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Biosystematics and Nomenclature.

Phylogenetic Species Concept.	Cracraft.
Biological Species.	Mayr.

Cohesive Species Concepts.

vs

Historical Species Concepts.

*Cracraft's ideas:

Conspecificity in the BSC is measured by relative phenotypic similarity, which Mayr claims functions as a surrogate for a direct measurement of reproductive compatibility. But look at Cracraft's paper.

*In some groups this is subjective.

Cinclosoma

-species limits -

-development of a true phylogeny- hindered because of the relational concept of BS.

Cracraft points out that a hybridization event between two species in the range is occurring,

-The BSC illustrates the idea that these two species could again overlap in range and hybridize on a wholesale scale if the climate changed.

HOWEVER, the phylogeny shows that these two species are not their closest relatives.

*Application of the BSC has created paraphyletic taxa. (Mistake - our own ideas superimposed in a true phylogeny.

*The problem is essentially solved when the phylogenetic species concept is applied in this case.

2- Speciation in *Daphoenositta*.

-Recognition of a single polytypic species - or MEGASUBSPECIES -

Convention: Ancestor with wide distribution - with 5 populations becoming isolated in humid refugia during a more xeric period. Populations the spread once the climate moderated.

Q's

1. What is the unit of evolution here? - the single species is not the unit. Here it has been treated as the sub-species.
2. Mayr 1982 indicated that subspecies are units of convenience not of evolution.
3. There is ontological confusion here - what are they species, subspecies, megasubspecies?
4. A phylogeny seems to really help here. However, many times - at levels below the species, phylogenetic methods break down.

-> Coding the characters and creating the table diagnoses:

- the analysis shows that the forms are not the same ages
- placing all them into a single spececies masks the historical pattern

How do we discover species?

First: We have to know what they are...

See page 106 of Brooks and McLennan.

Brooks starting on page 104 –

::**Cohesion Concepts of Species** - Species are groups of individuals held together by some cohesive systems.

Paterson (1978 - 1987).

::**Recognition Species Concept**: Groups of individuals held together by a specific mate recognition system.

Dobzhansky (1937) – Advocated by Mayr (1942 etc...).

::**Biological Species Concept**: A group of interbreeding or potentially interbreeding organisms reproductively isolated from other such groups.

Van Valen - (1976)

::**Ecological Species Concept**: Each species has its own unique niche and it is the niche that defines the species.

–These provide definition of what species are. That is after we know that they exist.

We need to find out how to discover species.

Brooks and McLennan consider the **Evolutionary Species Concept** as the fundamental Ontological species concept for evolutionary biology.

-Brooks and McLennan consider this concept non operational:

-Does not specify discovery criteria or evaluation criteria.

-The operational surrogate for the evolutionary species concept begins with a phylogenetic analysis of the collectoins of organisms given names by taxonomists.

-Not all organisms have the defining characters of the species - male characters, vs. female as in the paper by Cracraft.

:: Historical Concepts of Species.

Wiley from Brooks -

1. Species concept – must encompass species persistence through time as well as divergence.
2. Species are cohesive wholes
3. Inherent historical context of species (historicity ?????)

Brooks claims that the evolutionary species concept is non operational. We need an operational criterion for species.

*most taxonomists propose species names that do not require a particular species concept.

(Basically the typological species concept) -

*Brooks pointed out that The Operational Surrogate For the Evolutionary Species Concept starts with a Phylogenetic Analysis of the collection of organisms given names by taxonomists.

**Character analysis:: characters are not properties of membership, but evidence of inclusion or being part of a phylogenetic lineage.

Historical Species Concepts – Page 109 Brooks and McLennan

There are 3 distinct categories: They differ in how we recognize species on a phylogenetic tree.

1. Composite Species Concept - Conceived by Kornet in 1993.

-The CSC recognizes a distinct species for each character. This concept recognizes each instance of character fixation is evidence of past lineage splitting.

-Origination and fixation of each apomorphic trait requires permanent lineage splitting.

-Each apomorphic trait indicates the present or prior existence of a distinct species.

-No Anagenesis - No development of apomorphic traits within a species. Is anagenesis important? Yes. We want to study various evolutionary phenomena and can't do it if we do not recognize anagenetic evolution.

Thus: The CSC limits what we can understand about species - Placing constraints on the kinds of phenomena evolutionary biologists may study.

→This is not acceptable so I reject this species concept← AS DO Brooks and McLennan.

2. Phylogenetic Species Concept - 2 (PSC-2):

-From what we can get from the book: This concept may seem to be the most consistent of the HSC's

-It takes into account only the branching structure of the tree.

-It rules out the idea of persistent ancestors

-To me this was a difficult problem when I was first learning about and trying to apply the methods of phylogenetic systematics.

→> Since the PSC-2 rules out modes of speciation, then we reject it along with the CSC.

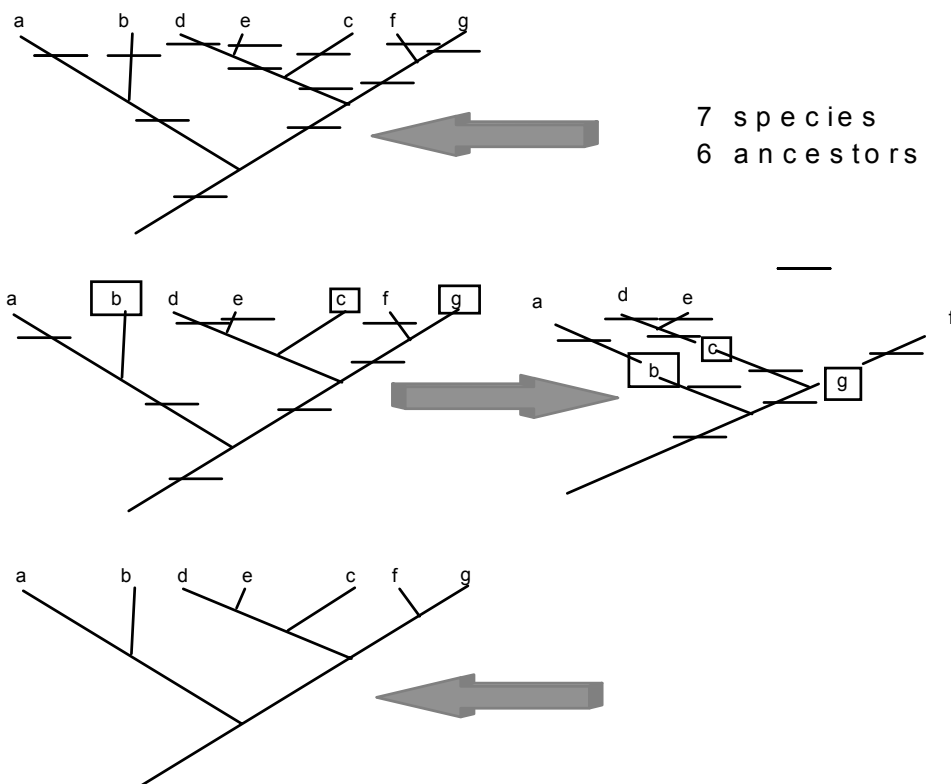
3. Phylogenetic Species Concept - 1 (PSC-1):

-Allows the recognition of persistent ancestors and budding of species from species that exist now.

-Most conservative approach --

Requires: Evidence of both lineage splitting and character evolution to recognize species.

Does Not A-Priori - Rule out any evolutionary processes that may occur. p 110



How do we evaluate species?

2 main research programs relative to evaluation of species.

-how they formed

-ways they maintain their identity once formed

- 1) How speciation started: Coupling of phylogenetic pattern with geographical distributions to determine conditions in which speciation was started.
- 2) How speciation was completed: Quantitative Genetics, demographics, mate choice experiments.

- Mayr 1963-

3 General classes of speciation.

1. Reductive speciation = *compilo-species* two species join to form a new one. There are no documented cases of this.

Draw.

2. Phyletic speciation = progression of forms within a single lineage are assigned species status at different points in time.

Draw. PSC-1 then allows each lineage evolving independently to undergo change - anagenesis. The CSC would not allow this.

3. Additive Speciation or Cladogenesis - Characterized by an increase in the number of species.

-most speciation models - while mechanistically different - are based on models of

additive speciation.

–Production of sister species is what we are studying.

Allopatric Modes of Speciation.

1. Allopatric Speciation Mode I (Passive Initiation) Vicariant Speciation.

-Environmental Harshness, Mountain Building, etc..

p117

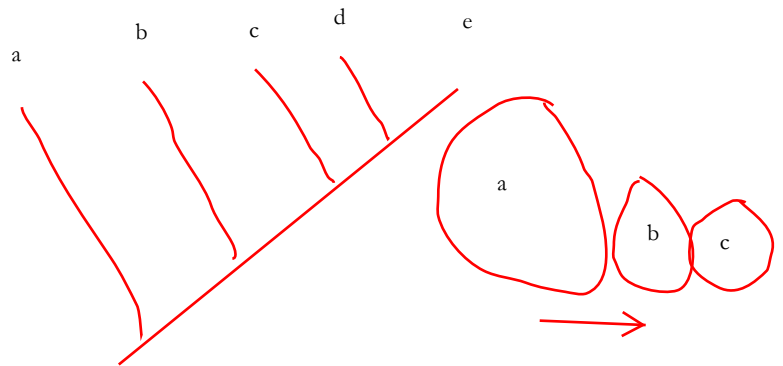
a) Dichotomous branching - sequential separation.

----->A-----> Range of A

range is split

A---->B and C

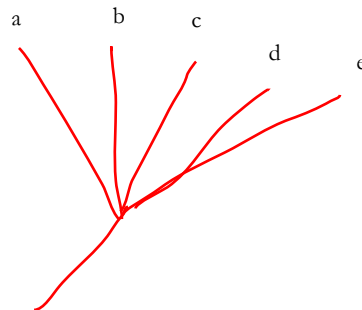
B
—A— |---- C----D and E



b) Polytomous branching due to microallopatric events.

-derived traits are not shared in the process of speciation - no way to see a dichotomous pattern.

It is a hard polytomy.



2. Allopatric Speciation Mode II. (Active Initiation)

Periphral isolates or Peripatric Speciation.

-Centrifugal Model-

-new species arising on the edges of the range of the parental species. Different habitats, different selective pressures and speciation begins.

-two patterns result.

- A) If isolation is due to random settling of individuals - we get hard polytomies. Repeated cycles of periphral isolation from same ancestor could produce a bifurcating tree.
- B) Alternating episodes of dispersal and isolation. (P. 121)

3. NON-ALLOPATRIC MODES

-Speciation initiation when there is incomplete separation of two or more populations.

-Speciation progresses despite continual gene flow between populations.

[Divergence with Gene Flow model]



-Sympatric speciation - Rice et al, found that species can diverge with gene flow.

Some Examples –

How do we test vicariance? Look at more than one species group. Similar patterns over geographic space will point to a similar process.

Vicariance seems to be the predominant mode of speciation.

How do we evaluate reproductive isolation?

-no general mechanism for completing speciation.

-no general combination of factors unique to a speciation mode.

1. Allopolyploidy - Occurs often in plants. Hybridization of two sets of chromosomes of different species of plants to produce a new species. Consisting of genetic contributions from both parentals.
that is: $AA \times BB = AABB$
-Examples in many different plant groups.
2. Heterochrony - Cricket example.
-Sympatric in space allopatric in time. Since we know that time and space are not separable, then we know that this is actually an allopatric mode of speciation.
-Microallopatric ? Syntopic but micro allopatric?
3. M.J.D. White. Moribane Grasshopper example. Sympatric Speciation - an example of sympatric speciation.

Remember that sympatry means geographic area, syntopic means same area and same niche space.

Speciation Models.

- allochronic
- allopatric
- centrifugal
- clinal
- dumbbell model
- explosive
- geographic
- parapatric
- quantum
- saltational
- sympatric

Stasipatric Speciation

1. Chromosomal Model
2. Species Range was replaced by the incipient species or groups of species
3. Identical karyotypes
4. One species is living ancestor - direct descendant
5. Field work showed - 1 fusion event; 1 pericentric inversion gave rise to acrocentric x-some.
6. Spreading from origin occurred despite segregational load at meiosis
7. Spreading was due to -
 - a. homozygote advantage
 - i. Homozygote for new arrangement was adaptively superior to homozygote for original karyotype.

- ii. Genetic Drift
- iii. Perhaps - Segregational advantage
- 8. Entire process involved fragmentation of original range and occupation by new types.
- 9. No general sympatry except in areas of hybridization.
 - a. Kangaroo Island - Zone of Overlap is 200 - 300 meters wide.
 - b. Hybrid females found no males
 - c. Evidence of limited gene flow
 - d. Meiosis normal
 - e. Some females transmit one chromosomal type more readily to offspring than the other type, indicating some meiotic load

Frequency of Initiation Modes in Speciation.

1. Allopatric Speciation.

-majority of speciation events fall in this arena -

2. Non-Allopatric Speciation

Evaluation of Speciation Event : Reproductive Isolation. How do we evaluate this?

-There is no one general mechanism for completion of speciation.

-There is no particular combination of these factors that are unique to a speciation mode.

-There are some general mechanisms that produce reproductively isolated groups instantaneously.

—>This is a case of initiation of speciation and completion simultaneously.

Ploidy in plants

Kornet et al., 1995. (From Brooks p 157).

Also See Maddison from handout.

Microspecies : **General term** All assemblages of conspecific organisms that we called subspecies – Combined complement of smaller lineages extending through time.

- term have implied links.
- 1st. Groups under study can be distinguished objectively in some manner.

- 2nd. There is a probability that this group will become a macrospecies not done so yet.

Expect extinctions, microspecies fusions, gene flow, etc. to limit macrospecies formation.

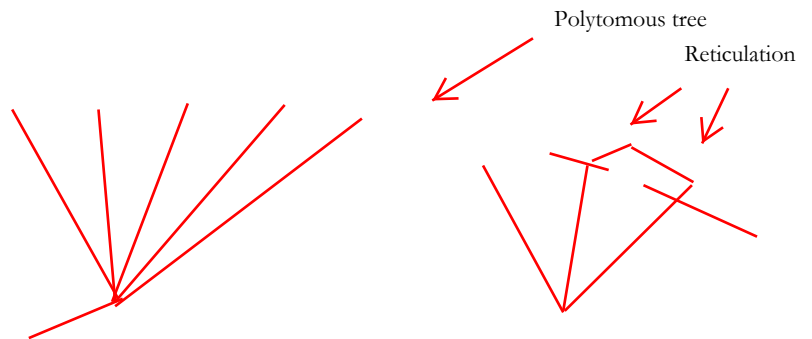
Macrospecies: A divergent lineage irreversibly split from its ancestor with no possibility of recombining with the parental species.

– In intraspecific phylogeography - the research program studies deployment of genetic variation within a species.

Generalization: relationships are complex and reticulated

- moderate to little resolution (many equally parsimonious trees).
- statistically indistinguishable trees.

reticulated and polytomous tree (show)



[This is predicted by Dobzhansky, Mayr, Simpson - SPECIES ARE THE KEY EVOLUTIONARY ENTITIES]

We predict:

- Microspecies should be more numerous than macrospecies.
- Macrospecies should be more easy to identify because they are created via historical non-reversible changes.

The Fish from Lake Victoria (400,000 yrs old) with 3 major dessication events.



The fish from Lake Tanganyika.

- show only 171 species
- these species display more extreme morphological and behavioral specializations than do the fish in the younger lakes. (Lake Victoria). See page 163-165

Fish from Lake Victoria and Lake Tanganyika.

Feb - 2014

Sticklebacks - Read the stickleback page example.

-*Gasterosteus aculeatus*

- look at the species patterns and see if they fit the results of what is expected with a centrifugal or peripatric speciation model.

You read on pages 166 - 167.

Two possible scenarios.

1. Sympatric speciation - benthic limnetic species pairs independently in each of 6 lakes.
2. 2 waves of anadromous colonists wafted into the lakes from the marine incursion.
 - a. First colonizer was closer to the benthic form.
 - b. Second colonizer was closer to the limnetic morph.

This has been termed – Ecological Speciation – speciation was completed via reinforcement (favoring premating isolation mechanisms) caused by selection against hybrids.

1. -Ecological Speciation (Dolf Schluter) -

Refers to specific involvement of ecological factors – ie.

-Competition or

-predator driven divergence.

What type of phylogenetic patterns are predicted?

1. Double invasion of the same ancestor at different times.

-Polytomy - Hard -

Both waves represent multiple instances of peripheral isolation from the same ancestor.

2. Sympatric speciation should also produce a polytomy.

Result of a phenetic analysis on page 170 shows a complicated relationship. However, a Wagner analysis of the genetic data (with bootstrap resampling) shows an almost complete polytomy.

-This is what is expected from multiple independent colonization events from a common ancestor population species!

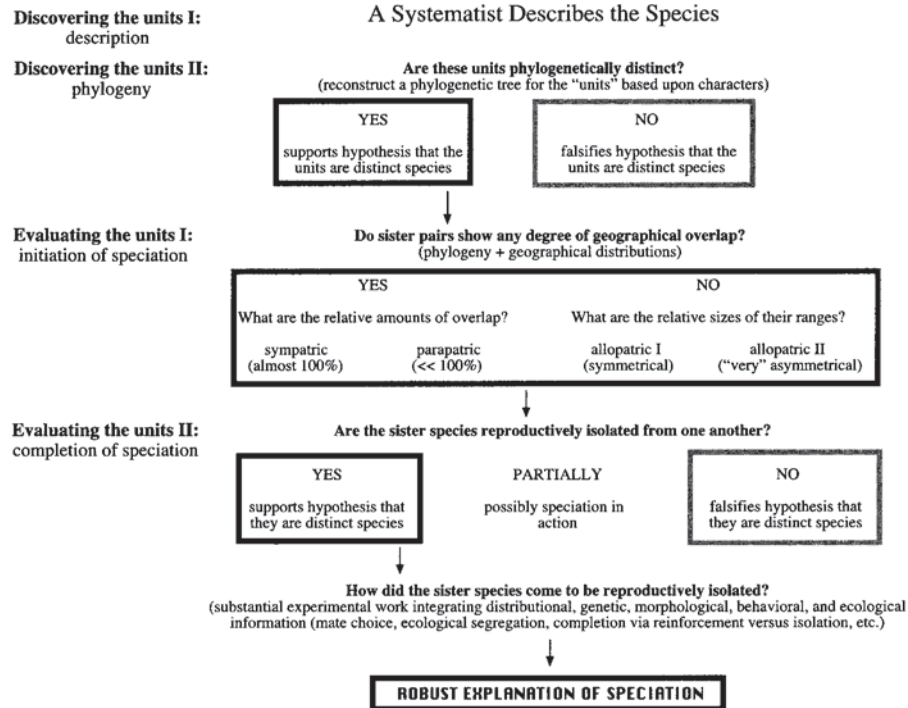


Figure 3.25. Flow chart showing the different steps needed to move from a description of a species to a robust explanation for the way in which that species was produced. Notice that information from both the historical and nondimensional species concepts is required in order to identify and evaluate the units we think might be species.



Chapter 4.

Historical Biogeography. History sensu Daniel Brooks.

3 major events in the mid 60's occurred:

1. Island Biogeography by MacArthur and Wilson 1963. Stimulated **Ecological Biogeography**
 - narrative in nature
 - discussing relationships between current environments and number and relative abundance of species in areas.
2. Continental Drift. Acceptance. 1960's
3. Phylogenetic Systematic Methods. 1960's onward.

Reliance only on contemporary ecology to look at patterns of species in areas (numbers of species on islands)

-This all led to the development of a system of biogeographic analysis called Vicariance Biogeography. This was based on "Component Analysis" for phylogenetic trees.

This method was shown to be somewhat workable, but it dropped data due to complexity of the analysis.

Meanwhile: == Farris 1970, 1982, 1988 developed methods of tree comparisons in cladistics that were applied by Brooks 1981 to look at host parasite phylogenies and later applied to biogeography.

-identify points of congruence and incongruence between host and parasite phylogenies and for historical biogeography.

Wiley called this **Brooks Parsimony Analysis (BPA)**.

-Questions are: which of the speciation events in the groups under study conform to a general pattern of vicariance?

And Which could be due to other modes of speciation / dispersal etc...?

Brooks -

Spatial scale influences complexity of phylogenetic influences on biogeographic patterns.

1. larger spatial scale -

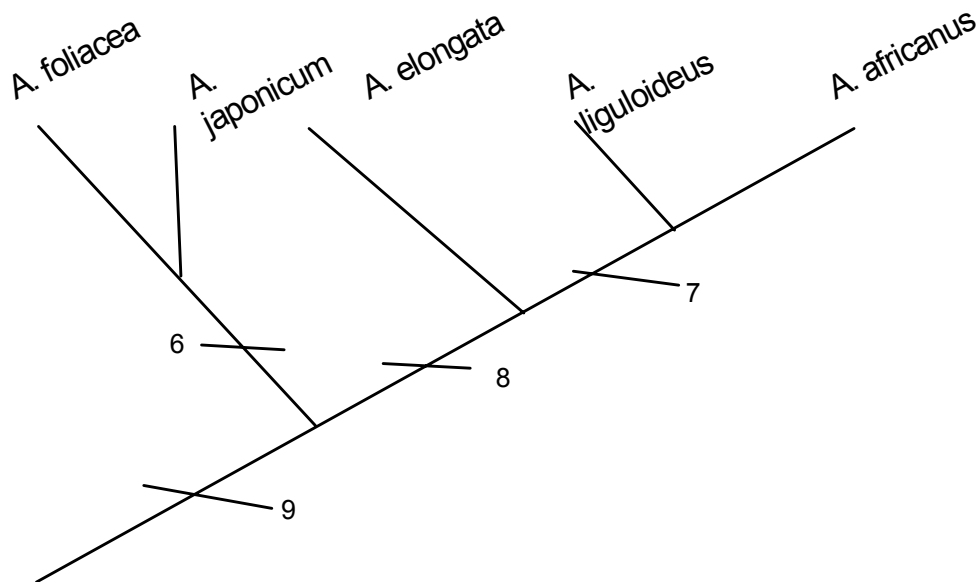
- more likely to find repeated or replicated speciation events.
- greater phylogenetic effects on diversity
- the older the origins of the biota studied.
- more complicated the historical explanations for the species composition in those biotas

2. Scale also influences the types of questions that can be asked.

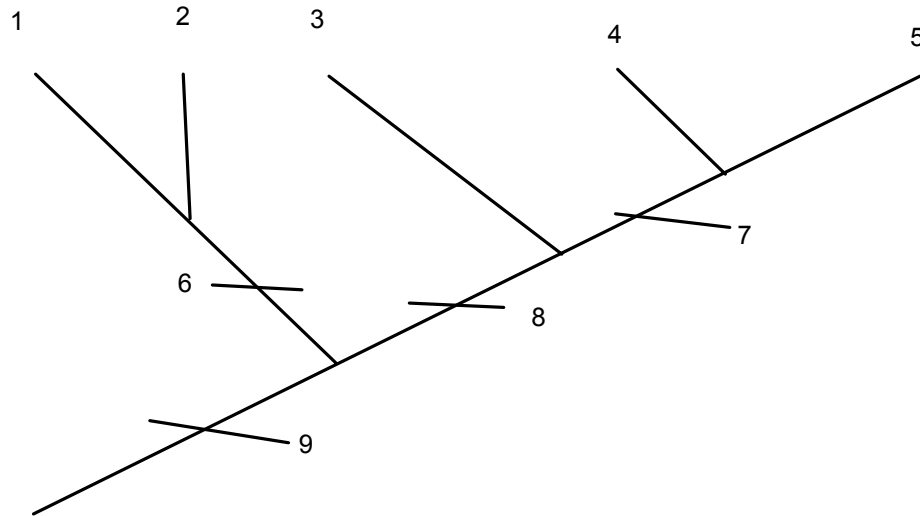
Cladogram = Branching diagram

Area Cladogram = Branching diagram of a biogeographic area

Phylogenetic Tree = estimate of relationships among species based on characters intrinsic to them.



Study of the Amphilinidea : Platyhelminthes (sister group to the tapeworms).
8 species known



Search for possible historical connections in association between these flatworms and their geographical distributions.

1. Reconstruct the phylogeny. Bandoni and Brooks, 1987 46 characters single tree with a CI of 87.5%
2. Designate areas in which the species occur as if they were taxa.

Area	Species	Species Name
A Eurasia	1	<i>Amphilina foliacea</i>
B North America	2	<i>A. japonica</i>
C Australia	3	<i>Gigantolina elongata</i>
D South America	4	<i>Schizochœrus liguloides</i>
E Africa	5	<i>S. africanus</i>

3. Now treat these as a completely polarized ordered multistate transformation series in which each branch of the tree is numbered.
4. Each species has a code that indicates its identity and its common ancestry.

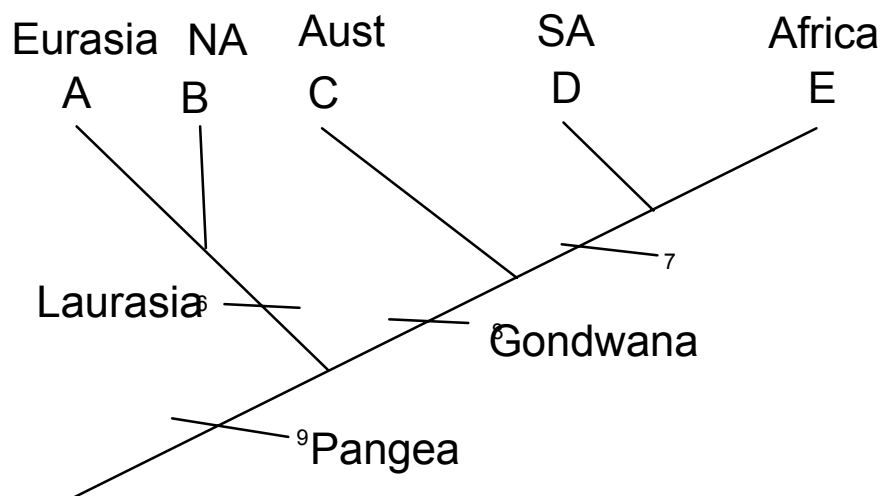
Binary codes representing the phylogenetic relationships among the 5 species of these amphilinid flatworms in our example.

	Species	Code
1	<i>Amphilina foliacea</i>	100001001
2	<i>A. japonica</i>	010001001
3	<i>Gigantolina elongata</i>	001000011
4	<i>Schizochœrus liguloideus</i>	000100111
5	<i>S. africanus</i>	000010111

- Replace the species names in table 4.2 with their geographic distributions.
- Construct an area cladogram based on the binary codes representing the phylogenetic relationships of the amphilinids.

	Species	Code
A	Eurasia	100001001
B	North America	010001001
C	Australia	001000011
D	South America	000100111
E	Africa	000010111

- Use geological evidence to produce an area cladogram showing the historical connections independent of any species living in them. It is not necessary to have a-priori information on the geological history to describe the pattern, but it helps to EXPLAIN the pattern.



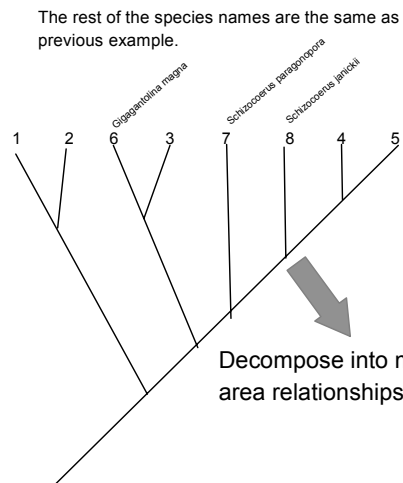
The area cladogram of the geological evidence and the area cladogram of the phylogenetic relationships are identical (CI = 100%).

Vicariant speciation.

What about Noise?

- Redundant species

(more than one member of clade endemic to same area)



2. Widespread species (one species in more than one area)
3. Missing species (one or more clades do not have species in an area).

Brooks Parsimony Analysis

Area Duplication Convention:

Whenever areas have reticulate histories with respect to the species inhabiting them, assumption 0 will be violated

unless those areas are represented as separate entities for each separate historical episode.

Primary BPA -Phylogenetic analyses that do not invoke the duplication rule.

Secondary BPA -Phylogenetic analyses that do invoke the duplication rule.

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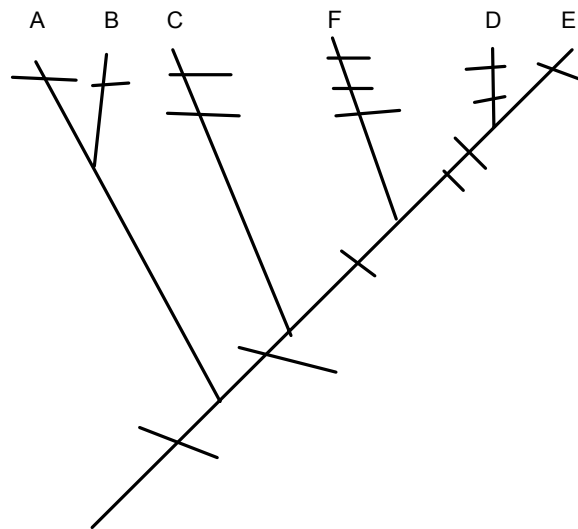
I. Redundant species in an area.

-complete phylogenetic tree for Amphilinidea.

1. Include complete data in tree - adding the three additional species.
2. Convert the tree (Fig 4.6) into a binary coded matrix. Table 4.4
-when more than one species occurs in an area - combine codes.
3. The area cladogram is reconstructed from Table 4.4.

label the tree by hand from page 184

A	100000001000001
B	010000001000001
C	001000000100011
D	000100010011111
E	000010000011111
F	000001100100111



label by hand from page 185.

The CI is 93.8% - 10 appears twice on the tree.

The common ancestor of species 3 and 6 ancestor 10 in fig above.

Problem: FIND AN EXPLANATION FOR THE HOMOPLASY.

- A. Species 3 evolved in area C (derived from ancestor 10 in same area).
- B. Ancestor 10 in area F must have been via a dispersal event.
- C. →occurrence of species 7 is due to common history
→occurrence of species 6 is due to dispersal of an ancestor into the area.

→a dispersal event by a part of species 10 that carried the synapomorphies that allows us to recognize these species.
- D. ∴Area F has a reticulate history with respect to this clade.
- E. Test dispersal of 10 and the reticulate history by using the taxon duplication convention.

Build our new tree with the matrix below:

A	Eurasia	100000001000001
B	NA	010000001000001
C	Australia	001000000100011
D	South Am	000100010011111
E	Africa	000010000011111
F1	Indo-Mal.	000001000100011
F2	Indo-Mal.	000000100000111

Problems and how to solve them:

1. Patterns of species distribution include dispersal events,
2. Either with speciation
3. Or without speciation.
4. →Result more than one species in same area←
::When this happens - binary code for area in primary BPA is a composite of the codes from all taxa in that area –
5. Codes for taxa 6 7 were combined to give composite code for area F.
6. Codes for taxa 4 8 were combined to give composite code for area D.
See Cressy et al., 1983 (inclusive Oring).
7. Dispersal appeared as homoplasy (reversal)
8. Two speciation events appeared as autapomorphies.
9. Ambiguity - solved by assuming indo-malaysia for species 6 was different from indo-malaysia for species 7.

I. Problem with BPA.

- a. Many Young Species Dispersing into Areas Inhabited by Older Members of the Clade.

This is solved by using the secondary BPA and duplicating the areas. See examples p 188 - 190. Know how to do this.

- b. Ambiguity Due to Widespread Species.

Any given species may occur in more than one of the areas being studied.

Dispersal from area of origin without speciating.

or

Failed to speciate due to vicariant events.

Secondary BPA seems to work to fix these problems using the area duplication convention. Compare matrix on page 191 with that on page 195.

See fig 4.18 on page 193. For dispersal schema

- c. What about Missing Species?

-what do we do if there were extinctions?

-what if we have not surveyed intensively enough to find all the species yet?

*** Primitive absence or secondary loss (or not enough data?).???