
Sense and nonsense of
SPECIES CONCEPTS
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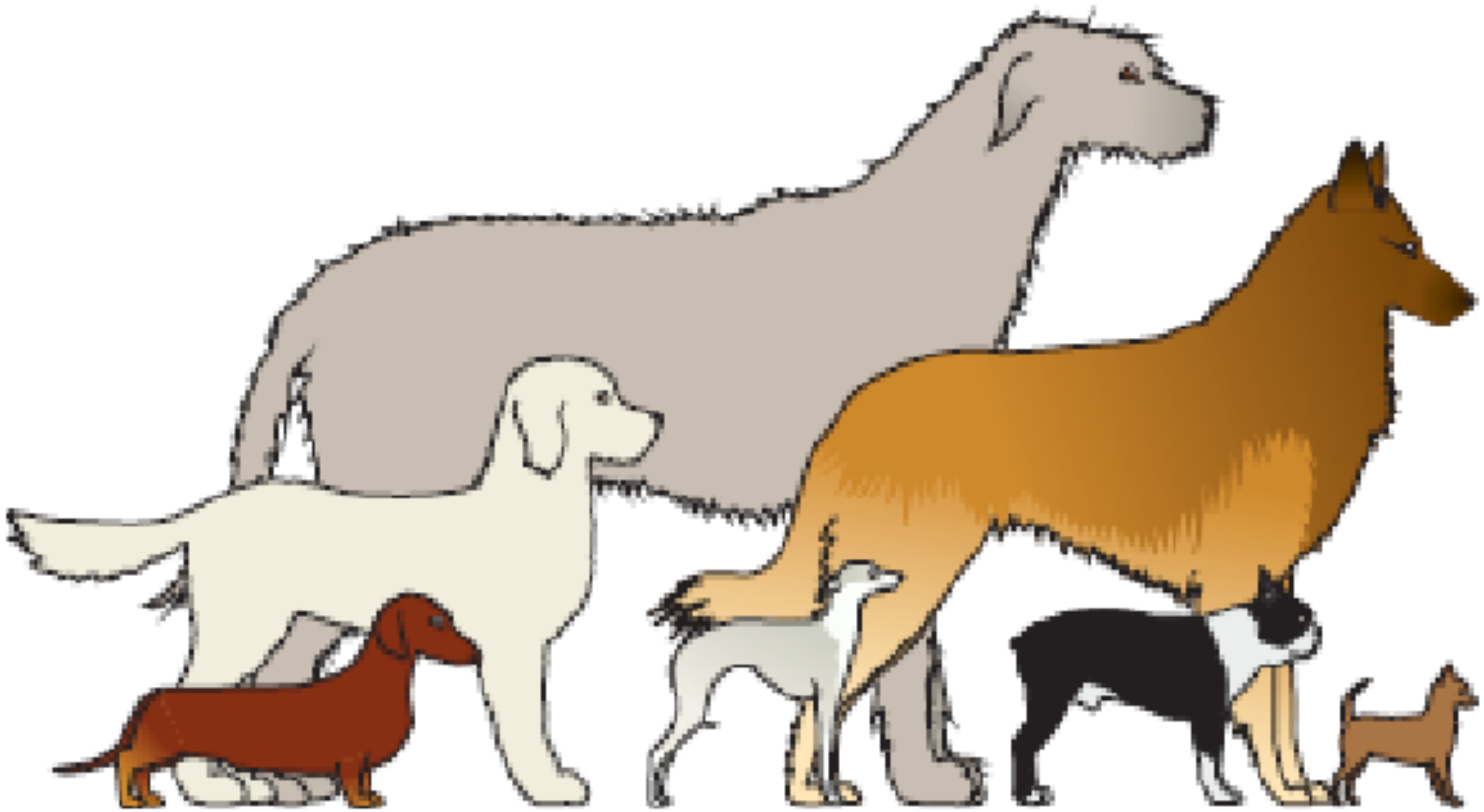
One species or many?



What criteria for species concepts?

Universality (generality)

- *Monism*: there exists a single way to divide the living world into kinds which are organised by a single hierarchy of laws
- *Pluralism*: there is no unified picture of nature; living things can be viewed from varying, equally legitimate perspectives

Applicability (operability)

- Species must be defined by taking into account the sort of data available

Theoretical significance (explanation)

- Species and the characters on which they are based provide evidence to arrive at a theoretical explanation

Do species concepts matter?

Conservation:

Example: the U.S. Endangered Species Act

- ✓ Lumpers recognize widespread species which are unlikely to become endagered;
- ✓ Splitters recognize more, range-restricted species which are more likely to be more vulnerable to become endangered.

A case made by a new preblesmouse species concept

Do species concepts matter?

Estimating biodiversity:

✓ Using different species concepts leads to comparing apples with oranges;

✓ Higher taxa are generally not comparable; species should be comparable, as they are generally considered as the units of conservation.

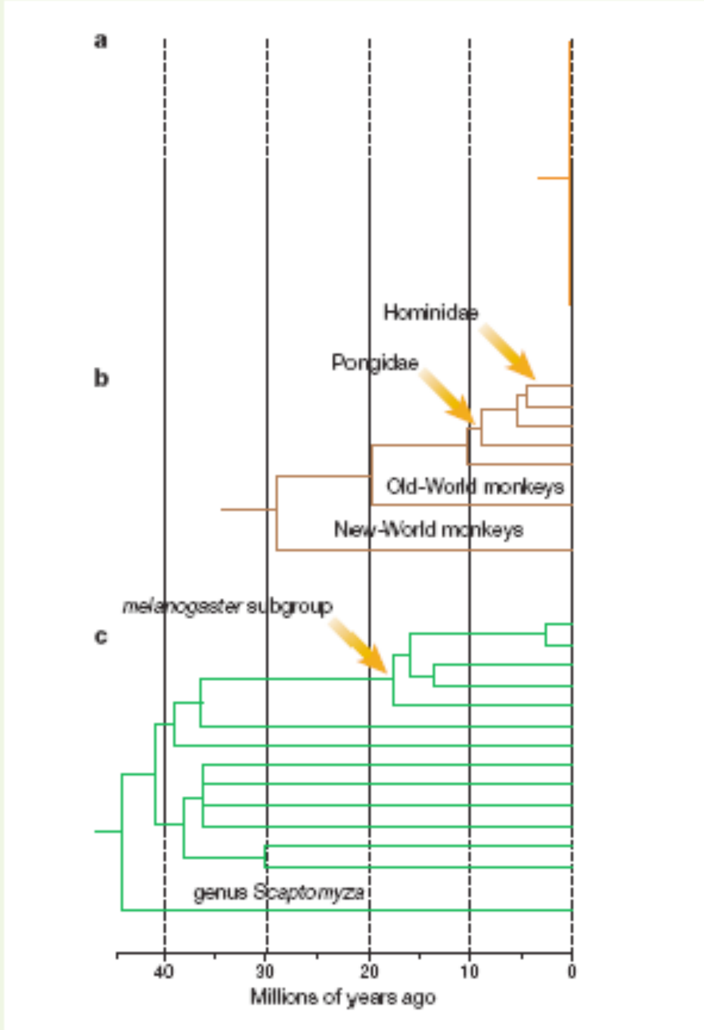


Figure 2 Taxonomic boundaries are not comparable among major groups. **a**, Fourteen species in nine genera representative of cichlid fish in Lake Victoria. **b**, Seven species representative of several families in anthropoid primates. **c**, Thirteen species representative of a single genus, *Drosophila*. Figure reproduced from ref 30, with permission.

Species concepts do matter!

Species concepts affect:

i. the specific status of diagnosable populations;
ii. estimates of species diversity;
iii. the historical analysis of these units
iv. an understanding of patterns of gene flow within and among these units;
v. delineation of areas of endemism;
vi. the demographic characterization of such units;
vii. decisions on captive breeding
viii. which units to receive protection under local, national, or international legal instruments.

(from Cracraft 2000: 7)

There is a need to universally:

- ✓ identify real species
- ✓ understand real species

↓

Progress in conservation efforts

Key questions to be answered

Do species really exist?

How to define species?

How to decide between species concepts?

Present-day species concepts

The pre-Darwinian species concept (cf. Linnaeus) was essentialistic (= typological)

Number of species concepts in use today

- ✓ Mayden (1997) identified no less than 24 species concepts
- ✓ Many of these concepts dwell on the same ideas

i. Agamospecies Concept;
ii. Biological Species Concept
iii. Cladistic Species Concept
iv. Cohesion Species Concept
v. Composite Species Concept
vi. Ecological Species Concept
vii. Evolutionary Significant Unit
viii. Evolutionary Species Concept
ix. Genealogical Concordance Concept
xix. Genetic Species Concept
xx. Genotypic Cluster Concept
xxi. Hennigian Species Concept
xxv. Internodal Species Concept
xxvi. Morphological Species Concept
xv. Non-dimensional Species Concept
xvi. Phenetic Species Concept
xvii. Phylogenetic Species Concept (Diagnosable version)
xviii. Phylogenetic species concept (Monophyly version)
xix. Phylogenetic Species Concept (Diagnosable and monophyly version)
xx. Polythetic Species Concept
xxi. Recognition Species Concept
xxii. Reproductive Competion Concept
xxiii. Succesional Species Concept
xxiv. Taxonomic Species Concept

How to see the forest for the trees

Three main breeds of species concepts

Similarity Concepts
Overall similarity and/or gaps in character distributions
(<MorphSC, PhenotSC, TaxSC,...)

Evolutionary Concepts
Theoretical commitment to evolutionary theory
(BioSC, EcolSC, EvolSC, RecogSC, CohSC,...)

Phylogenetic Concepts
Commitment to phylogenetics
(<CladSC,PhyloSC, HennigSC,...)

Some definitions

Biological species	A group of interbreeding natural populations that do successfully mate or reproduce with other such groups (and some would add, which occupy a specific niche) and have fertile offspring
Cohesion species	The smallest group of cohesive individuals that share intrinsic cohesive mechanisms (e.g. interbreeding ability, niche)
Ecological species	A lineage which occupies an adaptive zone different in some way from that of any other lineage in its range and which evolves seperately from all lineages outside its range
Evolutionary species	A single lineage of ancestor-descendant populations which is distinct from other such lineages and which has its own evolutionary tendencies and historical fate

Some definitions

Morphological species	The smallest natural populations permanently seperated from each other by a distinct discontinuity in heritable characteristics (e.g. morphology, behavior, biochemistry)
Phylogenetic species	The smallest group of organisms that is diagnostically distinct from other such clusters and within which there is parental pattern of ancestry and descent
Recognition species	A group of organisms that recognize each other for the purpose of mating and fertilization

✓Species definitions are made *ad hoc* and thus adopting a pluralistic attitude is key
✓Species concepts have theoretical and/or practical strengths and weaknesses

Species concept	Practical application	Strengths / weaknesses
Biological species	Difficult	Popular, explains why the members of a species resemble one another and differ from other species (shared gene pool + reproductive isolation). Not applicable to fossils, asexual organisms, complicated by natural hybridization, polyploidy, etc.
Ecological species	Difficult	Adaptive zones difficult to define, assumes two species cannot occupy the same niche for even a short period (but what to do with life stages…)
Evolutionary species	Difficult	Criteria vague and difficult to observe (see also PSC)
Cohesion species	Difficult	Cohesion is difficult to recognize, prezygotic and postzygotic isolating mechanisms are mostly unknown

Individuals of different species

PREZYGOTIC BARRIERS

Habitat isolation: populations live in different habitats and do not meet

Behavioral isolation: little or no sexual attraction between males and females

Temporal isolation: mating or flowering occurs at different seasons or times of day

Mating

Mechanical isolation: structural differences in genitalia or flowers prevent copulation or pollen transfer

Gametic isolation: female and male gametes fail to attract each other or are inviable

Fertilization

POSTZYGOTIC BARRIERS

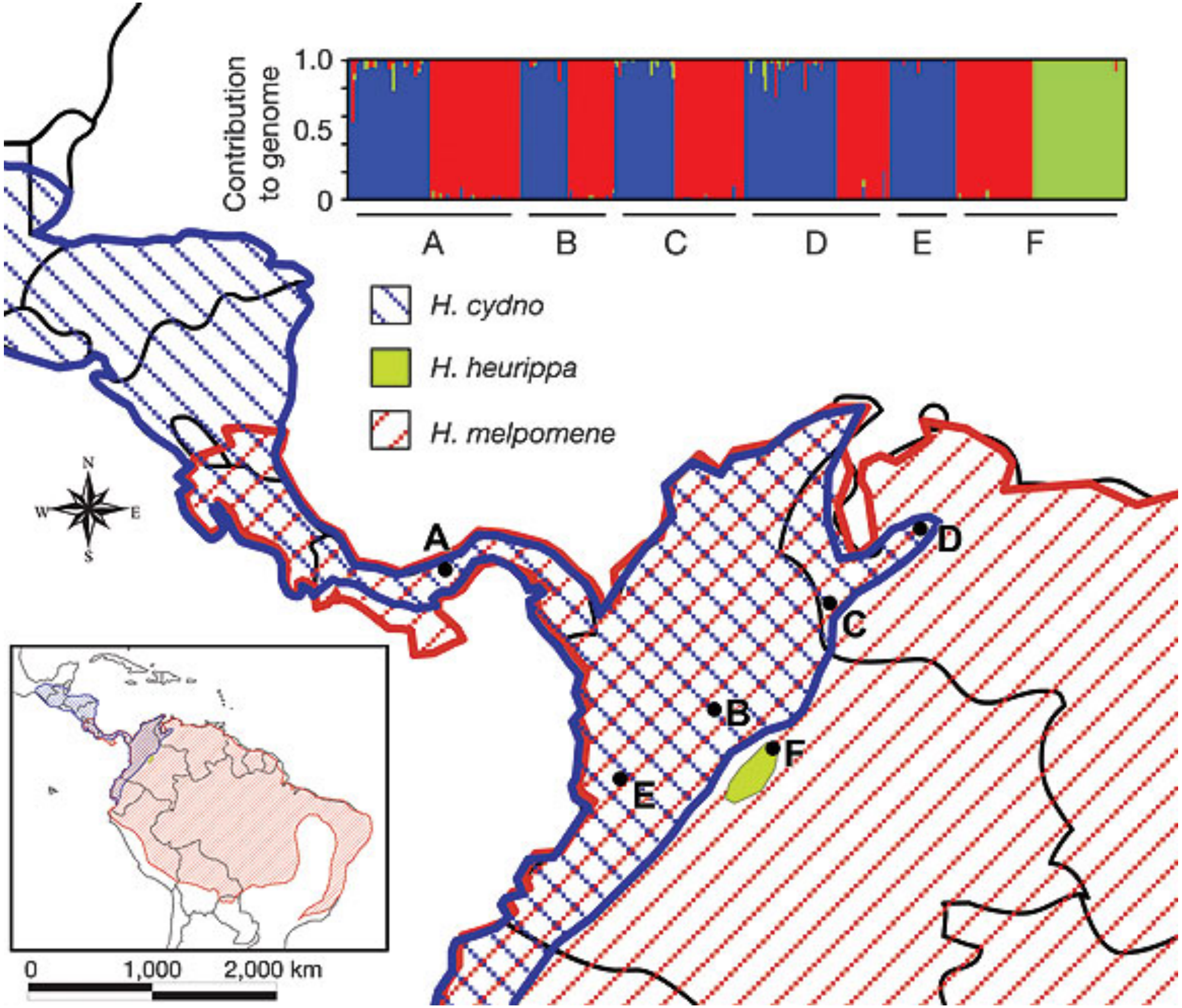
Reduced hybrid viability: hybrid zygotes fail to develop/fail to reach sexual maturity

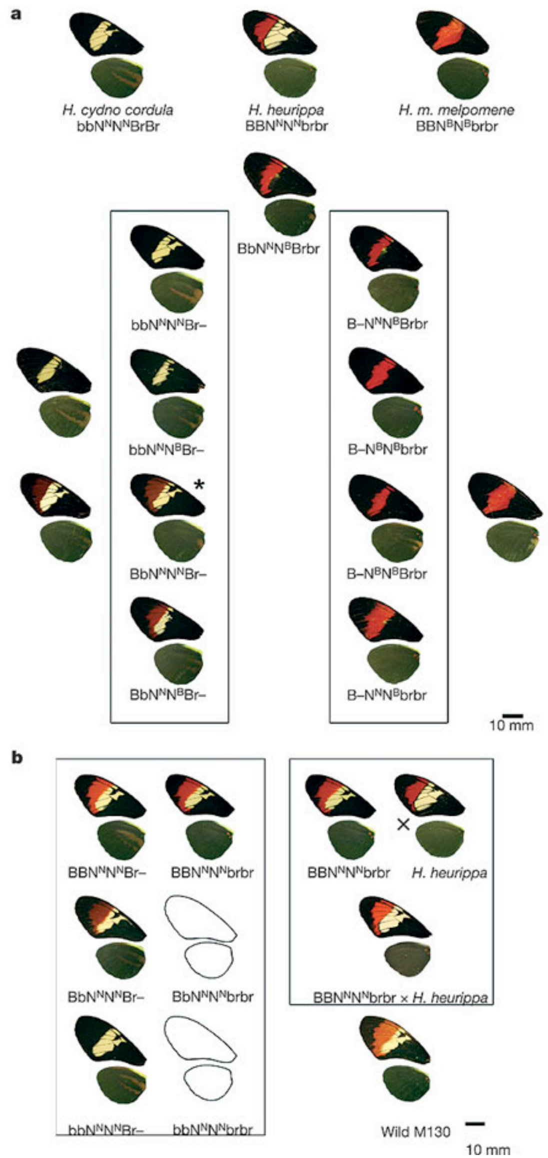
Reduced hybrid fertility: hybrids fail to produce functional gametes

Hybrid breakdowns: offspring of hybrids have reduced viability or fertility

Viable, fertile offspring

Barriers or not?
Homoploid hybrid speciation in *Heliconius butterflies*





(from Malvrez *et al*, 2006. Nature Vol 441: 868-871)

Barriers or not?
Hybridizing oaks

X

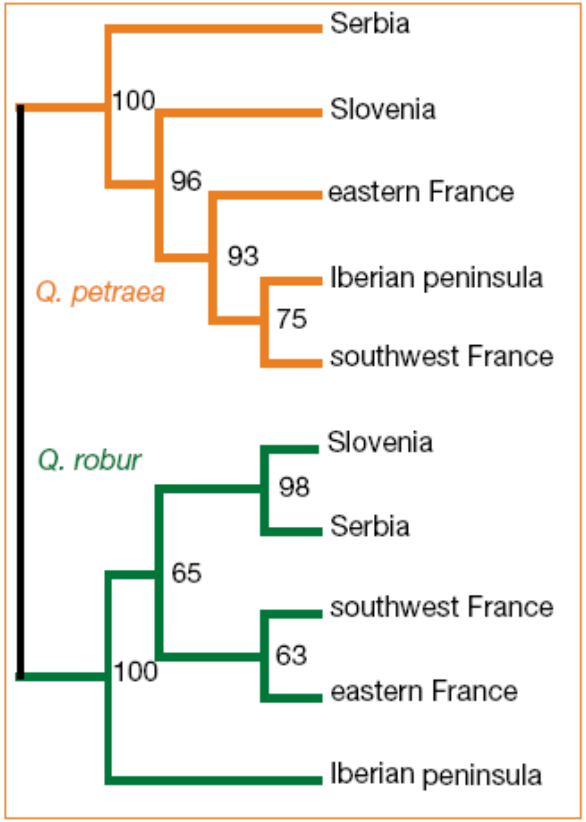


Figure 1 Dendrogram of 10 European *Quercus robur* and

Despite extensive gene flow, the sympatric *Q. petrae* and *Q. robur* remain distinct taxonomic units that can be designated by microsattelite data

(from Muir et al, 2000. Nature Vol 405: 1016)

Species concept	Practical application	Strengths / weaknesses
Morphological species	Easier	Morphological criteria may not reflect actual links that hold organisms together into a natural unit; only possibility for paleontologists; but what with cryptic species?
Phylogenetic species	Becoming easier; Increasing	Will give rise to recognition of many more species than more traditional concepts; but from what point onwards do we conceive differences to be 'statistically significant'?
Recognition species	Difficult	Determining if a feature is used to recognize potential mates is difficult or impossible in many populations (note that this concept has been succesfully demonstrated with amphibians, spiders…)

The Phylogenetic species concept

tokogenetic versus phylogenetic relationships

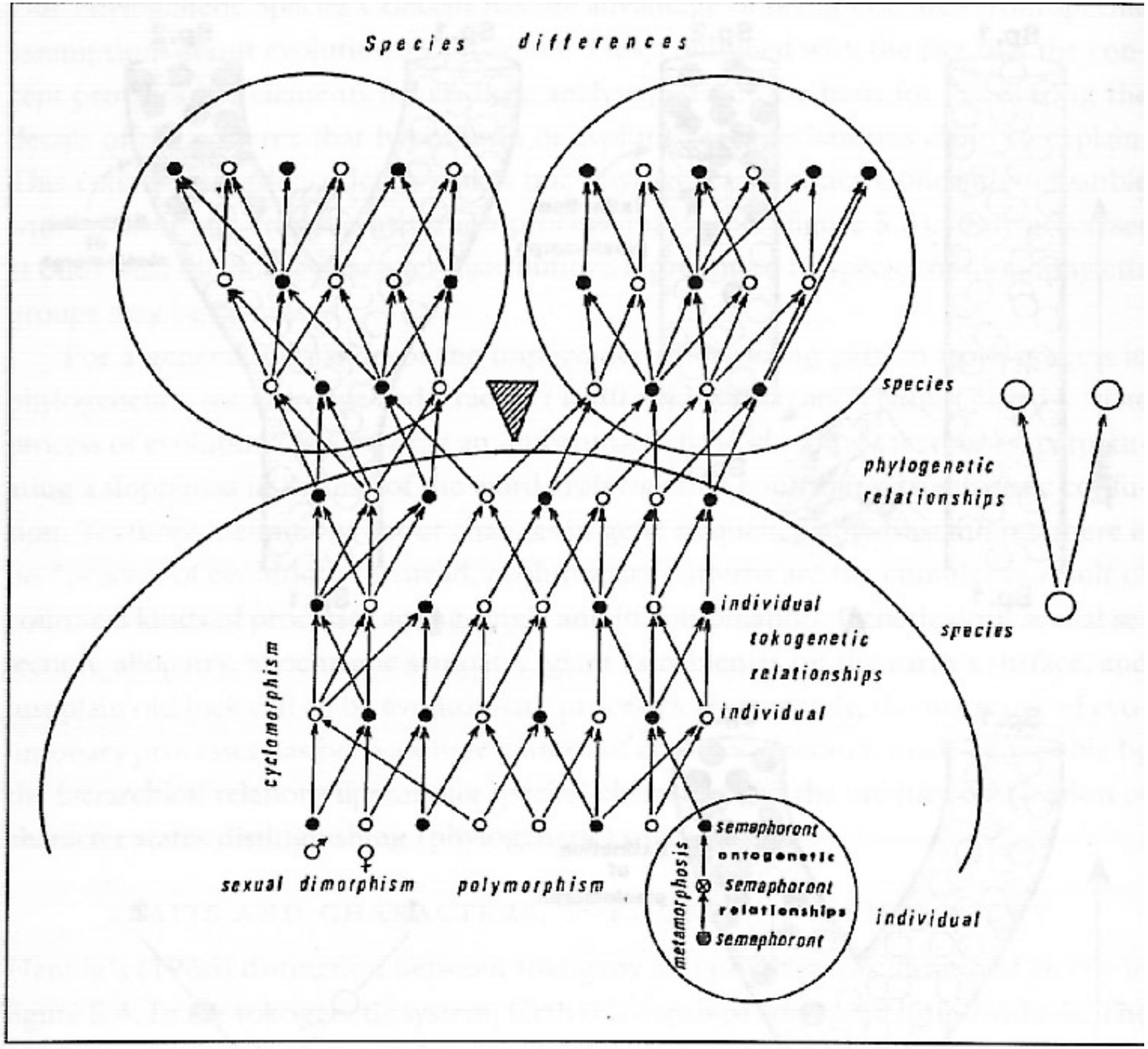
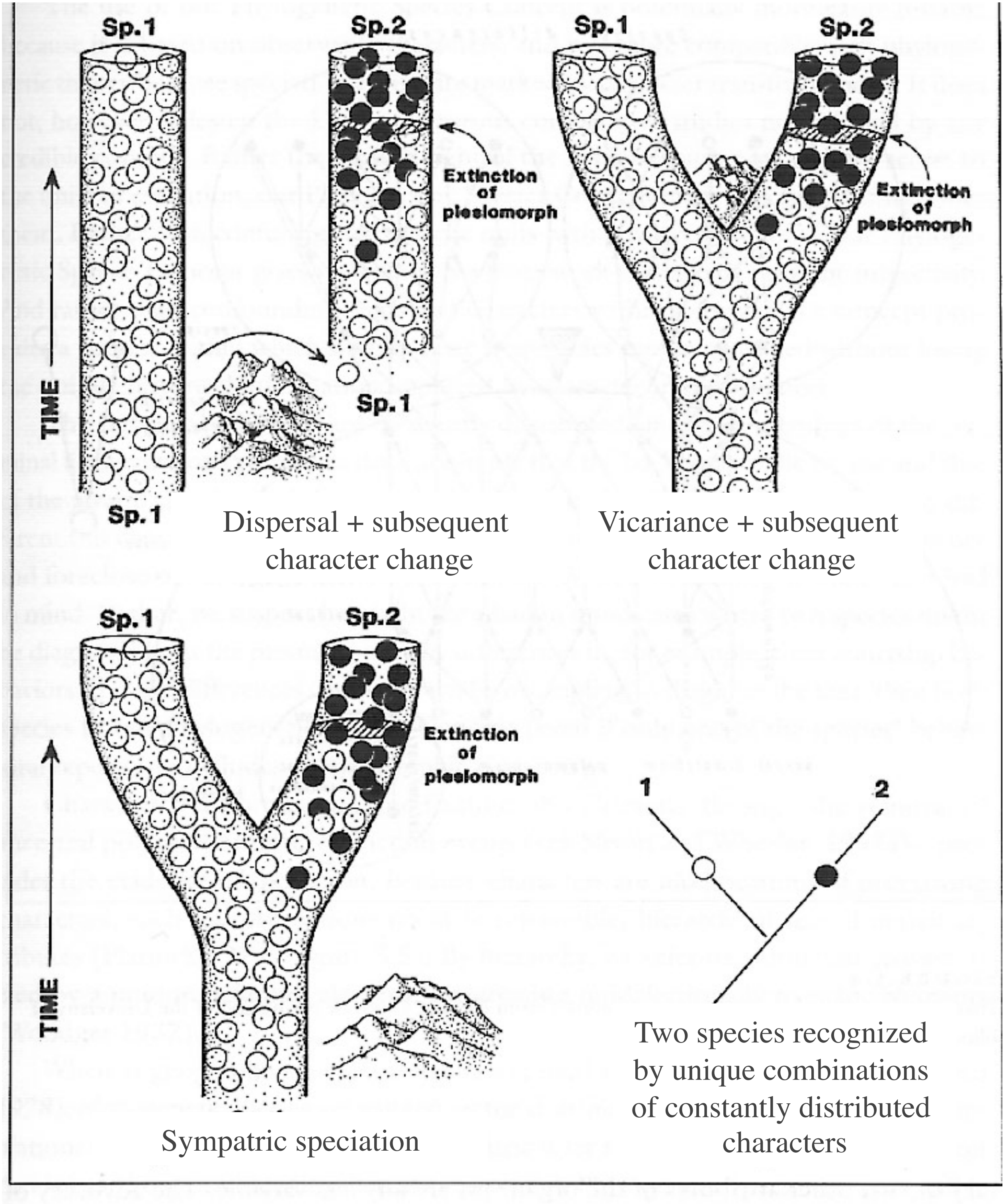


FIGURE 5.4.
Tokogenetic versus phylogenetic relationships. (From Hennig 1966, by permission of the University of Illinois Press.)

The phylogenetic species concept

Speciation and phylogenetic relationships

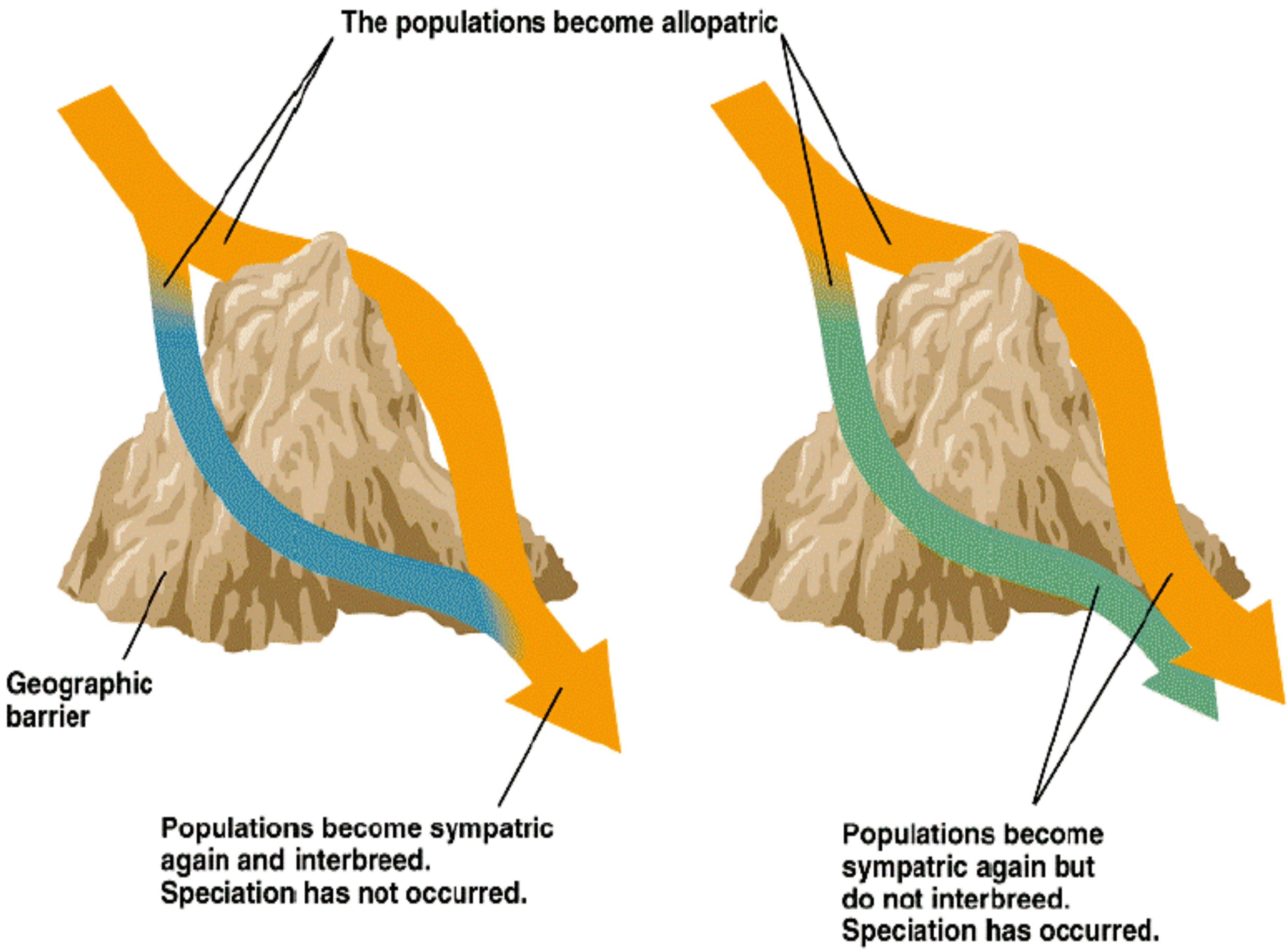


Dispersal + subsequent character change

Vicariance + subsequent character change

Sympatric speciation

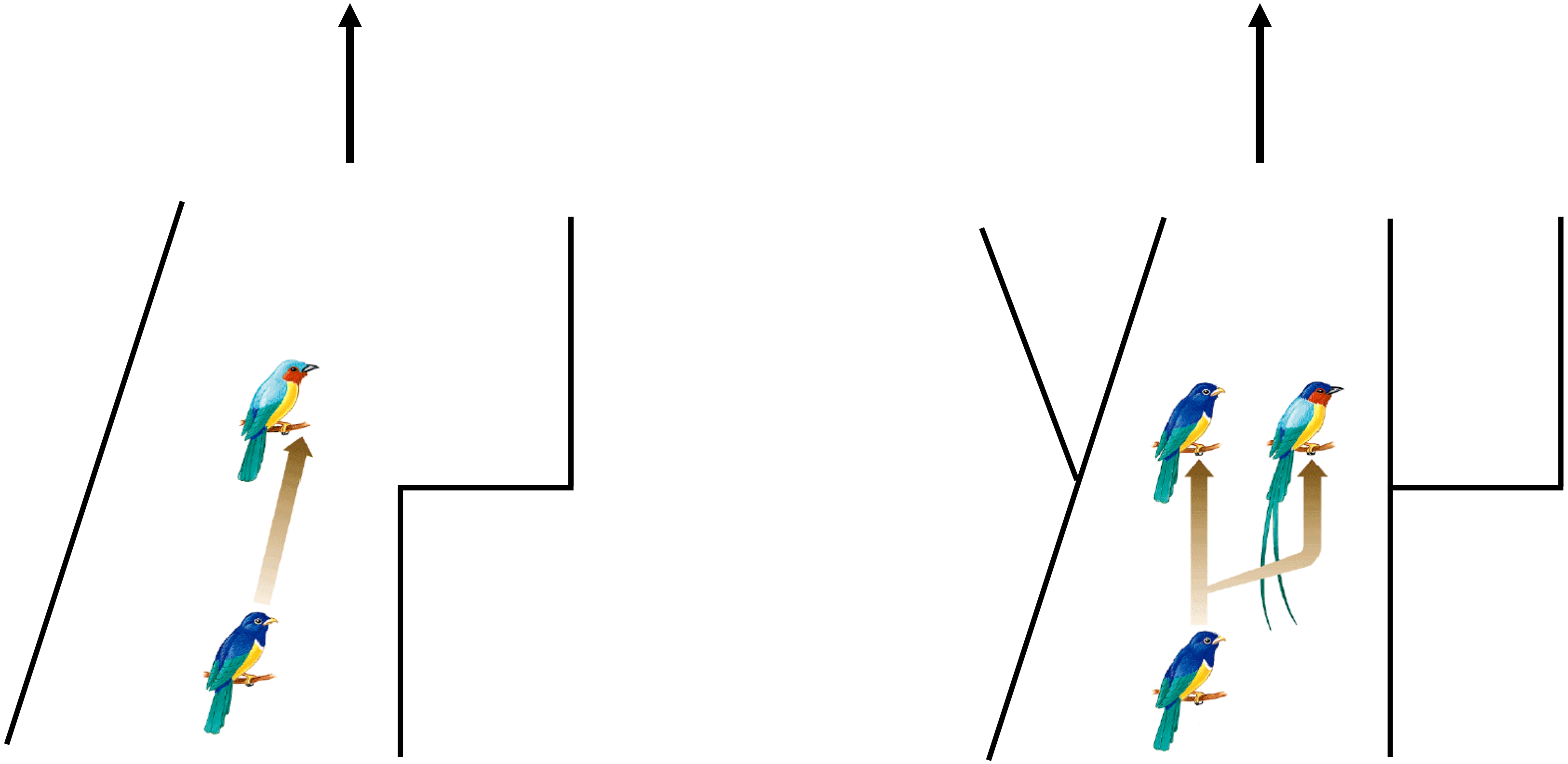
Two species recognized by unique combinations of constantly distributed characters


The populations become allopatric
Geographic
barrier
Populations become sympatric
again and interbreed.
Speciation has not occurred.
Populations become
sympatric again but
do not interbreed.
Speciation has occurred.

Anagenesis and cladogenesis

Phyletic speciation leading to new (chrono)species

True speciation leading to new species

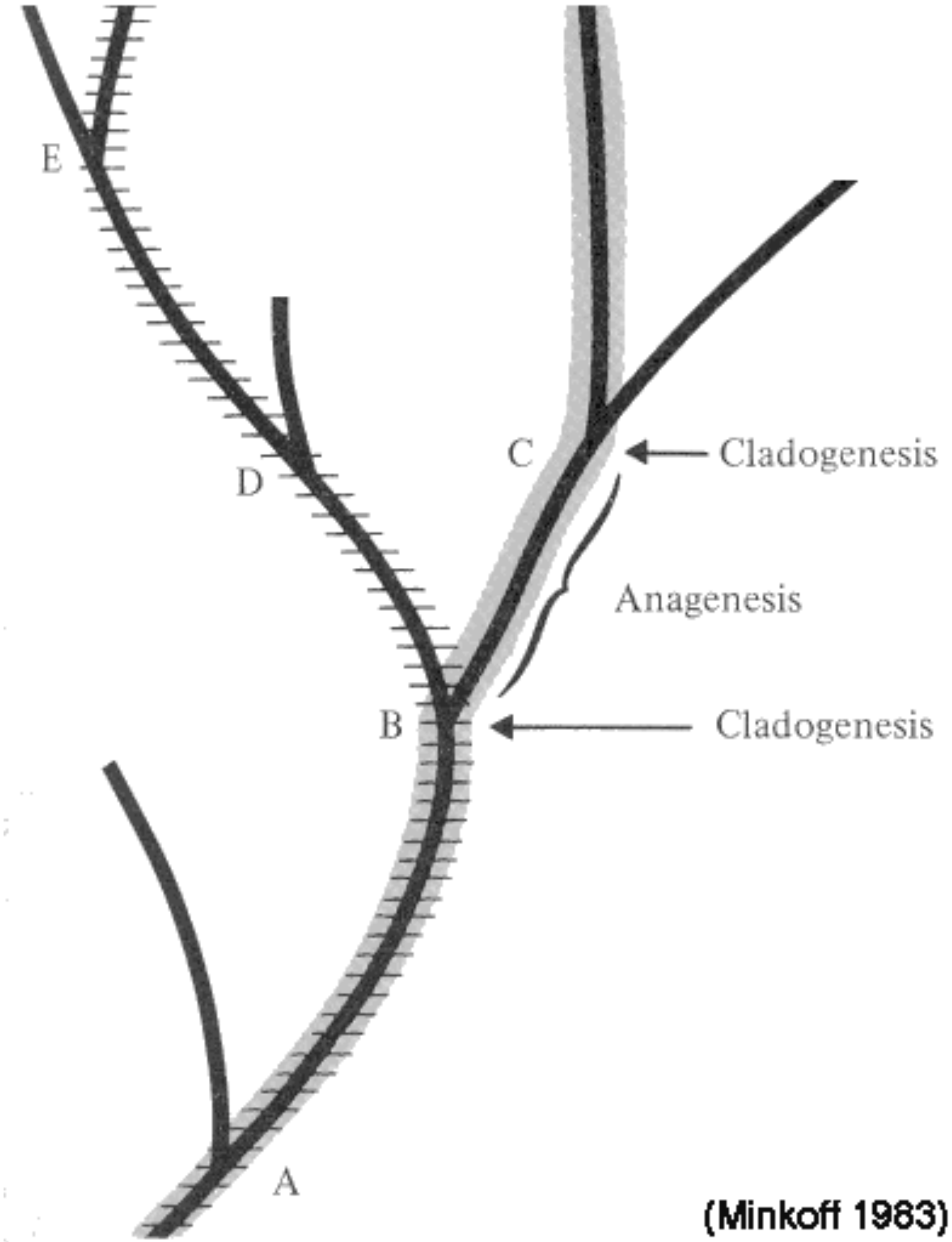


gradual abrupt

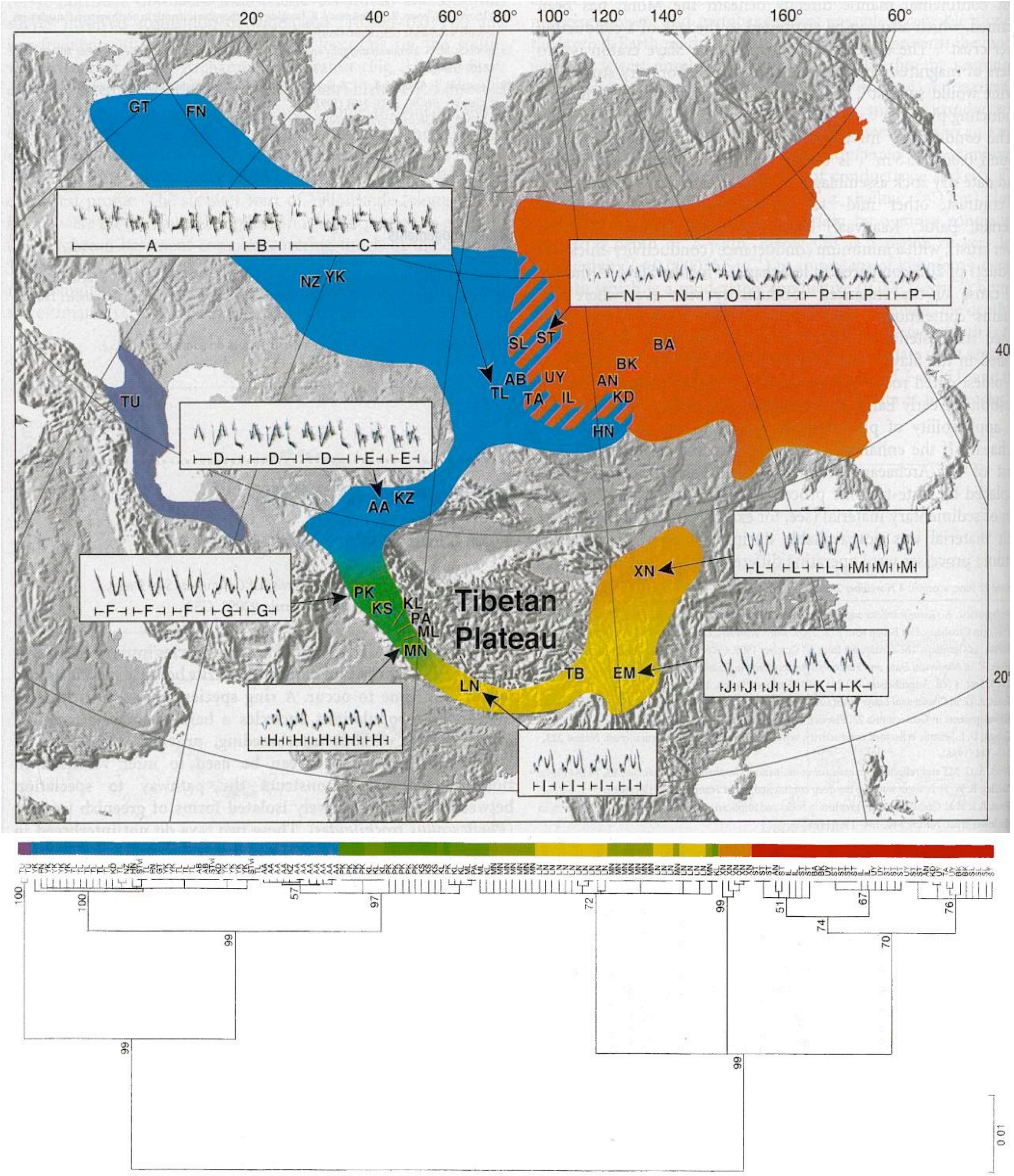
Anagenesis
(the same branch again)

gradual abrupt

Cladogenesis
(origin of a branch)



(Minkoff 1983)



Phylloscopus trochiloides

In order to understand species concepts we must grasp the evolution of species.

Ring species act as windows to this complexity.

Here distribution and song constitution of subspecies of greenish warbles

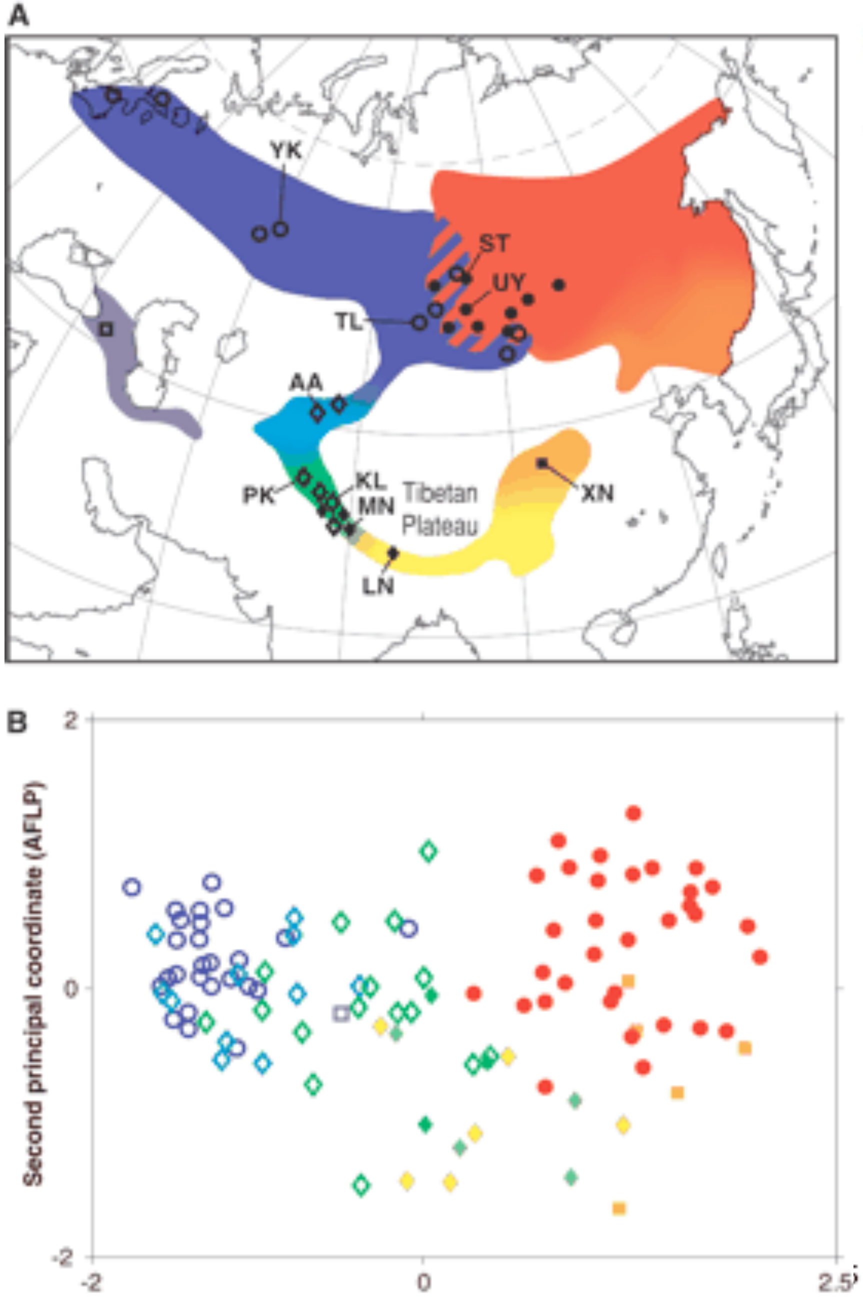


Fig. 1. (A) Map of Asia showing the range of greenish warblers in the breeding season. Different colors represent different subspecies as designated by Ticehurst (20) (*P. t. viridanus*, blue; *ludlowi*, green; *trochiloides*, yellow; *obscuratus*, orange; *plumbeitarsus*, red; and *nitidus*, violet). Colors grade together in areas where Ticehurst described gradual morphological change. The hatched area in central Siberia indicates the overlap zone between *viridanus* and *plumbeitarsus*. The gap in the ring in northern China is likely due to recent habitat destruction (10). Sampling sites are indicated by symbols corresponding to major mitochondrial clades [open symbols indicate western clade, and closed symbols eastern, see fig. S1 and (10)], with the most important sites indicated by two-letter codes. (B) Geographic variation in 62 AFLP markers as summarized by principal coordinates analysis. Each symbol represents a single individual, and distance between symbols corresponds roughly to genetic distance. Colors and symbols correspond to (A). Although the northern subspecies *viridanus* and *plumbeitarsus* differ distinctly in their genetic characteristics, there is gradual genetic change through the southern chain of populations. PC1 explains 19.4% of the variance, PC2 5.6%.

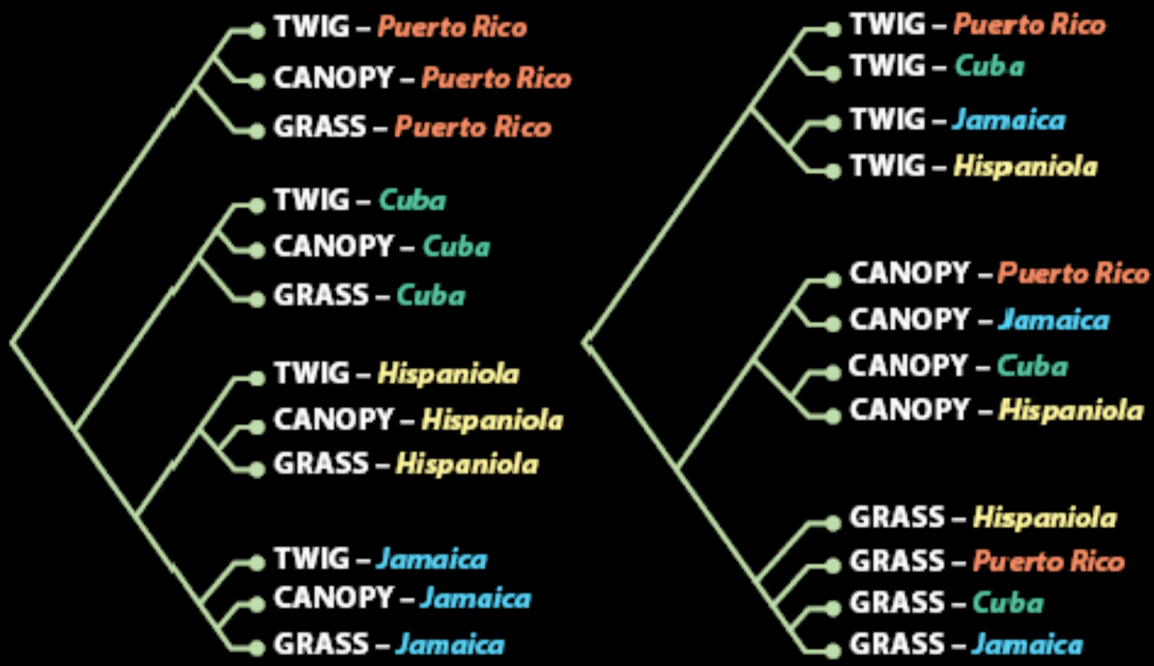
Phylloscopus trochiloides

In order to understand species concepts we must grasp the evolution of species.

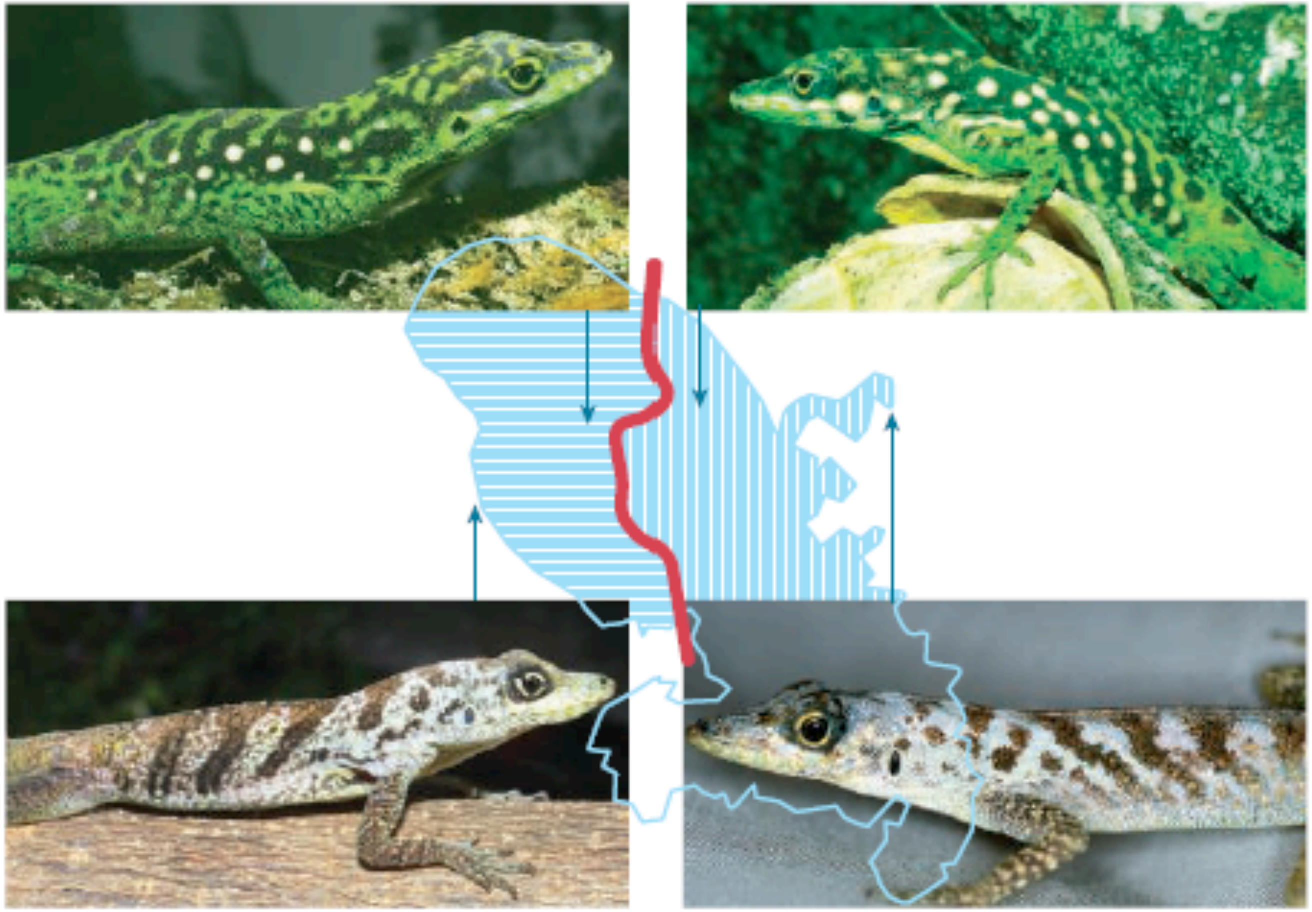
Ring species act as windows to this complexity.

Here distribution and genetic constitution of subspecies of greenish warbles

The different islands of the Greater Antilles all hold particular habitat specialists



EVOLUTIONARY TREES depict two of many possible hypotheses about the anole lizards' genetic relatedness. At one extreme, each kind of specialist evolved again and again, on different islands (*left*). At the other extreme, each specialist evolved only once and then ended up on various islands (*right*). DNA analysis suggests that a situation similar to the first scenario is more likely.



No evidence for the geographic speciation predicted by biogeographic pattern. Broad biogeographic pattern suggests geographic speciation in Lesser Antillean anoles, yet on Martinique, where once separate island species now meet in secondary contact (red line), population-based genetic studies show no evidence of their reproductive isolation (9). However, there is strong parallel adaptation to the habitat zonation and some evidence of reduced interbreeding among these habitat types (ecotypes) (9). Xeric coastal ecotypes of anoles are brown and striped (lower photographs; arrows indicate locality of origin). Where lineages meet, in the montane rainforest, they show parallel evolution of green montane ecotypes (upper photographs), irrespective of their independent island history and deep molecular phylogenetic divergence.

In order to understand species concepts we must grasp the evolution of species, but also population processes

(see f.i. Thorpe, 2005)

Thus, the PSC

identifies species by estimating the phylogeny of closely related populations and finding the smallest monophyletic groups

whereby

populations must have been independent long enough for diagnostic traits to emerge

And what species concept for bacteria?

Emphasis on evolutionary processes that lead to reproductive isolation, but in bacteria (and many other asexual forms) reproduction proceeds through mitosis and unidirectional gene transfer.

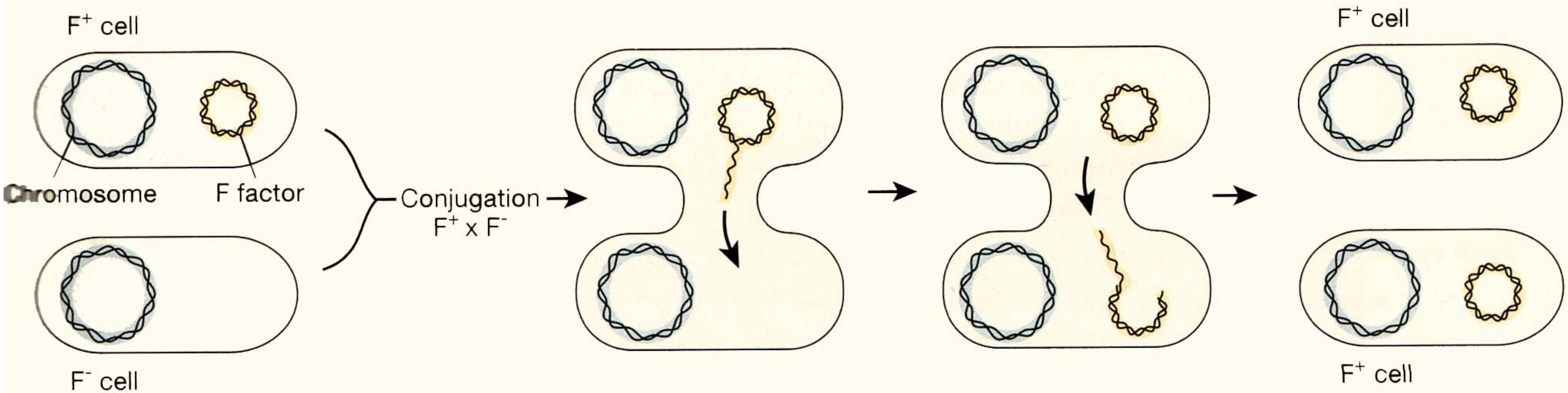
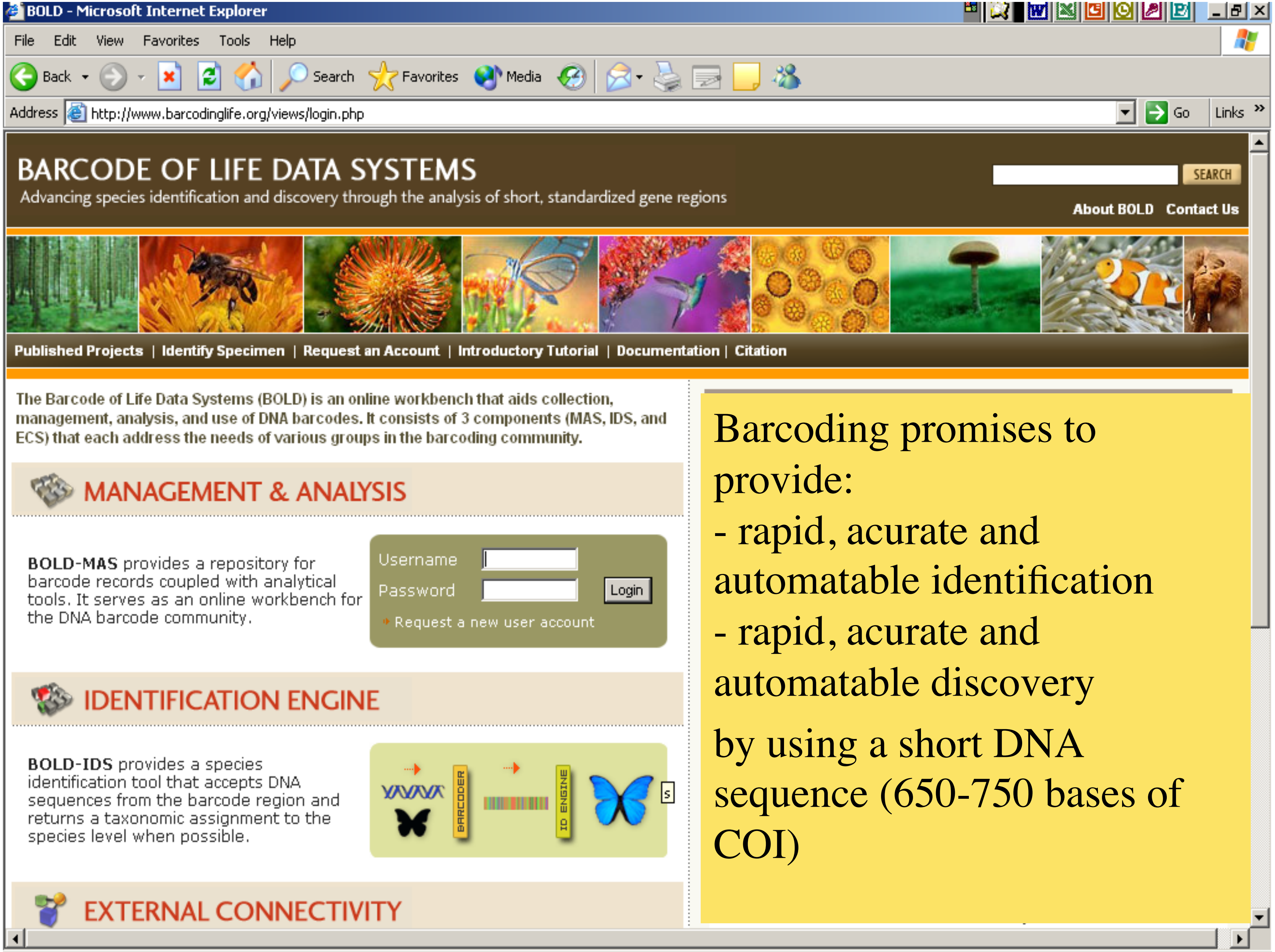


FIGURE 12.1 Genetic recombination in bacteria *Escherichia coli* cells with an extrachromosomal loop of DNA called an F (for fertility) factor can engage in recombination. The process starts when cells with F factors form conjugation tubes with F^- cells. A copy of the F factor migrates through the conjugation tube, converting the recipient cell from F^- to F^+. Occasionally F factors will integrate into the chromosome. These integrated sequences can later leave the chromosome. When they do, they frequently take chromosomal sequences (that is, new genes) with them. In this way, F factors can transfer alleles between bacterial chromosomes.

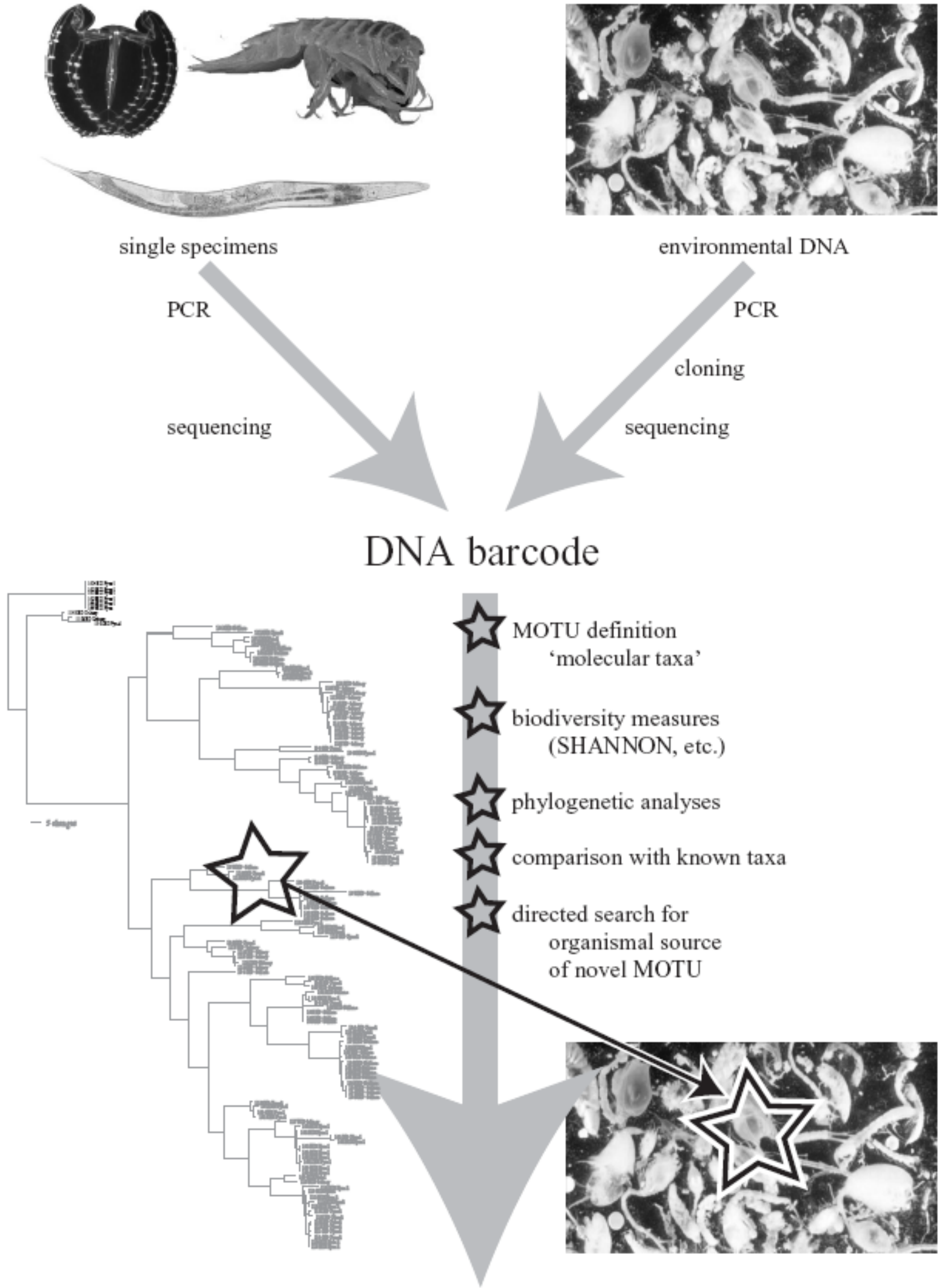


Barcoding promises to provide:

- rapid, acurate and automatable identification
- rapid, acurate and automatable discovery

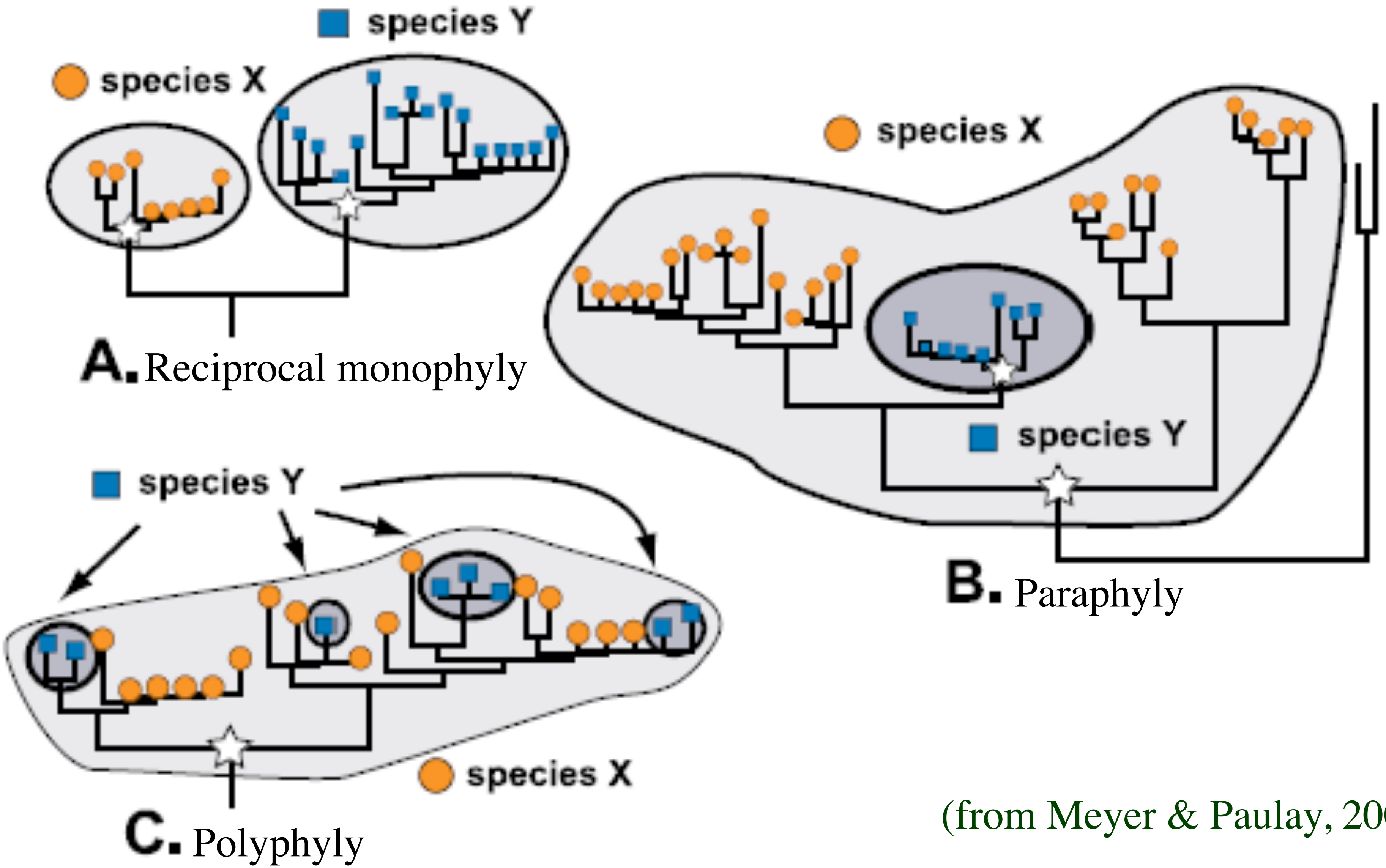
by using a short DNA sequence (650-750 bases of COI)

How does it work?



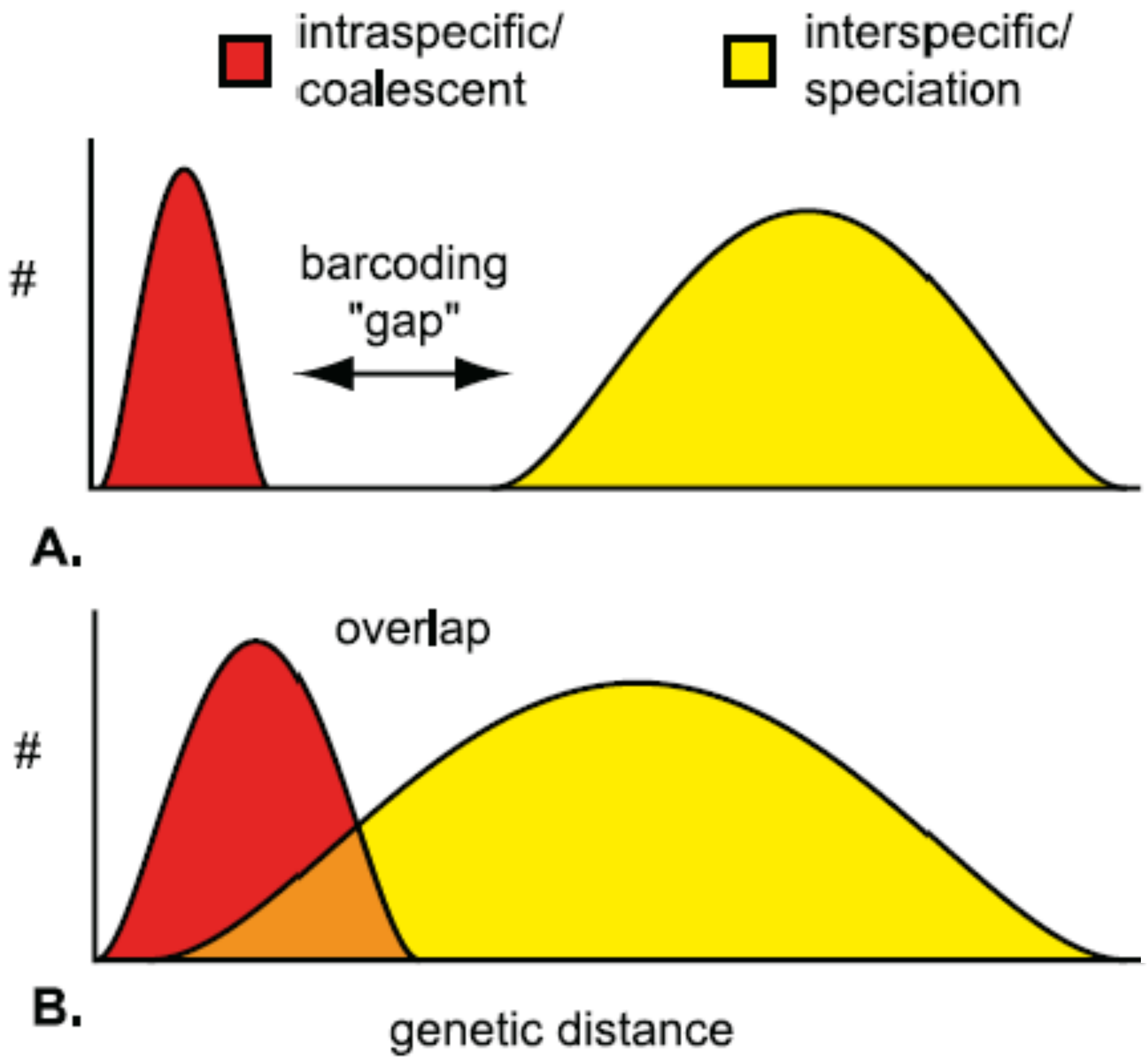
(from Blaxter, 2004)

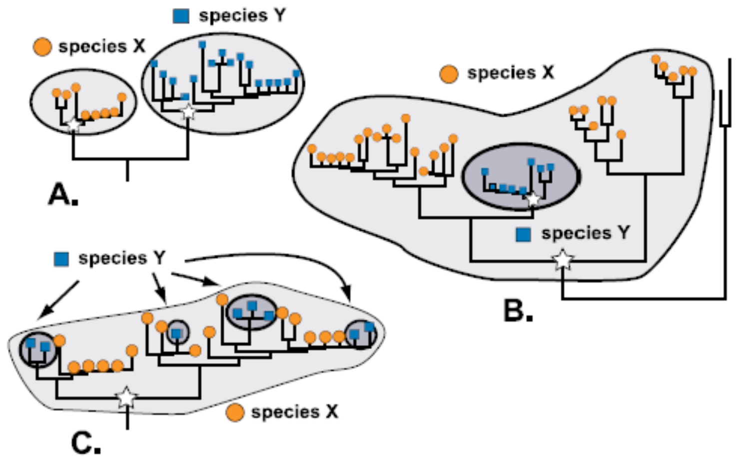
Does it work?



(from Meyer & Paulay, 2005)

Does it work?





(from Meyer & Paulay, 2005)

Hey, 2006

Species definition cannot solve the problem of species identifcation

But remember also this...

We have described some 1.7 to 1.9 million species

At least 8 million species are yet to be discovered and described

Most of our existing (and comming) species knowledge comes (will come) from a **single point in space** (single locality) **and time** (no fossil evidence to back up) and hence populational variability and concern with the process of speciation remain “luxury concerns”

J. Ray (1653): “Species are merely what competent naturalists says they are” ... We need more competent naturalists, and hence taxonomists!


Thank you for
your attention