**

= phenotypic variation among individuals in a single population

- \* polymorphisms
- \* sexual dimorphism

## **Phenotypic Variation Within Genotypes**

- \* ontogenetic changes
- \* seasonal forms and cyclomorphosis
- \* sexual vs. asexual life forms
- \* phenotypic plasticity



Darker  
variant

Lighter  
variant

## The Carniolan honey bee *Apis mellifera carnica*

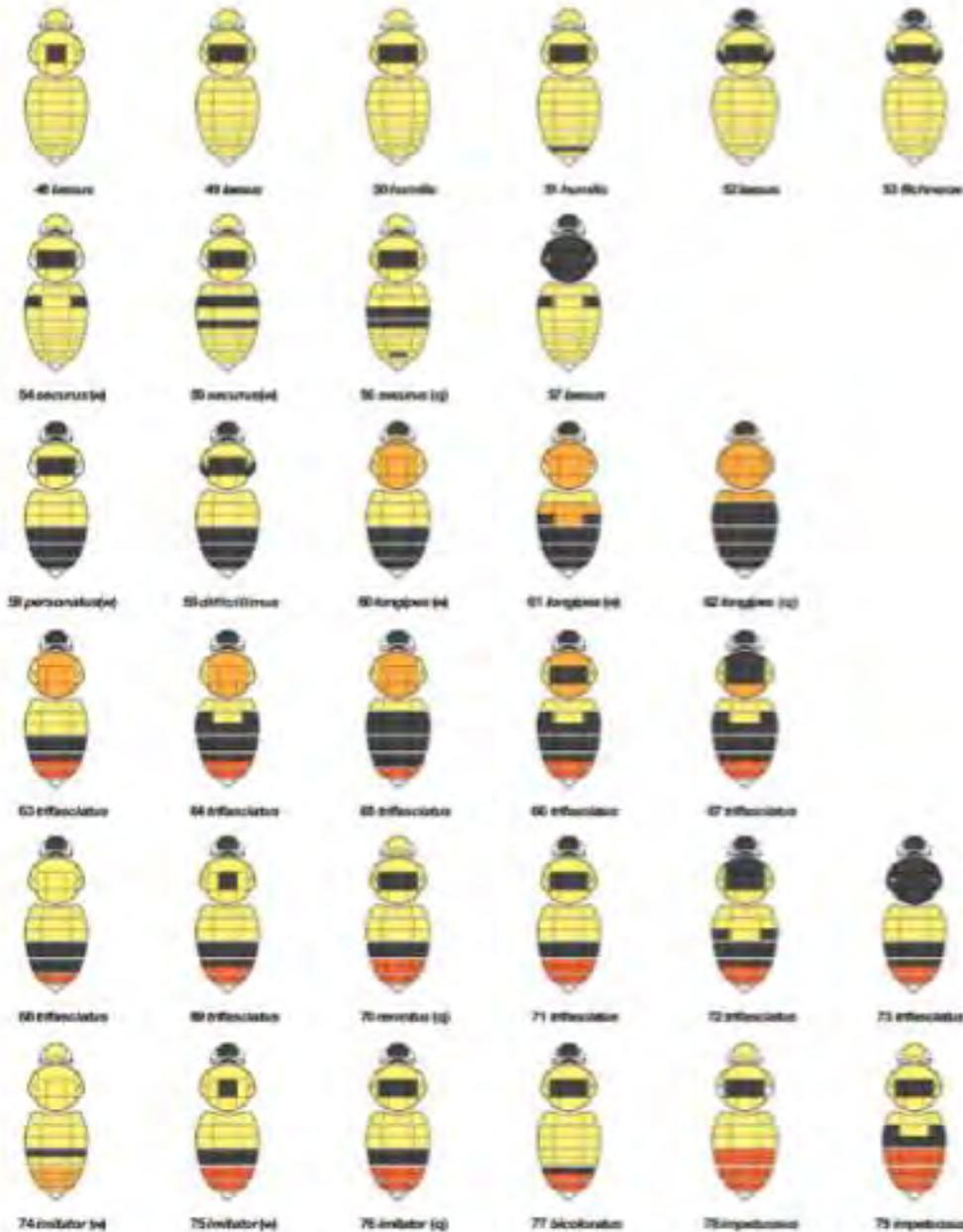
Subspecies of the western honey bee, *Apis mellifera*

# Infrasubspecific variation

Color morphs of the  
bumblebees of Sichuan, China

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Figures 48–79 Guide to species by simplified colour-pattern diagrams for females (queens [q] and workers [w]). The dorsum of the body is artificially divided into an arbitrary set of regions, which are classified into seven colour classes.

& 1/2 China's bee diversity and 1/5 world diversity of bumblebees in this area

& 65 recognized species that have 847 names

& Many different color patterns, some infrasubspecific



# More Bears in BC

*Ursus americanus kermodei* Hornoday, 1905

"The Spirit Bear"

Restricted to costal BC and islands inside the Hecate Strait. White form estimated at 10%.



*Platycotis vittata*, the Oak Treehopper



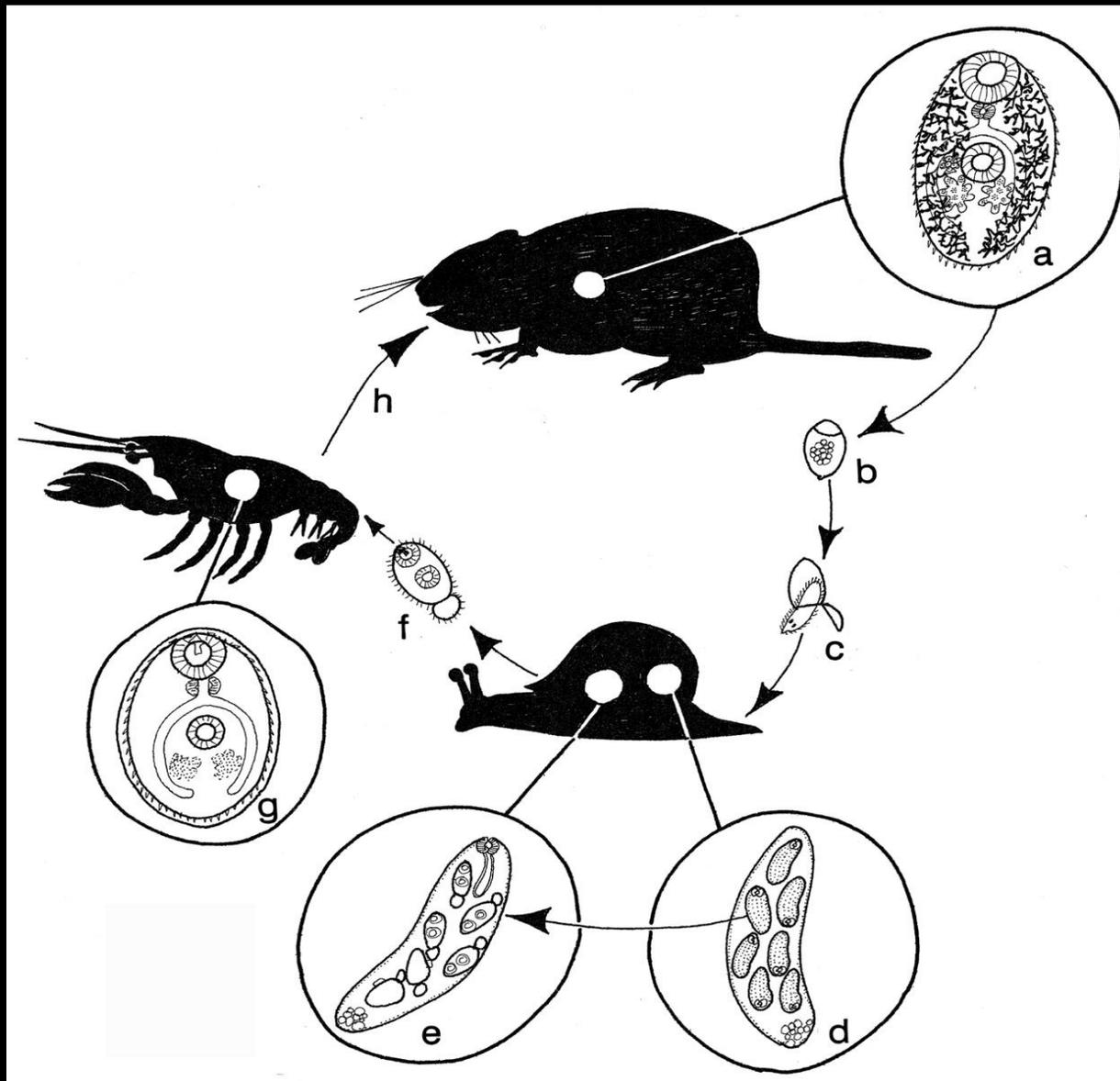




left: exposed to predators; right: same species and sex, not exposed to predators; source: [Agrawal \(2001\)](#)



Ptarmigan sexual and season dimorphism



7 Life stages in many Trematodes

*Brassica oleracea*

