

Start: 30 September, 2013

**TABLE 7-1**  
**KINDS OF TAXONOMIC CHARACTERS**

- 1 Morphological characters
  - a General external morphology
  - b Special structures (e.g., genitalia)
  - c Internal morphology (anatomy)
  - d Embryology
  - e Karyology and other cytological differences
- 2 Physiological characters
  - a Metabolic factors
  - b Body secretions
  - c Genic sterility factors
- 3 Molecular characters
  - a Immunological distance
  - b Electrophoretic differences
  - c Amino acid sequences of proteins
  - d DNA hybridization
  - e DNA and RNA sequences
  - f Restriction endonuclease analyses
  - g Other molecular differences
- 4 Behavioral characters
  - a Courtship and other ethological isolating mechanisms
  - b Other behavior patterns
- 5 Ecological characters
  - a Habitats and hosts
  - b Food
  - c Seasonal variations
  - d Parasites
  - e Host reactions
- 6 Geographic characters
  - a General biogeographic distribution patterns
  - b Sympatric-allopatric relationship of populations

**Character:** trait or attribute

**Character States:** various forms or expression of a character

Ex.: beetle elytra (forewing)

Character: punctation of tiger beetle elytra

States: punctures shallow or punctures deep

### New Characters

#### Molecular

- \* microsatellite DNA
- \* SNPs (single nucleotide polymorphisms)
- \* next-generation sequence fragments
- \* whole genomes

#### Ultrastructure

- \* sperm ultrastructure very conservative

CT Scans (=computer-processed X-rays to produce tomographic images or slices of an object)

**Apomorphic:** derived or evolved character state

**Plesiomorphic:** the ancestral or pre-existing state of a character

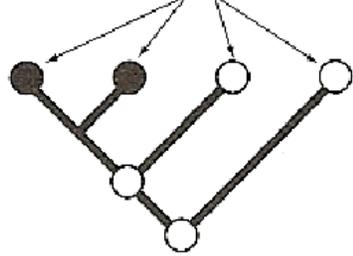
**Apotypic and plesiotypic:** can use for (non-morphological) behavioral, ecological, and physiological characters

**Autapomorphic:** unique (unshared) derived state

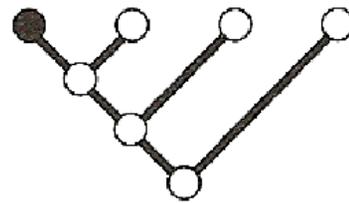
**Synapomorphic:** uniquely shared derived state

**Symplesiomorphic:** shared primitive state

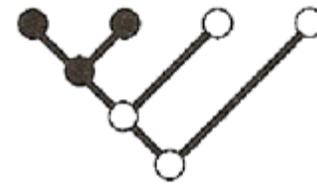
Apomorphy    Plesiomorphy



**Autapomorphy**



**Synapomorphy**



## *Autapomorphic, Synapomorphic & Sympleiomorphic*

\* *relative terms*: i.e., relative to other taxa under study

\* usage depends on level of analysis or inquiry

Ex.: feathers are

- autapomorphic for the class Aves(birds) (relative to other vertebrates)
- synapomorphic for all bird orders (relative to other vertebrates)
- sympleiomorphic for ratites and other flightless birds (when trying to infer relationships of bird orders to one another)

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Monday, October 5, 2009

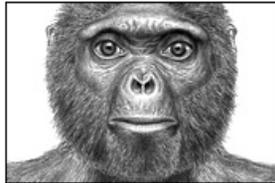
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## Oldest "Human" Skeleton Found-- Disproves "Missing Link"

Jamie Shreeve  
 Science editor, [National Geographic magazine](#)  
 Updated 6:44 p.m. ET, October 1, 2009

**Move over, Lucy. And kiss the missing link goodbye.**

Scientists today announced the discovery of the oldest fossil skeleton of a [human](#) ancestor. The find reveals that our forebears underwent a previously unknown stage of evolution more than a million years before [Lucy](#), the iconic early human ancestor specimen that walked the Earth 3.2 million years ago.



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- [Human Genome Shows Proof of Recent Evolution, Survey Finds](#)
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The centerpiece of a treasure trove of new fossils, the skeleton—assigned to a species called *Ardipithecus ramidus*—belonged to a small-brained, 110-pound (50-kilogram) female nicknamed "Ardi." (See [pictures of Ardipithecus ramidus](#).)

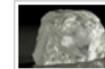
The fossil puts to rest the notion, popular since Darwin's time, that a [chimpanzee](#)-like missing link—resembling something between humans and today's apes—would eventually be found at the root of the human family tree. Indeed, the new evidence suggests that the study of chimpanzee anatomy and behavior—long used to infer the nature of the earliest human ancestors—is largely irrelevant to understanding our beginnings.

(Interactive time line: [how the Ardipithecus ramidus discovery changes human evolutionary theory](#).)

Ardi instead shows an unexpected mix of advanced characteristics and of primitive traits seen in much older apes that were unlike chimps or gorillas ([interactive: Ardi's key features](#)). As such, the skeleton offers a



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# Trees

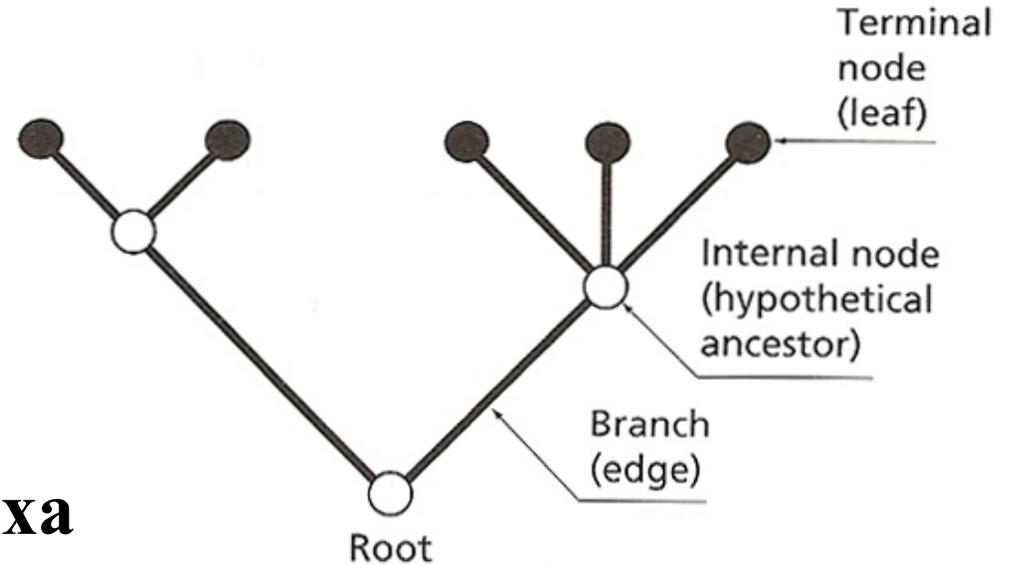
**Nodes: branching points**

**Branches (internodes, edges)**

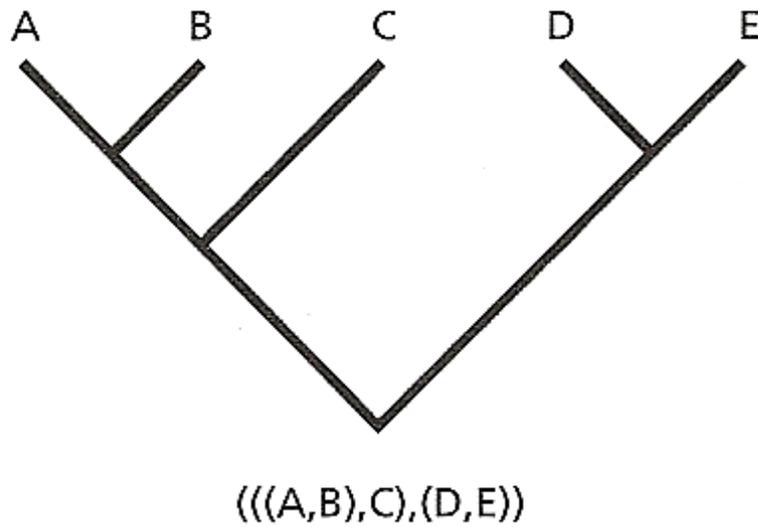
- **terminal nodes: terminal taxa**
- **the entities in the analysis**

**Internal nodes: hypothetical ancestors**

**Root: basal ancestor**



# Tree Notation



**Fig. 2.4** A tree and its shorthand representation using nested parentheses.

# Tree resolution

- \* Partially or fully resolved trees
  - fully resolved: all branches bifurcating
  - partially resolved trees have *polytomies*
- \* *Polytomy* = 3 or more branches (descendants) from single node
  - soft polytomy: waiting for more data (unsure of sequence)
  - hard polytomy: polytomy thought to be reflective of true evolutionary history

# Types of branching diagrams

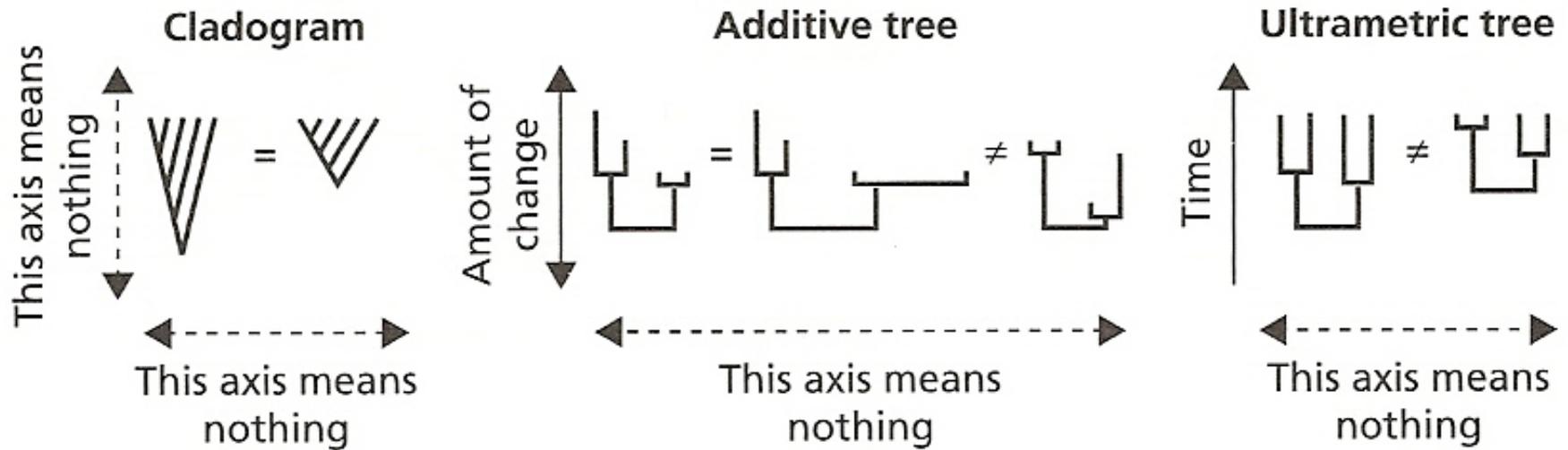
A **dendrogram** is a broad term for any diagrammatic representation of a phylogenetic tree.

A **cladogram** is a tree formed using cladistic methods. This type of tree only represents a branching pattern, i.e., its branch lengths do not represent time.

\* A synapomorphy mapping scheme of sorts as its topology is determined by mapping of shared derived characters.

A **phylogram** (additive tree) is a phylogenetic tree that represents the amount of character change by its branch lengths.

An **ultrametric tree** or **chronogram** is a phylogenetic tree that explicitly represents evolutionary time through its branch lengths.



a. cladograms

- simply branching sequence, relationships
- branch lengths unknown or not estimated

b. additive trees

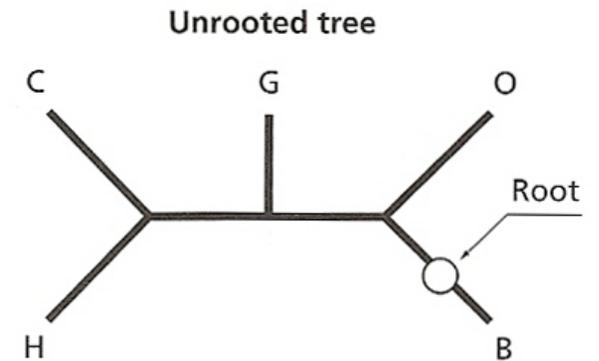
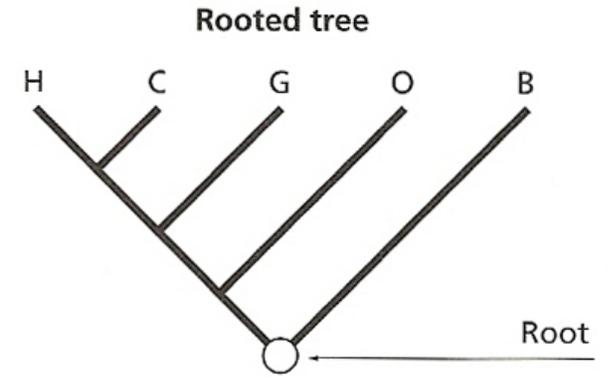
- branching sequence plus branch lengths
- distance from root to tips differs among lineages
- root to tip specifies degree of divergence

c. ultrametric trees

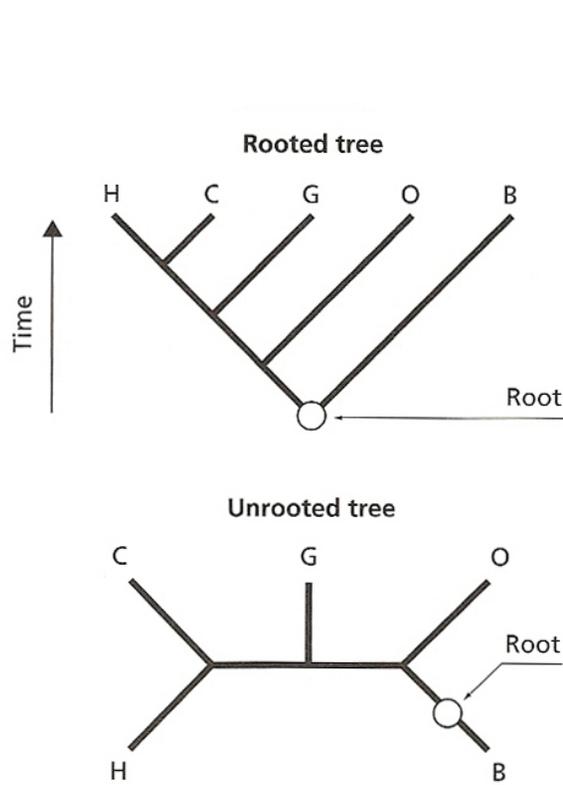
- tips equidistant from root (assuming all taxa extant)
- branching sequence plus *time*
- lengths of branches specify *time* since splits

# Rooting Trees

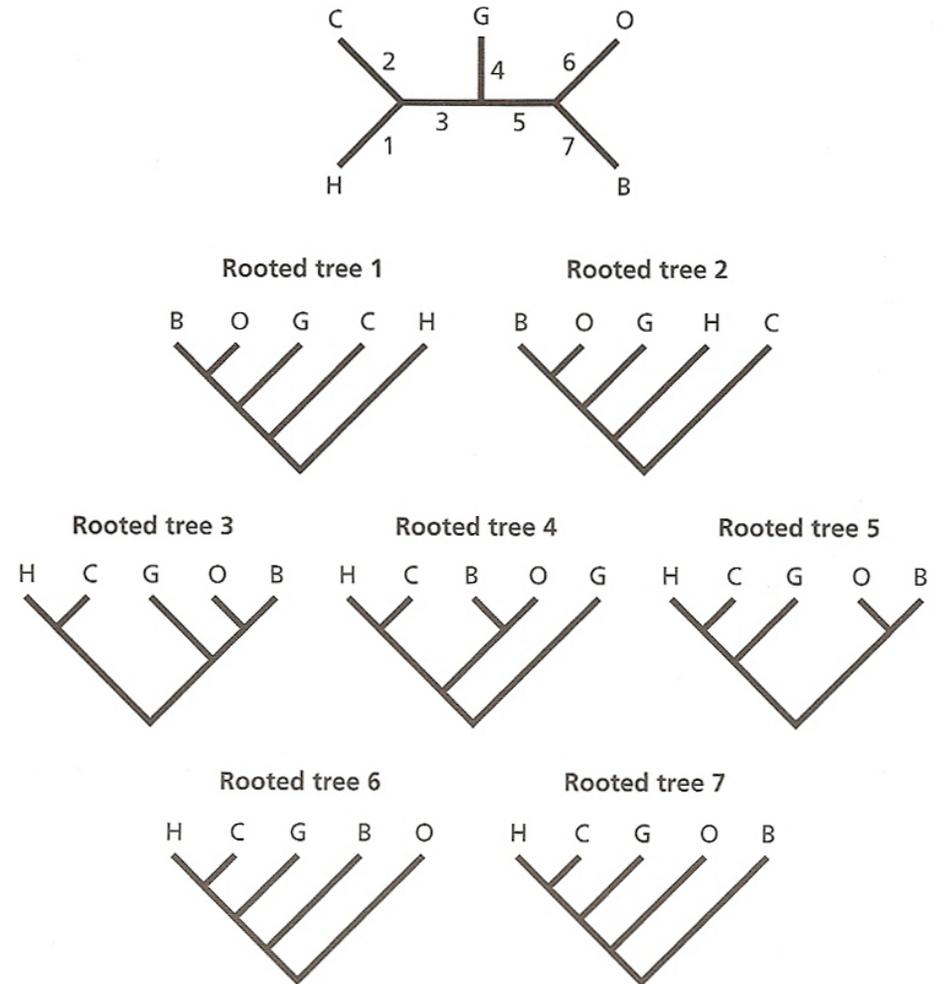
- \* Trees may be rooted or unrooted
- \* unrooted trees = networks or graphs
  - no base or origin implied
- \* if no constraints on character evolution (directionality), all trees are of same length no matter where the root is placed



# Rooting Trees



**Fig. 2.6** Rooted and unrooted trees for human (H), chimp (C), gorilla (G), orang-utan (O), and gibbon (B). The rooted tree (top) corresponds to the unrooted tree below.

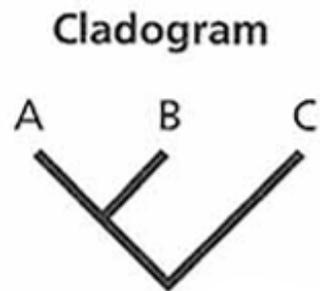


**Fig. 2.7** The seven rooted trees that can be derived from an unrooted tree for five sequences. Each rooted tree 1–7 corresponds to placing the root on the corresponding numbered branch of the unrooted tree. (Sequence labels as for Fig. 2.6.)

Rooting determines everything...

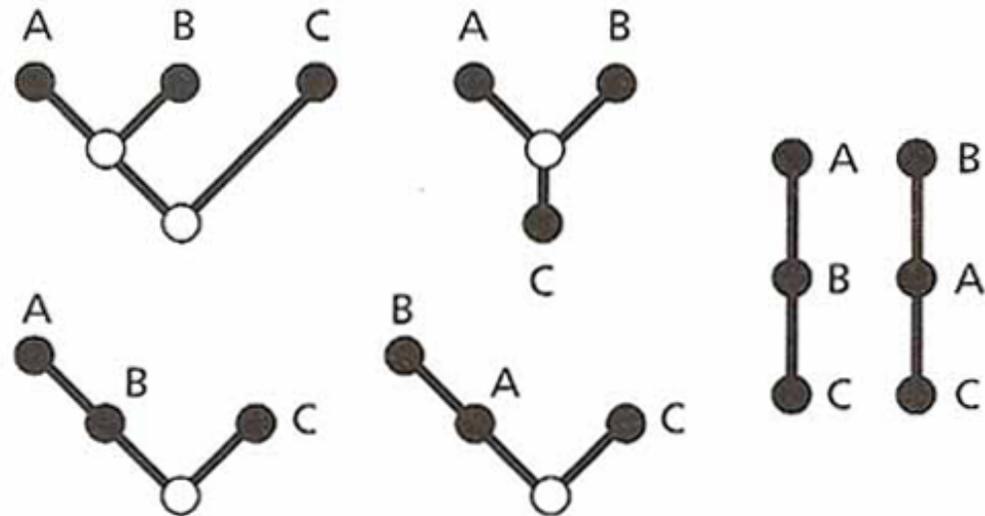
## Cladograms $\neq$ Evolutionary Trees

- \* a *cladogram* is often equated with an evolutionary tree but
  - many phylogenetic/evolutionary trees possible from even a simple cladogram (see Pages and Holmes 1998: 24)

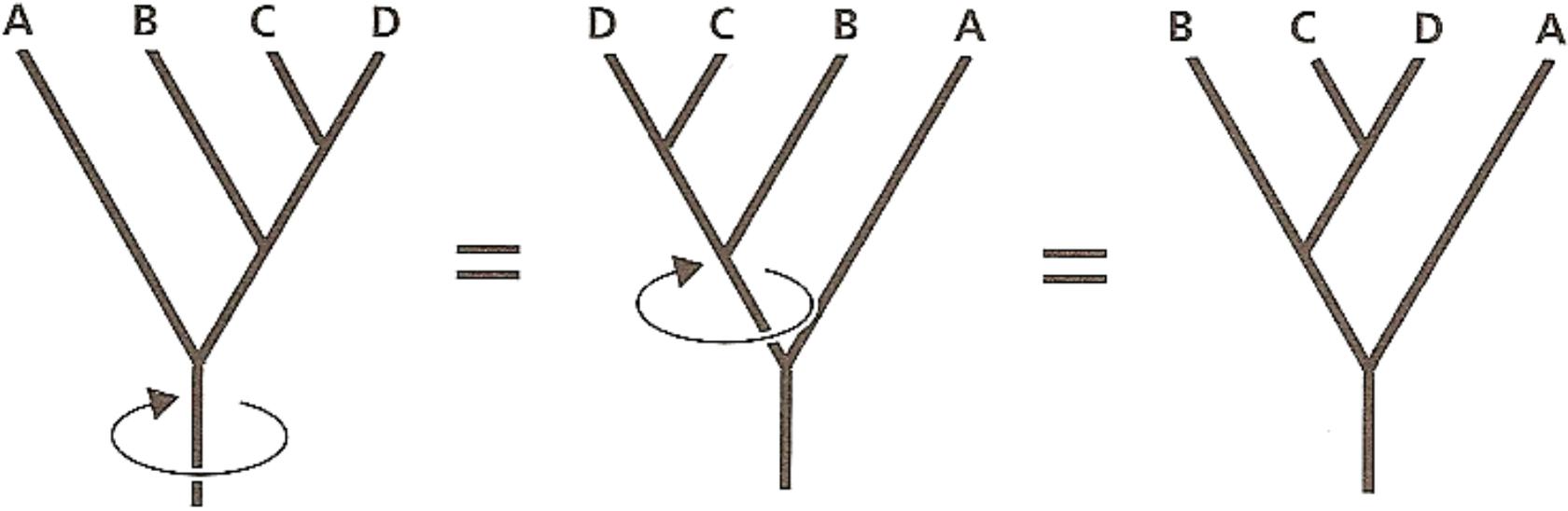


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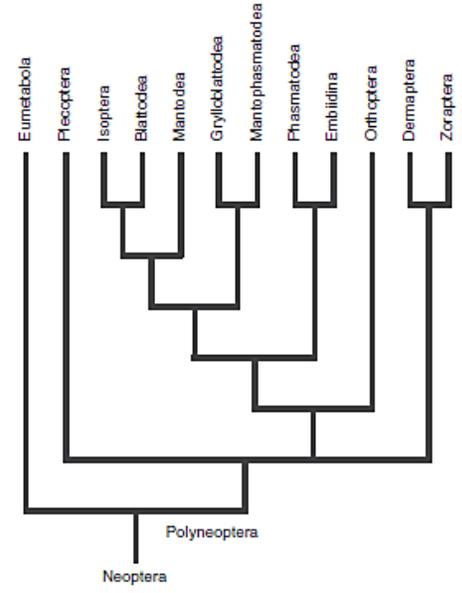
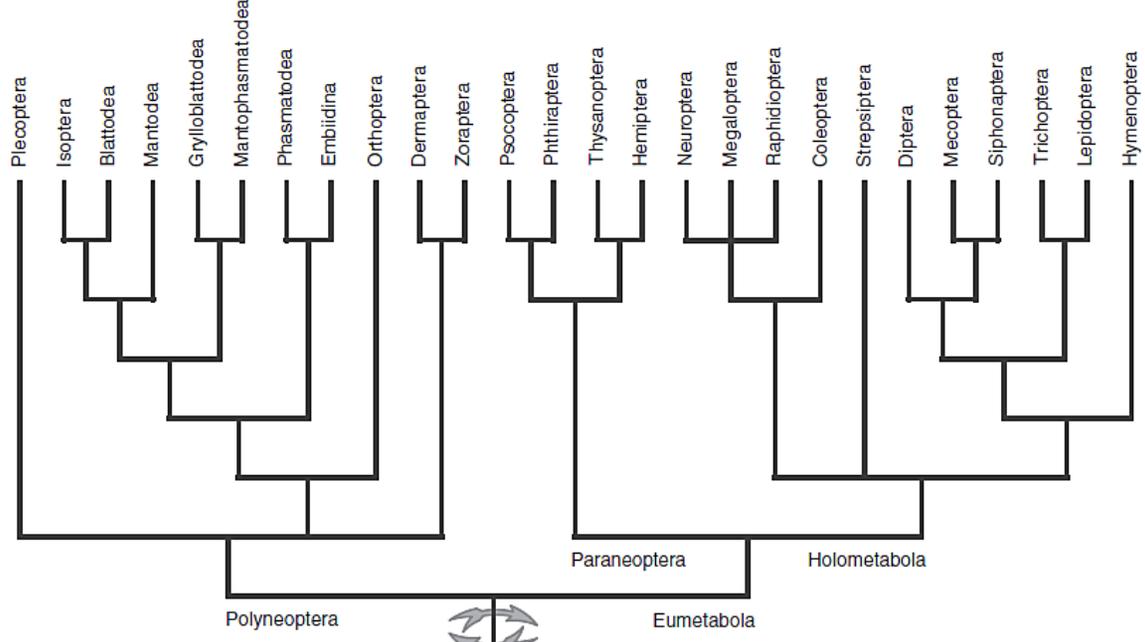
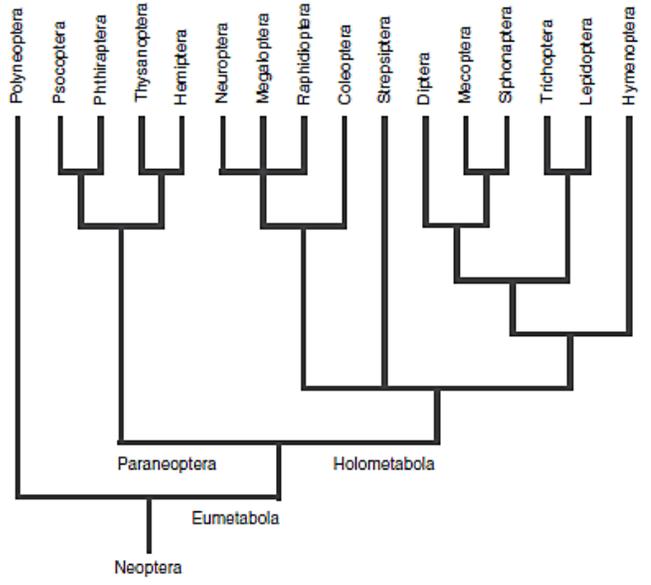
Evolutionary trees



# Branches Can Rotate on Node



**...taxon on right is not most derived**



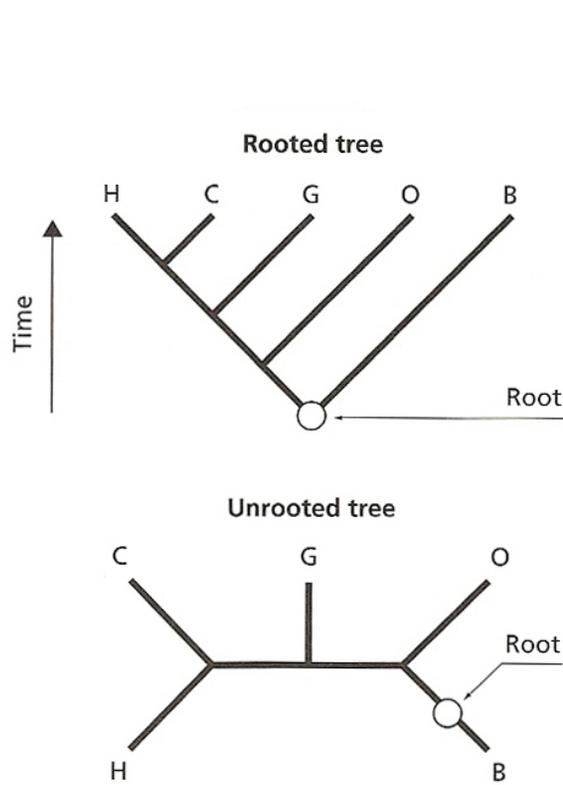
Krell and Cranston 2004. Which side of the tree is more basal?

# Announcements

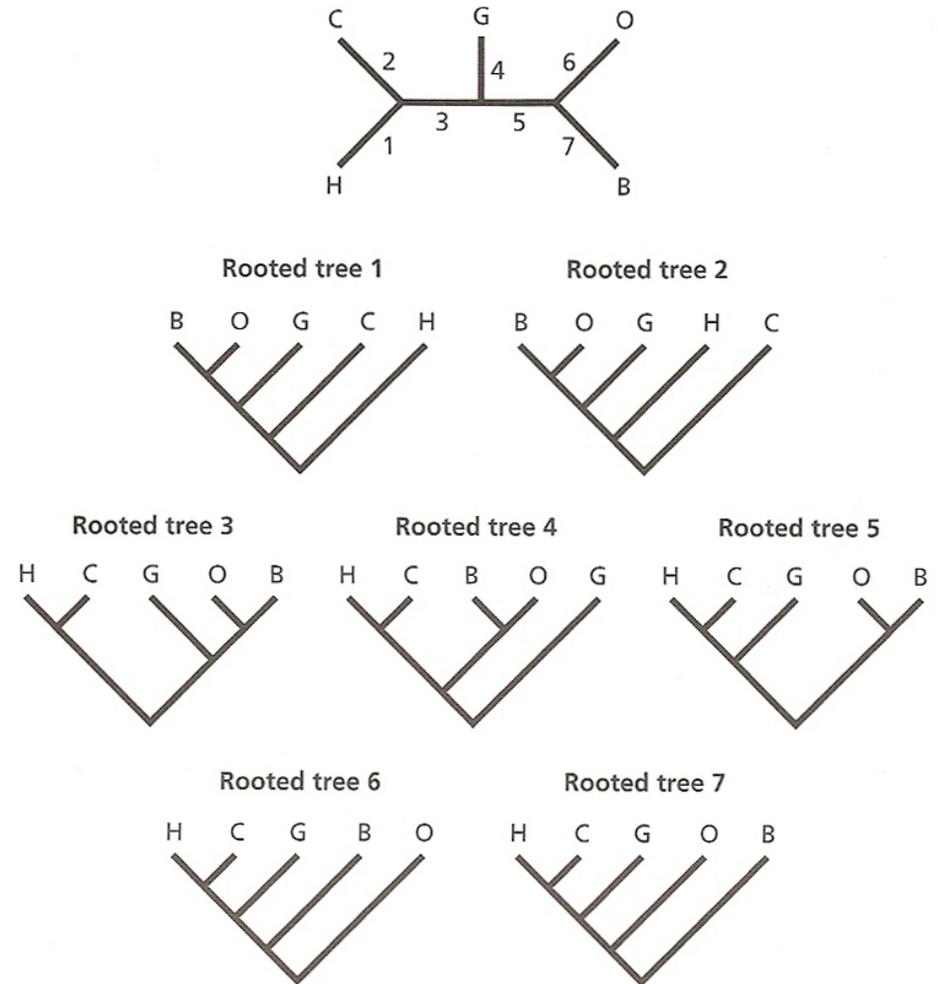
2 October, 2013

- \* Field trip receipts: approx. \$85 available
- \* black jacket
- \* Readings
- \* Paper topic
- \* ?Wagner away at Smithsonian after noon on Thursday

# Rooting Trees



**Fig. 2.6** Rooted and unrooted trees for human (H), chimp (C), gorilla (G), orang-utan (O), and gibbon (B). The rooted tree (top) corresponds to the unrooted tree below.



**Fig. 2.7** The seven rooted trees that can be derived from an unrooted tree for five sequences. Each rooted tree 1–7 corresponds to placing the root on the corresponding numbered branch of the unrooted tree. (Sequence labels as for Fig. 2.6.)

Rooting determines everything...

Number of possible unrooted trees

$$\frac{(2n - 3)!}{2^{n-2}(n - 2)!}$$

Number of possible rooted trees

$$\frac{(2n - 5)!}{2^{n-3}(n - 3)!}$$

Number of sequences	Number of unrooted trees	Number of rooted trees
2	1	1
3	1	3
4	3	15
5	15	105
6	105	945
7	945	10395
8	10395	135135
9	135135	2027025
10	2027025	34459425

# Qualitative versus Quantitative Characters

1. Qualitative characters
2. Quantitative (measurement) characters
  - a. continuous: height
  - b. meristic: count measurements  
e.g., number of antennal segments

All three character types may appear in same matrix.

# **Discrete versus non-discrete (continuous) characters**

- \* Discrete characters most commonly employed character type in phylogenetic analyses because the various states may be unambiguously coded with respect to one another.
- \* If measured variation (states) is not discrete, i.e., the taxa exhibit overlapping states, there is disagreement on how such data can/should be incorporated into a phylogenetic analysis.
- \* Keep in mind that much apparently discrete data may, in fact, be pseudo-discrete data
  - states might be defined as if they were discrete: e.g., leaf shapes;
  - absence of intermediates may simply reflect incomplete sampling;
  - even presence/absence can be tricky (a feature may appear absent until you view it under greater magnification).

# Coding Discrete Characters

## \* Binary Characters

- two states, coded by 0 and 1
- ordered by default

## \* Multistate Character

- more than two states
- two broad types with several possible attributes:

### a) linear transformation series (Compleat Cladist Fig. 3.13)

i) linear coding (Compleat Cladist Table 3.6)

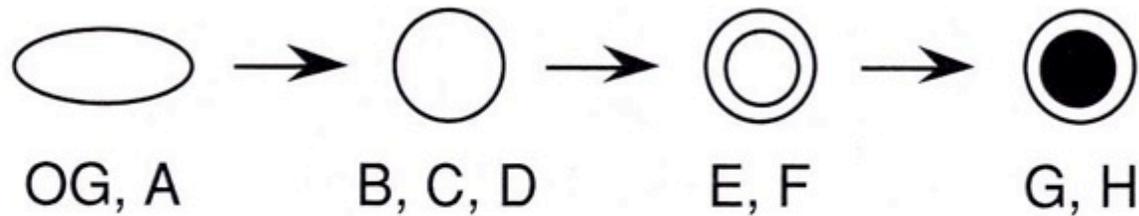
ii) additive binary (Compleat Cladist Table 3.6)

### b) branching transformation series (Compleat Cladist Fig. 3.14)

i) nonadditive binary coding (Compleat Cladist Table 3.7)

ii) mixed coding (Compleat Cladist Table 3.7)

## Optional



A simple linear character tree of four characters. Letters represent taxa in which each character

Table 3.6.—Data matrix for a simple linear transformation series coded by the linear and the additive binary methods (Example 3.2).

Taxon	Linear coding	Additive binary coding*		
		C + C/C + C/D	C/C + C/D	C/D
OG	0	0	0	0
A	0	0	0	0
B	1	1	0	0
C	1	1	0	0
D	1	1	0	0
E	2	1	1	0
F	2	1	1	0
G	3	1	1	1
H	3	1	1	1

\* Column heads are apomorphic (1) characters. C = circle; C/C = circle/circle; C/D = circle/dot.

# Optional

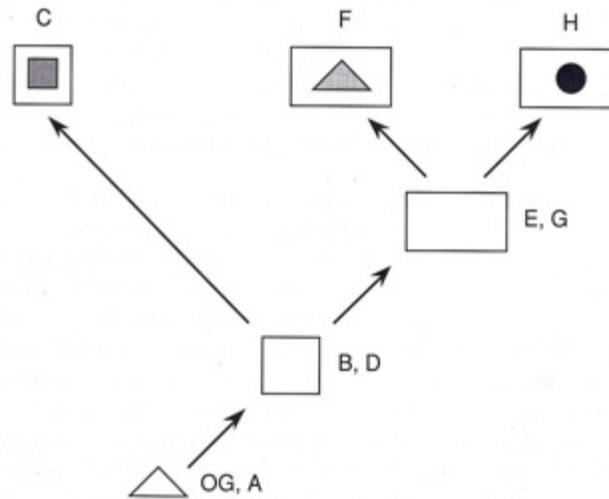


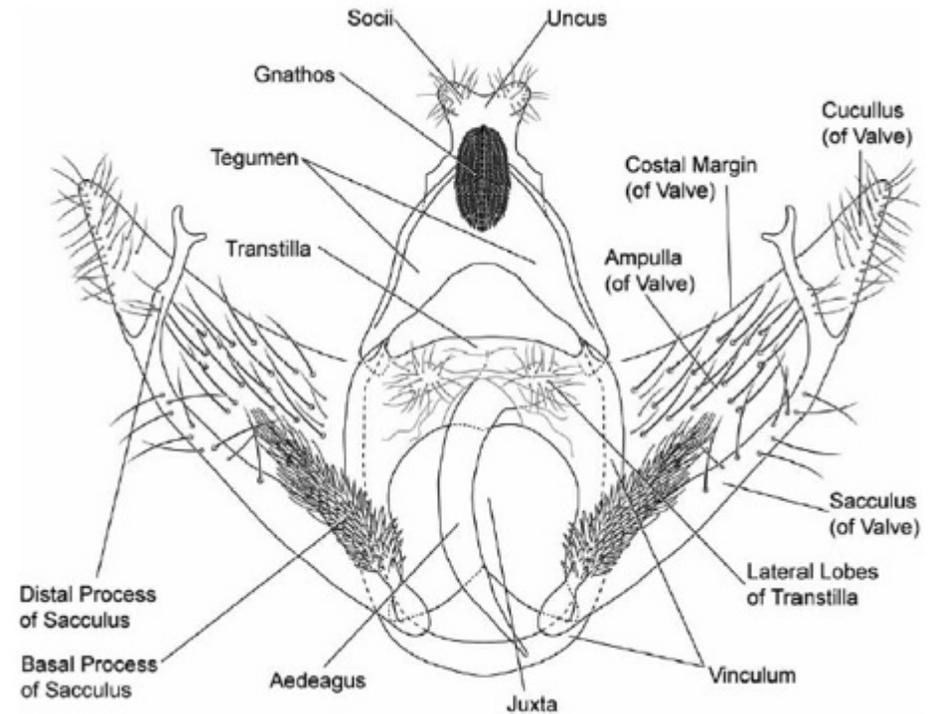
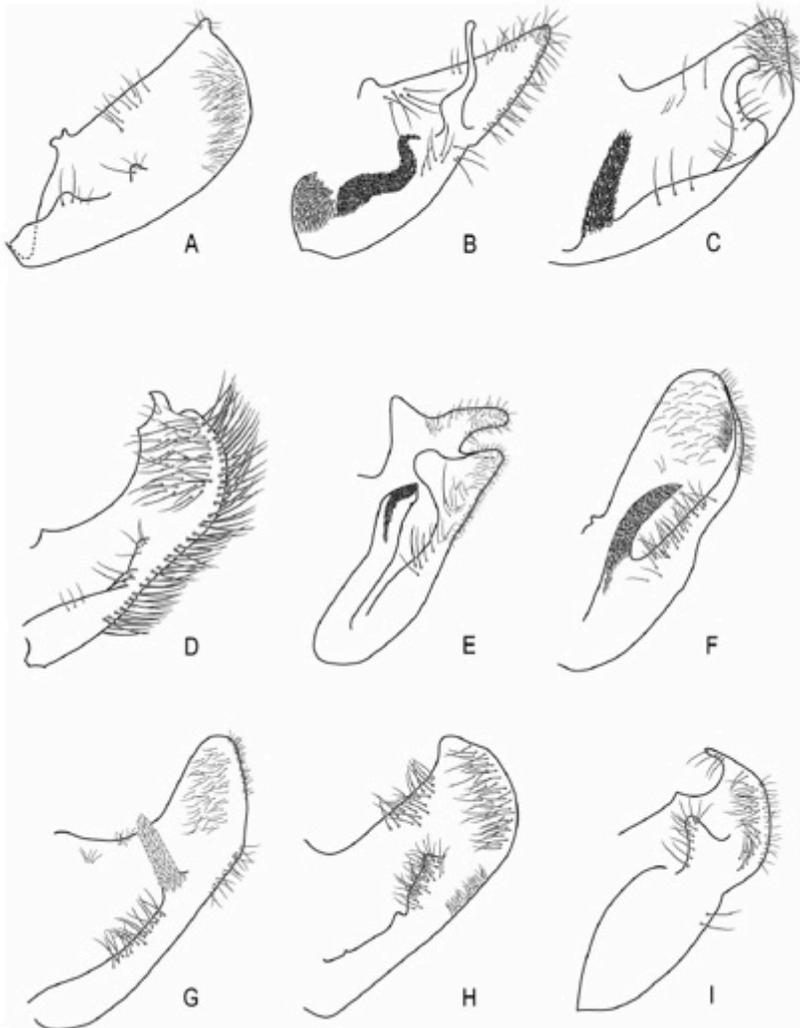
Fig. 3.14.—A complex branching character tree of six characters. Letters represent taxa in which each character is found.

Table 3.7.—Data matrix for a branching transformation series coded by the nonadditive binary and the mixed methods (Example 3.3).

Taxon	Nonadditive binary coding*					Mixed coding*		
	All except T	S/S	R+	R/D	R/T	T+S+R+R/D	S/S	R/T
OG	0	0	0	0	0	0	0	0
A	0	0	0	0	0	0	0	0
B	1	0	0	0	0	1	0	0
C	1	1	0	0	0	1	1	0
D	1	0	0	0	0	1	0	0
E	1	0	1	0	0	2	0	0
F	1	0	1	1	0	2	0	1
G	1	0	1	0	0	2	0	0
H	1	0	1	0	1	3	0	0

\* Column heads are apomorphic ( $\geq 1$ ) characters. T = triangle; S = square; S/S = square/square; R+ = rectangle and all descendants; R/D = rectangle/dot; R/T = rectangle/triangle.

No rules on how to code complex (morphological) characters:  
How many characters do you derive from a single character or  
character system?



# Coding Continuous Characters

**gap coding** – some statistical measure of the variance is used as a yard-stick for identifying sufficiently large gaps in the raw data.

**segment coding** – the total range in variation in a character is divided into an arbitrarily chosen number of equal-sized, non-overlapping ranges.

**divergence coding** – makes prior knowledge of taxa; mean character values for each taxon are ranked; taxon by taxon matrix is filled with either 1s, -1s or 0s depending on whether the means for each pair of taxa are greater or less than that of other taxa; the total score of 1s, -1s, and 0s is calculated for each taxon and that value is used as the character state.

**generalized gap coding** – taxa are again arranged in order according to their mean values and pooled data for all possible sets of contiguous taxa are compared statistically with data for adjacent taxa or contiguous sets of adjacent taxa; if a statistically significant difference is obtained then the boundary between the two groups is taken as a “gap.”

See Quicke, D. L. J. (1993): Principles and Techniques of Contemporary Taxonomy, Tertiary Level Biology Series, Blackie Publishing Group, Glasgow.

# Character Analysis

- \* Character analysis sits at the heart of phylogenetic construction and systematic analysis
- \* "Knowing where useful characters are to be found and establishing their specific value is perhaps the most important skill of a systematist..." Mayr and Ashlock (1991)
- \* They go on to write: "The entire zoological classification is based on the proper evaluation of taxonomic characters. This operation, then, is the most important as well as one of the most difficult tasks of the taxonomist."
- \* cladograms and phylogenetic trees are only as good as the *character analysis* that goes to generating them (garbage in...garbage out)

# Character selection

- \* find characters that are variable but not too variable
  - characters should be appropriate for the questions being asked
- \* objectivity is important when selecting non-molecular characters
  - easy to bias an analysis by choosing the characters that fit your preconceived notions (glass slipper phenomenon)
- \* choose independent characters
  - avoid suites of correlated characters
  - avoid characters known to be under strong selection (e.g., 1° and 2° sex. characters)



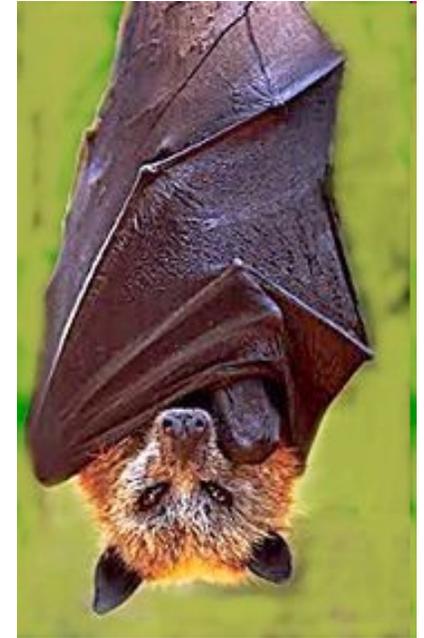
**Golden crowned fruit bat**



**Big brown bat**

# Character selection and Bat Phylogeny

- \* External morphology argues for common, and unique ancestry (monophyly),
  - but many of these are characters associated with flight and the flight musculature.
- \* Neurological wiring of brain suggests two lineages, and that bats are polyphyletic
  - but again same problem because Megachiroptera do not echolocate



**Golden crowned fruit bat**



**Big brown bat**

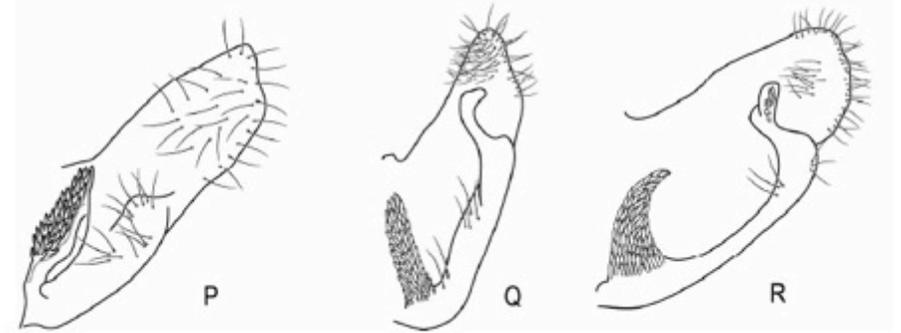
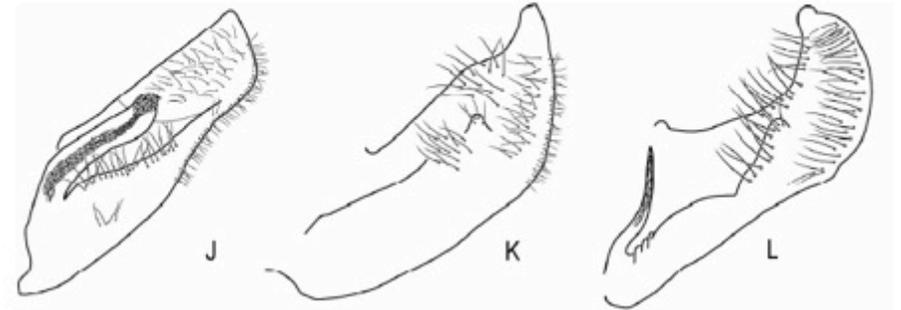
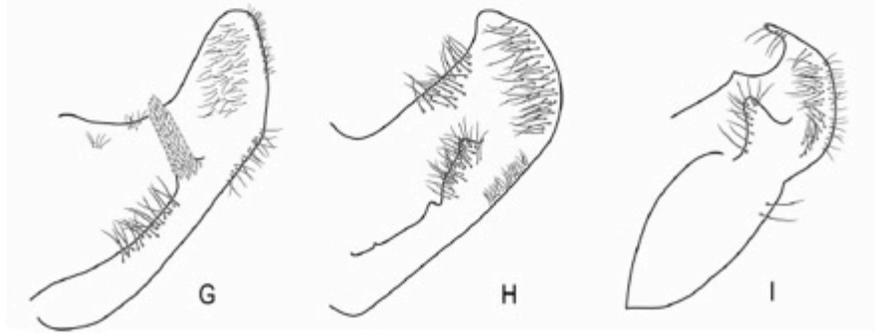
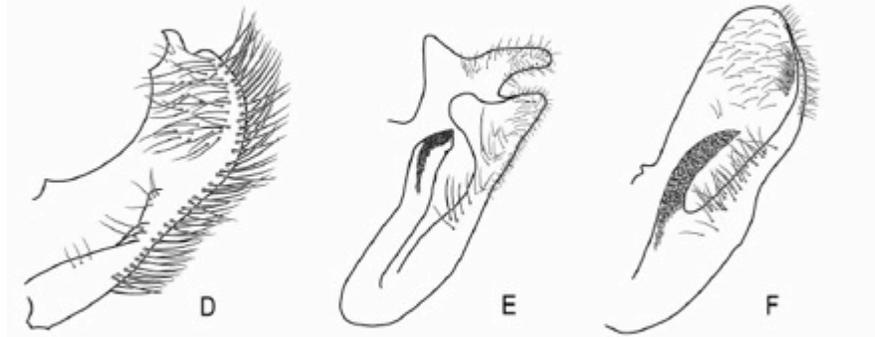
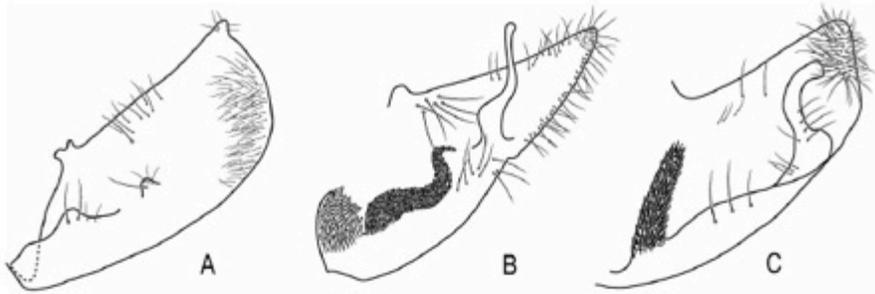
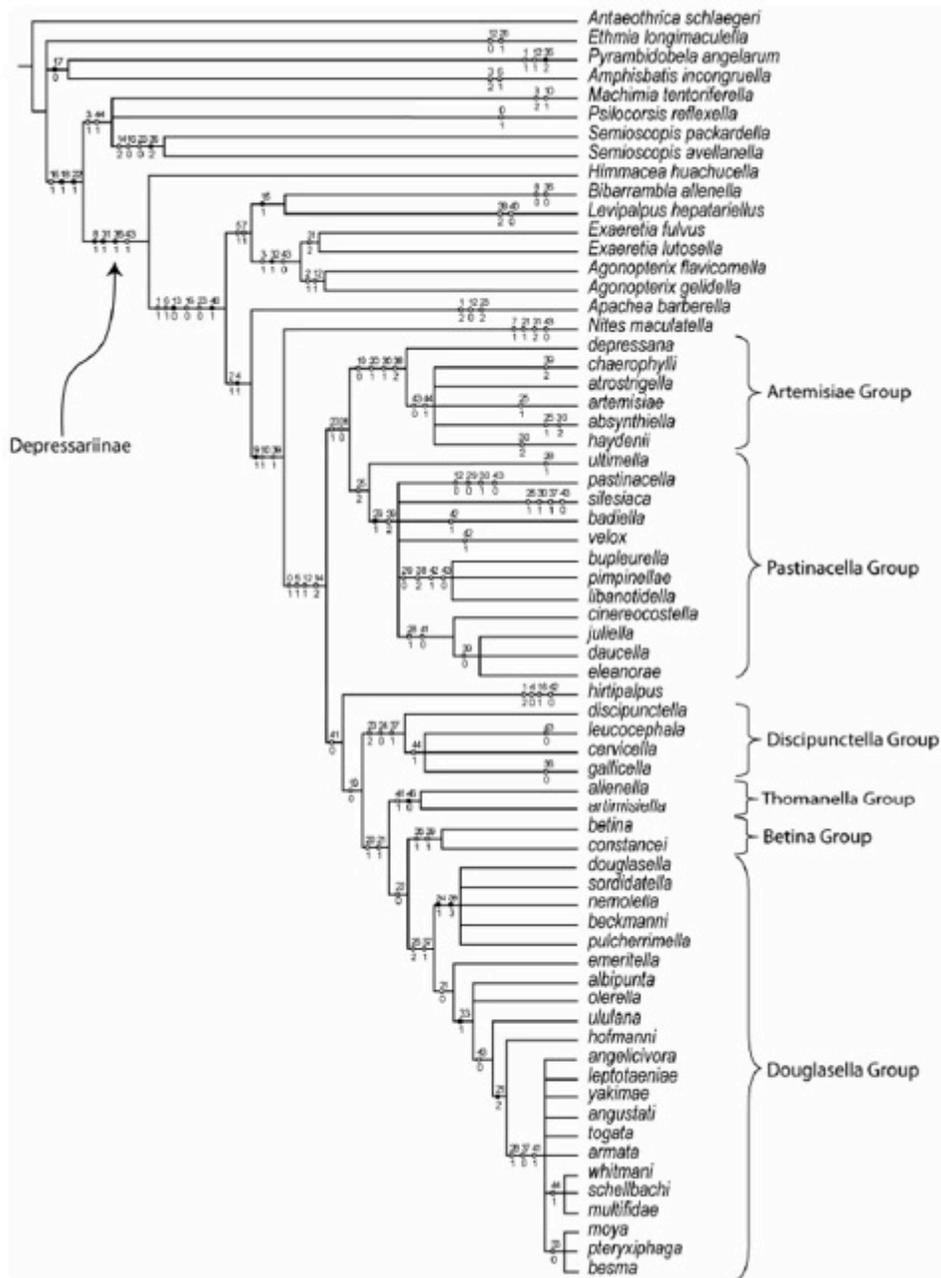
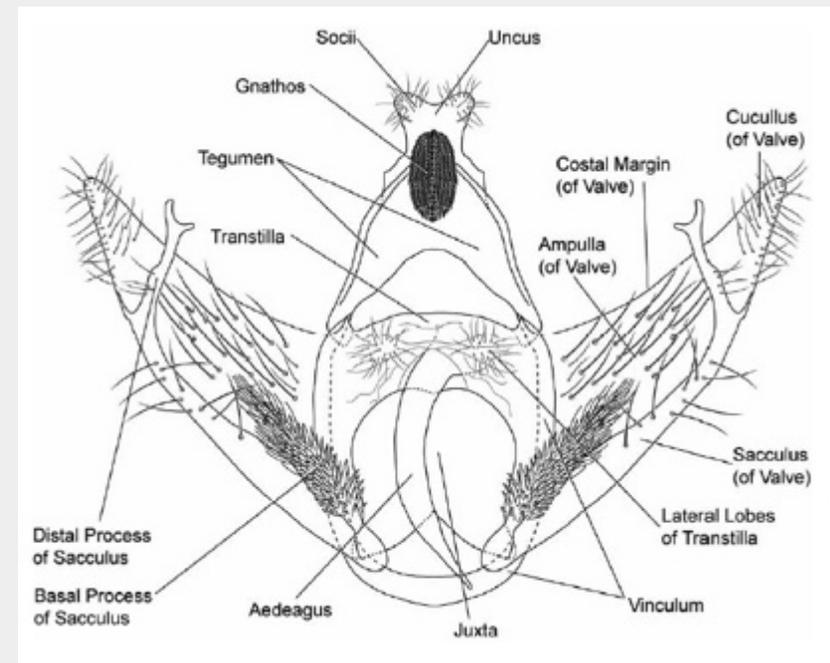


Fig. 3



## 46 Characters in analysis:

- 29 based on male genitalia
- 15 based on male valve



*Cerma cerintha*



Moved into Acronictinae because of DNA data and pupation behavior, but initially regarded as problematic because *Cerma* possessed very complex (derived) male pheromone system believed to have evolved later in Noctuidae

“The male scent system consists of a (1) fascicle of long scent scales, a (2) lever system that deploys the androconial brush during courtship, an (3) apodeme associated with the lever, a (4) pheromone-releasing gland, a (5) pocket on the side of the third and fourth abdominal segments that receives the brush at rest, plus (6) all the associated musculature and innervation.”

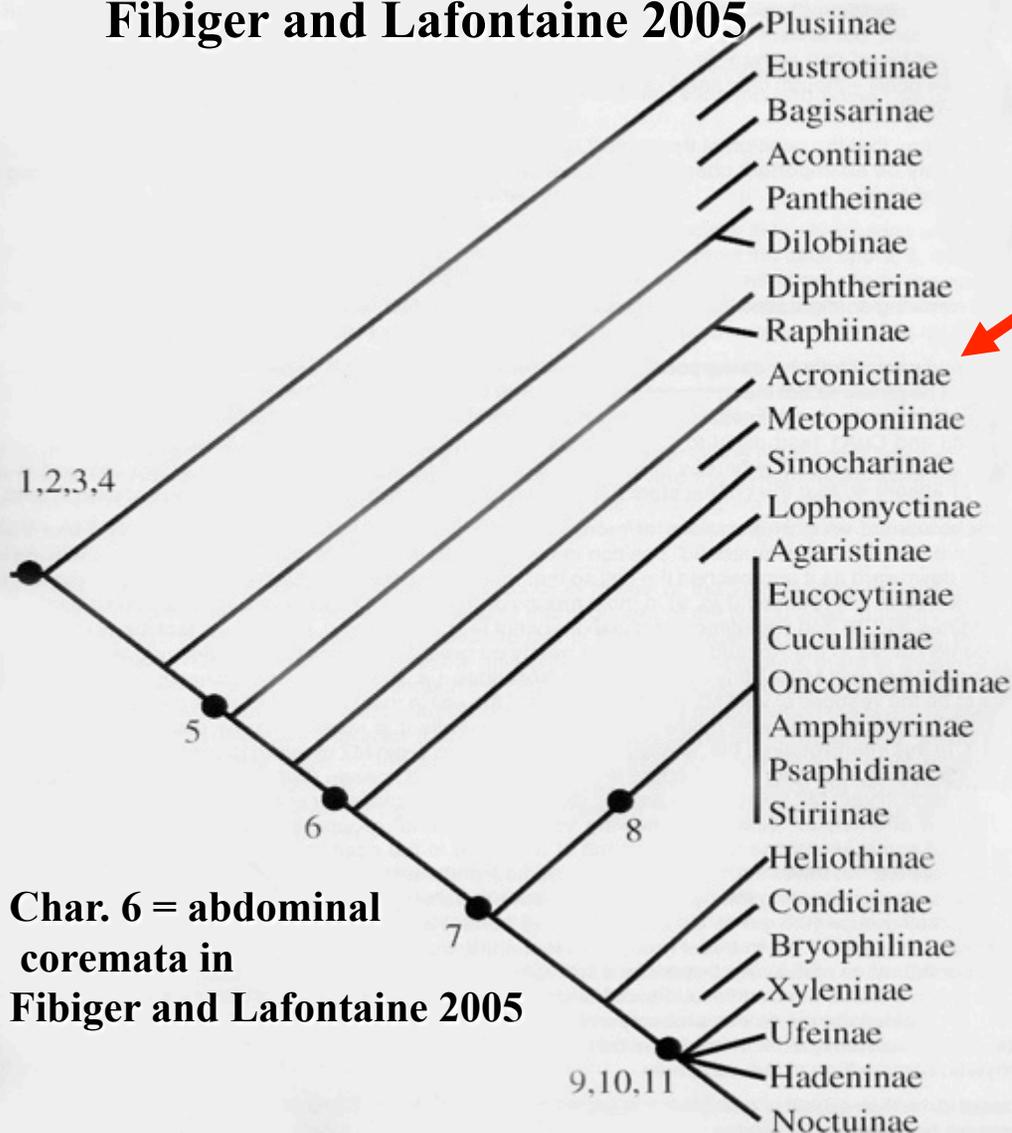
Wagner (2007)



*Cerma cerintha*

# Abdominal Brush Organ in *Cerma cerintha*

Fibiger and Lafontaine 2005



Char. 6 = abdominal coremata in Fibiger and Lafontaine 2005



If *Cerma* is an acronictine, then:

- (1) abdominal coremata must evolve more basally
- (2) abdominal coremata must be surprisingly labile (evolutionarily)
- (3) elevation of Sinocharinae and Lophonyctinae based on presence of coremata seems ill-considered, and *Sinocharis* and *Lophonycta* could be returned to Acronictinae

Bottom line: male sexual characters can evolve rapidly and workers need to regard cautiously

## Scoring Synapomorphies: Homology Criteria

- \* Similarity in position  
ex. forelimbs in vertebrates
- \* Similarity of quality or function  
ex. all vertebrate eyes
- \* Continuance through intermediate forms  
*taxonomic, fossil, or ontogenetic intermediates*  
ex. our inner ear bones are homologous to the jaw bones of reptiles,  
i.e., hydromandibular, quadrate, & articular bones  
- fossils can be key here (as in horses and their toe fusion...)

## Regressive and Loss Characters

- \* difficult to determine homology
  - because there are so many ways to lose a character
  - for example, phylogenetic reconstruction of parasitic lineages based on morphology has been problematic historically

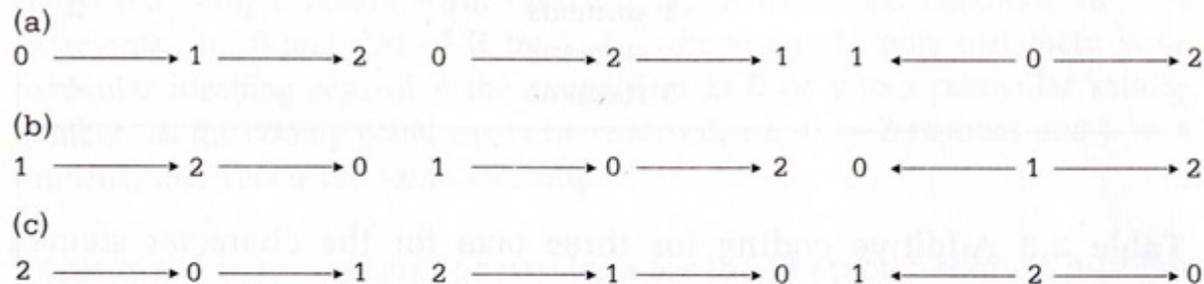
Analogous problems when aligning nucleotide sequences:  
gaps, insertions, and deletions become homology problems

<b>Taxon</b>	<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>	<b>5</b>	<b>6</b>	<b>7</b>	<b>8</b>	<b>9</b>
<b>A</b>	<b>A</b>	<b>G</b>	<b>G</b>	<b>T</b>					<b>C</b>
<b>B</b>	<b>A</b>	<b>G</b>	<b>G</b>	<b>G</b>			<b>G</b>		<b>C</b>
<b>C</b>	<b>A</b>	<b>G</b>	<b>G</b>	<b>G</b>			<b>G</b>		<b>C</b>
<b>D</b>	<b>A</b>	<b>C</b>	<b>C</b>	<b>T</b>			<b>C</b>		<b>C</b>
<b>E</b>	<b>A</b>	<b>C</b>	<b>C</b>	<b>T</b>					<b>C</b>
<b>F</b>	<b>A</b>	<b>C</b>	<b>C</b>	<b>T</b>			<b>C</b>		<b>C</b>

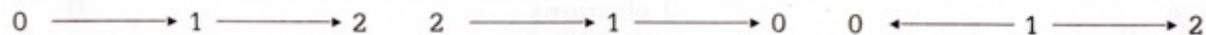
Is the loss at position 7 homologous in taxon A and E?

# Unordered versus Ordered Characters

- \* unordered characters – any state can transform into any other state with equal cost
- \* ordered – the relationships of character states are specified (for example, below character state 0 may transform into character state 1, and character state 1 may transform into character state 2).



**Fig. 2.1** The nine possible transformations among three character states.



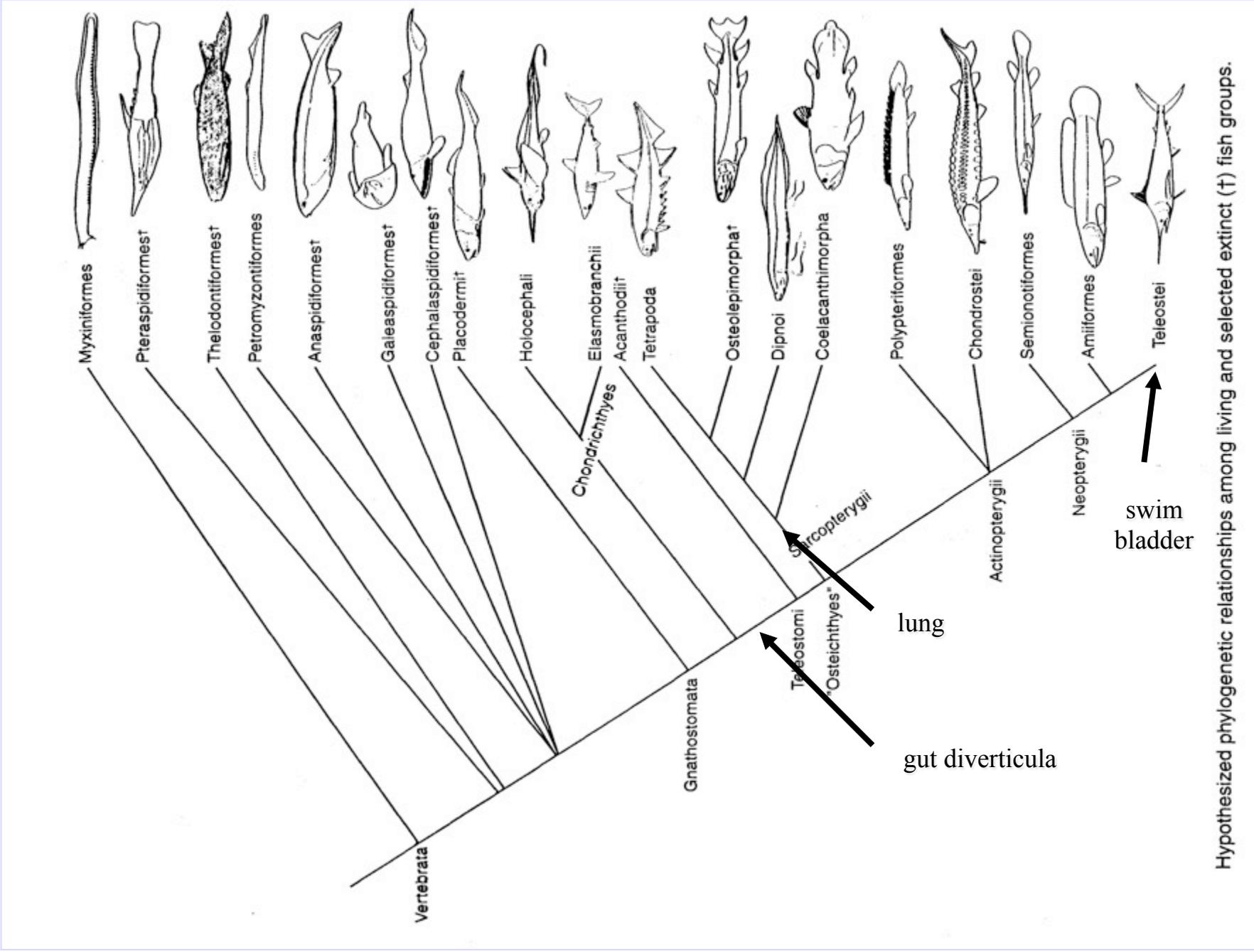
**Fig. 2.2** Imposition of order reduces the nine possibilities of Fig. 2.1 to a set of 3; the three possibilities if the order is for incremental gain or loss.

## Modern Analyses Use Indirect (Outgroup) Method to Determine Character Polarities

- \* characters are not a priori polarized
  - \* run characters as ordered/unordered
  - \* specification of outgroup taxon (taxa)
- choice of outgroup(s) (and rooting) determines character polarities.

# Polarity

- \* Polarity (direction of character change) is critical to our understanding of evolution
- \* Darwin's misunderstanding of fish swim bladder/tetrapod lung
  - common sense would suggest lungs are derivative of the swim bladder
  - but wrong
  - swim bladders and lungs are homologous but lungs did not evolve from swim bladder
  - at least one placoderm had a breathing structure off of the pharynx (pharyngeal pouch)
    - transformation series: gut diverticula → lung
    - gut diverticula → swim bladder



Hypothesized phylogenetic relationships among living and selected extinct (†) fish groups.

Outgroup Rule: given two character states within a monophyletic group, the state also found in the outgroup is plesiomorphic, whereas that found only in the ingroup is apomorphic.

outgroup	ingroup	ingroup
a	a'	a

Transformation series: a ----> a'

ingroup = study group

outgroup = any taxon of equal or higher rank outside  
ingroup

sister group: outgroup taxon that shares the most recent  
common ancestor with the ingroup.

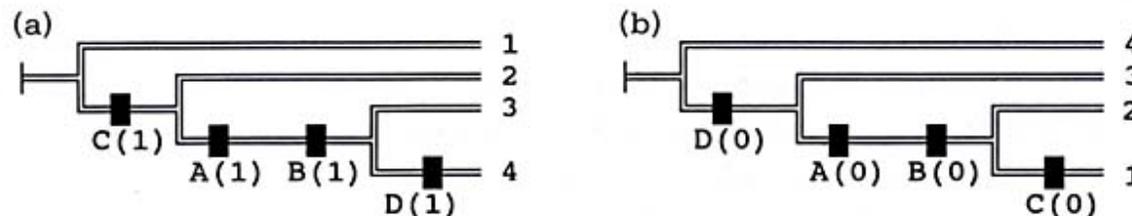
- sister group provides best estimate of ancestral character  
states combinations in ingroup (best outgroup taxon)
- true sister lineage often extinct (or unavailable)
- when you can, use closest available taxon in analyses

\* Outgroup selection profoundly affects polarity decisions which ultimately determines:

- (1) tree topology
- (2) all monophyly decisions

**Table 2.6** Binary coding for four taxa (1 – 4) and four characters (A – D); data for Fig. 2.10

Taxa	ABCD
1	0000
2	0010
3	1110
4	1111



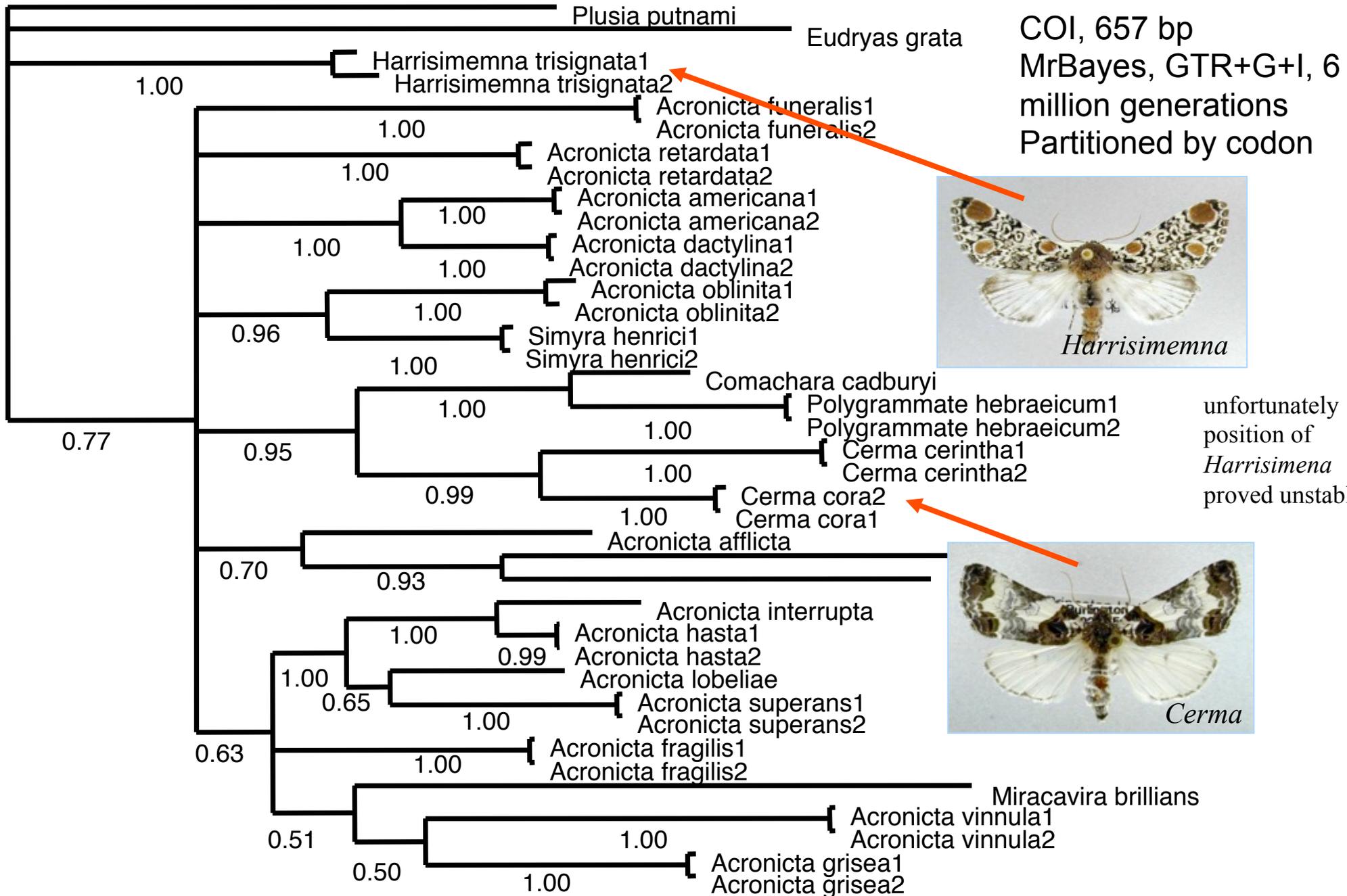
**Fig. 2.10** Rooting, apomorphy and monophyly. (a) The most parsimonious tree taking taxon 1 as the root; characters A(1), B(1) and C(1) are synapomorphic and D(1) autapomorphic. (b) An alternative interpretation rooted on taxon 4: taxon (1 2 3) is monophyletic; and characters A(0), B(0) and D(0) are synapomorphic and C(0) is autapomorphic.

TAXON	1	2	3	4	5
Tribe X-ini					
Genus <i>Hirsutus</i>					
Species A	1'	2	3'	4'	5'
Species B	1	2	3	4'	5
Species C	1'	2'	3'	4	5'
Species D	1	2'	3	4'	5
Genus <i>Prohirsutus</i>					
Species E	1	2'	3	4	5

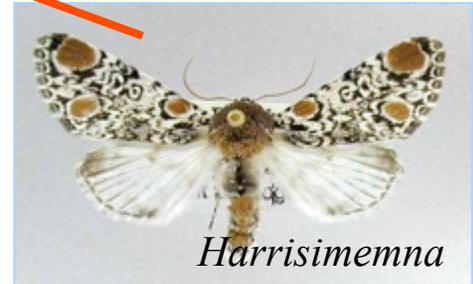
TAXON	1	2	3	4	5
Tribe X-ini					
Genus <i>Hirsutus</i>					
Species A	1'	2	3'	4'	5'
Species B	1	2	3	4'	5
Species C	1'	2'	3'	4	5'
Species D	1	2'	3	4'	5
Genus <i>Prohirsutus</i>					
Species E	1	2'	3	4	5
Tribe Y-ine					
Species F	1	2	3'	4'	5'

- \* Outgroup selection profoundly affects polarity decisions which determines:
  - (1) tree topology
  - (2) monophyly decisions
  
- \* consider outgroup selection in when you're evaluating papers and grant proposals (or your own work)
  - might results hinge on a single outgroup taxon?
- \* avoid distant outgroups when possible
  - sometimes unavoidable (when there has been much extinction)
  - this is why fossils are needed for reconstruction of tetrapods (?and angiosperms)





COI, 657 bp  
 MrBayes, GTR+G+I, 6 million generations  
 Partitioned by codon



unfortunately position of *Harrisimemna* proved unstable!



## When Relationships Around Ingroup are Poorly Understood

(common for species-level analyses in large, unstudied families)

- \* use multiple outgroups
- \* perform sensitivity analysis
  - if results stable to outgroup addition, phylogeny is more believable
- \* sometimes have to eliminate rogue taxon
- \* if sister group too distant explore assigning FIG's and FOG's (assigning functional in group and functional outgroup from your ingroup taxa)
  - for example, if you have an idea about which ingroup is likely to be sister to rest of the members in your analysis, based on biogeography, fossil data, unusual characters, etc.

# Character Weighting

- \* some characters are more valuable than others and could be accorded greater weight in our analyses  
coding versus non-coding regions; synonymous versus non-synonymous substitutions
- \* but how you go about determining weights can get subjective esp. for morphological characters
  - a priori* – done before the analysis
  - a posteriori* – after the analysis, re-weigh characters relative to the amount of homoplasy they show; rerun analysis

# Homoplasy: Character Conflict

\* In a perfect world each character evolves only once (i.e., map onto the tree at a single position) and all our phylogenetic algorithms will allow us to reconstruct the tree of life correctly. But in essentially all molecular and larger morphological data sets, many characters map on in more than one spot.

\* Sources of character conflict:

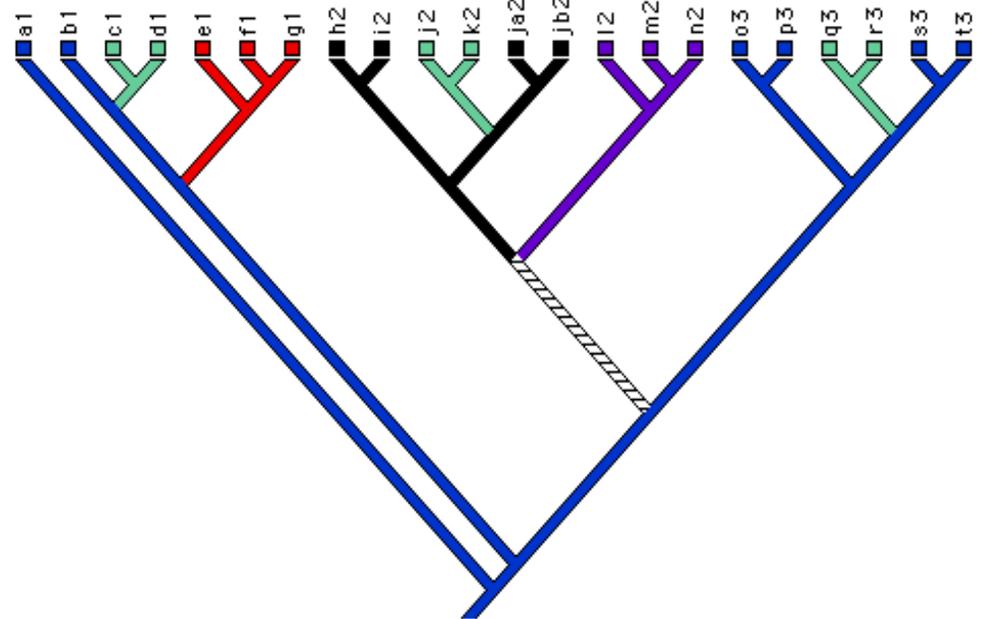
(1) incorrect homology decisions

(2) homoplasy

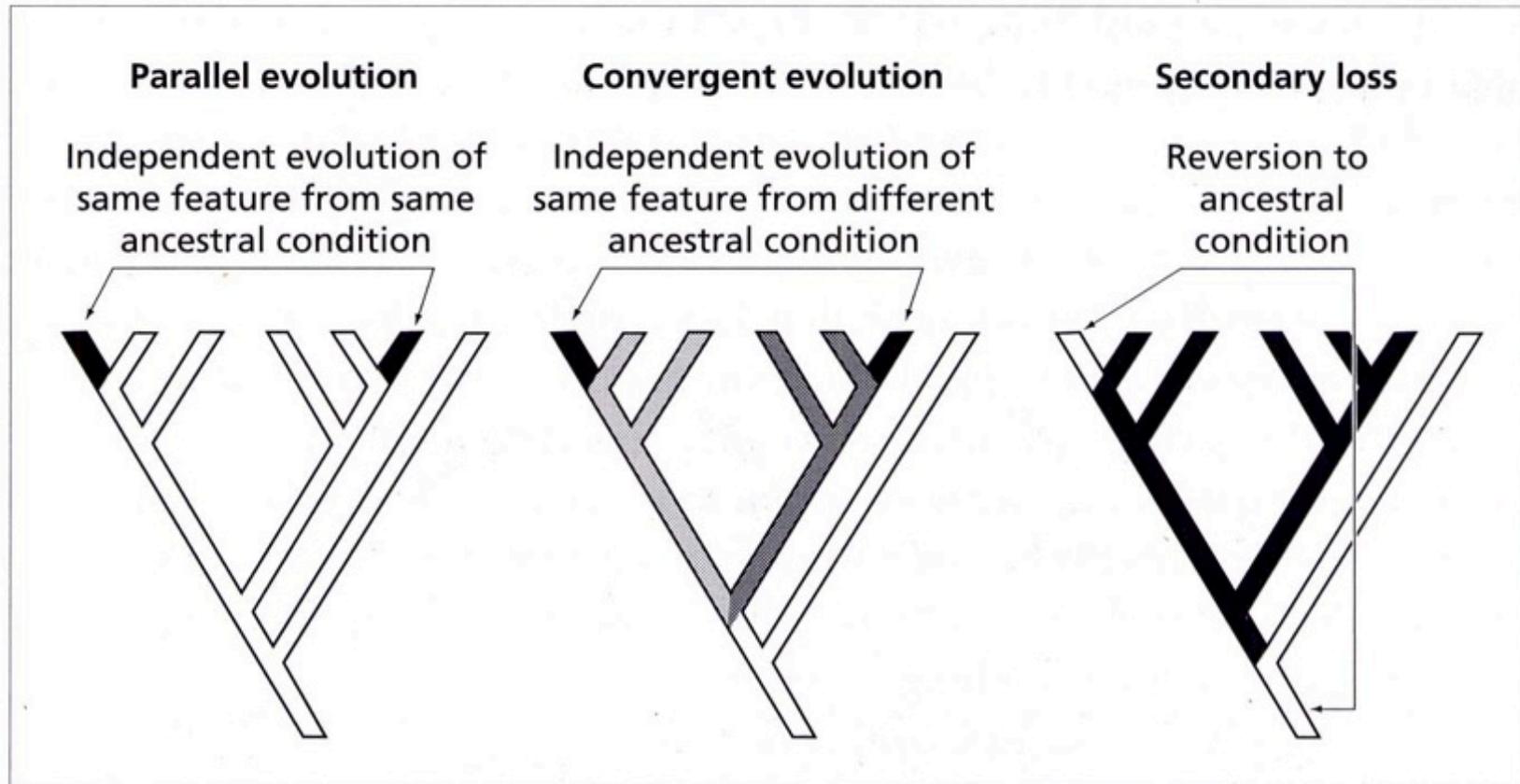
a. reversal

b. parallelism

c. convergence

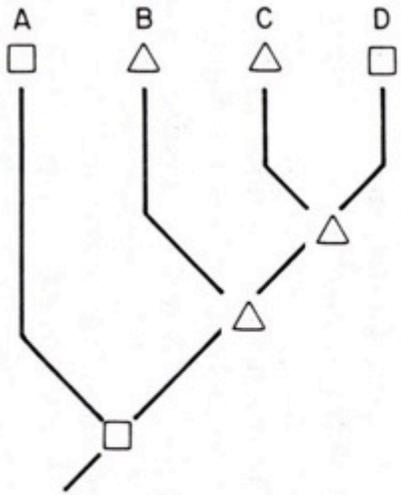


# Homoplasy

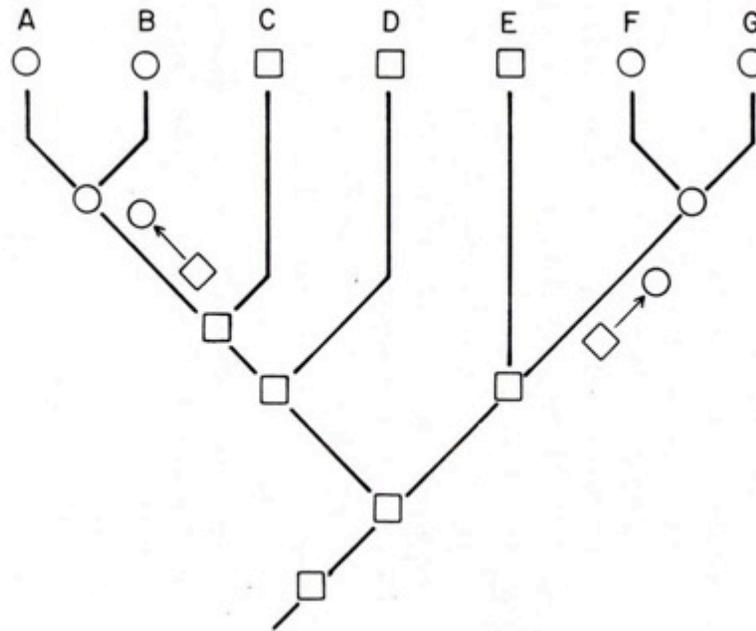


**Fig. 2.12** Three different kinds of homoplasy.

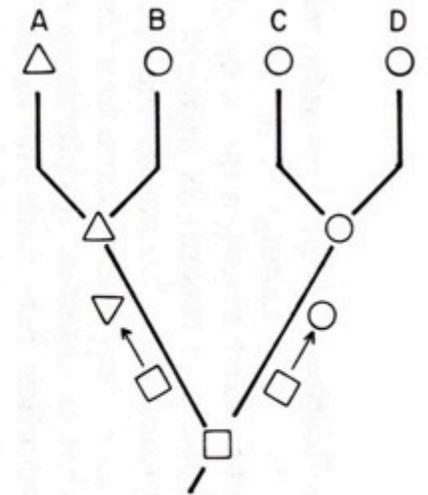
# Three kinds of homoplasy



**reversal**



**parallelism**



**convergence**