9.xi.

1. Wagner algorithm

2. outgroup

3. homoplasy & homology

4. character congruence

5. summary

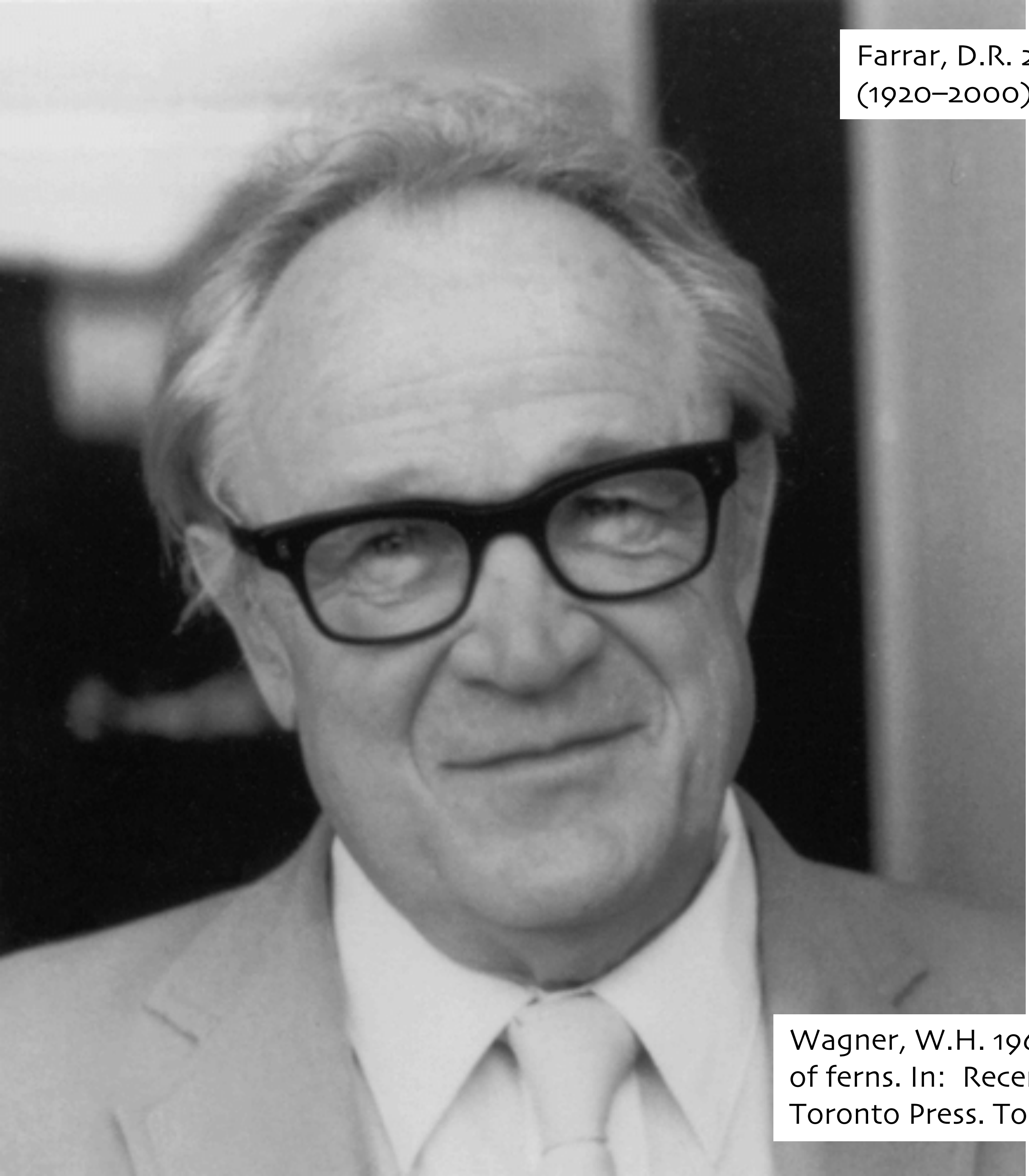
6. home exercise

Wagner algorithm

Kluge, A. G. & Farris, J. S. 1969. Quantitative phyletics and the evolution of anurans. *Systematic Zoology* 18:1-32.

Farris, J. S. 1970. Methods for computing Wagner trees. *Systematic Zoology* 19:83-92.

Farrar, D.R. 2002. Obituary: Warren H. Wagner, Jr. (1920–2000). *American Fern Journal* 92:39-49.



Wagner, W.H. 1961. Problems in the classification of ferns. In: Recent advances in botany. Univ. Toronto Press. Toronto pp. 841-844.

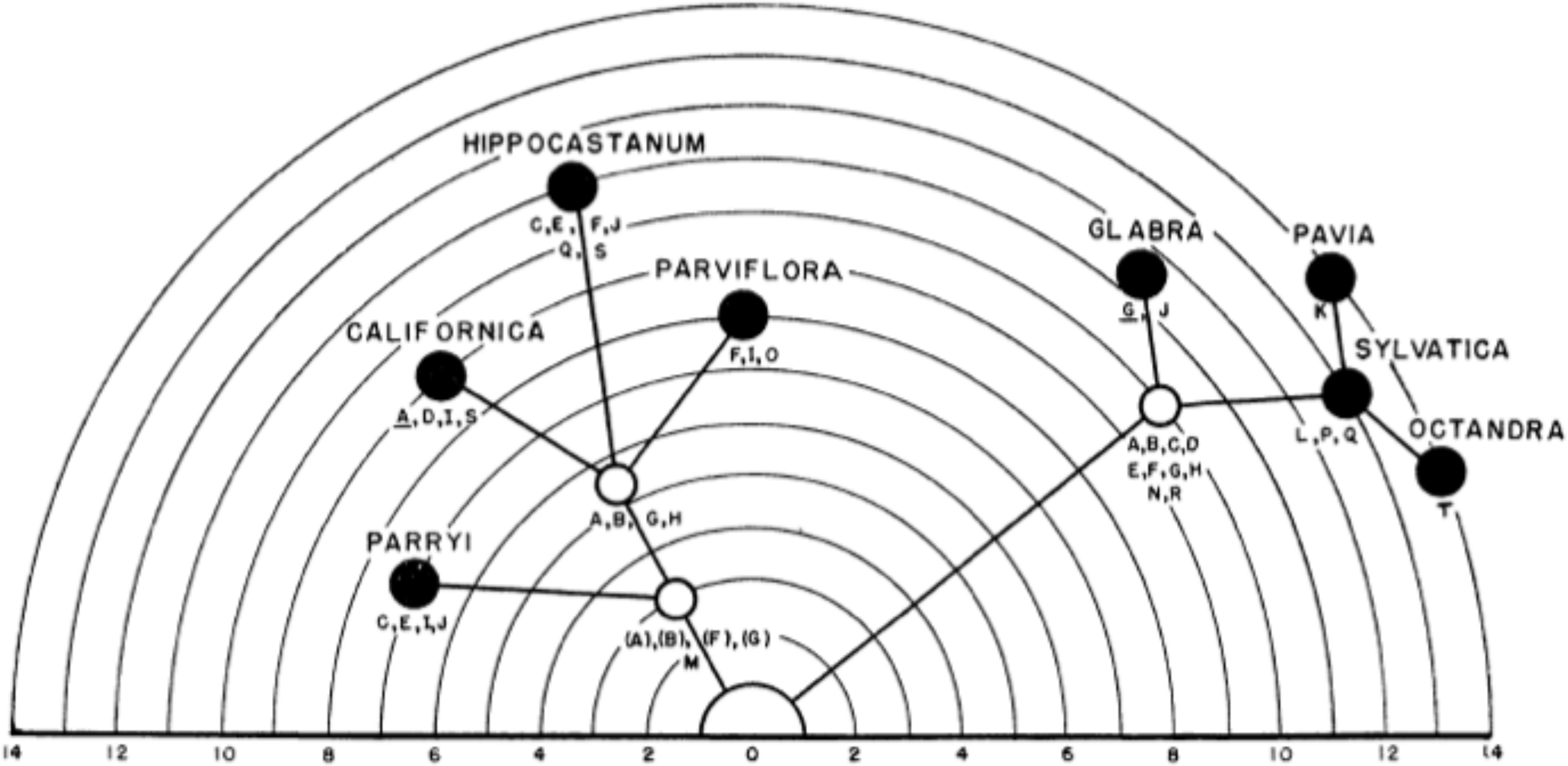


FIG. 15. Evolution in *Aesculus*.

Hardin, J. W. 1957. A revision of the American Hippocastanaceae. *Brittonia* 9:145-171.

Wagner algorithm

Lipscomb pp. 16-18:
upper part of p. 16

```
    A    1000110001
    C    0000000011
 differences: 1   11  1


         A   1000110001
         C   0000000011
 differences:1   11  1
```

error on upper part of p. 18:

that characters 1,5,6, and 10 .....

should read:
that characters 2,3,7,8, and 10.....

Wagner algorithm

page 13:

1. Find the organism with the lowest number of derived character states and connect it to the outgroup

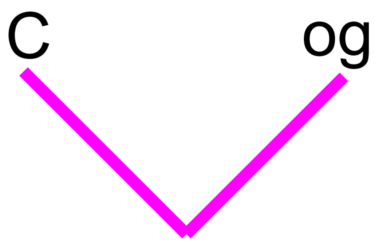
in practice ANY of the organisms can be used as outgroup

next search for a terminal to pair with it so that the number of observed differences between the two are minimized

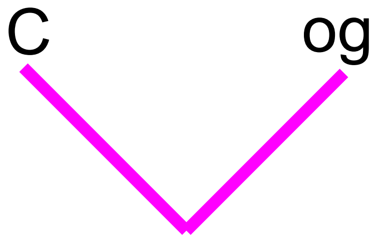
	1	2	3	4	5	6	7	8	9	10	differences from outgroup
og	0	0	0	0	0	0	0	0	0	0	-
A	1	0	0	0	1	1	0	0	0	1	4
B	1	0	0	0	1	0	0	0	0	1	3
C	0	0	0	0	0	0	0	0	1	1	2
D	0	1	1	0	0	0	1	1	0	1	5
E	0	1	1	1	0	0	0	1	0	1	5

Wagner formula

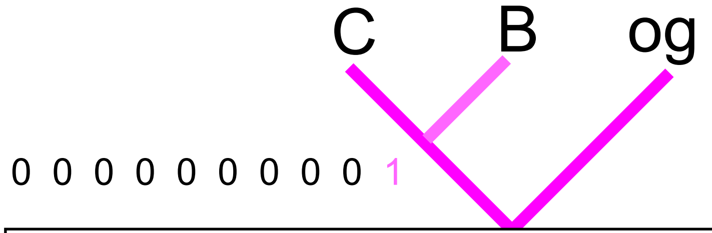
$$d(A, B) = \sum | X(Ai) - X(Bi) |$$



	1	2	3	4	5	6	7	8	9	10	differences from outgroup
og	0	0	0	0	0	0	0	0	0	0	-
A	1	0	0	0	1	1	0	0	0	1	4
B	1	0	0	0	1	0	0	0	0	1	3
C	0	0	0	0	0	0	0	0	1	1	2
D	0	1	1	0	0	0	1	1	0	1	5
E	0	1	1	1	0	0	0	1	0	1	5

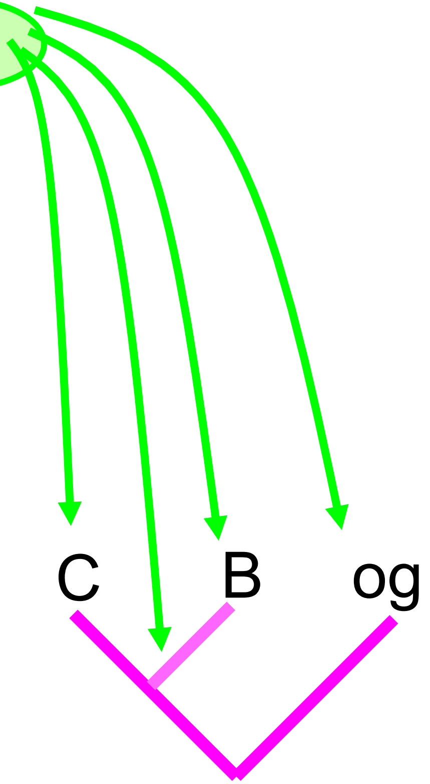


	1	2	3	4	5	6	7	8	9	10	differences from outgroup
og	0	0	0	0	0	0	0	0	0	0	-
A	1	0	0	0	1	1	0	0	0	1	4
B	1	0	0	0	1	0	0	0	0	1	3
C	0	0	0	0	0	0	0	0	1	1	2
D	0	1	1	0	0	0	1	1	0	1	5
E	0	1	1	1	0	0	0	1	0	1	5



internal node on tree
hypothetical ancestor of C & B

	1	2	3	4	5	6	7	8	9	10	differences from outgroup
og	0	0	0	0	0	0	0	0	0	0	-
A	1	0	0	0	1	1	0	0	0	1	4
B	1	0	0	0	1	0	0	0	0	1	~~3~~
C	0	0	0	0	0	0	0	0	1	1	~~2~~
D	0	1	1	0	0	0	1	1	0	1	5
E	0	1	1	1	0	0	0	1	0	1	5



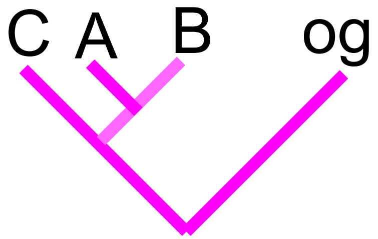
A	1	0	0	0	1	1	0	0	0	1	**4**
C	0	0	0	0	0	0	0	0	1	1	

A	1	0	0	0	1	1	0	0	0	1	**3**
BC	0	0	0	0	0	0	0	0	0	1	

A	1	0	0	0	1	1	0	0	0	1	**1**
B	1	0	0	0	1	0	0	0	0	1	

A	1	0	0	0	1	1	0	0	0	1	**4**
og	0	0	0	0	0	0	0	0	0	0	

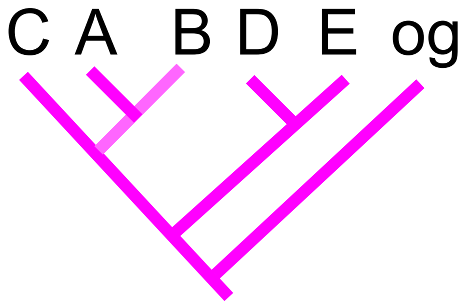
	1	2	3	4	5	6	7	8	9	10	differences from outgroup
og	0	0	0	0	0	0	0	0	0	0	-
A	1	0	0	0	1	1	0	0	0	1	4
B	1	0	0	0	1	0	0	0	0	1	~~3~~
C	0	0	0	0	0	0	0	0	1	1	~~2~~
D	0	1	1	0	0	0	1	1	0	1	5
E	0	1	1	1	0	0	0	1	0	1	5



continued until all terminals are included

	1	2	3	4	5	6	7	8	9	10	differences from outgroup
og	0	0	0	0	0	0	0	0	0	0	-
A	1	0	0	0	1	1	0	0	0	1	4
B	1	0	0	0	1	0	0	0	0	1	~~3~~
C	0	0	0	0	0	0	0	0	1	1	~~2~~
D	0	1	1	0	0	0	1	1	0	1	5
E	0	1	1	1	0	0	0	1	0	1	5

the problem of Wagner algorithm is that the order where terminals are added to tree affects the tree finally obtained



continued until all terminals are included

	1	2	3	4	5	6	7	differences from taxon C
A	1	0	0	1	1	1	1	4
B	0	1	0	0	1	0	1	6
C	0	0	1	1	0	1	0	-
D	0	0	0	1	0	0	1	3

Wagner formula

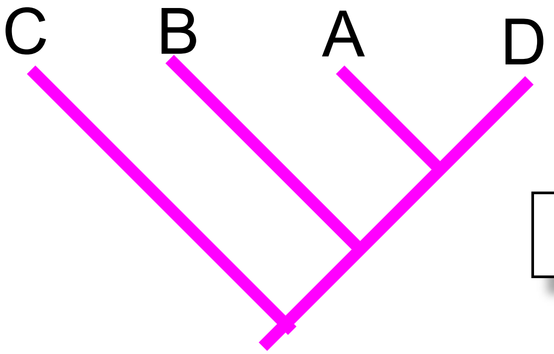
C defined as outgroup

$$d(A, B) = \sum | X(Ai) - X (Bi) |$$

Lipscomb pp. 34-35

	1	2	3	4	5	6	7	differences from taxon C
A	1	0	0	1	1	1	1	4
B	0	1	0	0	1	0	1	6
C	0	0	1	1	0	1	0	–
D	0	0	0	1	0	0	1	3

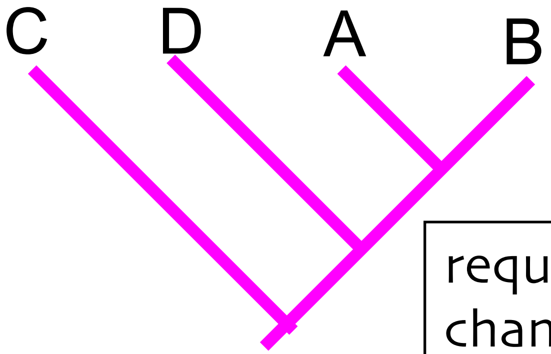
Wagner algorithm and starting from pair C & D will give tree:



10 evolutionary changes

	1	2	3	4	5	6	7	
A	1	0	0	1	1	1	1	4
B	0	1	0	0	1	0	1	6
C	0	0	1	1	0	1	0	–
D	0	0	0	1	0	0	1	3

however, a tree exists:



requiring only 9 character state changes

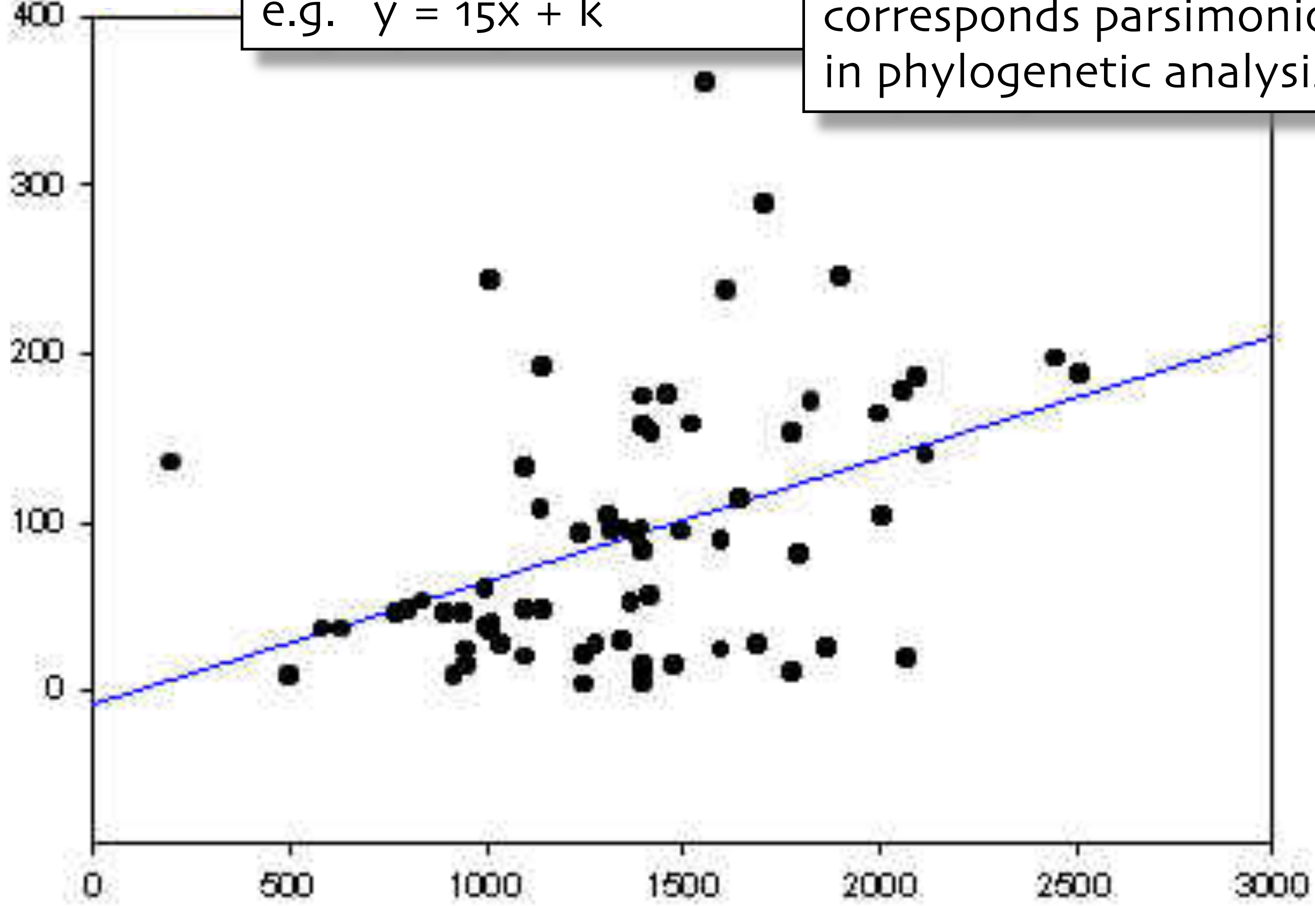
Wagner algorithm helps (A GREAT DEAL!) in finding optimal solutions BUT order of addition of terminals affects final tree obtained

PARSIMONY

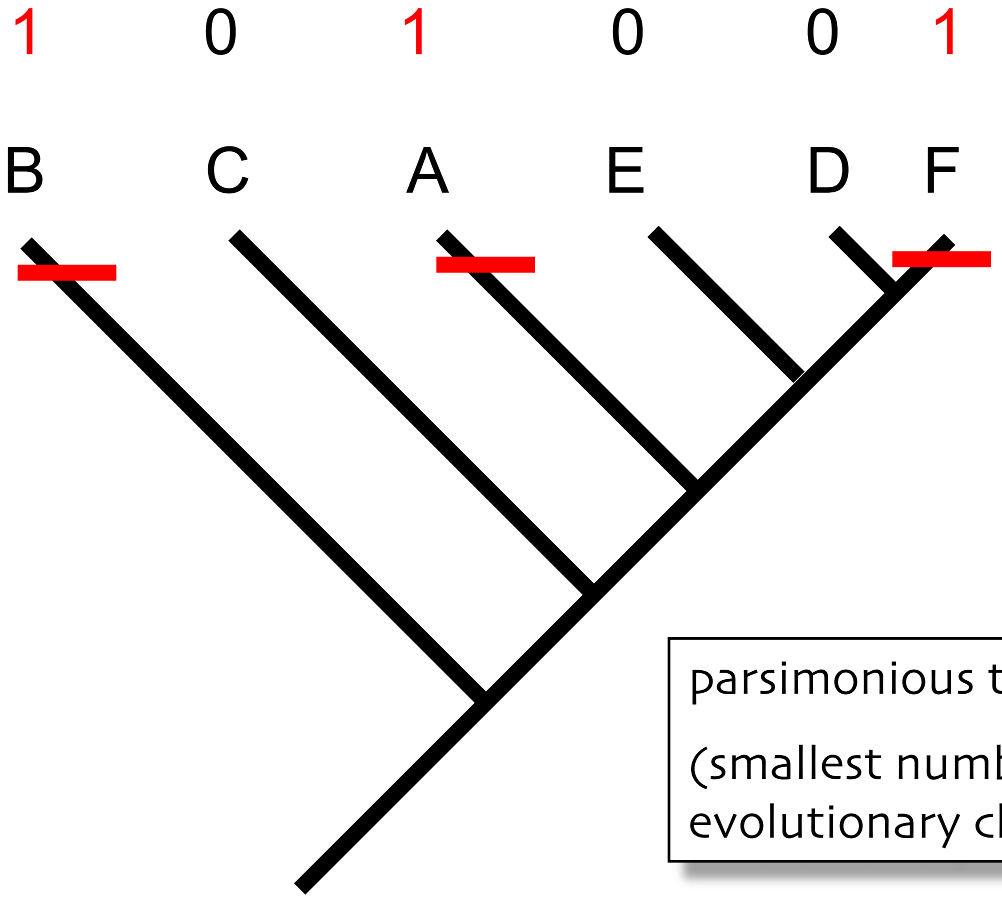
it has been erroneously claimed that use of parsimony as optimality criterion requires unrealistic assumption that evolution & evolutionary history are simple line represents dependence between two variables

e.g. $y = 15x + k$

corresponds parsimonious tree in phylogenetic analysis

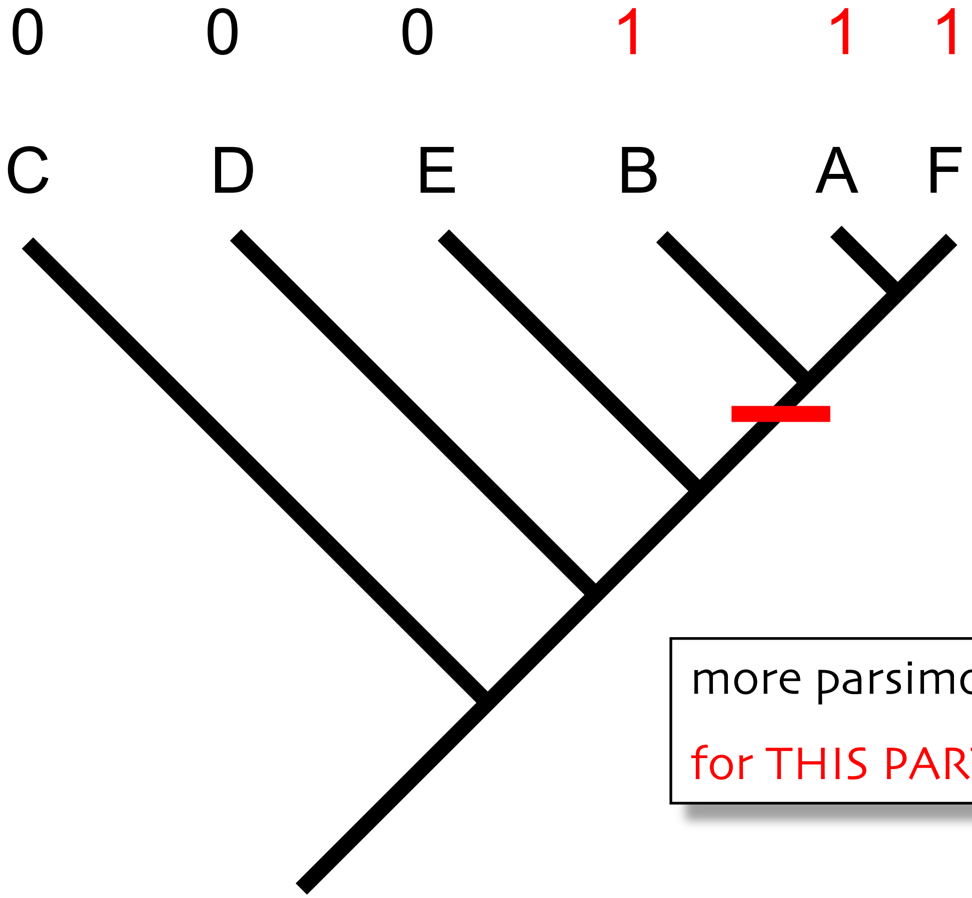


www2.hawaii.edu/~donaldp/Biostatitics/



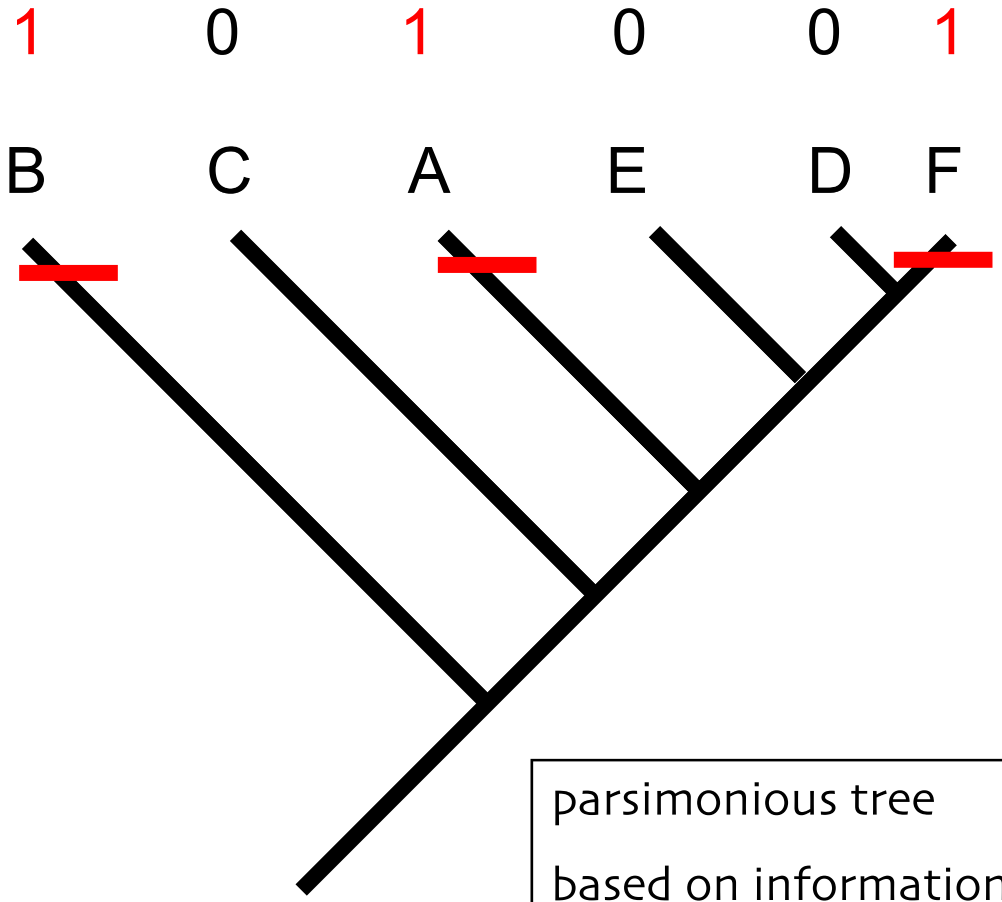
parsimonious tree

(smallest number of evolutionary changes)



more parsimonious tree

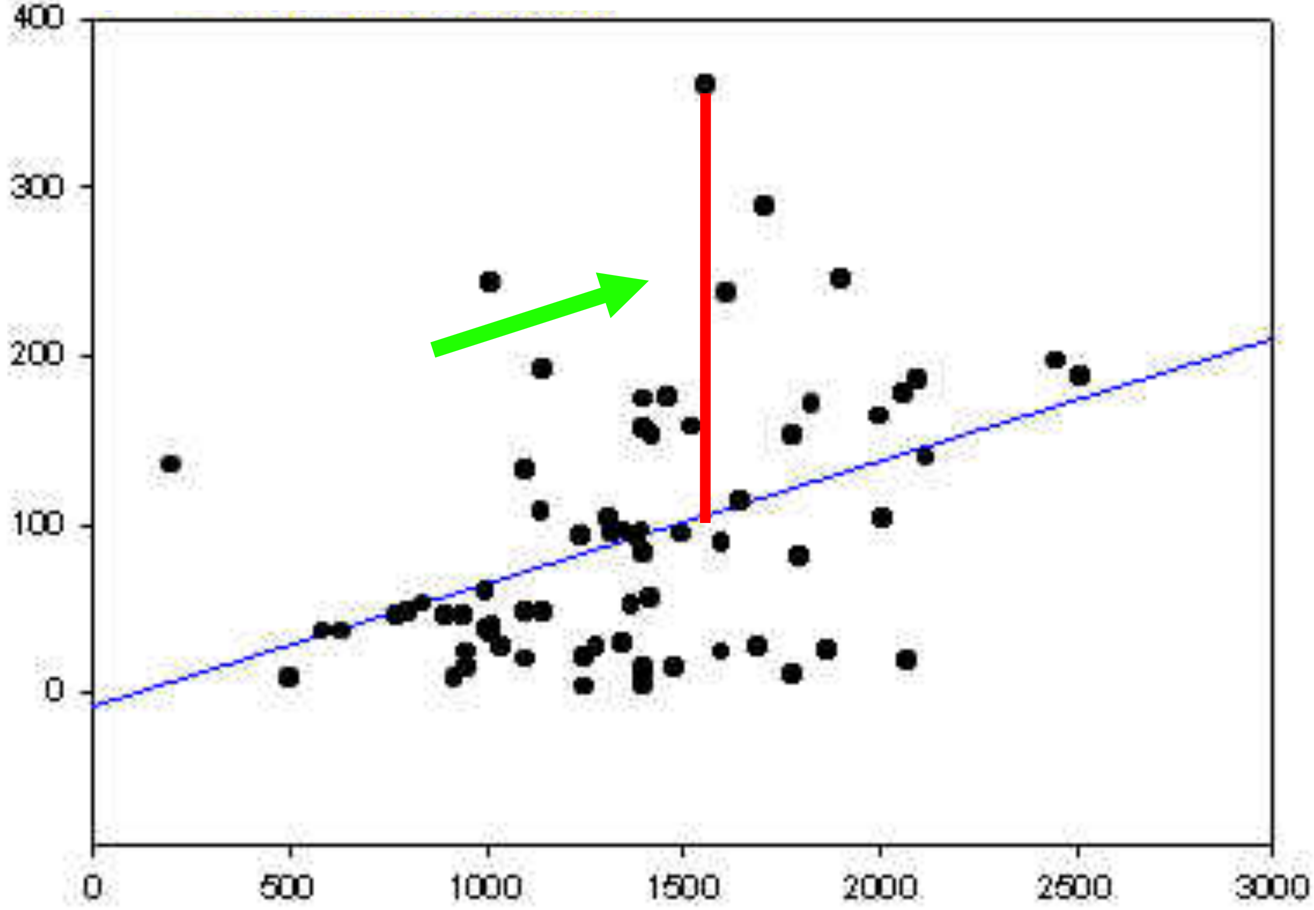
for THIS PARTICULAR character



parsimonious tree

based on information from ALL characters

$$d(A, B) = \sum | X(A_i) - X(B_i) |$$



numbe r of lvs

stem height (mm)

www2.hawaii.edu/~donaldp/Biostatitics/

APOMORPHY

= evolutionary novelty

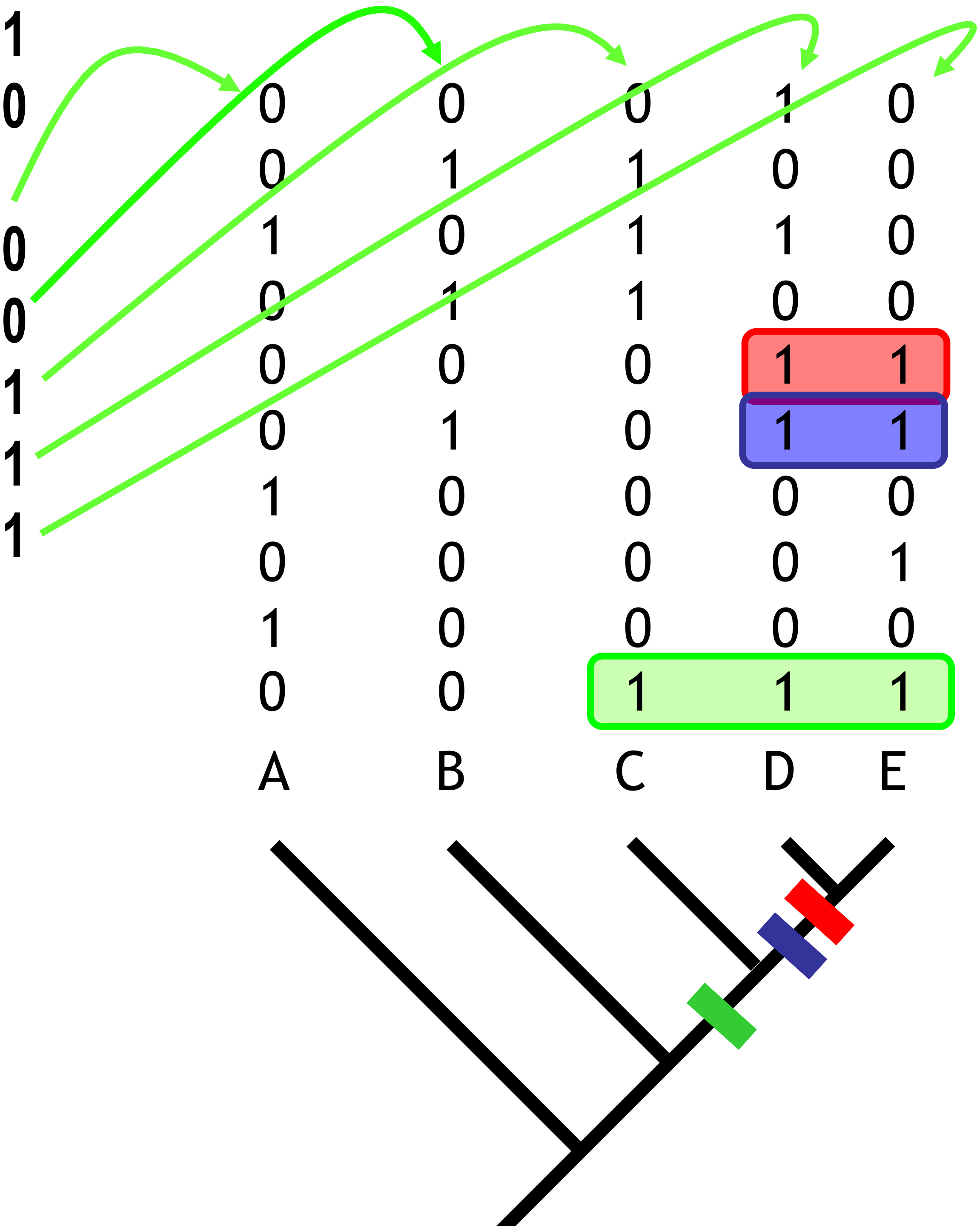
PLESIOMORPHY

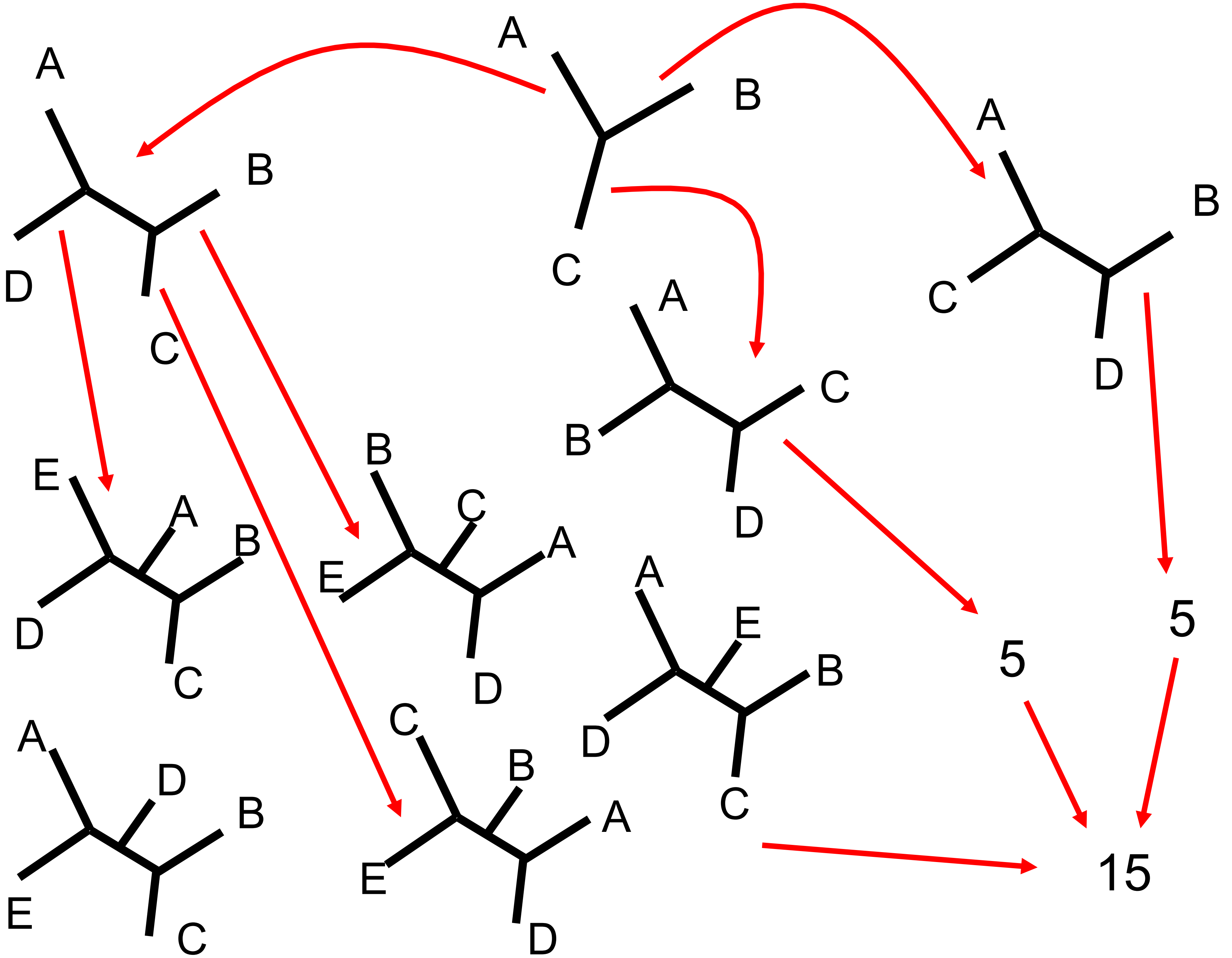
= OLD, inherited character

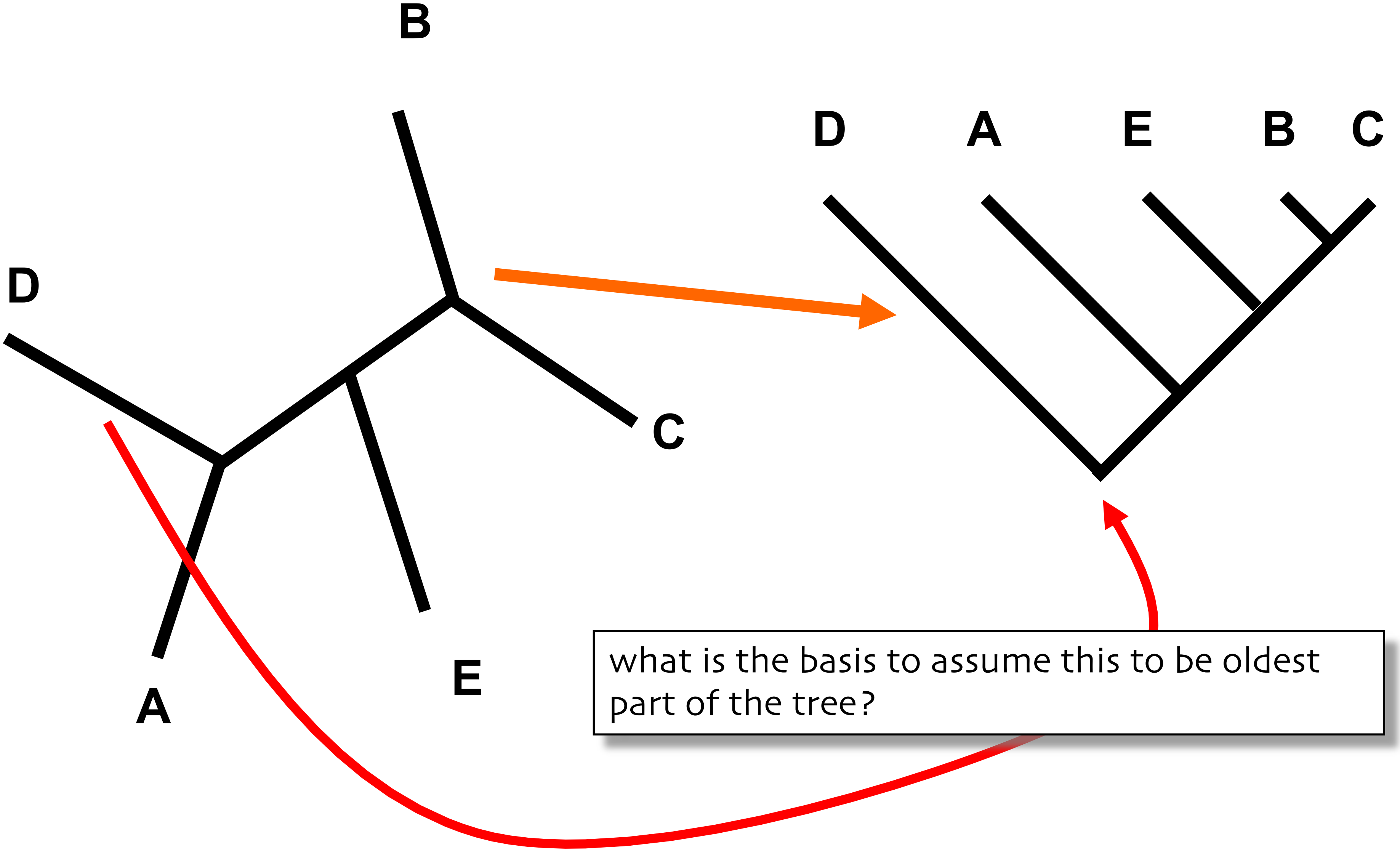
how to distinguish apo- & plesiomorphies?

how to introduce time in our hypothesis?

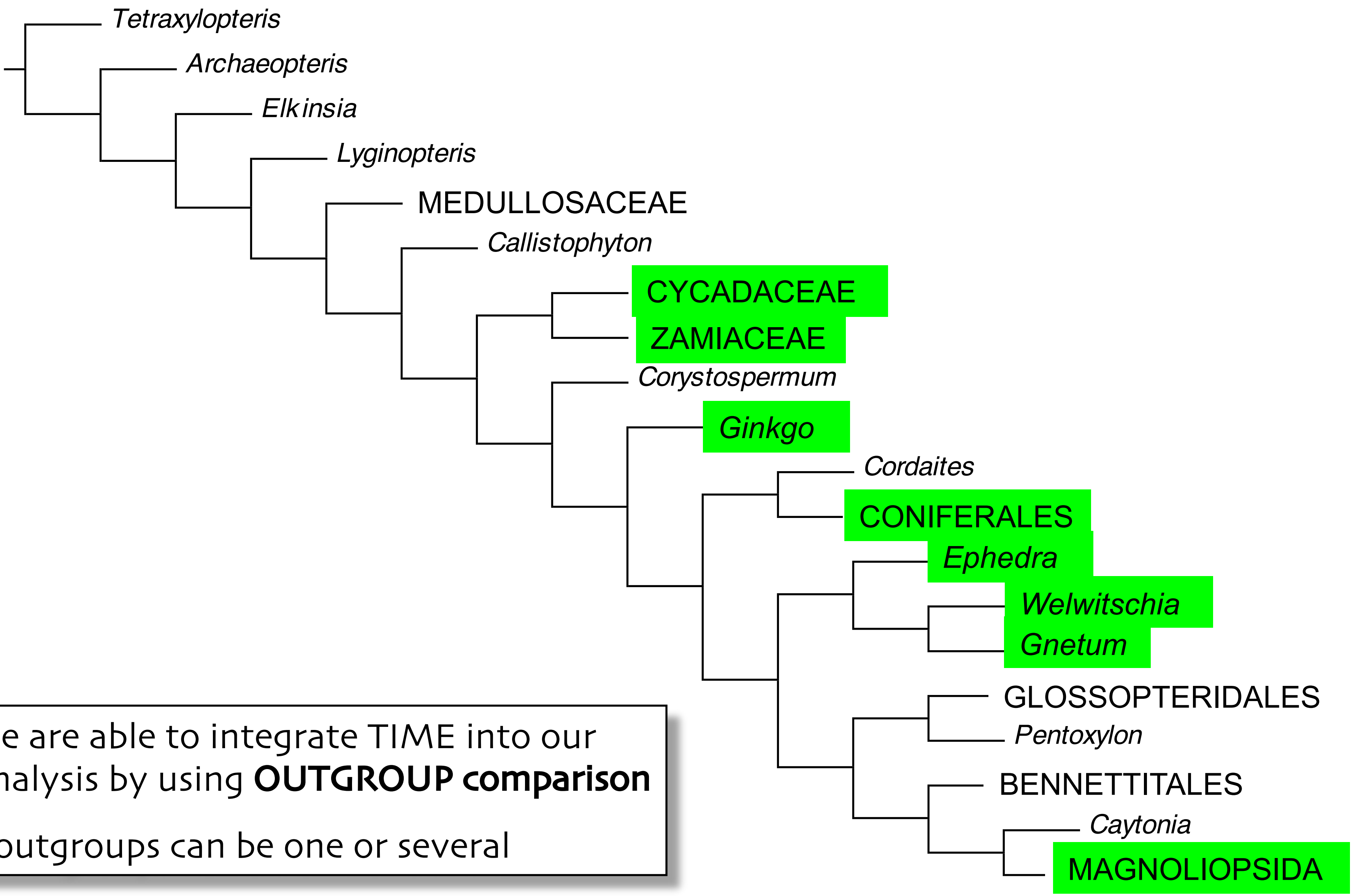
	01	02	03	04	05	06	07	08	09	10
A	0	0	1	0	0	0	1	0	1	0
B	0	1	0	1	0	1	0	0	0	0
C	0	1	1	1	0	0	0	0	0	1
D	1	0	1	0	1	1	0	0	0	1
E	0	0	0	0	1	1	0	1	0	1




A
B
C
A
B
C
D
A
B
C
D
A
B
C
D
E
A
B
C
D
B
C
A
E
D
A
E
B
D
C
5
5
A
D
B
E
C
C
B
A
E
D
15



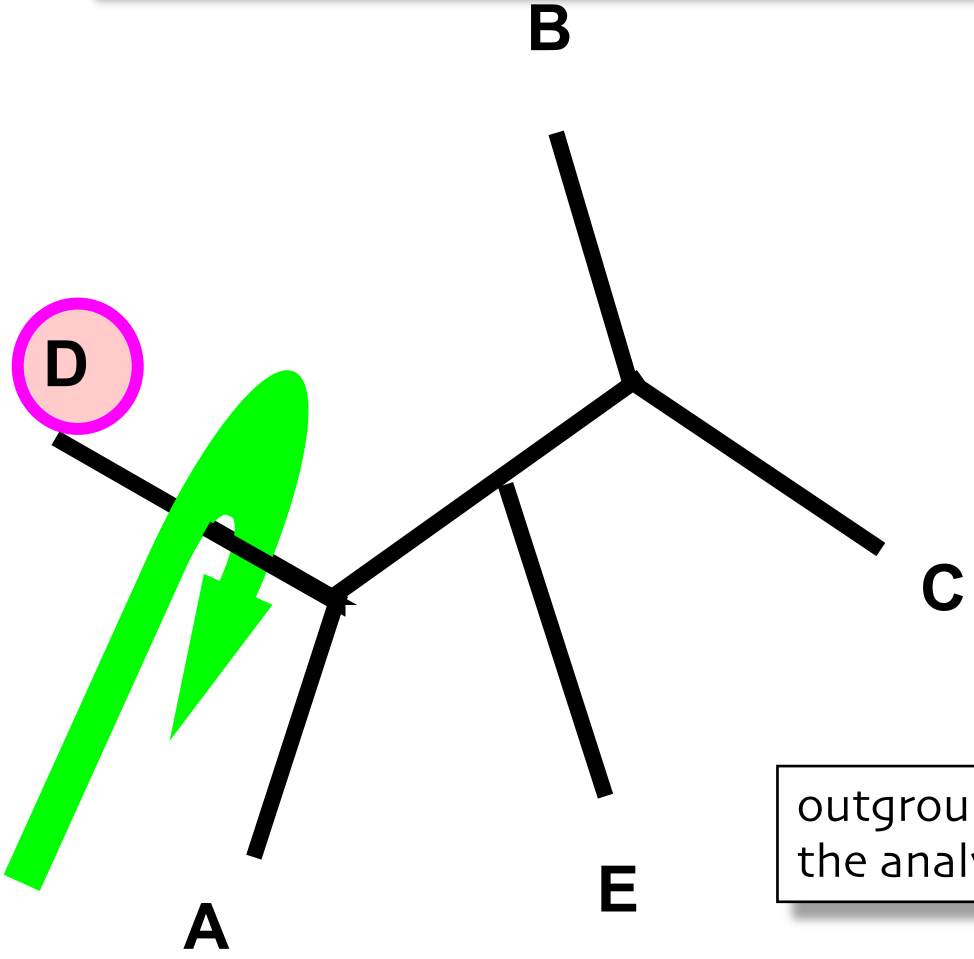
what is the basis to assume this to be oldest part of the tree?

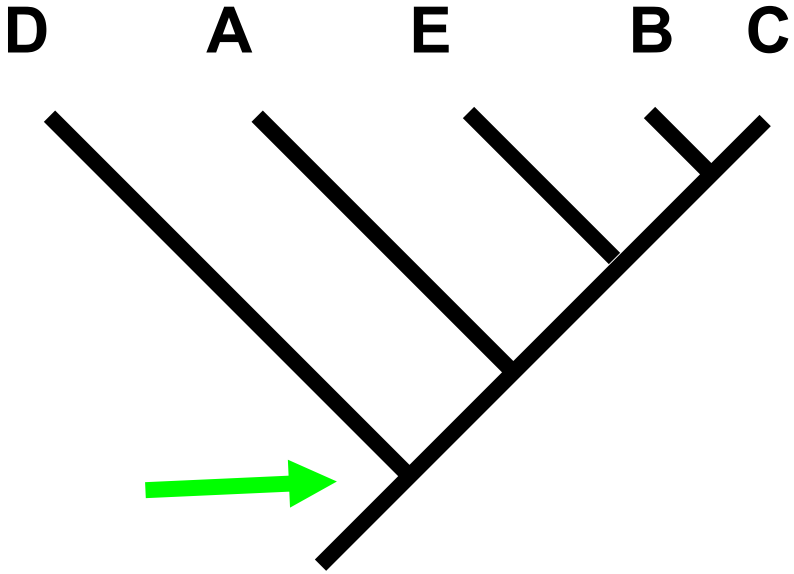


we are able to integrate TIME into our analysis by using **OUTGROUP comparison**

- outgroups can be one or several

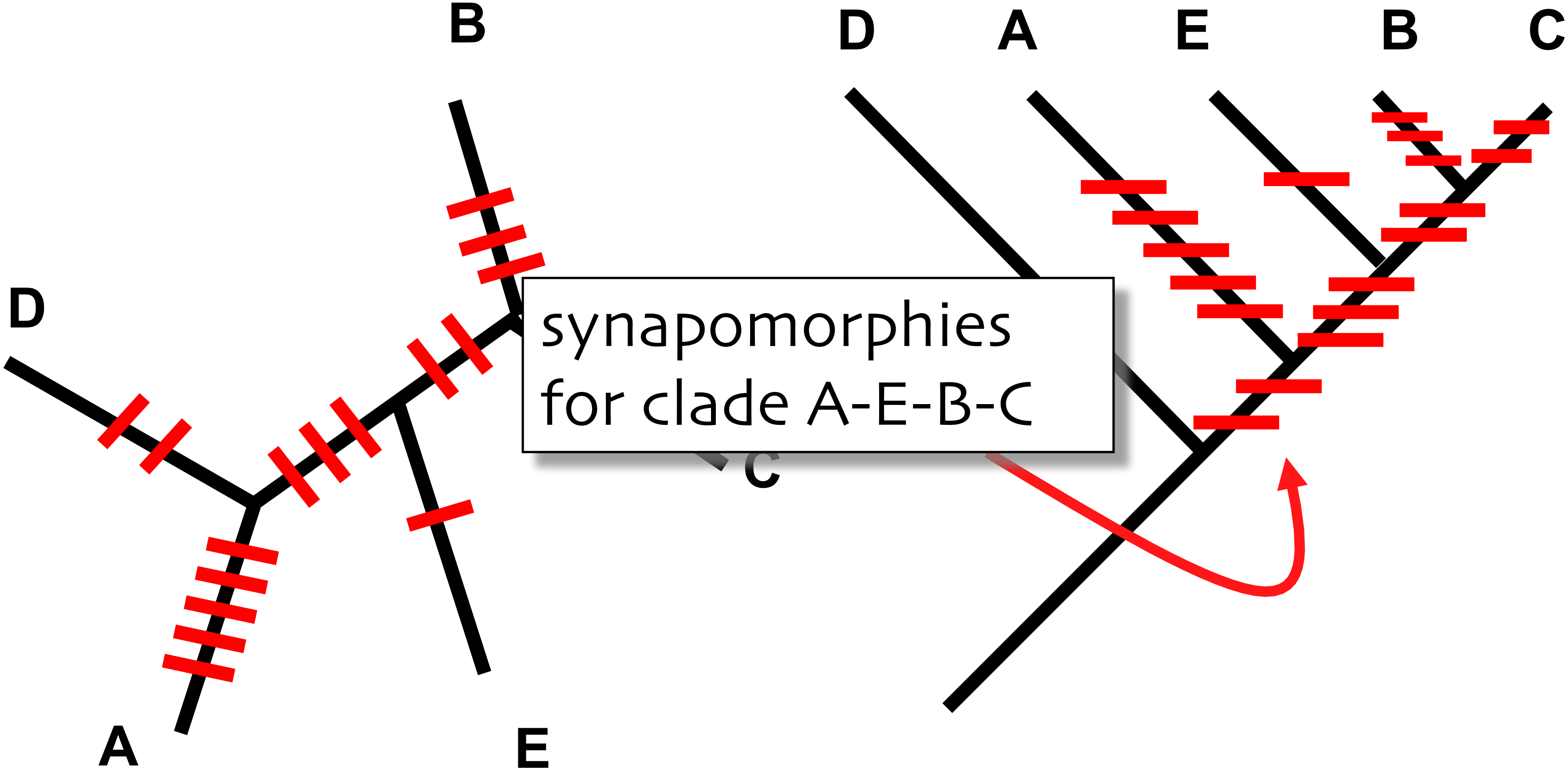
Nixon, K. & Carpenter, J. 1993. On outgroups. Cladistics 9: 413-426.



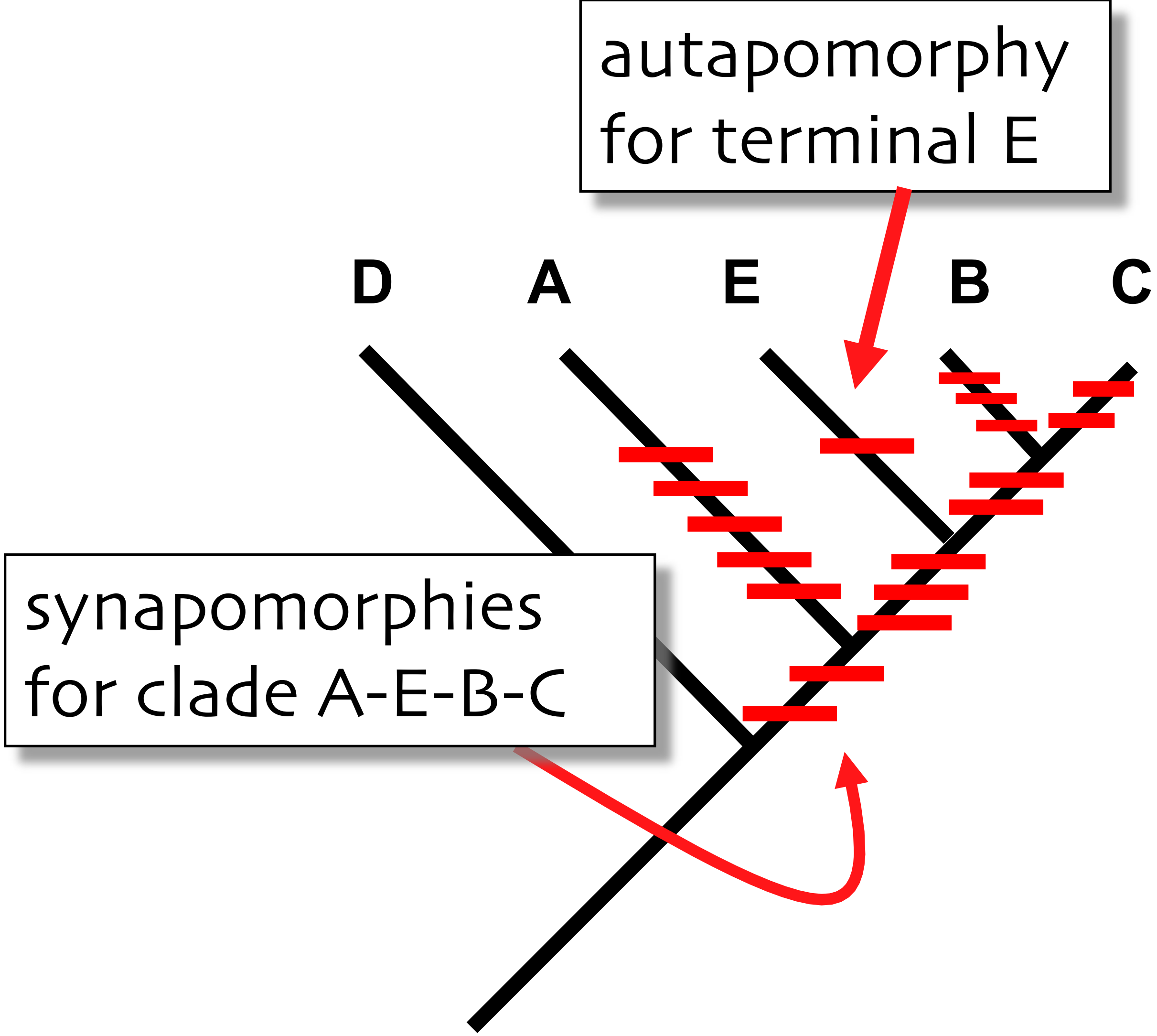


outgroup terminals should be treated in the analyses AS ANY OTHER TERMINAL

they should be included in the analyses FROM THE VERY START

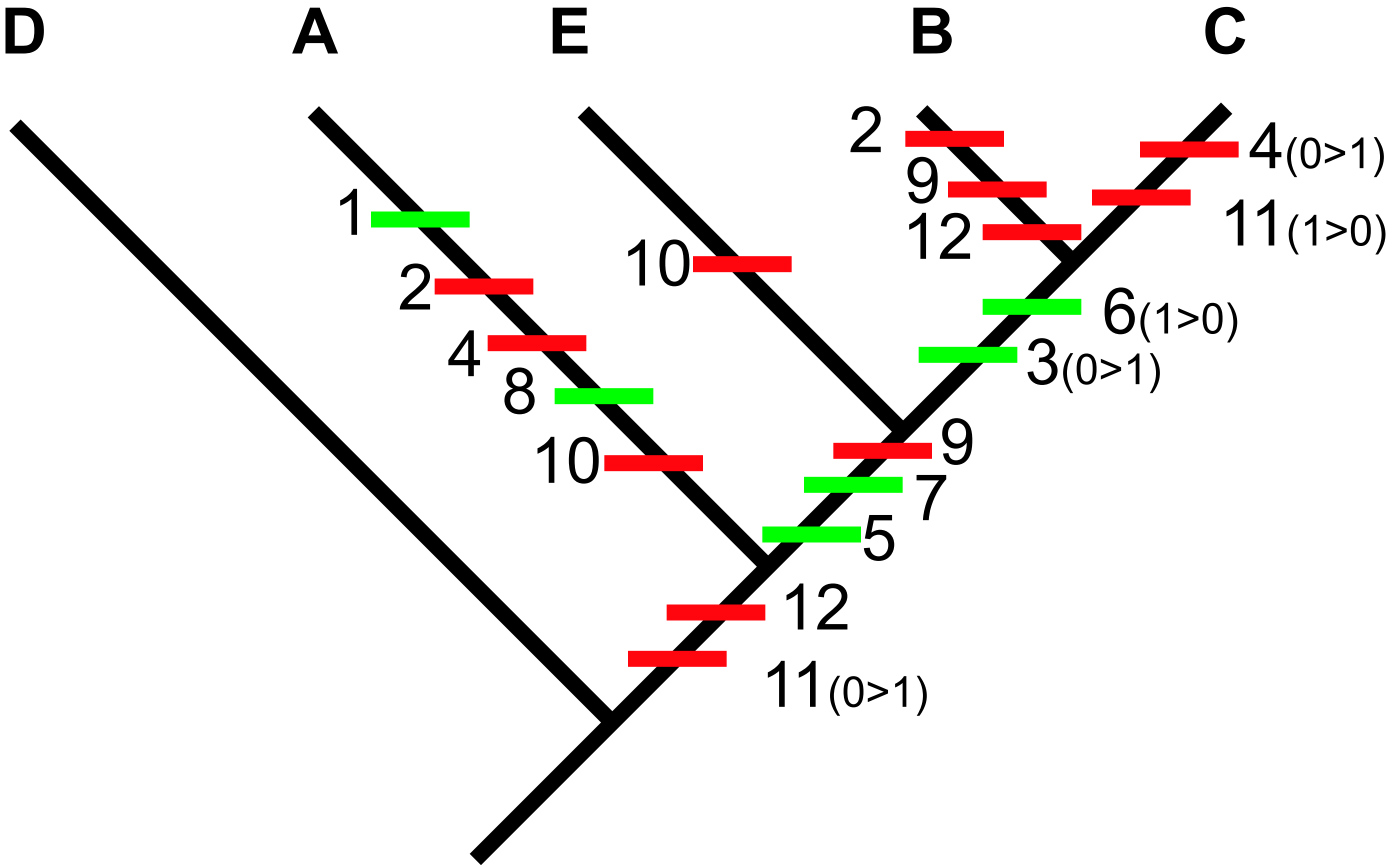


synapomorphies
for clade A-E-B-C



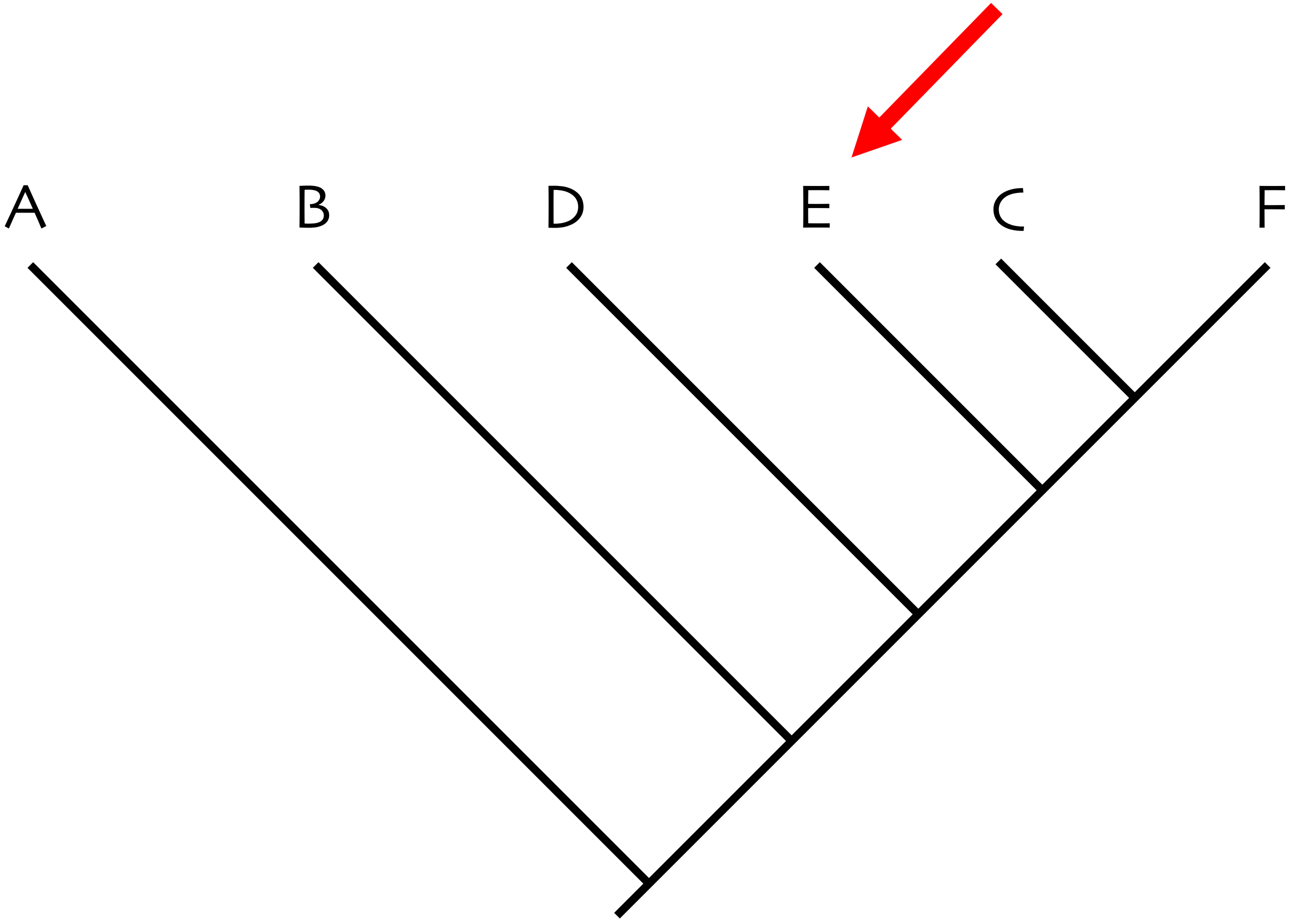
autapomorphy
for terminal E

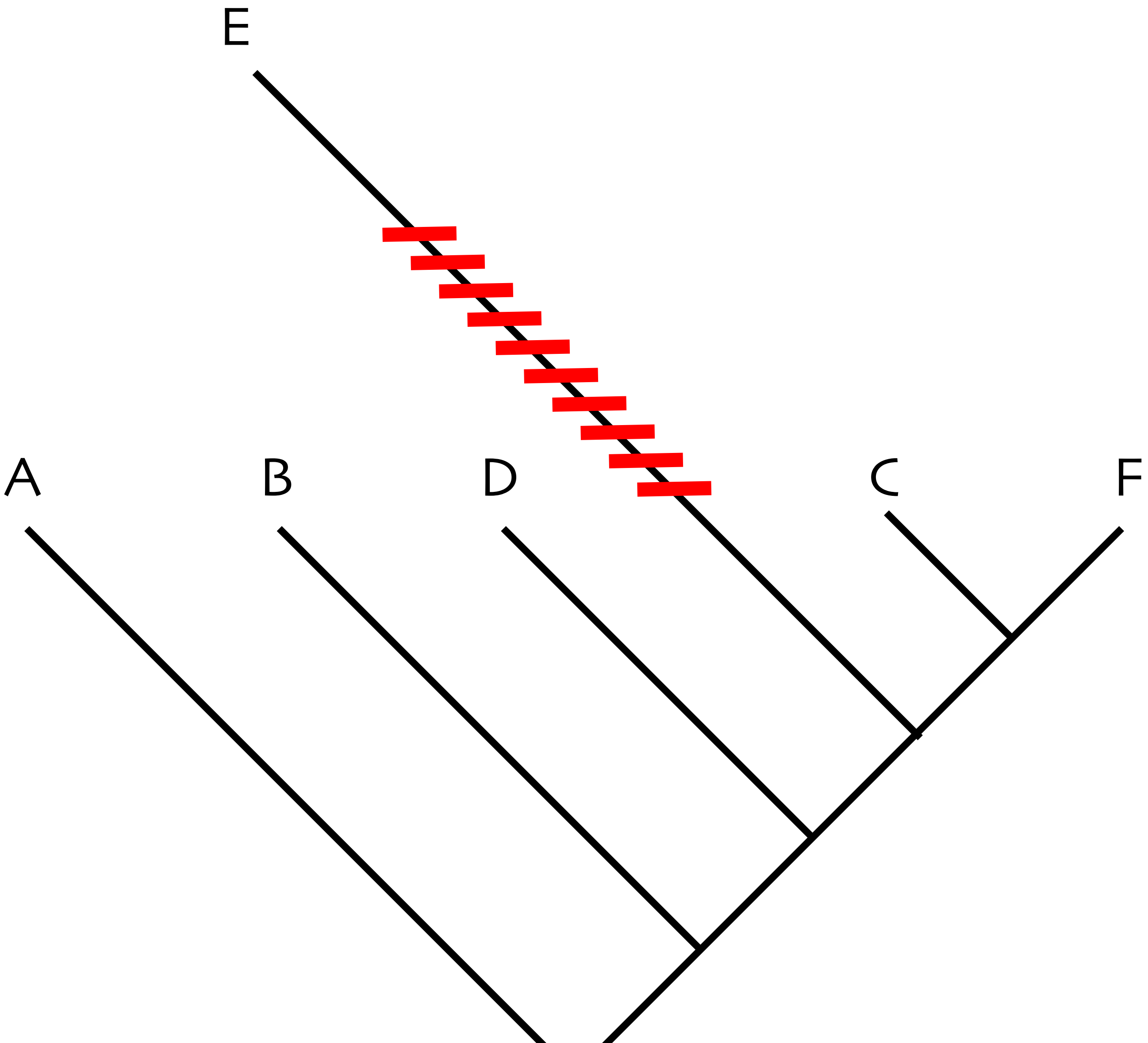
synapomorphies
for clade A-E-B-C


D
A
E
B
C
1
2
4
8
10
10
2
9
12
4(0>1)
11(1>0)
6(1>0)
3(0>1)
9
7
5
12
11(0>1)

Based on previous classification spp.
A-D & C & F belong to same genus

Species E has been distinguished as a genus of its own

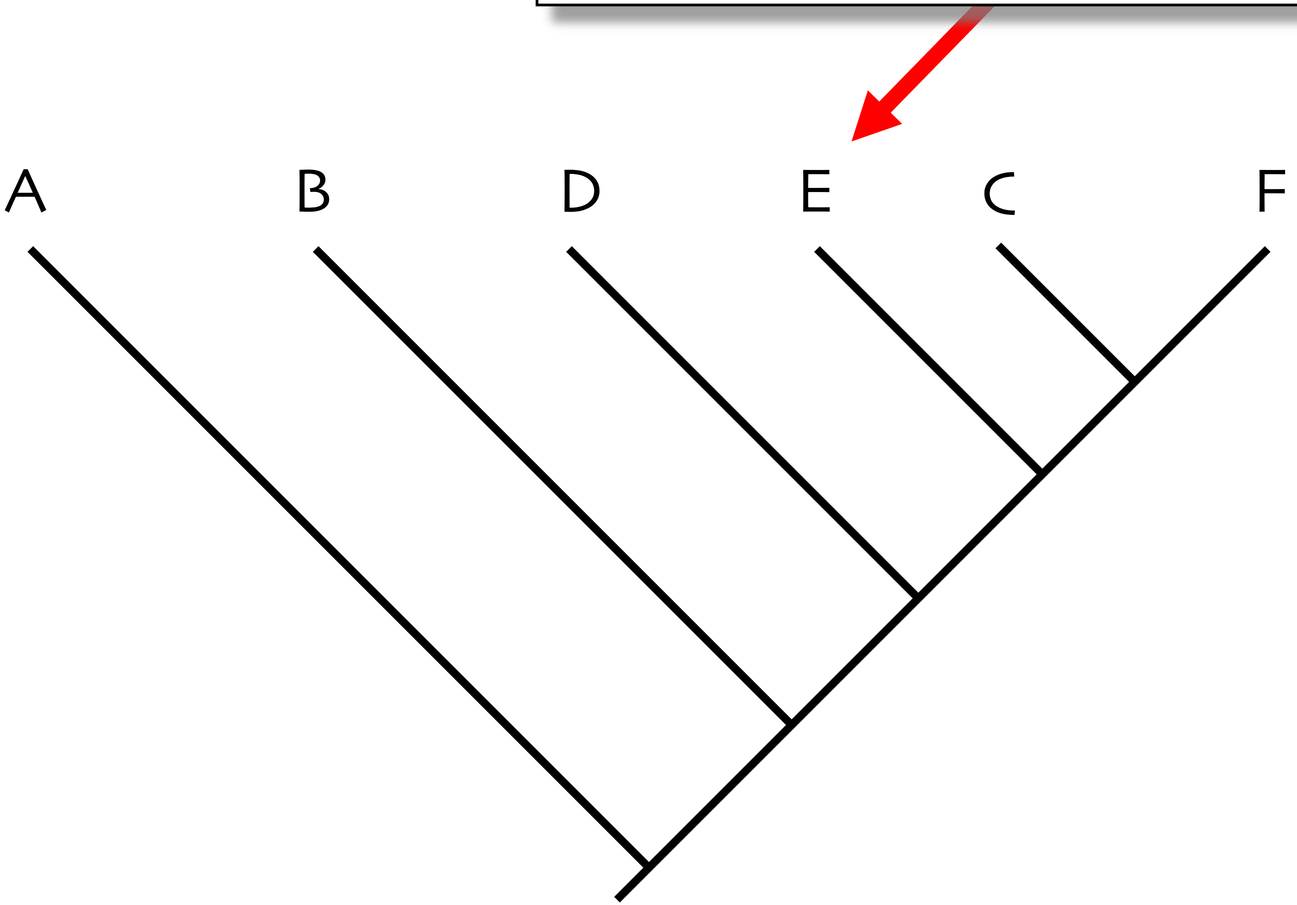



E
A
B
D
C
F

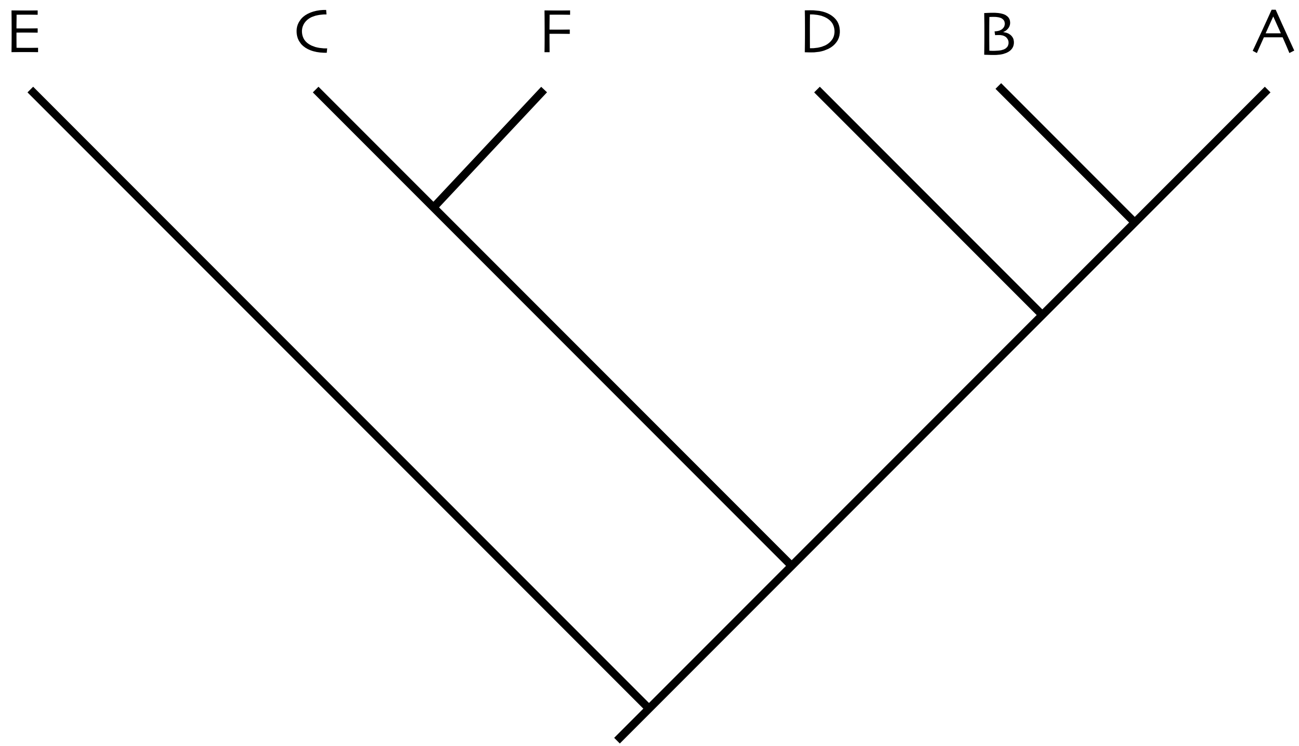
Based on previous classification spp. A-D & C & F belong to same genus

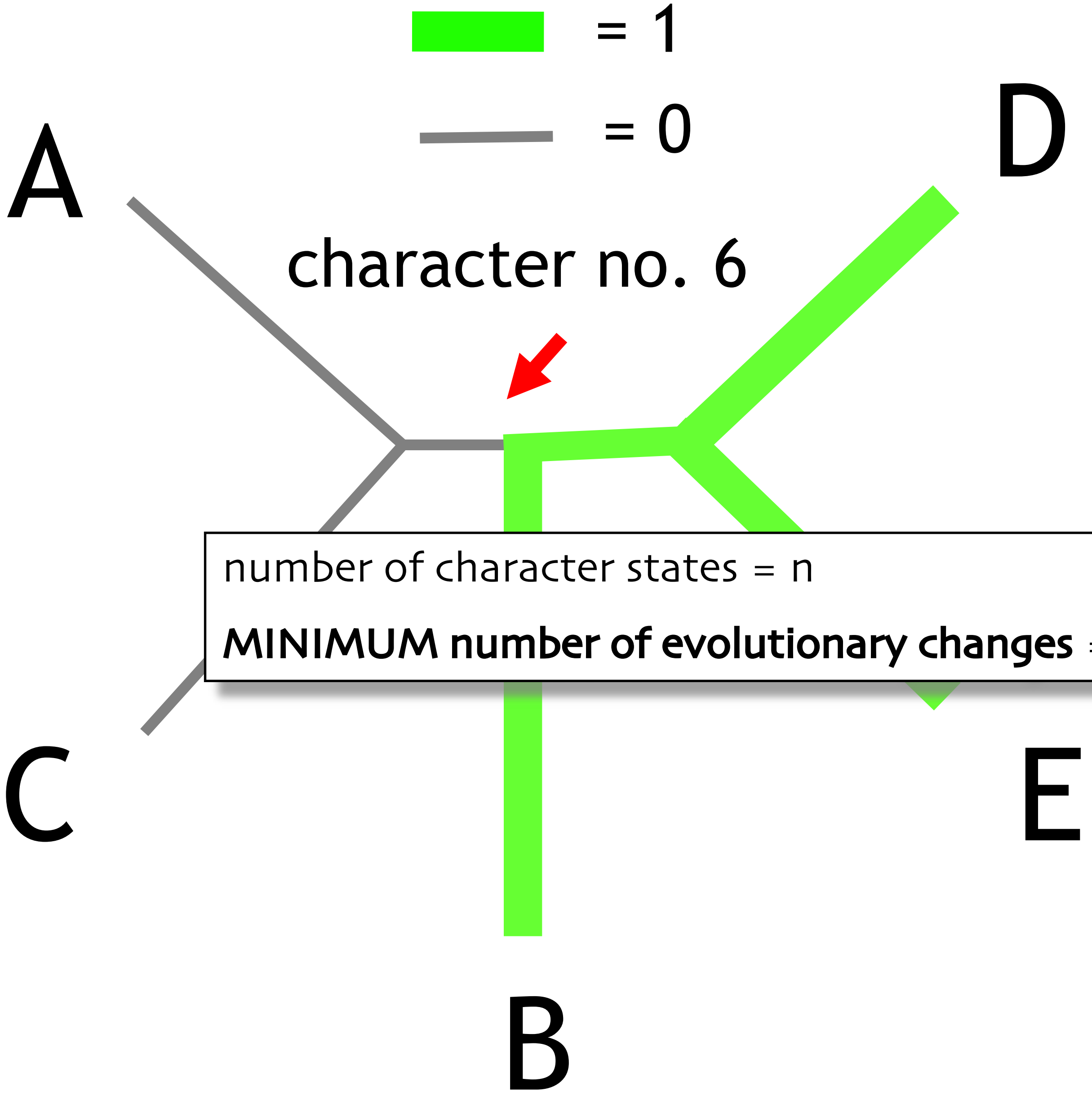
Species E has been distinguished as a genus of its own

If the species E would have been chosen as a sole outgroup this would have resulted in a tree →



in order to avoid these kind of mistakes it is recommended to use SEVERAL OUTGROUPS in analysis





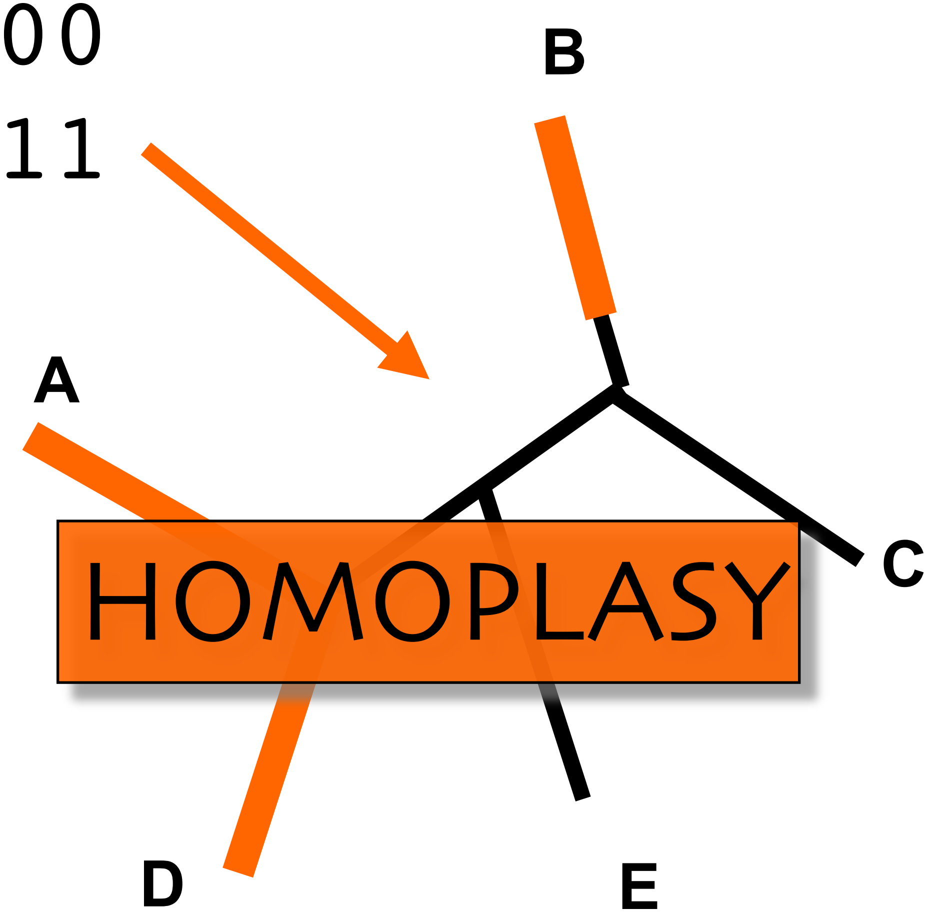
number of character states = n

MINIMUM number of evolutionary changes = n-1

	characters												
trees	01	02	03	04	05	06	07	08	09	10	11	12	Σ
1	1	1	2	2	2	2	2	1	2	2	1	2	20
2	1	1	2	2	2	2	2	1	2	2	2	2	21
3	1	1	2	2	2	2	2	1	1	2	2	2	20
4	1	2	2	1	2	2	2	1	2	2	2	2	21
5	1	2	2	1	2	2	2	1	2	2	2	1	20
6	1	2	2	1	2	2	2	1	2	2	2	2	21
7	1	2	2	2	2	2	2	1	2	1	1	2	20
8	1	2	1	2	2	1	2	1	2	1	2	2	19
9	1	2	2	2	2	2	2	1	2	1	2	1	20
10	1	2	2	2	2	2	2	1	1	2	2	1	20
11	1	2	2	2	2	2	2	1	2	2	1	2	21
12	1	2	1	2	2	1	2	1	2	2	2	2	20
13	1	2	2	2	1	2	1	1	1	2	2	2	19
14	1	2	2	2	1	2	1	1	2	2	2	2	20
15	1	2	1	2	1	1	1	1	2	2	2	2	18

A	010111011111
B	111000101010
C	101100100001
D	100011001000
E	100001100111

(most) parsimonious, i.e.
shortest tree 18 (16+2)
evolutionary changes



HOMOPLASY

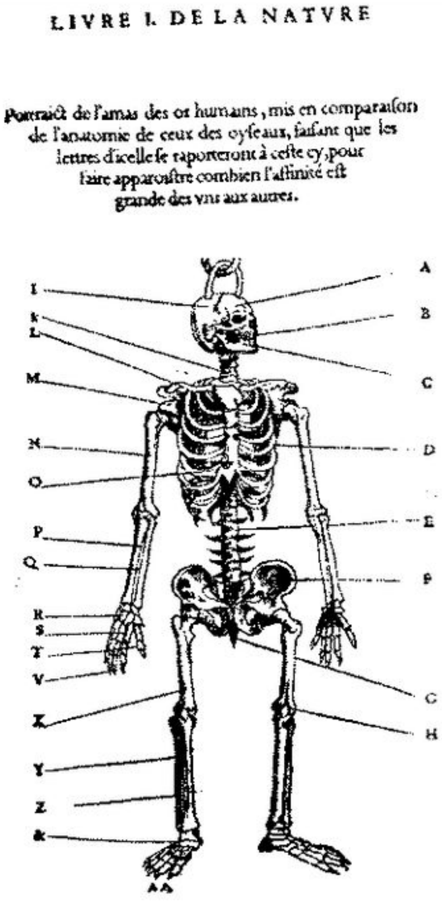
e.g. character 9
2 evolutionary changes

also characters 2, 4, 10-12

HOMOLOGY

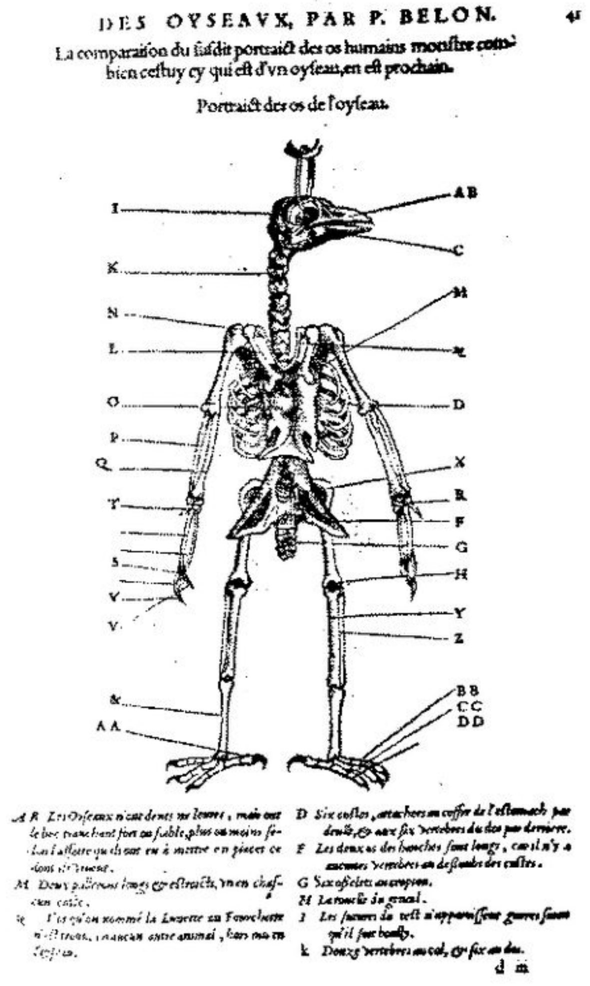
Richard Owen (1804-1892) originally presented (1848) concept of HOMOLOGY for similar structures of organisms that represent ARCHETYPE

Pierre Belon (1517-1564)



LIVRE I. DE LA NATVRE

Portraict de l'amas des os humains, mis en comparaiſon de l'anatomie de ceux des oyſeaux, faiſant que les lettres d'icelle ſe raporteront à ceſte cy, pour faire apparoiſtre combien l'affinité eſt grande des vns aux autres.



DES OYSEAVX, PAR P. BELON. 41

La comparaiſon du ſuſdit portraict des os humains monſtre combien ceſtuy cy qui eſt d'vn oyſeau, en eſt prochain.

Portraict des os de l'oyſeau.

A B Les Oyſeaux n'ont dents ne levres, mais ont le bec tranchant fort ou foible, plus ou moins ſelon l'affaire qu'ils ont eu à mettre en pieces ce dont ils viuent.

M Deux palerons longs & eſtroicts, vn en chaſcun coſté.

K Os qu'on nommé la Lunette ou Fourchette n'eſt trouvé en aucun autre animal, hors mis en l'oyſeau.

D Six coſtes, attachees au coffre de l'eſtomach par deuāt, & aux ſix vertebres du dos par derriere.

F Les deux os des hanches ſont longs, car il n'y a aucunes vertebres au deſſoubs des coſtes.

G Six oſſelets au croupion.

H La rouelle du genoil.

I Les ſutures du teſt n'apparoiſſent gueres ſinon qu'il ſoit bouilly.

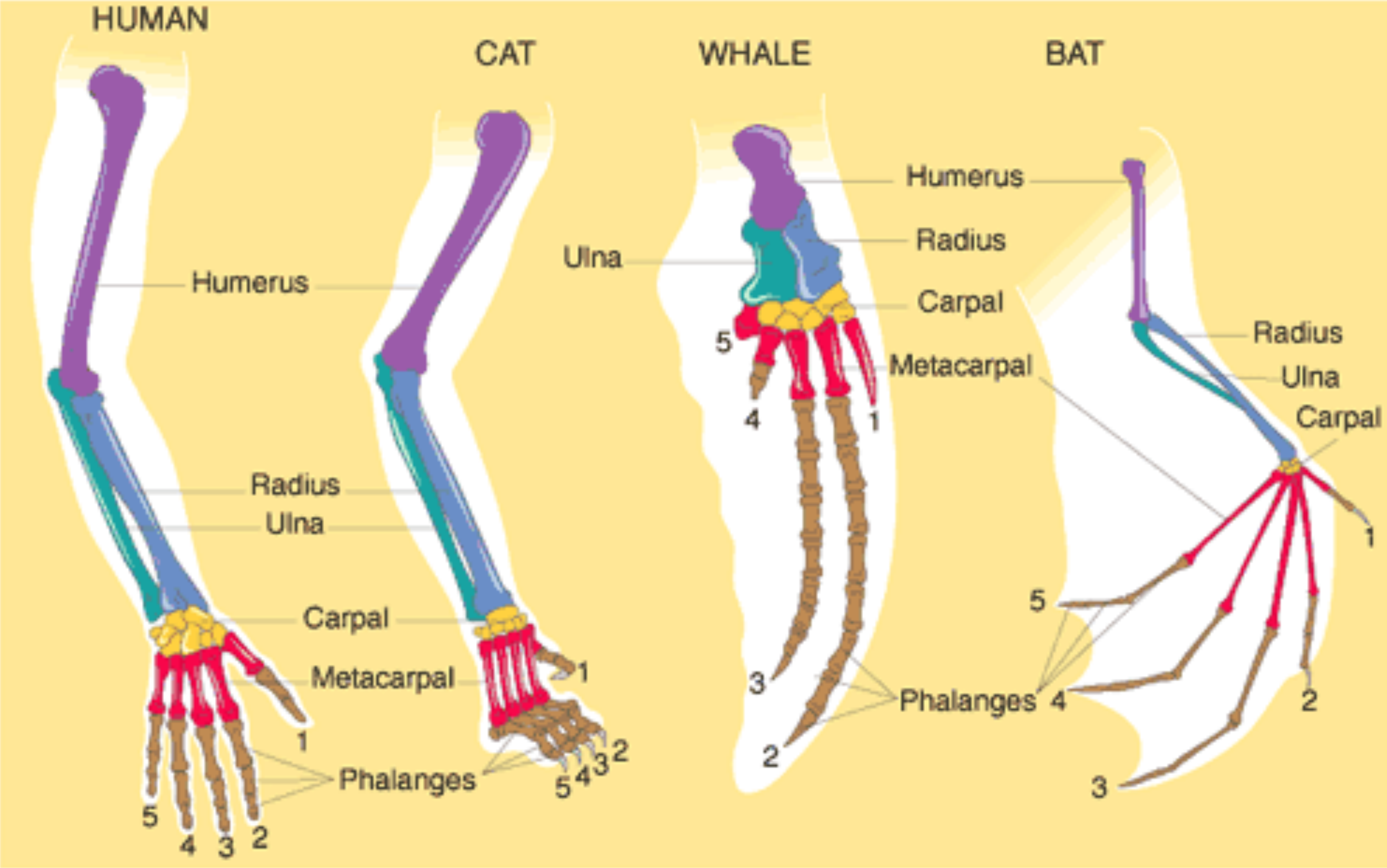
k Douze vertebres au col, & ſix au dos.

d iii

HOMOLOGY & ANALOGY

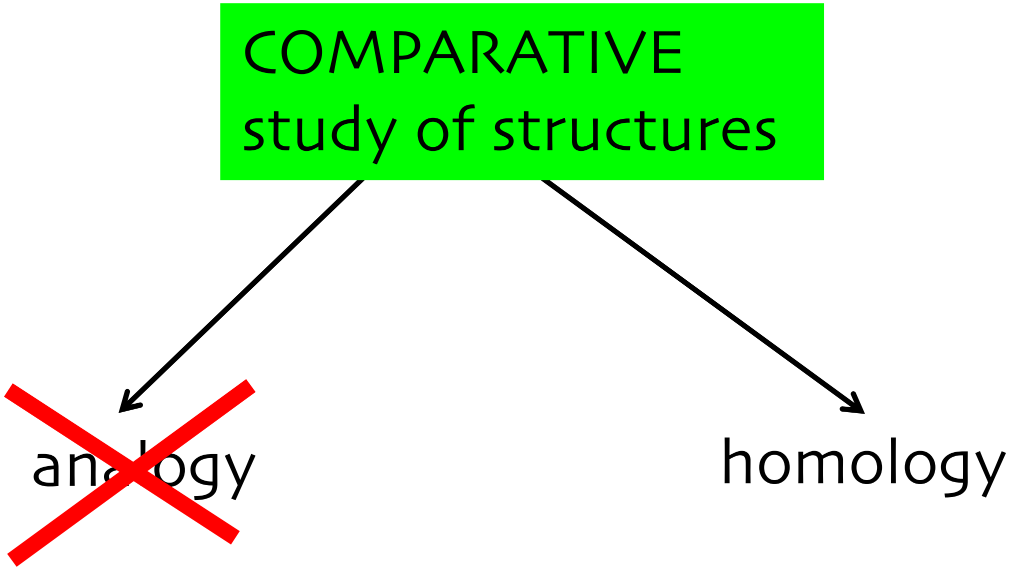
HOMOLOGY
same organ in different animals under every variety of form and function

ANALOGY
a part or organ in one animal which has the same function as another part or organ in a different animal


HUMAN
CAT
WHALE
BAT
Humerus
Radius
Ulna
Carpal
Metacarpal
Phalanges
1
2
3
4
5
Ulna
Humerus
Radius
Carpal
Metacarpal
Phalanges
1
2
3
4
5
Radius
Ulna
Carpal
Phalanges
1
2
3
4
5

HOMOLOGY & ANALOGY

homology informs about history, part of historical signal,
ANALOGY does NOT

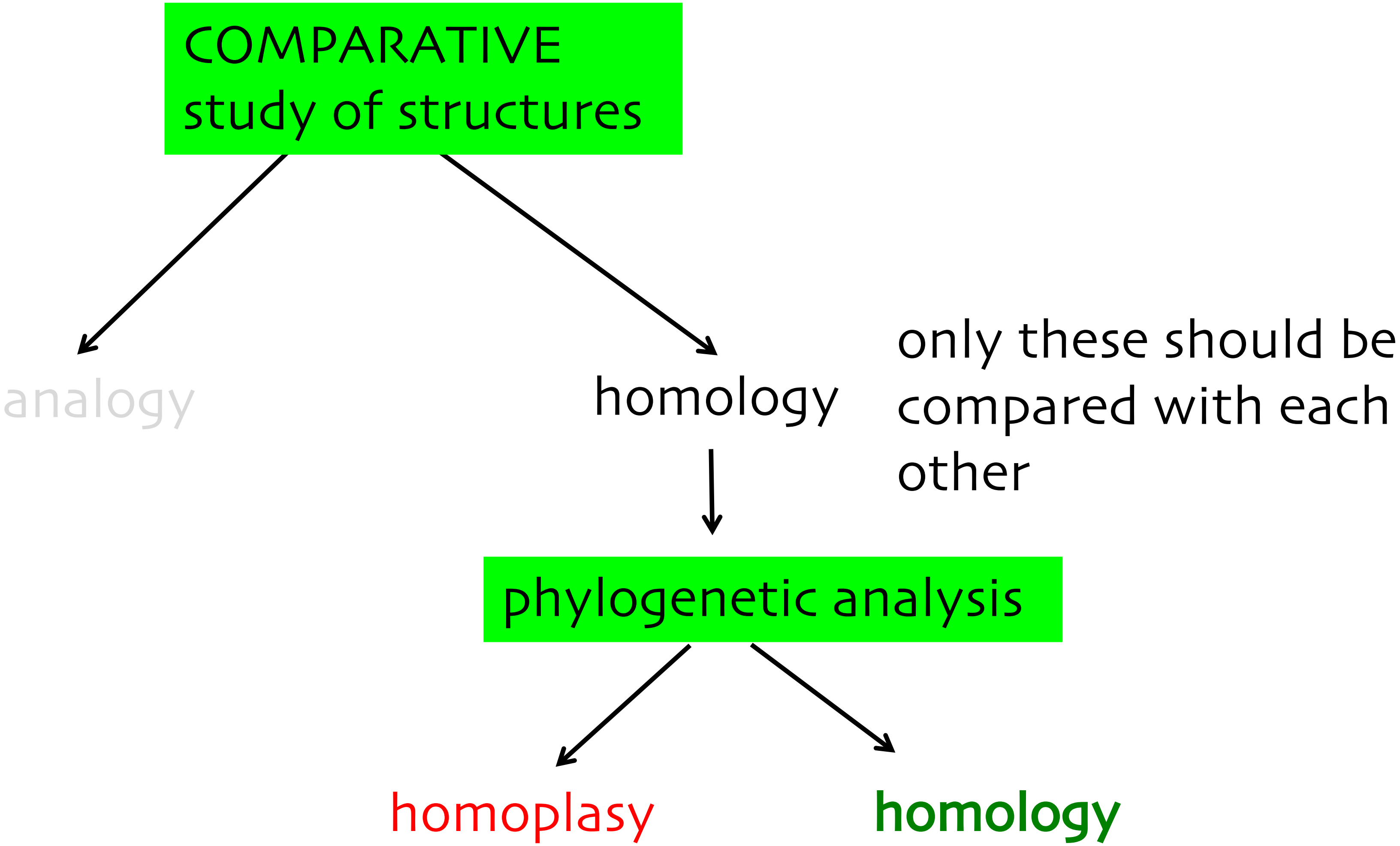


COMPARATIVE
study of structures

~~analogy~~

homology

only these should be compared with each other



COMPARATIVE
study of structures

analogy

homology

only these should be compared with each other

phylogenetic analysis

homoplasy

homology

preliminary assumption
about homology failed

might still define SMALLER
clades > **still valuable**

HOMOLOGY & HOMOPLASY

characters are ALWAYS in conflict to some extent →
HOMOPLASY = EXTRA STEPS, i.e. more ch. state changes than the minimum, AFTER phylogenetic analysis has been performed

homology informs about history, part of historical signal,
homoplasy ONLY PARTIALLY, it is NOISE to some extent & at some level

HOMOLOGY & HOMOPLASY

earlier assumptions about homology have to be denied (at least at this level)

HOMOLOGY = shared feature inherited from common ancestor

for example wings of birds & bats
flippers of penguins & seals

homologies as limbs **NOT** as wings/flippers

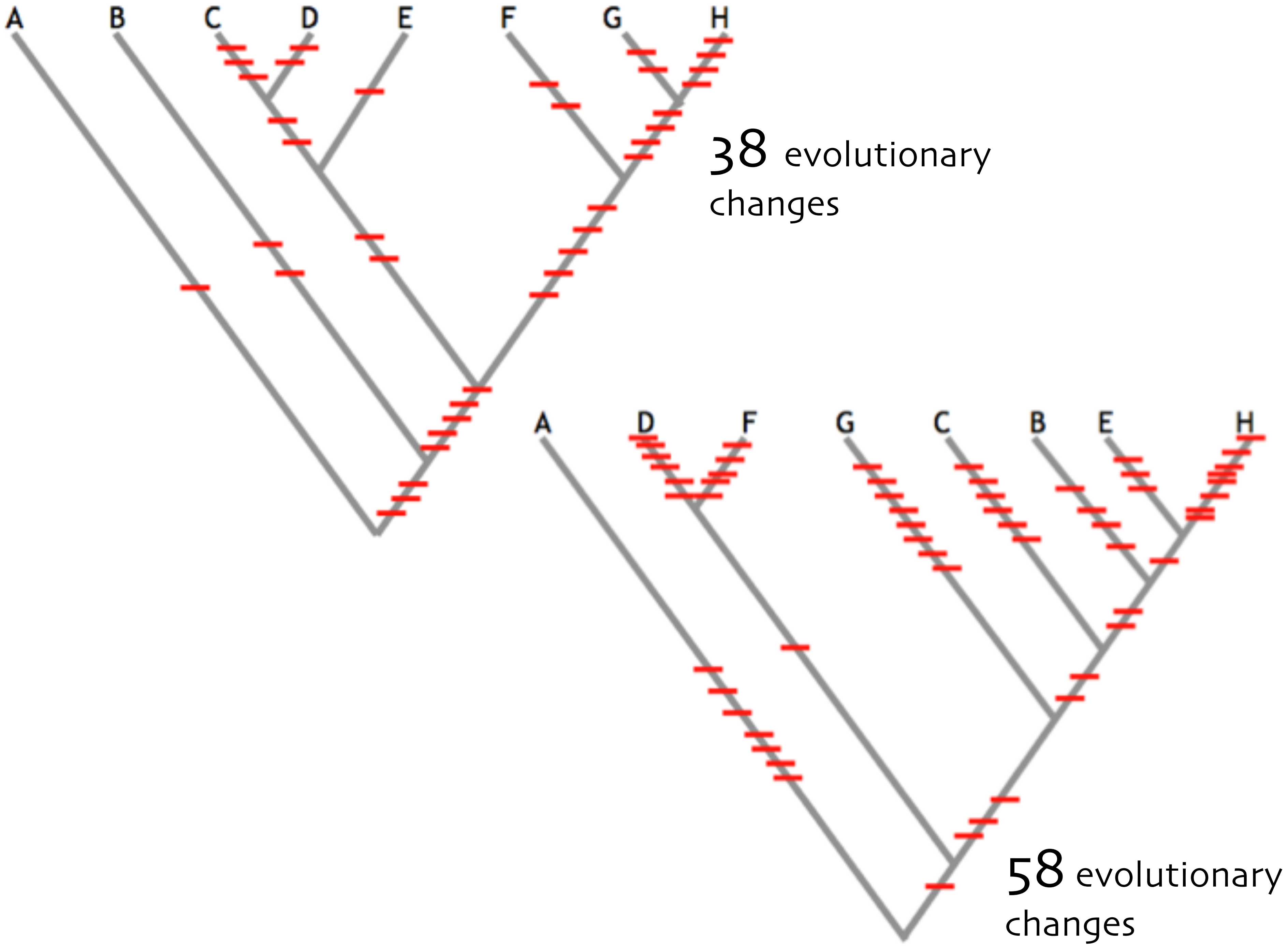
homoplasy is due to convergence or reversals

e.g. during ontogeny development of structure is not completed

	characters												
	0	0	0	0	0	0	0	0	0	1	1	1	Σ
trees	1	2	3	4	5	6	7	8	9	0	1	2	
1	1	1	2	2	2	2	2	1	2	2	1	2	20
2	1	1	2	2	2	2	2	1	2	2	2	2	21
3	1	1	2	2	2	2	2	1	1	2	2	2	20
4	1	2	2	1	2	2	2	1	2	2	2	2	21
5	1	2	2	1	2	2	2	1	2	2	2	1	20
													21
7	1	2	2	2	2	2	2	1	2	1	1	2	20
8	1	2	1	2	2	1	2	1	2	1	2	2	19
9	1	2	2	2	2	2	2	1	2	1	2	1	20
10	1	2	2	2	2	2	2	1	1	2	2	1	20
11	1	2	2	2	2	2	2	1	2	2	1	2	21
12	1	2	1	2	2	1	2	1	2	2	2	2	20
13	1	2	2	2	1	2	1	1	1	2	2	2	19
14	1	2	2	2	1	2	1	1	2	2	2	2	20
15	1	2	1	2	1	1	1	1	2	2	2	2	18

What is the CONCRETE reason for length differences between trees?

CHARACTER CONGRUENCE

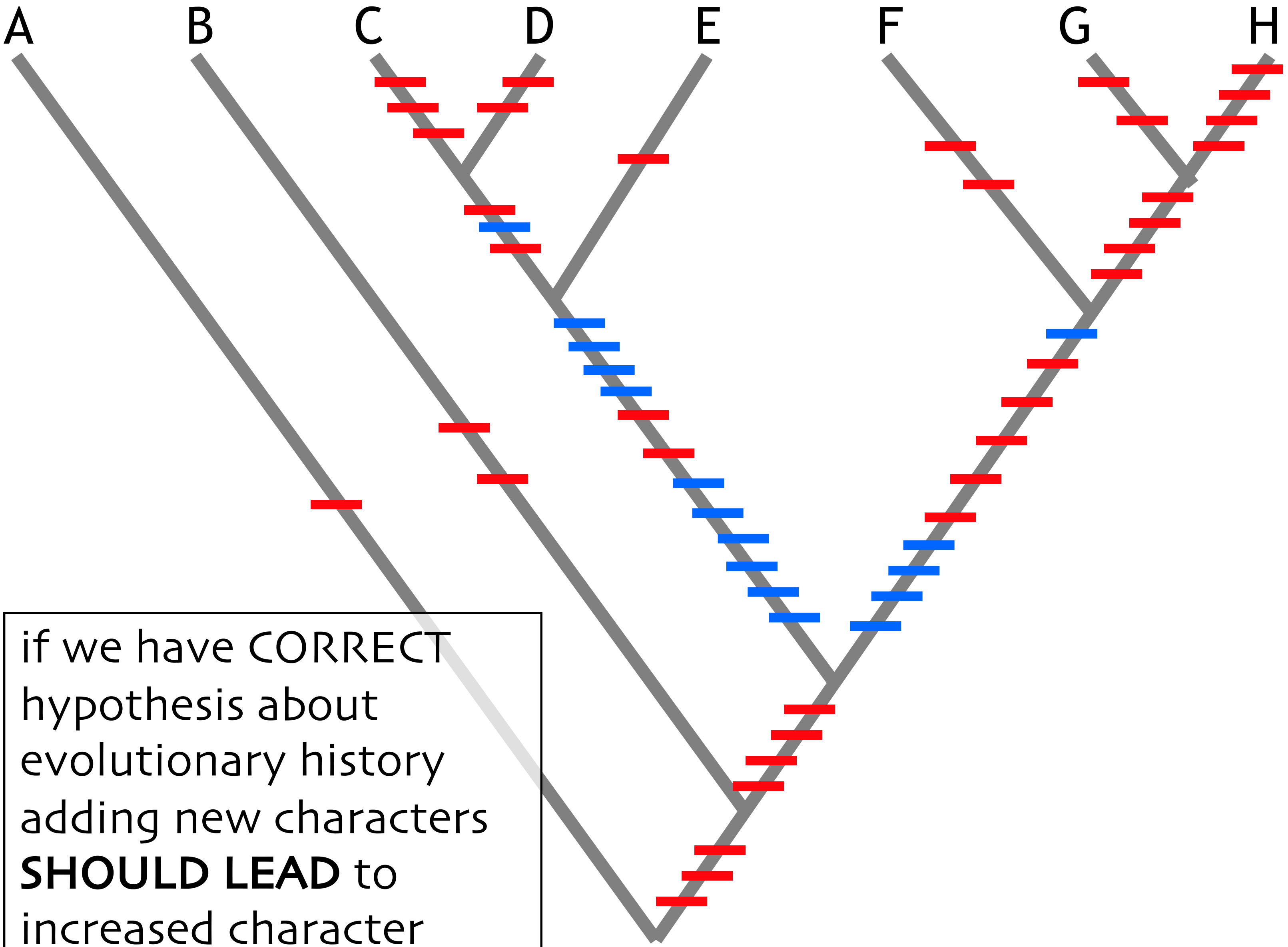

A
B
C
D
E
F
G
H
38 evolutionary changes
A
D
F
G
C
B
E
H
58 evolutionary changes

CHARACTER CONGRUENCE

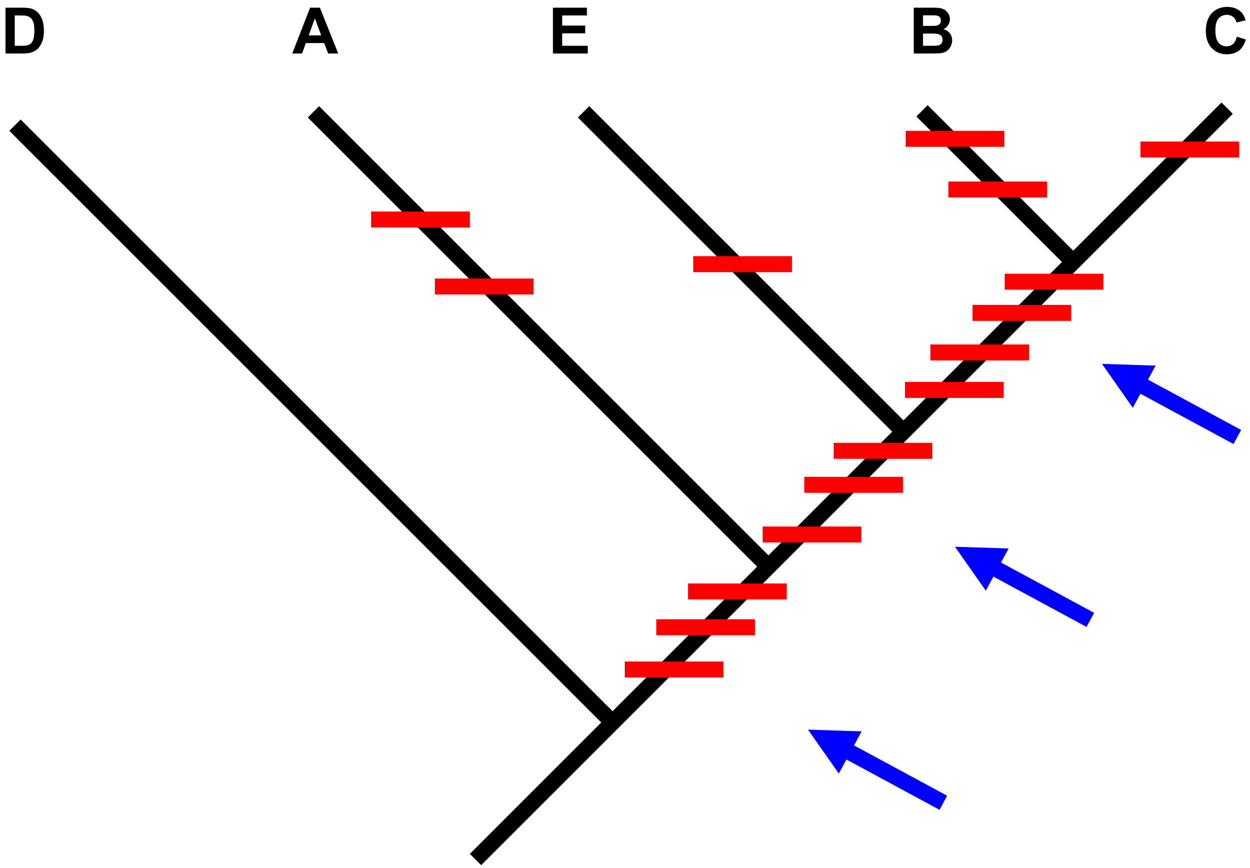
is the concrete reason for the fact that we find short tree(s)

on the shortest tree evolutionary changes are CONGRUENT, i.e. CONCENTRATED ON SAME BRANCHES of the tree (less homoplasy)

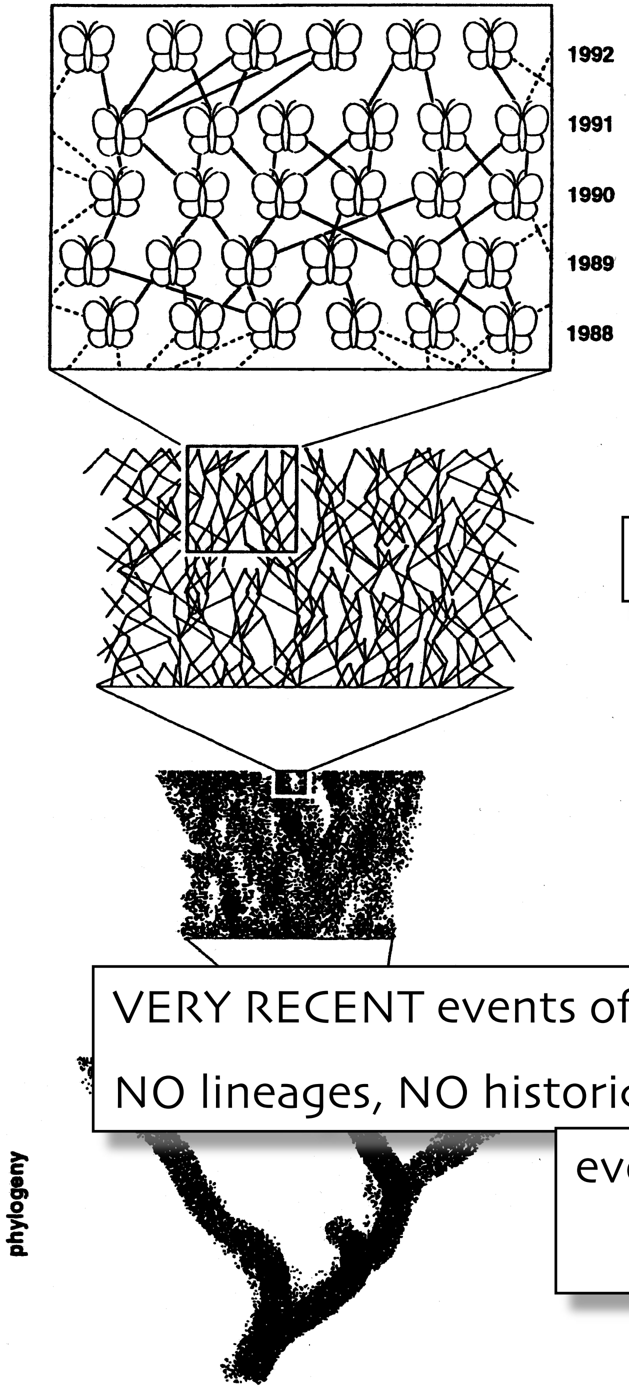
1. Is this accidental?
2. Or have we possibly found a hypothesis that is a good approximation about evolutionary history and this is why so MANY characters are congruent?



if we have CORRECT hypothesis about evolutionary history adding new characters **SHOULD LEAD** to increased character congruence


D
A
E
B
C

TOKOGENY
vs.
PHYLOGENY



INDIVIDUALS

POPULATIONS

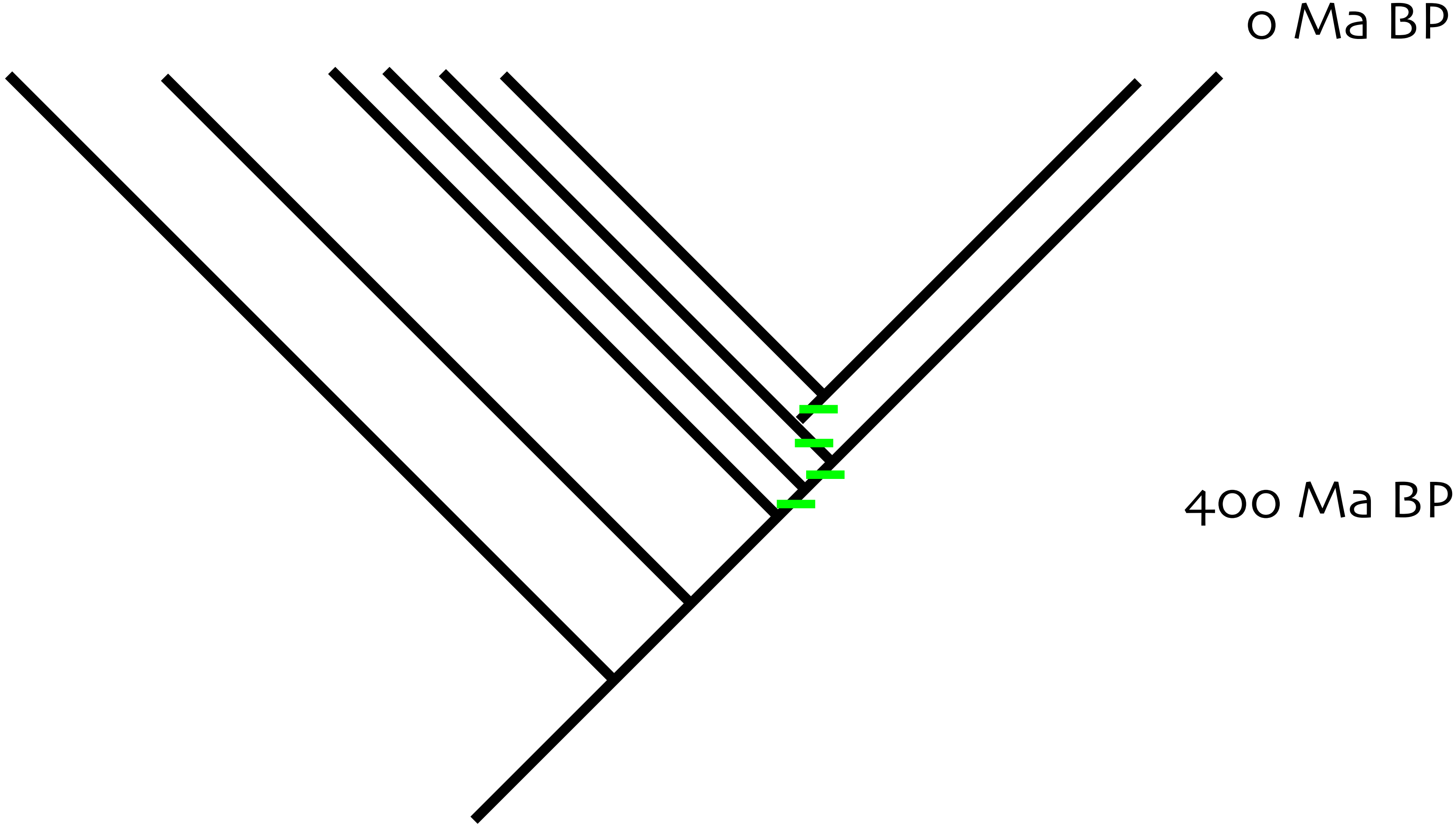
SPECIES

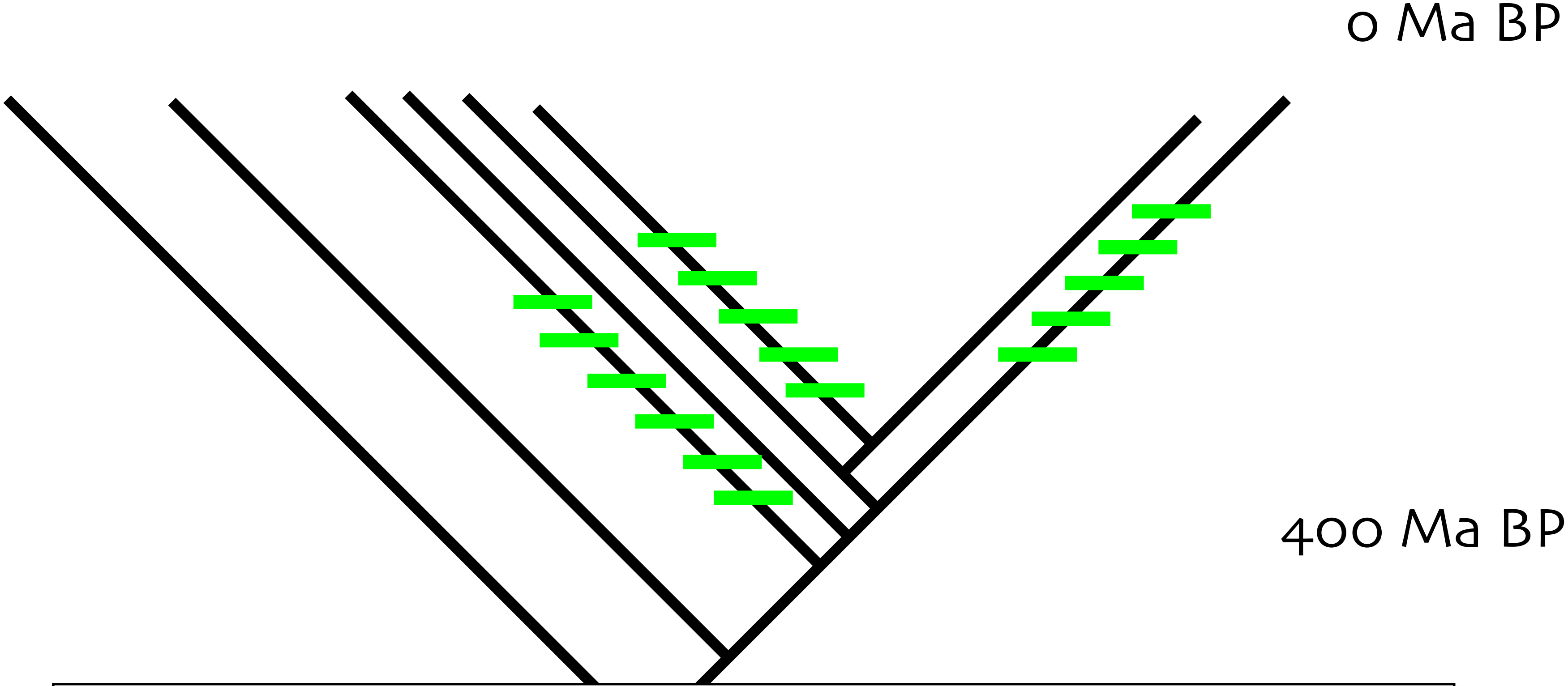
VERY RECENT events of evolutionary history

NO lineages, NO historical signal

evolutionary **process**

evolutionary **pattern**

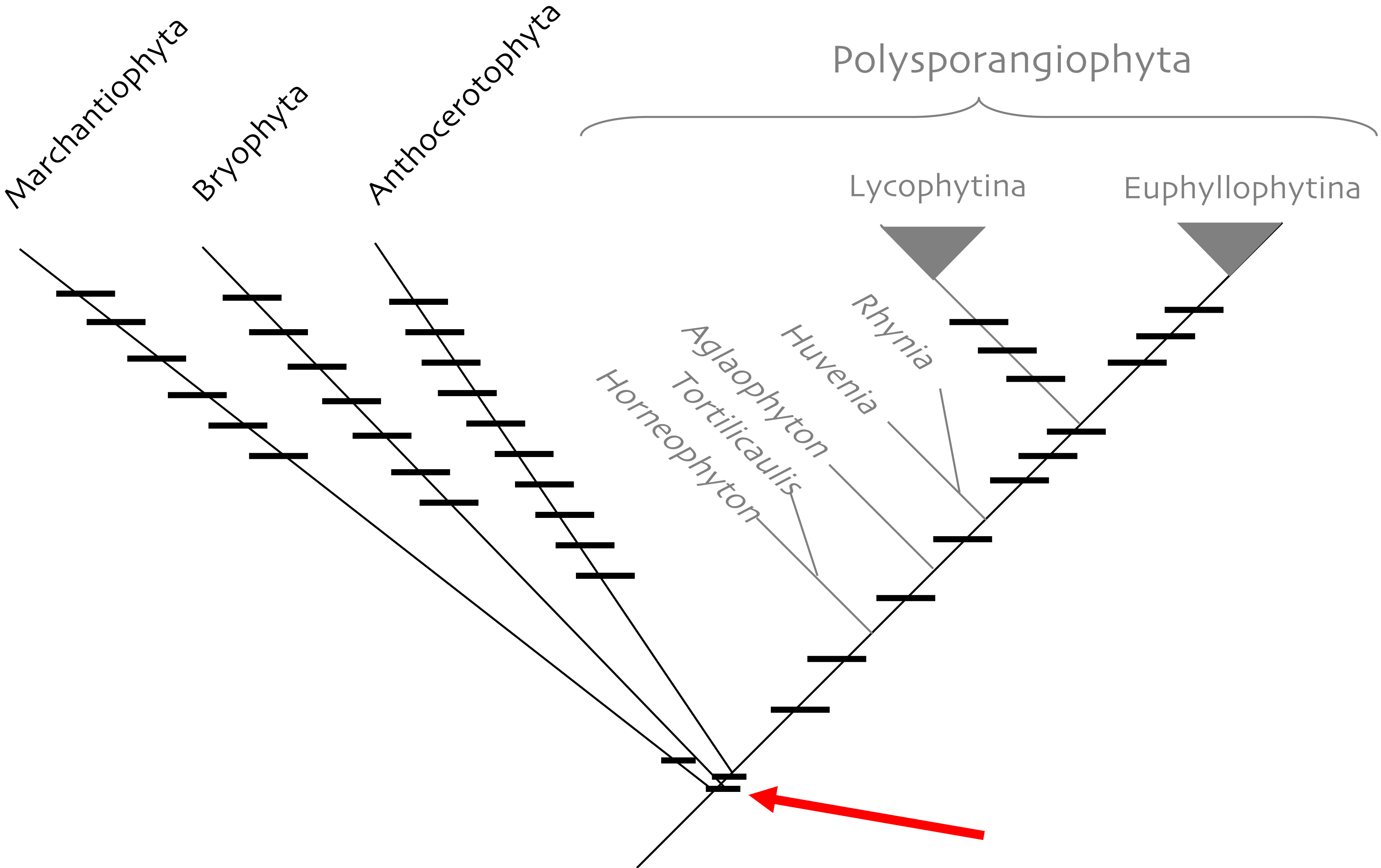

0 Ma BP
400 Ma BP



…or such VERY OLD lineages that have diverged from each other VERY RAPIDLY

SHARED HISTORY, as compared to the one that followed, is very short

EMBRYOPHYTES



SUMMARY

Wagner algorithm is fast & efficient way for finding close estimate of the parsimonious tree

order of addition of terminals affects performance of the algorithm

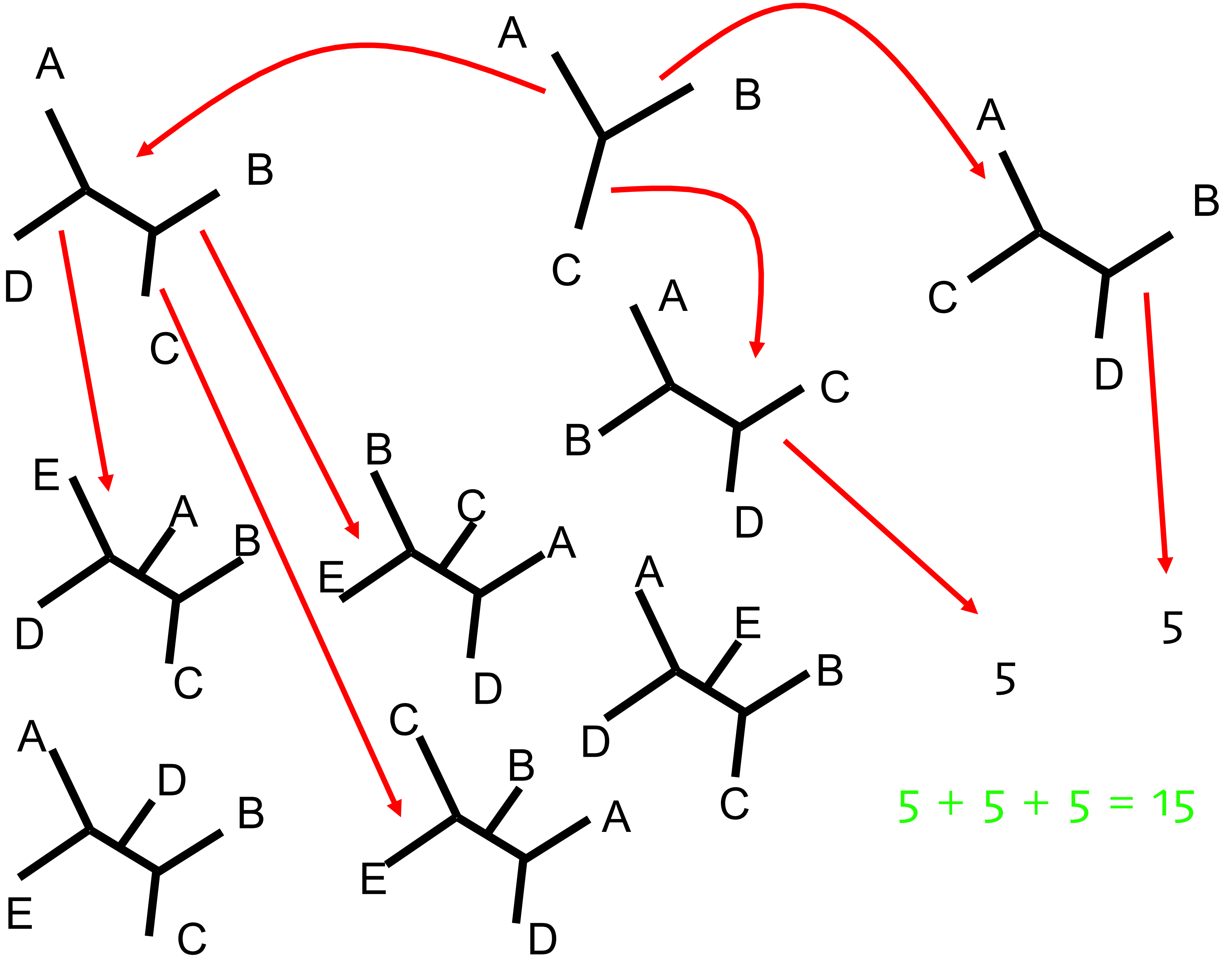
apo- & plesiomorphies can be distinguished using **OUTGROUP comparison**

concrete reason for length differences between trees is character **CONGRUENCE**

for how many characters does the SAME tree give simplest (=parsimonious) evolutionary explanation

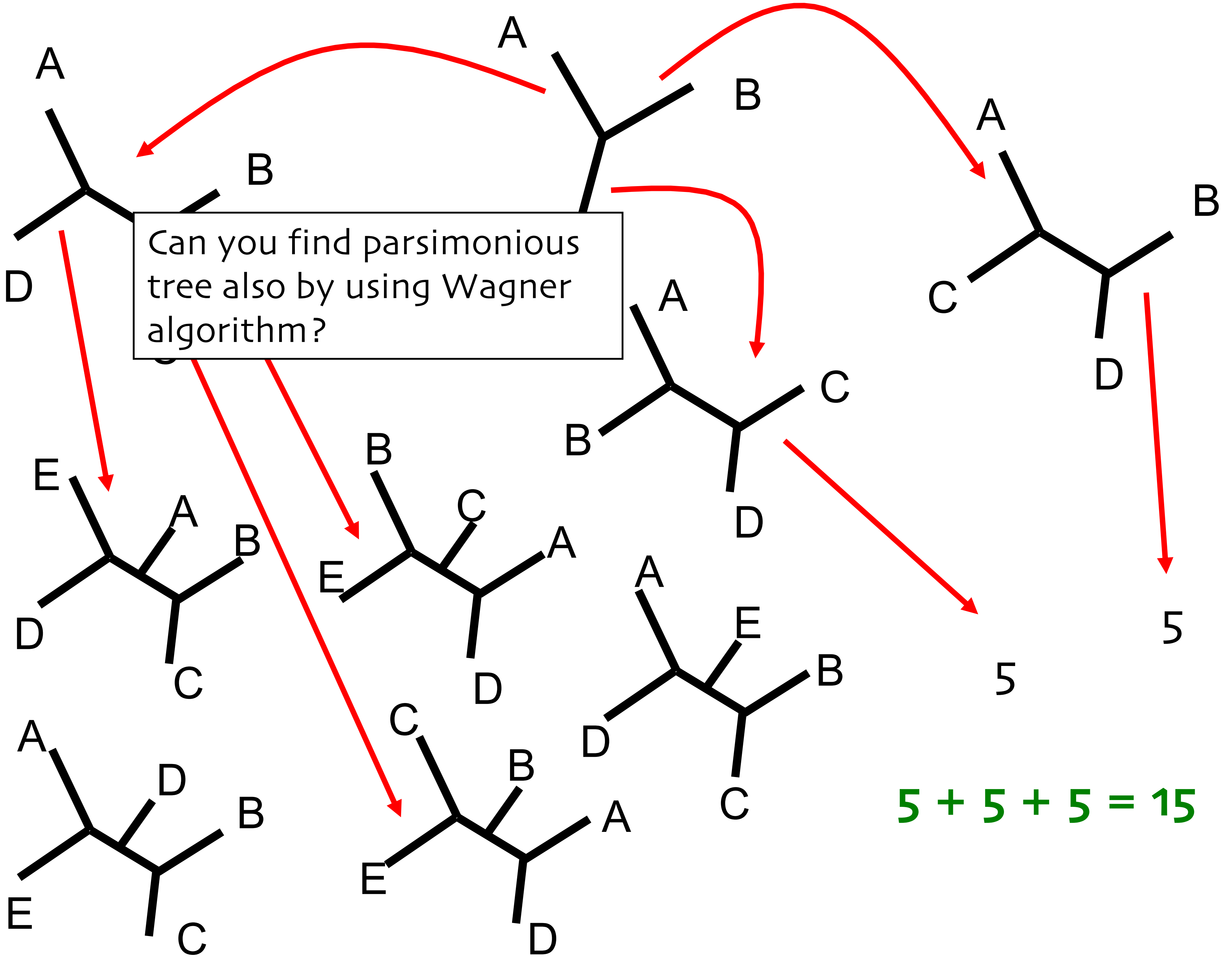
analyses will ALWAYS reveal homoplasy

HOMOLOGY is the NULL hypothesis for resemblance between terminals


A
B
C
A
B
C
D
A
B
C
D
A
B
C
D
E
A
B
C
D
E
B
C
A
D
A
E
B
D
C
A
D
B
E
C
C
B
A
E
D
5
5
5 + 5 + 5 = 15

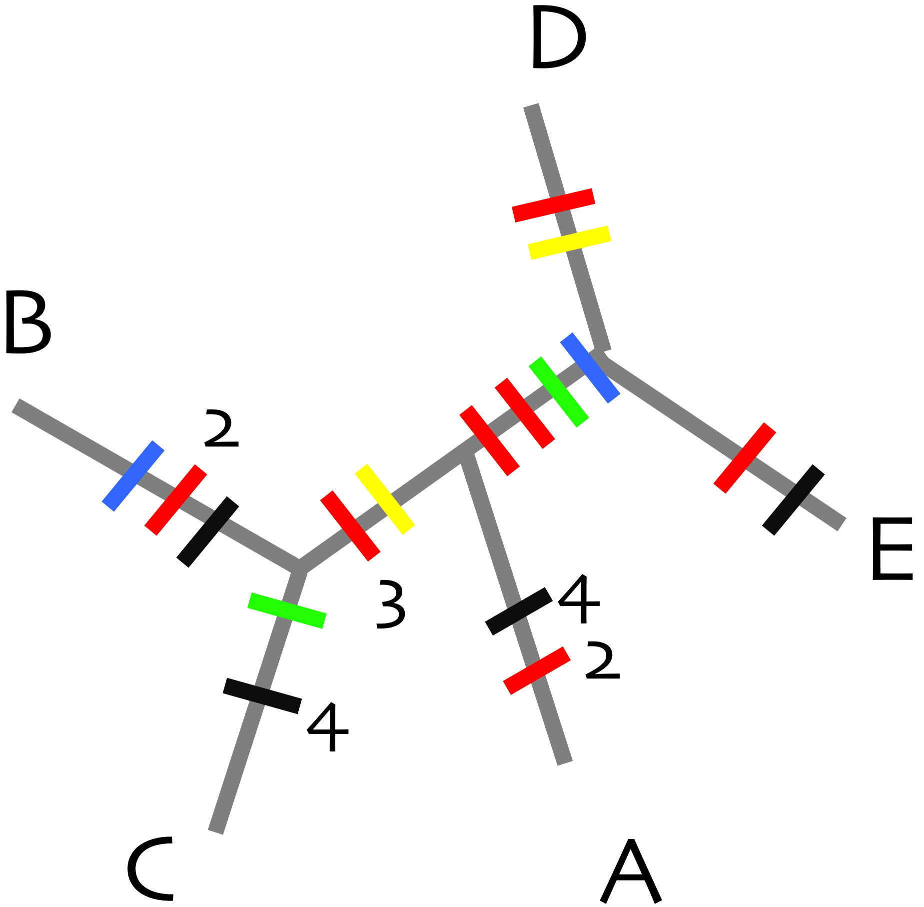
HOME EXERCISE

terminals \ characters	01	02	03	04	05	06	07	08	09	10	11	12
A	0	1	0	1	1	1	0	1	1	1	1	1
B	1	1	1	0	0	0	1	0	1	0	1	0
C	1	0	1	1	0	0	1	0	0	0	0	1
D	1	0	0	0	1	1	0	0	1	0	0	0
E	1	0	0	0	0	1	1	0	0	1	1	1



Can you find parsimonious tree also by using Wagner algorithm?

5 + 5 + 5 = 15


D
B
2
3
4
2
E
4
C
A

HOME EXERCISE

lecture slides available in pdf-format AFTER the lectures

www.helsinki.fi/~jhyvonen/ec18

	characters											
terminals	01	02	03	04	05	06	07	08	09	10	11	12
A	0	1	0	1	1	1	0	1	1	1	1	1
B	1	1	1	0	0	0	1	0	1	0	1	0
C	1	0	1	1	0	0	1	0	0	0	0	1
D	1	0	0	0	1	1	0	0	1	0	0	0
E	1	0	0	0	0	1	1	0	0	1	1	1