12.xi.

1. home exercise

1. characters

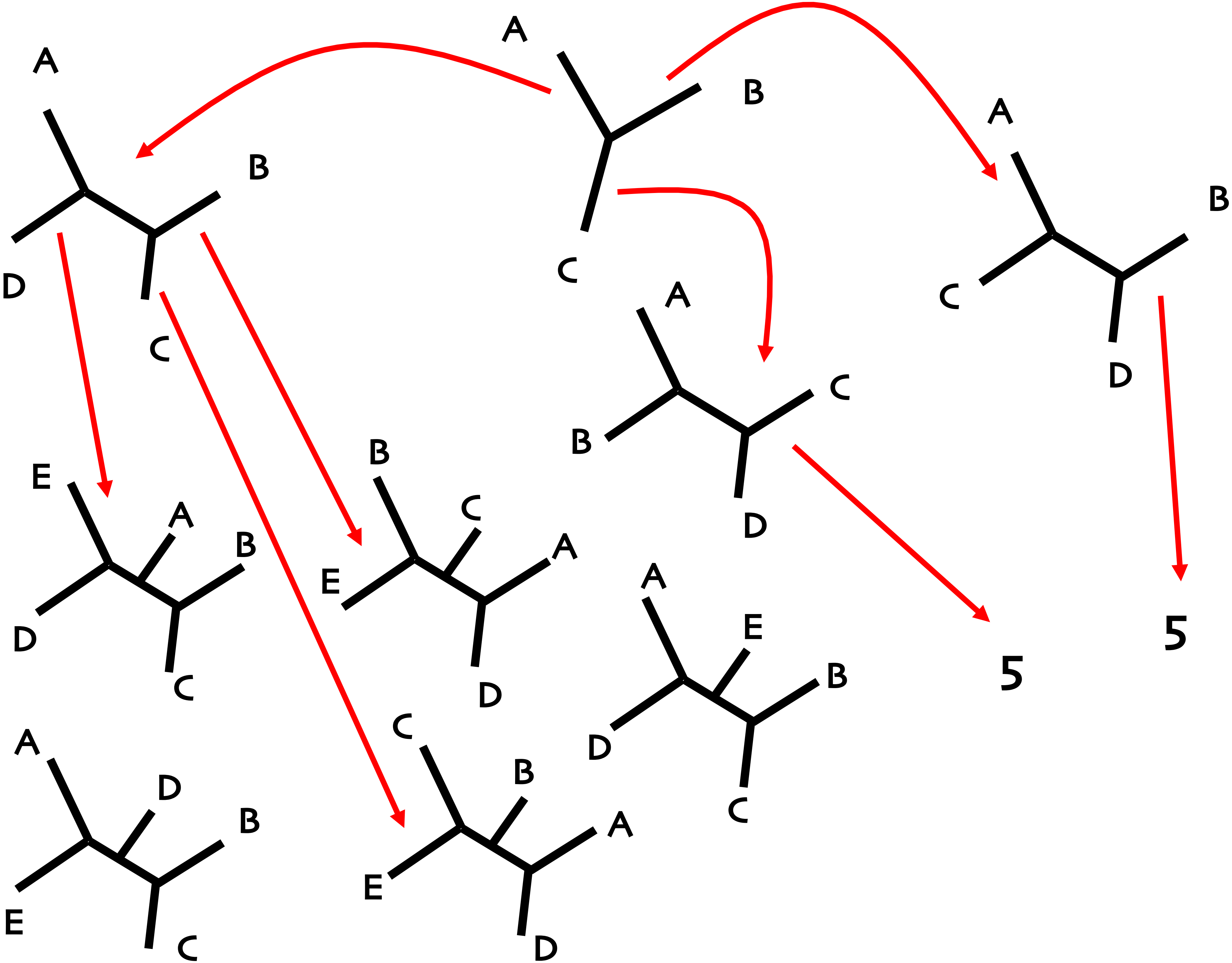
2. character weighting

3. indices describing characters

4. summary

HOME EXERCISE

terminals	characters 000000000111 123456789012
A	010111011111
B	111000101010
C	101100100001
D	100011001000
E	100001100111



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

trees	characters 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

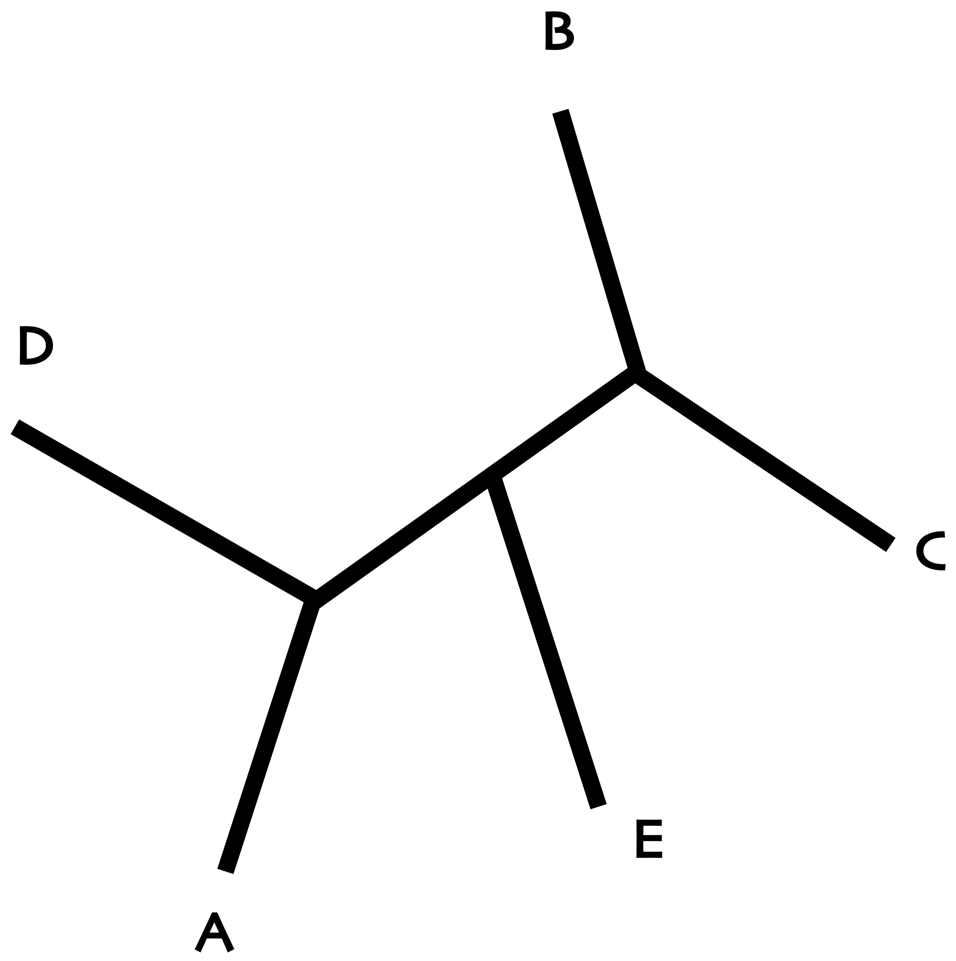
characters

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
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

BEST HYPOTHESIS

- smallest number of changes from one character state to another

- largest part of resemblance between terminals explained by their shared HISTORY (descent from common ancestor)


B
D
C
E
A

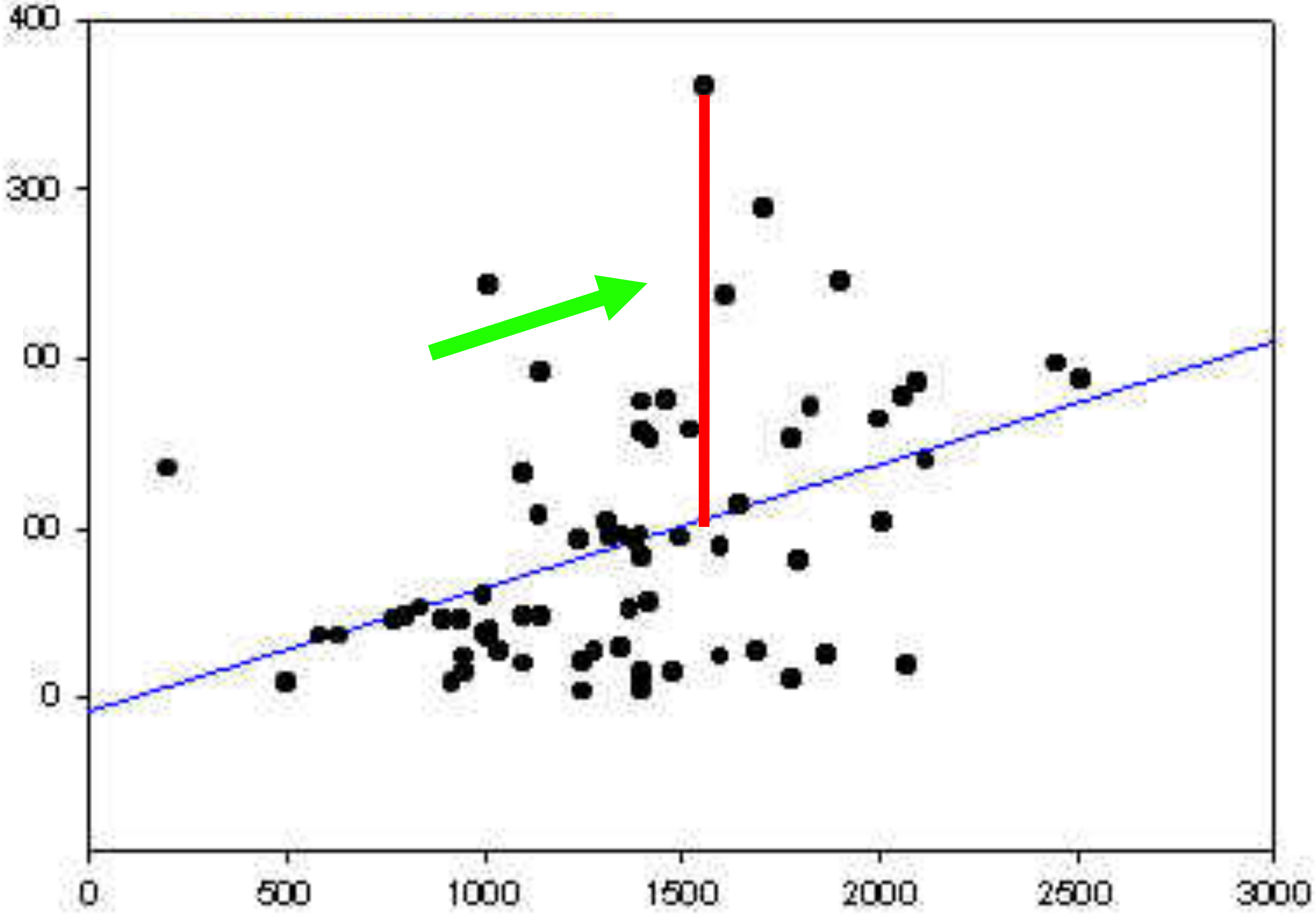
trees	characters 01	02	03	04	05	06	07	08	09	10	11	12	Σ
1	1	1	2	2	2	2	2	1	2	2	1	2	20
2	1	1	2	2	2	2	2	1	2	2	2	2	21
3	1	1	2	2	2	2	2	1	1	2	2	2	20
4	1	2	2	1	2	2	2	1	2	2	2	2	21
5	1	2	2	1	2	2	2	1	2	2	2	1	20
6	1	2	2	1	2	2	2	1	2	2	2	2	21
7	1	2	2	2	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
8	1	2	1	2	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
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

number of character states= n

MINIMUM number of evolutionary changes= n-1

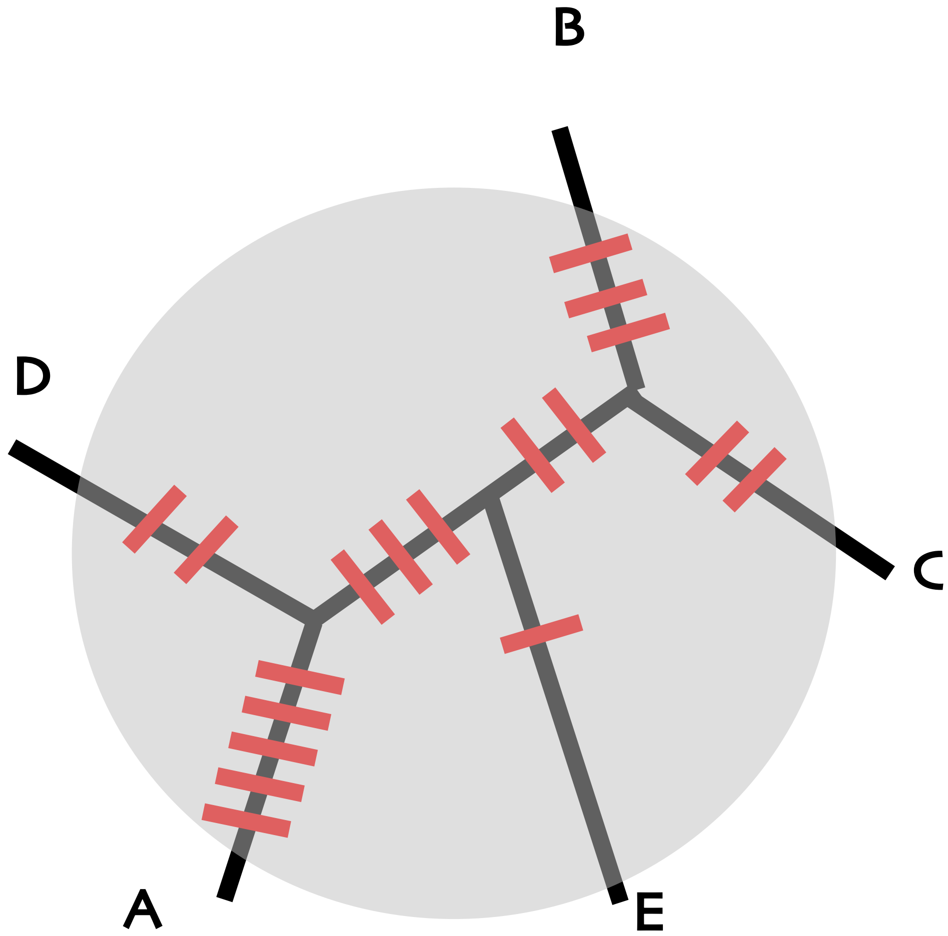
$$d(A, B) = \sum | X(Ai) - X(Bi) |$$

number of lvs

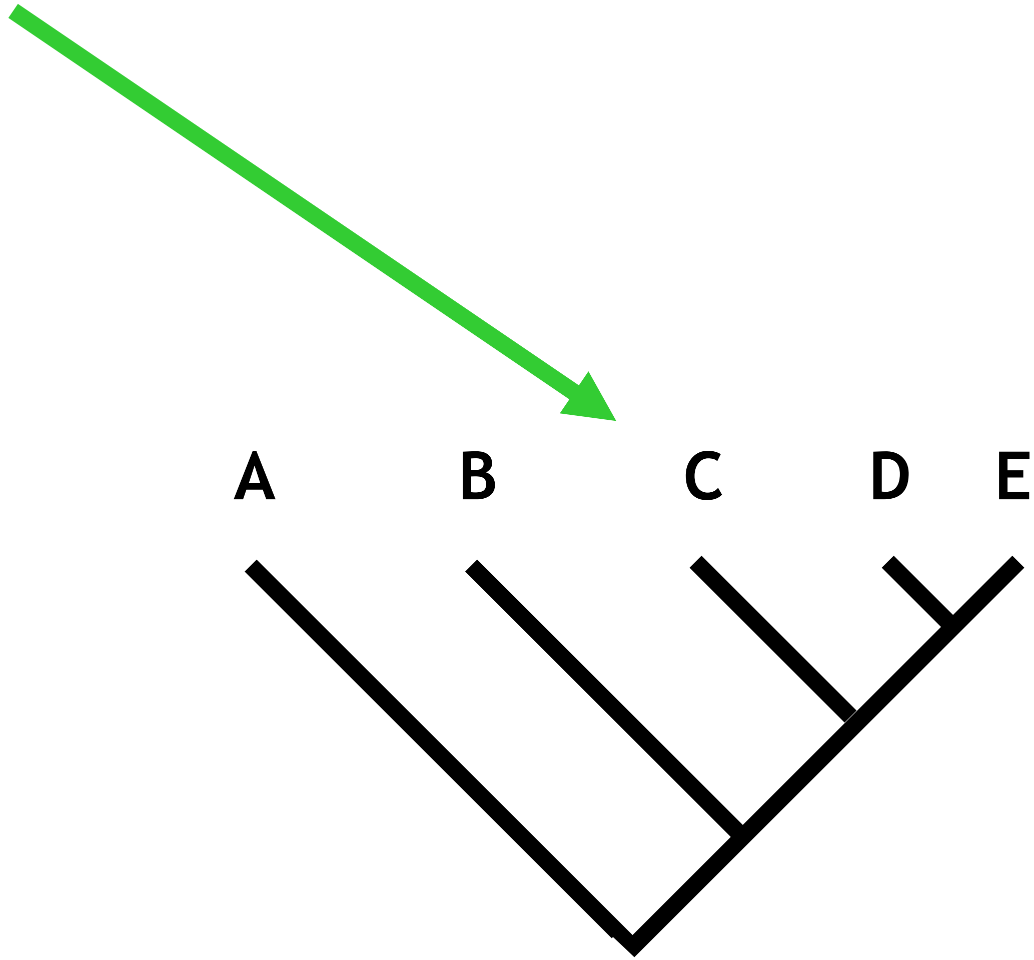


stem height

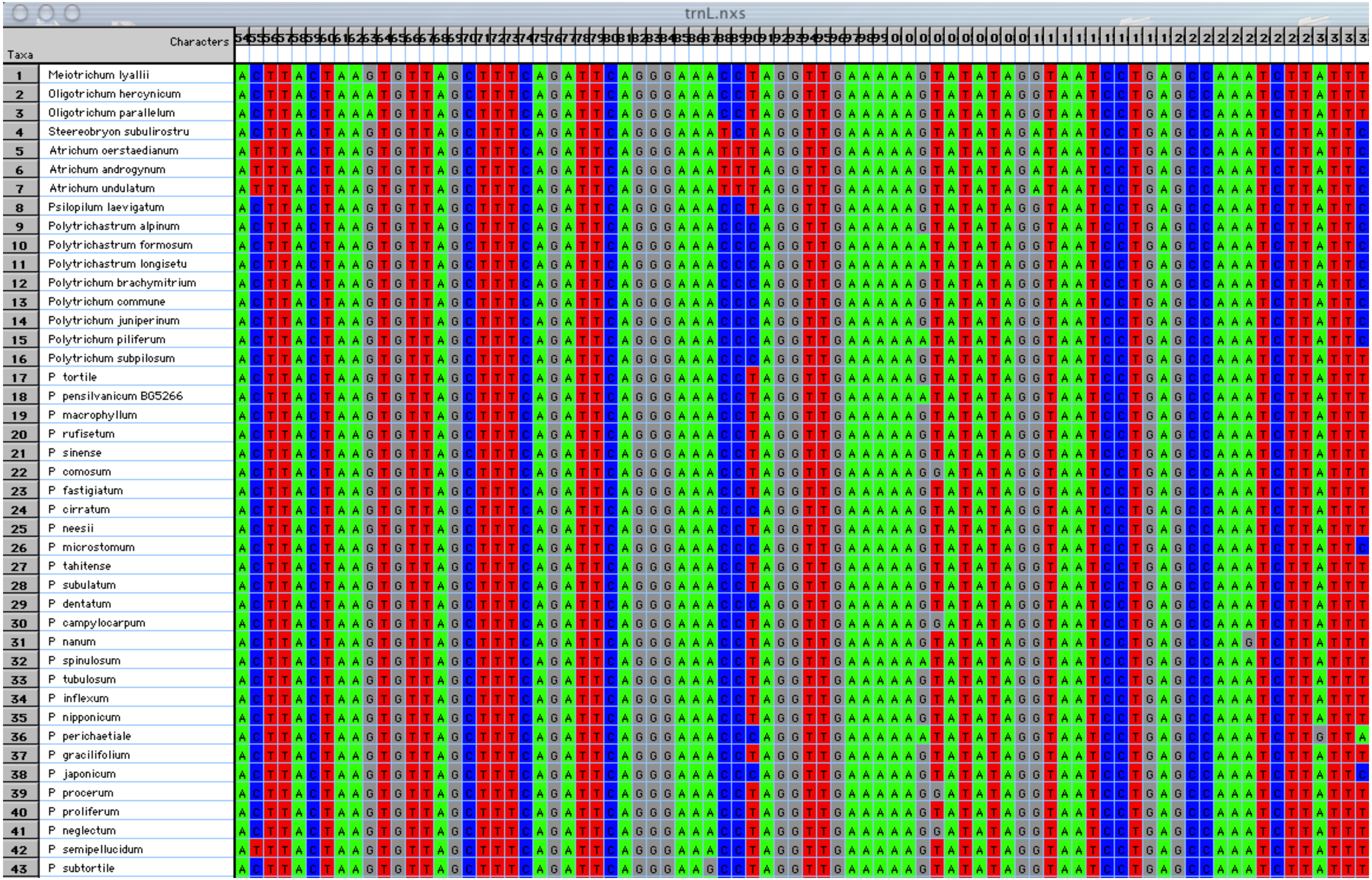
www2.hawaii.edu/~donaldp/Biostatitics/


B
D
C
A
E

	0	0	0	0	0	0	0	0	0	1
	1	2	3	4	5	6	7	8	9	0
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



terminals \ characters	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
A	1	0	0	0	0	1	0	0	0	0
B	1	0	1	1	1	1	1	1	1	1
C	0	1	1	0	0	1	1	1	1	0
D	1	0	0	0	0	1	1	0	0	0
E	1	0	1	0	1	1	1	1	1	0


trnL.nxs
Characters
Taxa
1 Meiotrichum lyallii
2 Oligotrichum hercynicum
3 Oligotrichum parallelum
4 Steereobryon subulirostru
5 Atrichum oerstaedianum
6 Atrichum androgynum
7 Atrichum undulatum
8 Psilopilum laevigatum
9 Polytrichastrum alpinum
10 Polytrichastrum formosum
11 Polytrichastrum longisetu
12 Polytrichum brachymitrium
13 Polytrichum commune
14 Polytrichum juniperinum
15 Polytrichum piliferum
16 Polytrichum subpilosum
17 P tortile
18 P pensilvanicum BG5266
19 P macrophyllum
20 P rufisetum
21 P sinense
22 P comosum
23 P fastigiatum
24 P cirratum
25 P neesii
26 P microstomum
27 P tahitense
28 P subulatum
29 P dentatum
30 P campylocarpum
31 P nanum
32 P spinulosum
33 P tubulosum
34 P inflexum
35 P nipponicum
36 P perichaetiale
37 P gracilifolium
38 P japonicum
39 P procerum
40 P proliferum
41 P neglectum
42 P semipellucidum
43 P subtortile

observations about compared organisms

↓

interpretation

↓

coding as characters and their states

TAXONOMIC CHARACTERS

= potentially useful for phylogenetic analysis

COMPARATIVE STUDY OF CHARACTERS

TAXONOMIC CHARACTERS

transformation series, character
character, character state

Wiley´s 3 conditions for characters to be useful in cladistic analysis:

1. variation between compared terminals

2. observed variation shows regularity

3. variation controlled genetically, not induced by environment

from the level of single nucleotides to macromorphology

ALL assumedly homologous characters that show **VARIATION** between terminals are POTENTIALLY useful for infering phylogeny

TAXONOMIC CHARACTERS

we can use for example the following when trying to find potential homologies:

1. topology (position)
2. external similarity
3. “continuum” between character states

TAXONOMIC CHARACTERS

1. PRELIMINARY hypothesis about homology

   observed similarities between compared terminals are interpreted as homologies (**NULL** hypothesis)

2. distinguish character STATES
3. with cladistic analysis we "test" these preliminary hypotheses against those made for other characters-->

TAXONOMIC CHARACTERS

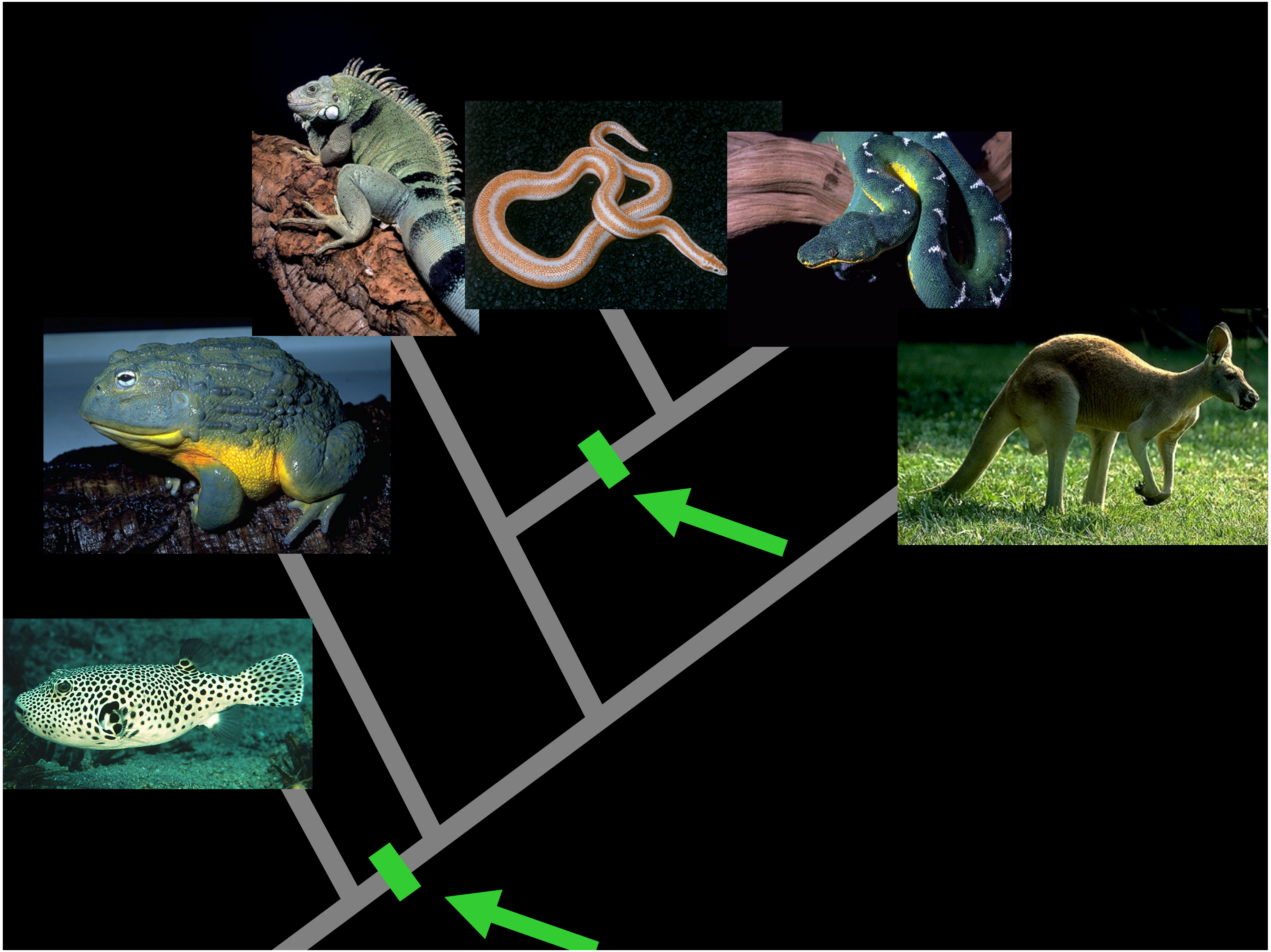
hypothesis about homology either **accepted** or **rejected**

HOMOLOGY = shared feature inherited from common ancestor

ALL SYNAPOMORPHIES are homologies

all homologies ARE NOT synapomorphies

ATTENTION! level of observation



TAXONOMIC CHARACTERS

binary characters (only 2 character states)
coded 0 & 1

teeth by lf margins : present (0), absent (1)

in many characters numerous character states can be
distinguished , coded 0, 1, 2, 3, 4, etc.

A C G T

petal color: white (0), yellow (1), orange (2)
red (3), blue (4)

TAXONOMIC CHARACTERS

transformation series, character
character, character state

Wiley´s 3 conditions for characters to be useful in cladistic analysis:

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from the level of single nucleotides to macromorphology

ALL assumedly homologous characters that show VARIATION between terminals are POTENTIALLY useful for infering phylogeny

TAXONOMIC CHARACTERS

continuous characters & landmark data

QUANTITATIVE characters, ch. state distinction impossible/problematic

VARIATION still observed between terminals

numerous case studies have shown that also these kind of characters DO include valuable phylogenetic information

most advanced applications allow use of these characters directly & together with other kind of characters

e.g. with program TNT

Catalano, S.A. & al. 2010. Phylogenetic morphometrics (1): the use of landmark data in a phylogenetic framework. Cladistics 26: 539-549.

$$\mathrm{Min}\ (D_{AP} + D_{BP} + D_{CP}$$

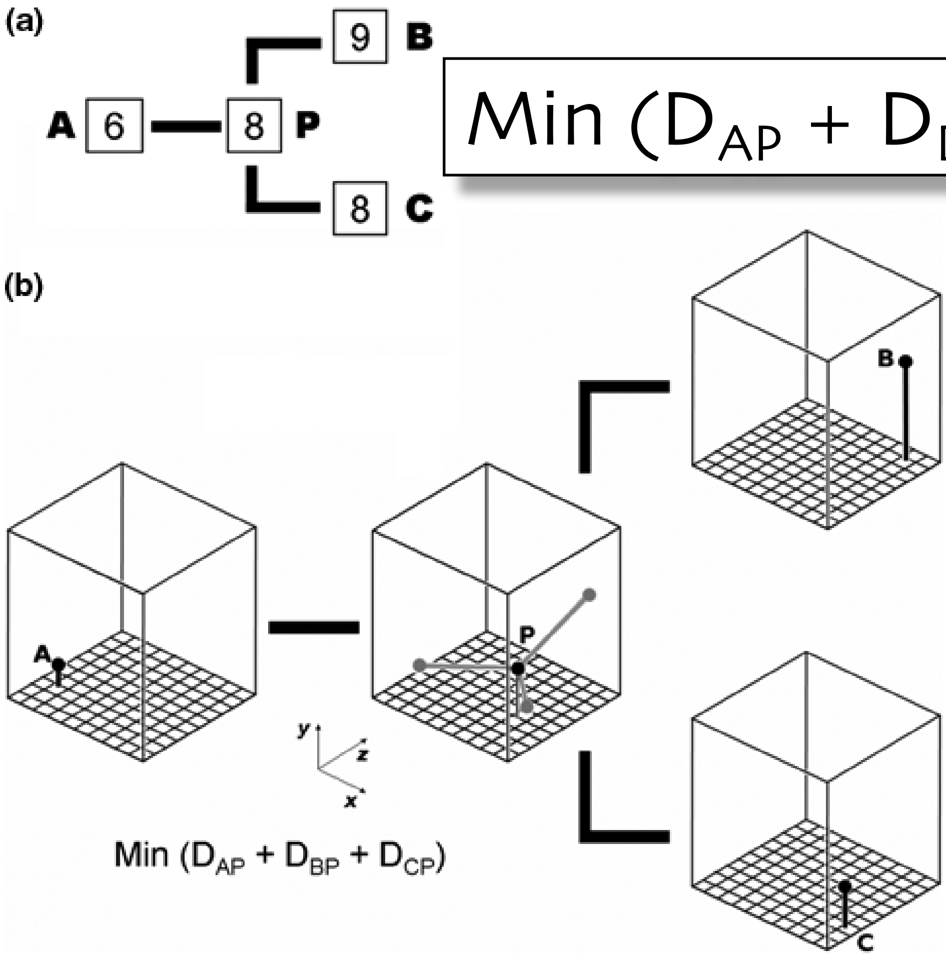
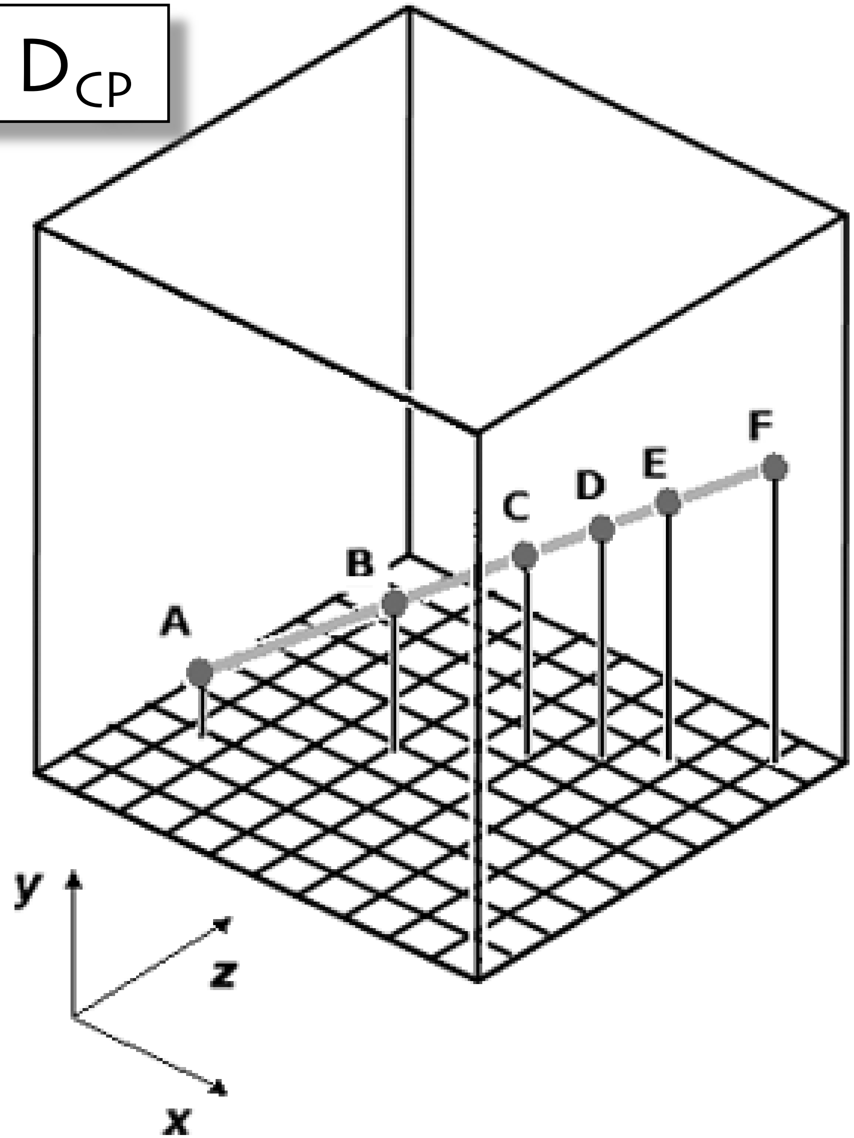
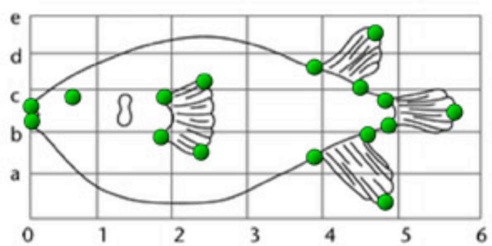
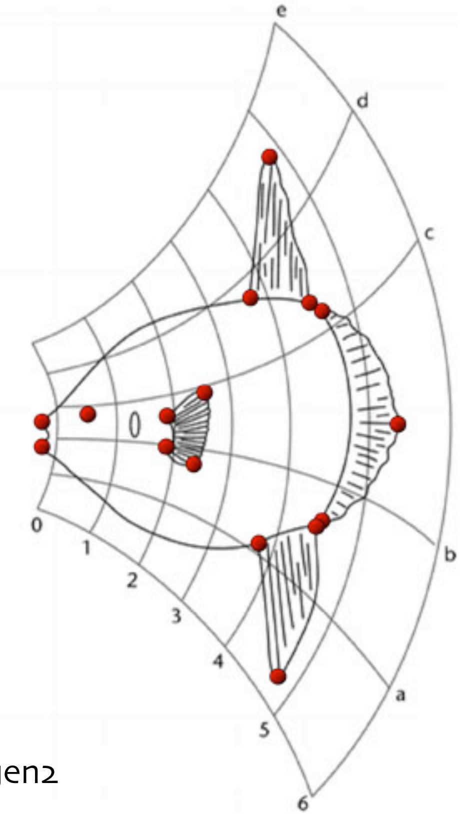


Fig. 1. Comparison between (a) Farris optimization and (b) 3D landmark optimization. In Farris optimization, the sum of the numerical differences between states is minimized. In landmark optimization, the distances between landmark positions are minimized.

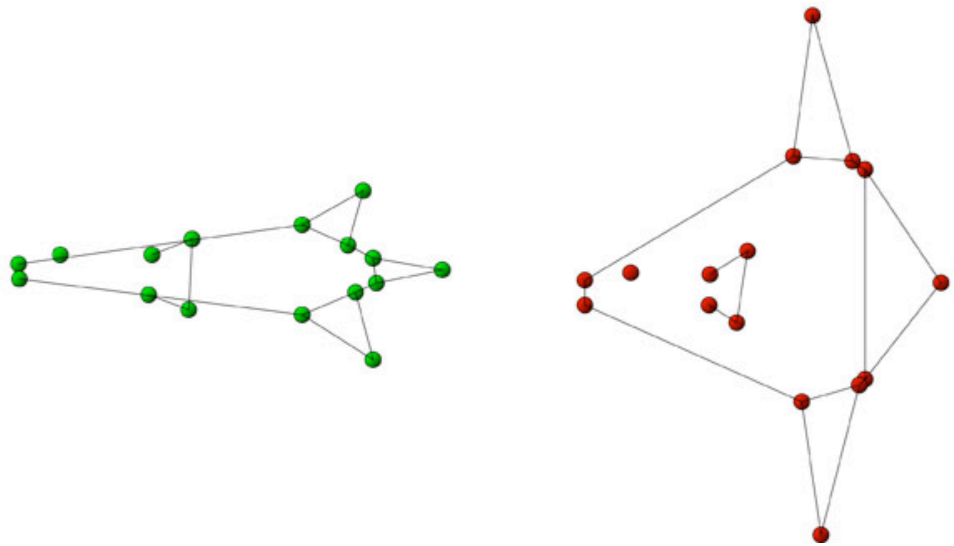


Diodon *Orthagoriscus*

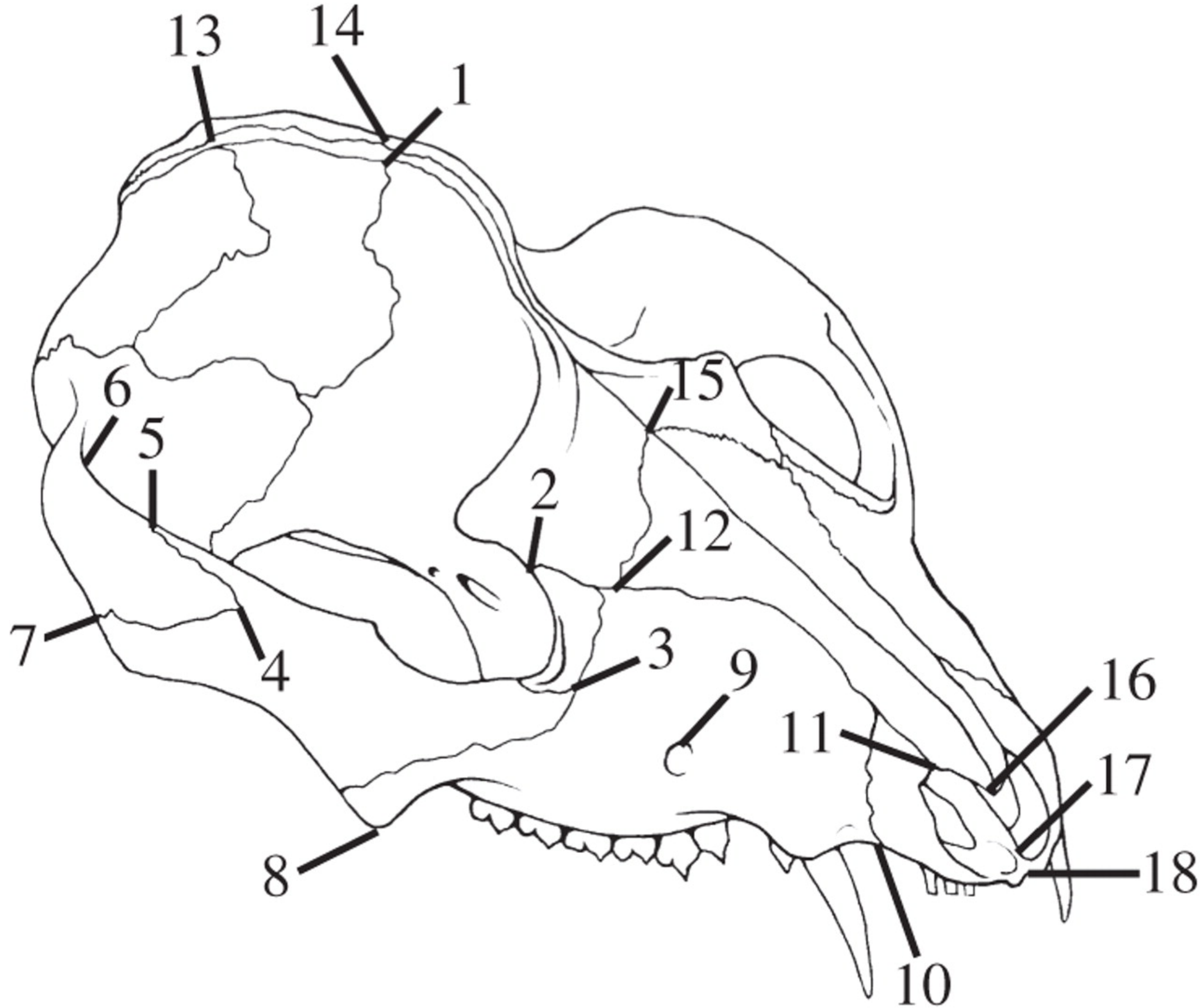




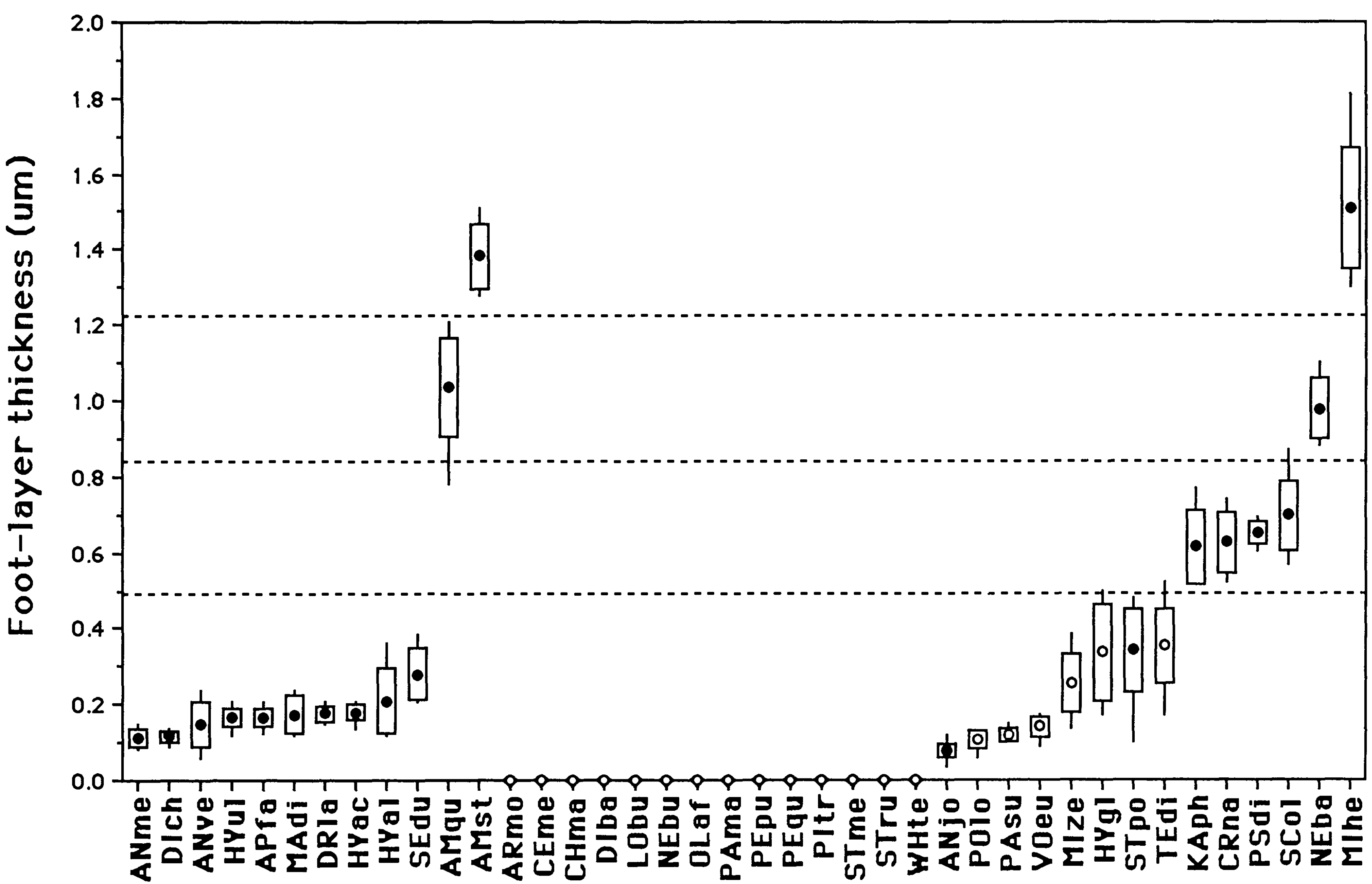
http://cdn.palass.org/palaeomath_101/moribund/images/eigen2
/Fig2.jpg



Goswami, A. & al. 2011. Biting through constraints: cranial morphology, disparity and convergence across living and fossil carnivorous mammals. *Proceedings of the Royal Society, B Biological Sciences 27*8: 1831-1839.



Levin, G.A. & Simpson, M.G. 1994. Phylogenetic implications of pollen ultrastructure in the Oldfieldioideae (Euphorbiaceae). *Annals of the Missouri Botanical Garden* 81: 203-238.



WILEY-BLACKWELL

Cladistics

Cladistics 26 (2010) 539–549

10.1111/j.1096-0031.2010.00302.x

Phylogenetic morphometrics (I): the use of landmark data in a phylogenetic framework

Santiago A. Catalano[a,b,*], Pablo A. Goloboff[a,c] and Norberto P. Giannini[a,d]

Goloboff, P. & al. 2006. Continuous characters analyzed as such. *Cladistics* 22: 589-601.

k/(m+k); k = constant, m = min. number of steps between ch. states

Ch. A binary

B 8 states

3/(2+3) = 0,6

3/(8+3) = 0,27

WILEY-BLACKWELL

Cladi

10.1111/cla.12160

TNT version 1.5, including a fu… genetic morphometrics

Pablo A. Goloboff[a,*] and Santiago A. Catalano[a,b]

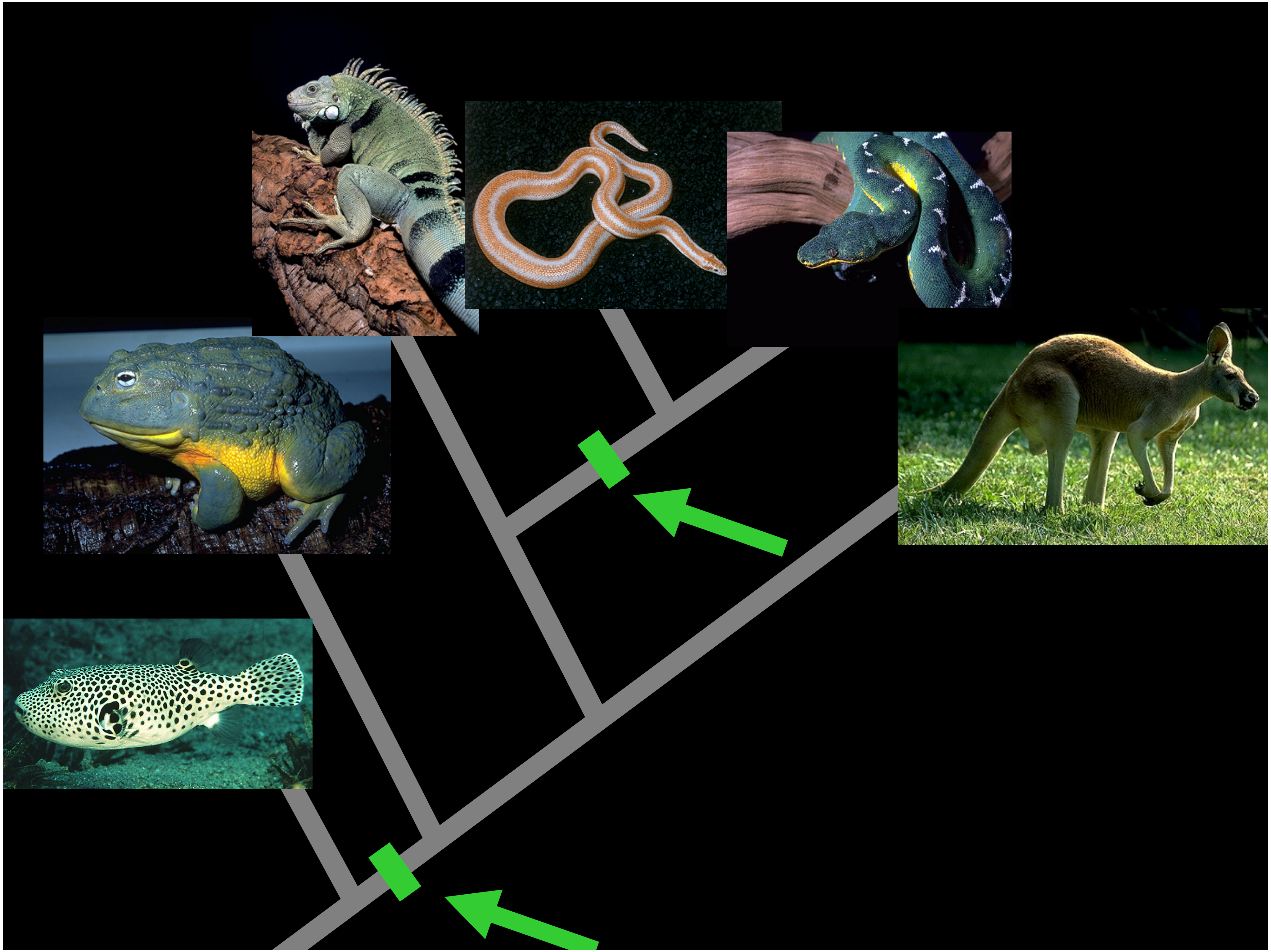
[a]*Unidad Ejecutora Lillo, Consejo Nacional de Investigaciones Científicas y Técnicas, Miguel Lillo 251, 4000 S.M. de Tucumán, Argentina;* [b]*Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Miguel Lillo 205, 4000 S.M. de Tucumán, Argentina*

Accepted 29 February 2016

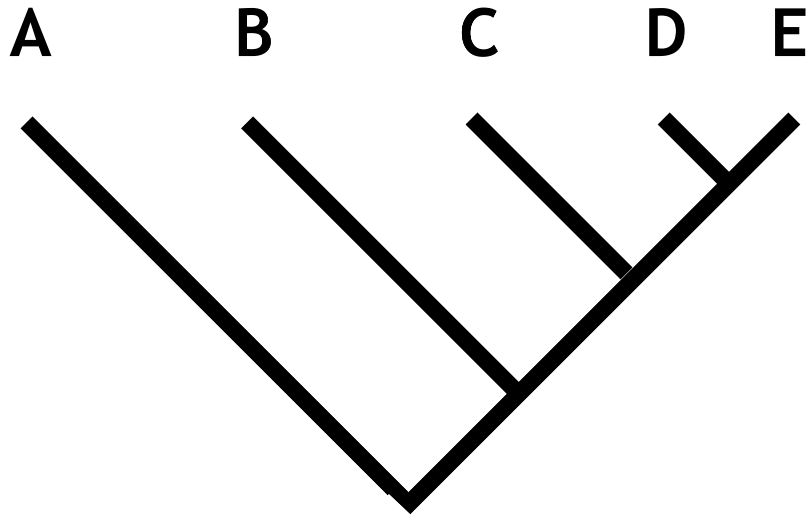
TAXONOMIC CHARACTERS

also LACK of some structure might provide useful information

reduction, neoteny



	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



TAXONOMIC CHARACTERS

characters ------> matrix <------- cladistic analysis

much homoplasy, suspicious -----> return to study & evaluation of characters

reciprocal illumination

SUPERFICIALLY TWO THINGS ARE SAME BUT PROVE TO BE DIFFERENT WITH DETAILED STUDY

TAXONOMIC CHARACTERS

characters used in phylogenetic analyses are assumed to be independent of other characters

NO genetic correlation

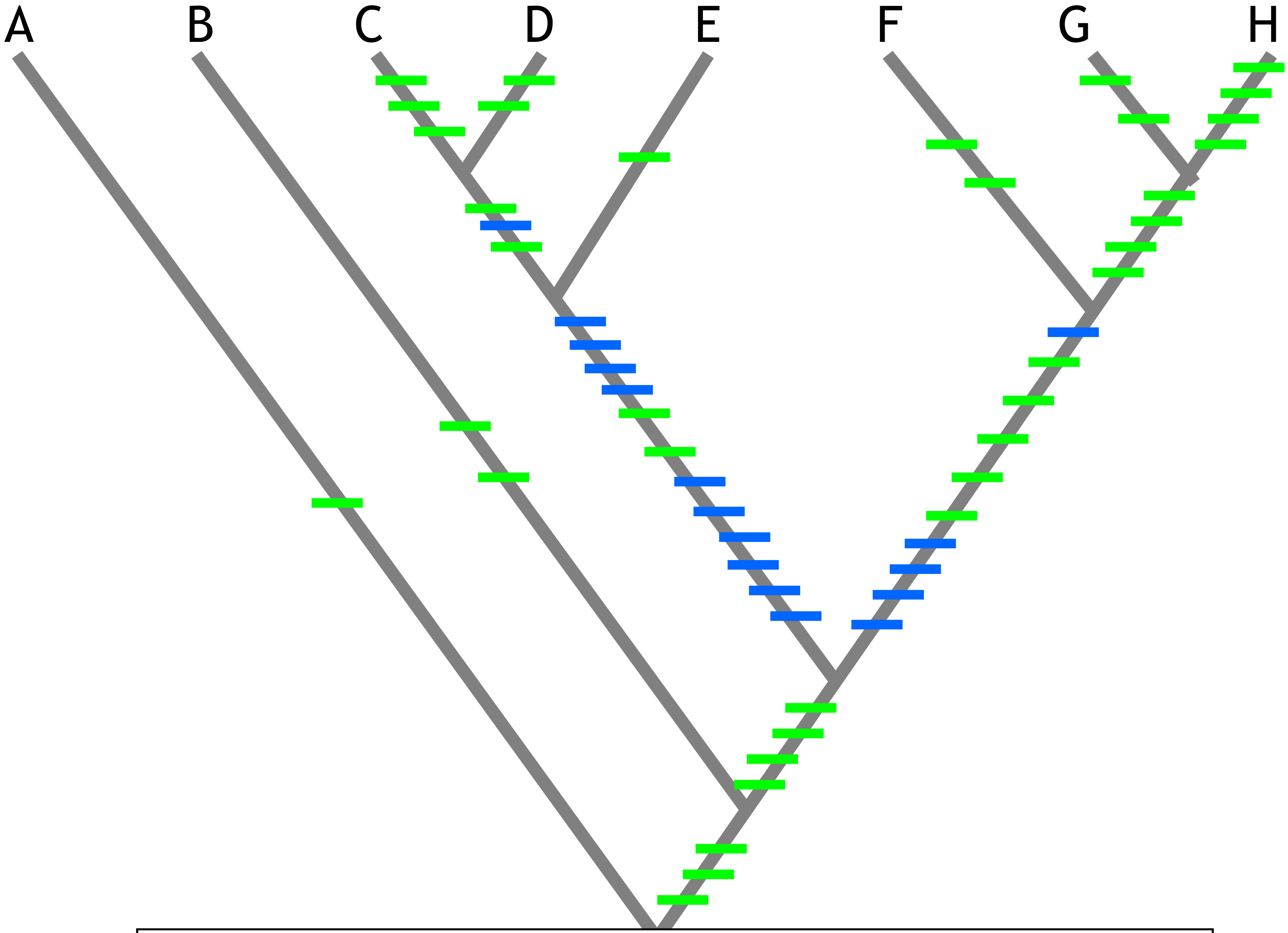
ALL these considered to be equally valuable =
potentially useful for phylogenetic analyses

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

identical distribution
of character states

characters 2-6
from the same part of organism

genetic correlation?



phylogenetic correlation = character congruence

TAXONOMIC CHARACTERS & their states

1. order

2. direction

3. weight

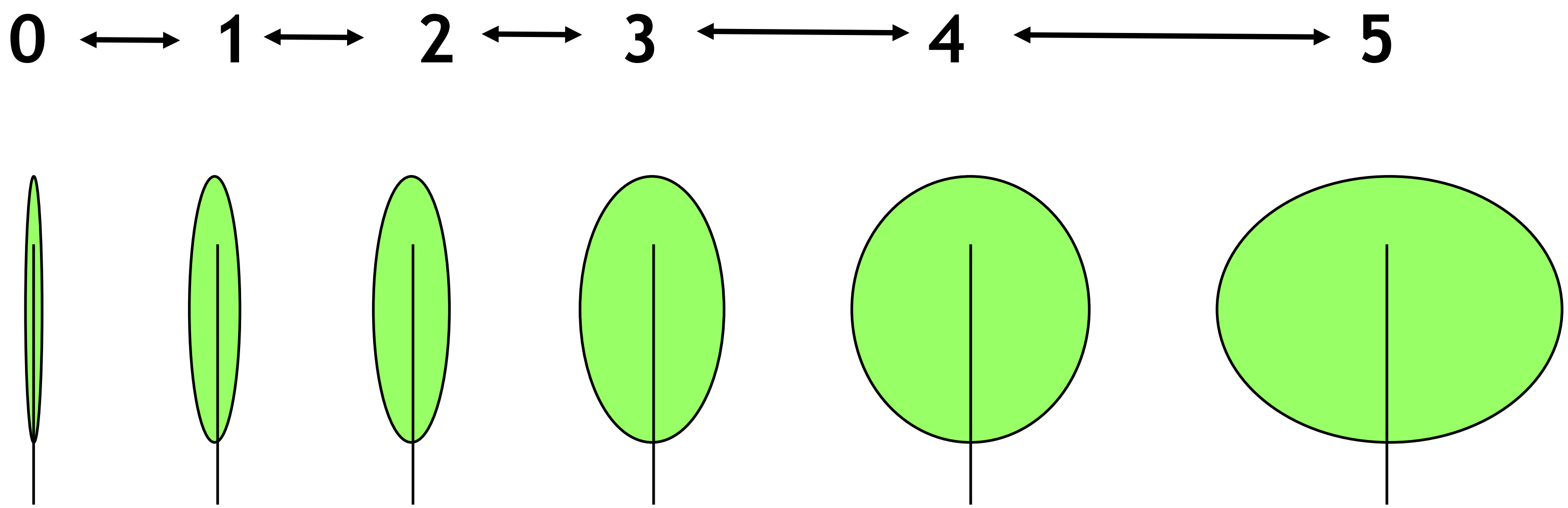
TAXONOMIC CHARACTERS & their states

1. order

"If you have obvious order in your character states, do not ignore this information"

Slowinski, J. B. 1993. "Unordered" versus "ordered" characters.
Systematic Biology 42: 155-165.

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



0 ---> 1 ≠ 0 ---> 5 ?

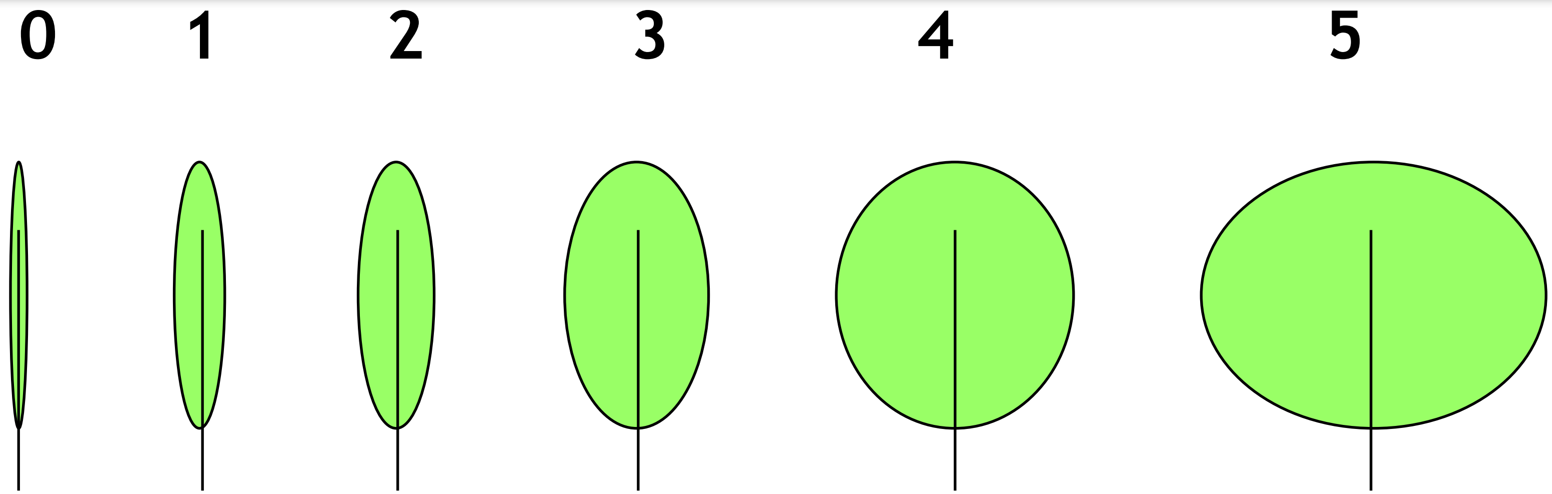
ordered/additive characters

Wagner (Farris) parsimony

0 ---> 1 = 1 evolutionary change

0 ---> 5 = 5 evolutionary changes

Fitch, W. M. 1971. Toward defining the course of evolution: minimum change for a specific tree topology. *Systematic Zoology* 20: 406-416.



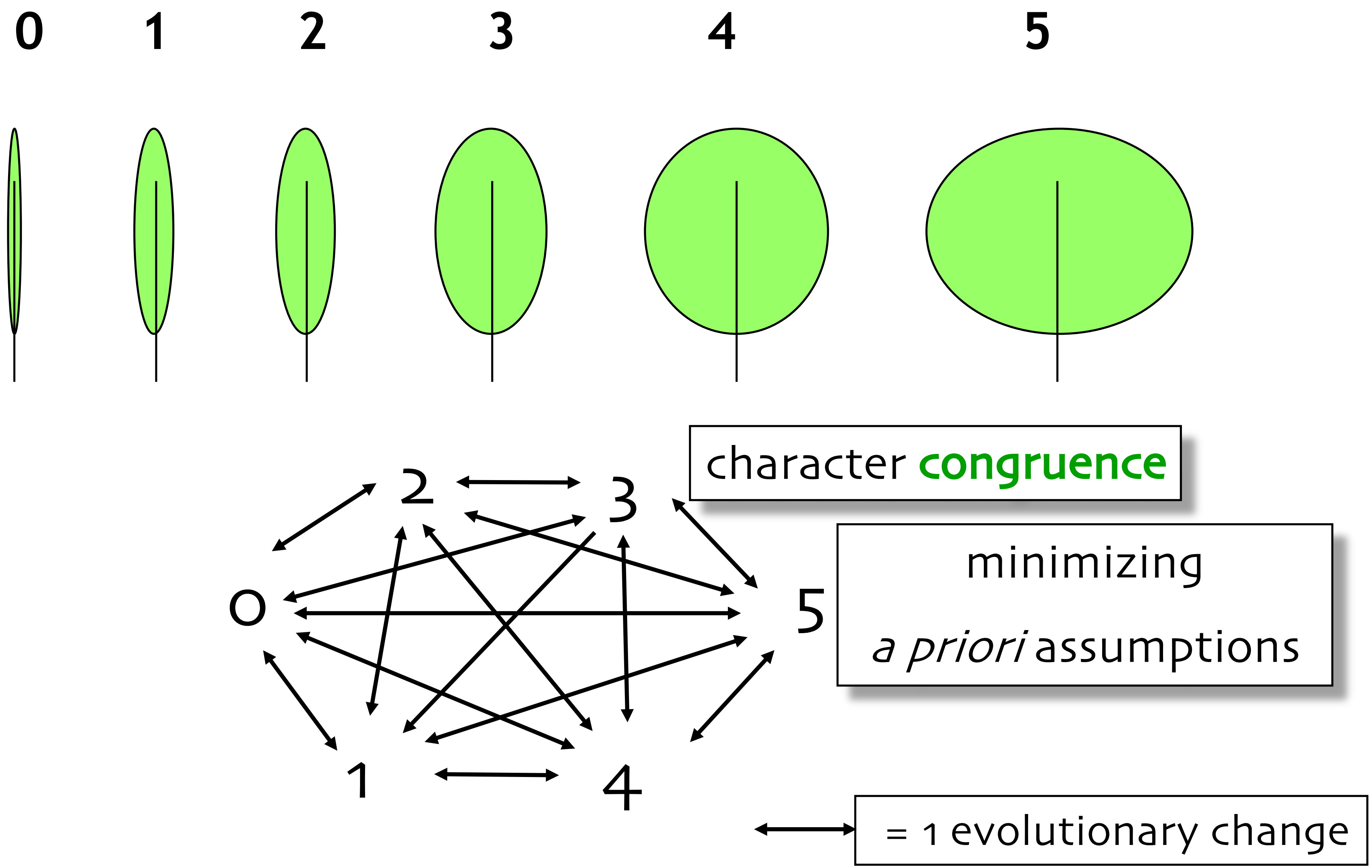
0 ---> 1 = 0 ---> 5

unordered/non-additive characters

Fitch parsimony

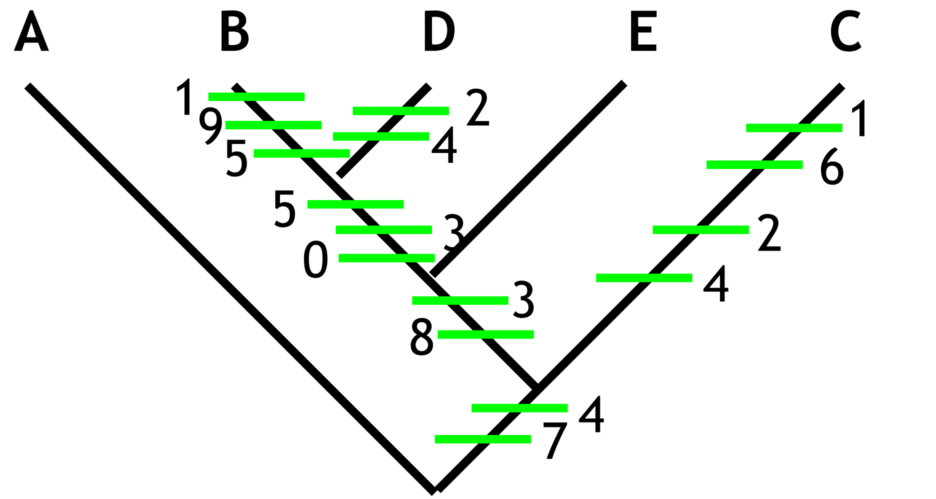
0 ---> 1 = 1 evolutionary change

0 ---> 5 = 1 evolutionary change

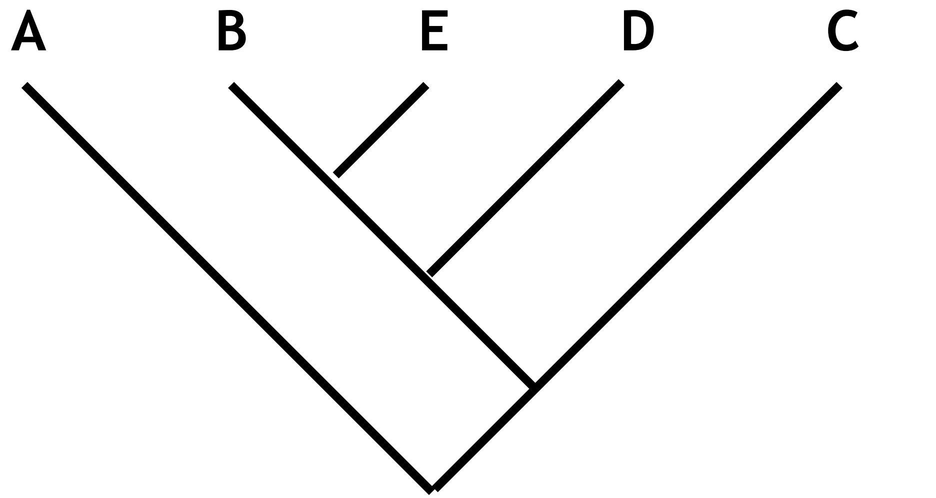


0
1
2
3
4
5
character congruence
minimizing
a priori assumptions
= 1 evolutionary change

	0	1	2	3	4	5	6	7	8	9
A	1	1	2	1	2	2	1	1	0	1
B	0	0	2	2	1	0	1	0	1	0
C	1	0	1	1	0	2	0	0	0	1
D	0	1	0	2	0	1	1	0	1	1
E	1	1	2	0	1	2	1	0	1	1

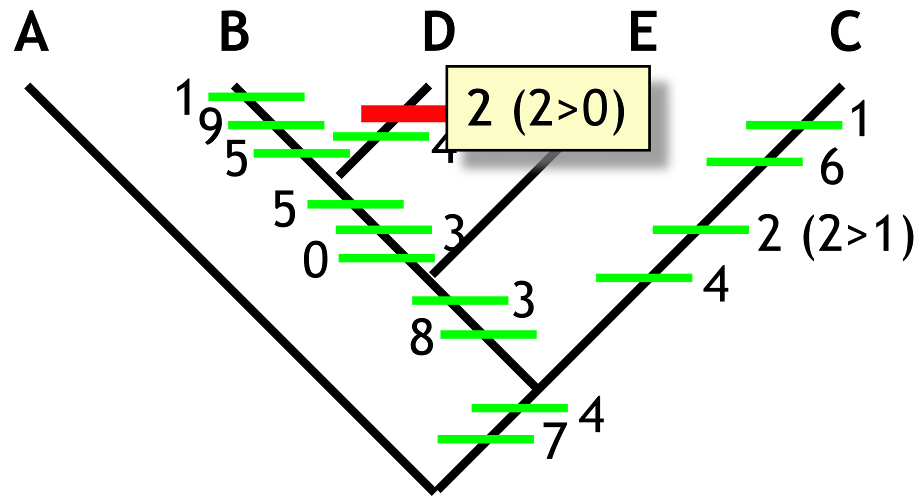


16 evolutionary changes



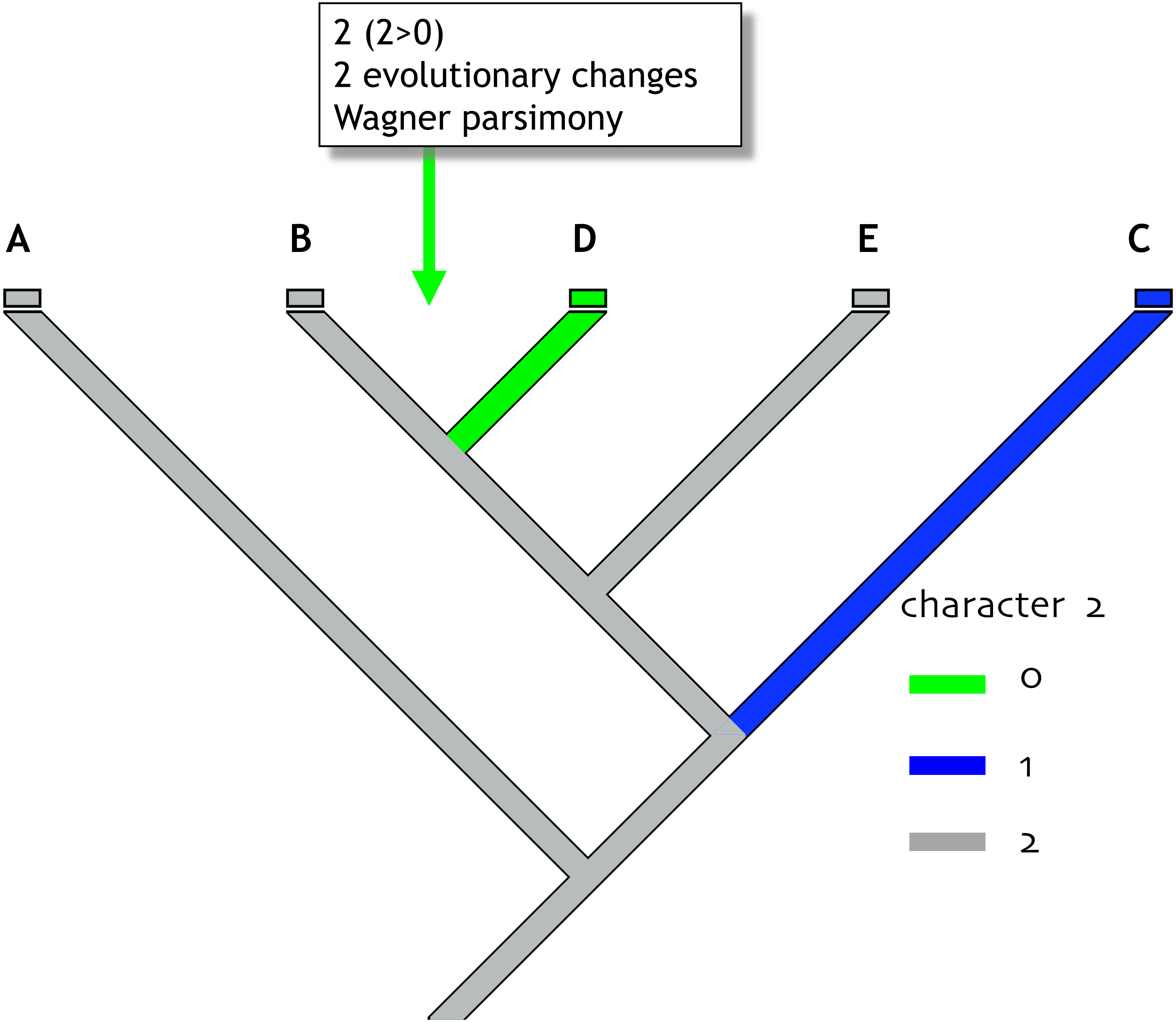
Fitch parsimony

	0	1	2	3	4	5	6	7	8	9
A	1	1	2	1	2	2	1	1	0	1
B	0	0	2	2	1	0	1	0	1	0
C	1	0	1	1	0	2	0	0	0	1
D	0	1	0	2	0	1	1	0	1	1
E	1	1	2	0	1	2	1	0	1	1

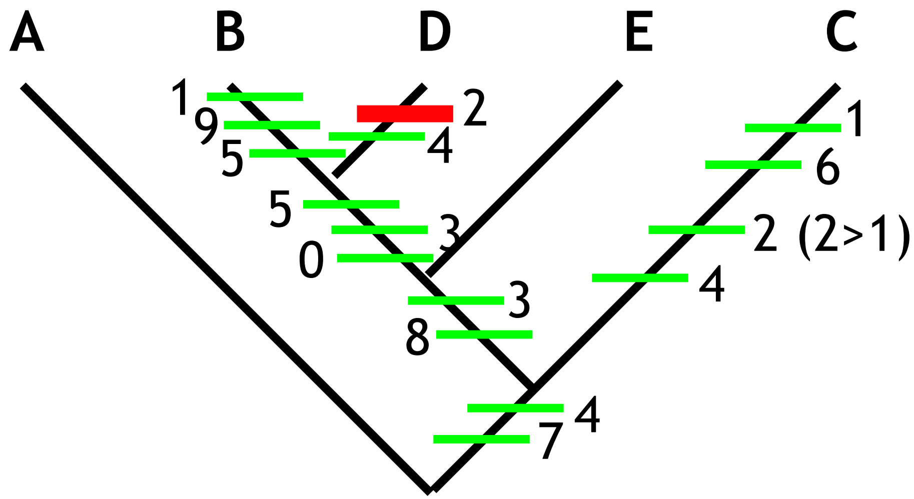


17 evolutionary changes

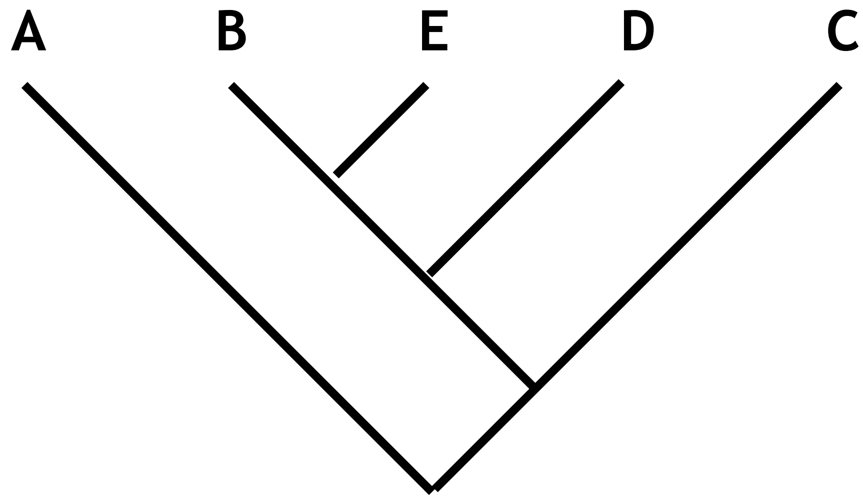
Wagner parsimony


2 (2>0)
2 evolutionary changes
Wagner parsimony
A
B
D
E
C
character 2
0
1
2

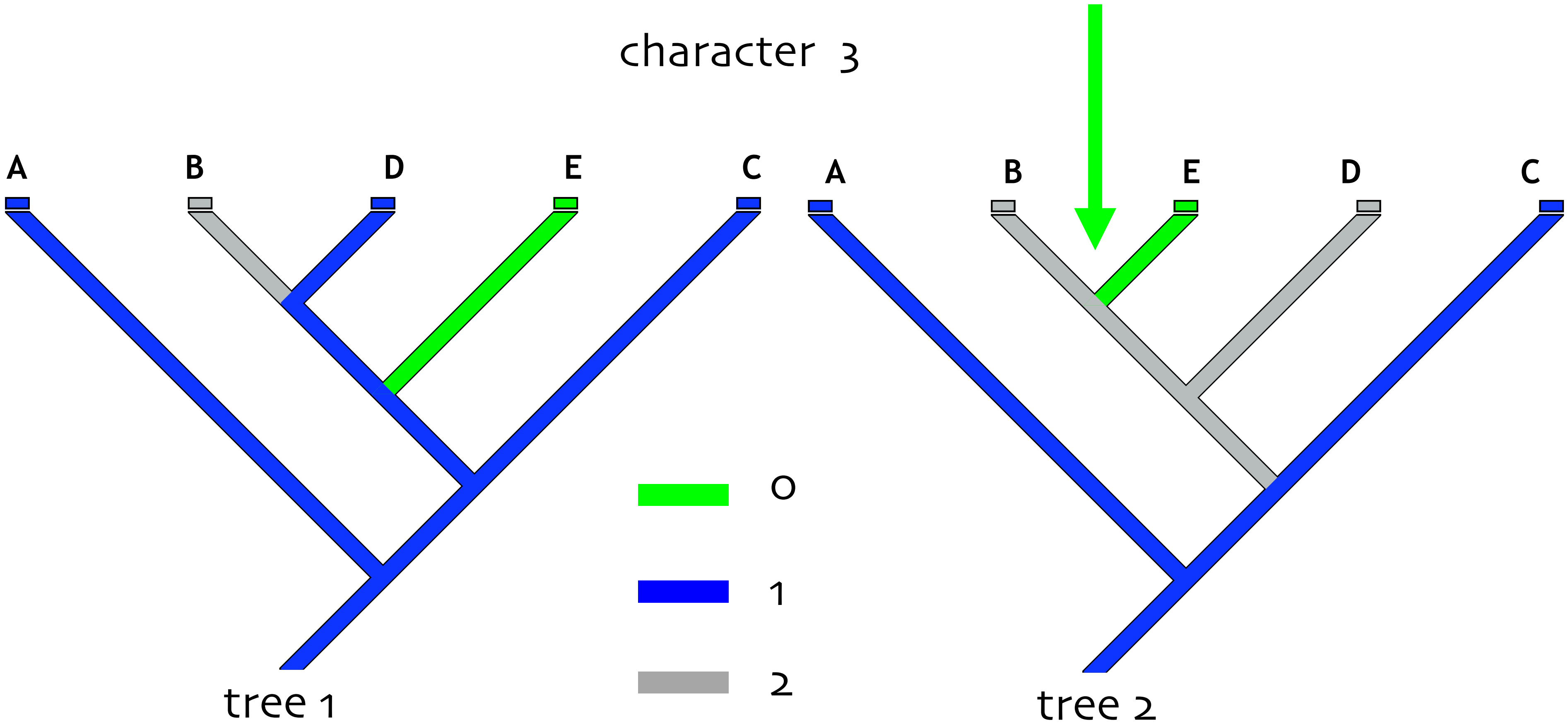
	0	1	2	3	4	5	6	7	8	9
A	1	1	2	1	2	2	1	1	0	1
B	0	0	2	2	1	0	1	0	1	0
C	1	0	1	1	0	2	0	0	0	1
D	0	1	0	2	0	1	1	0	1	1
E	1	1	2	0	1	2	1	0	1	1



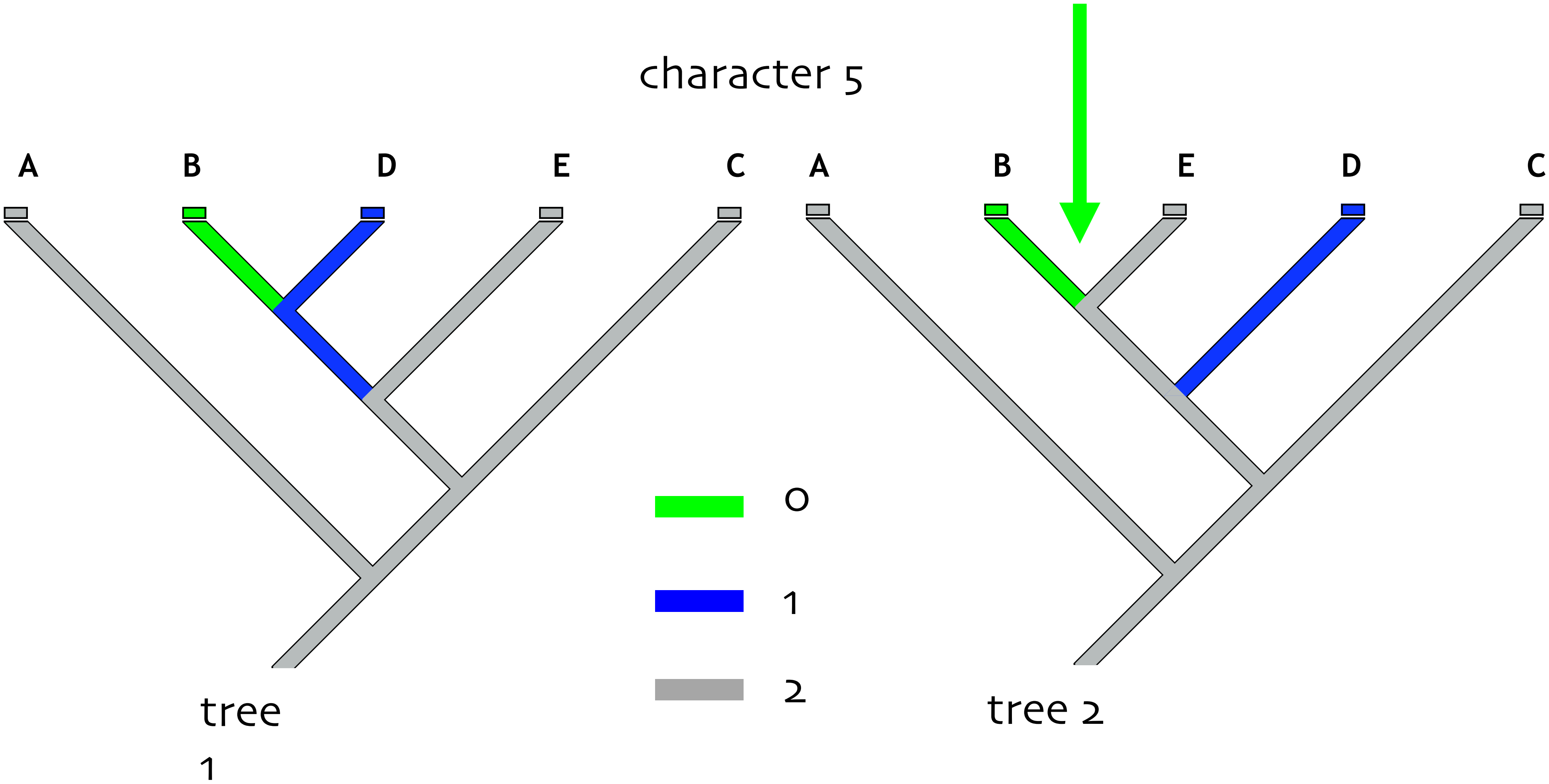
17 evolutionary changes



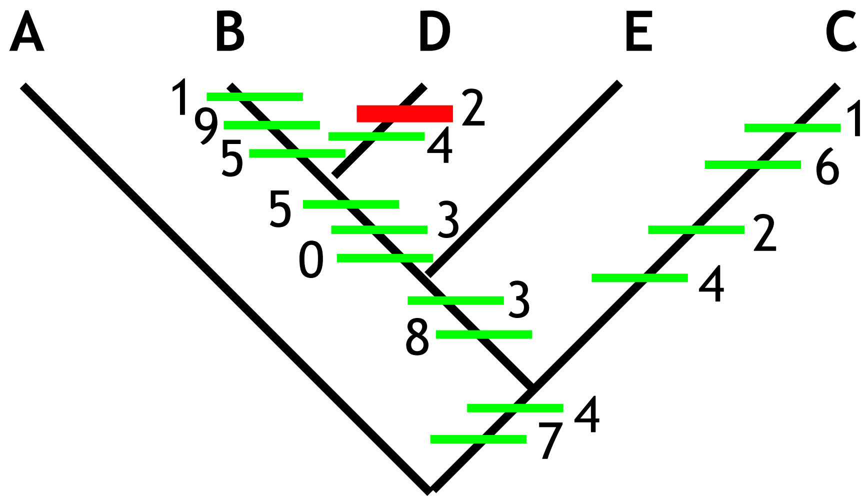
Wagner parsimony

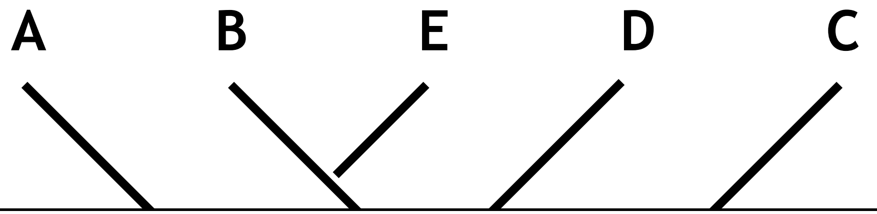


character 3
A
B
D
E
C
A
B
E
D
C
0
1
2
tree 1
tree 2


character 5
A
B
D
E
C
A
B
E
D
C
0
1
2
tree 1
tree 2

	0	1	2	3	4	5	6	7	8	9	Σ
tree 1	1	2	3	2	3	2	1	1	1	1	17
tree 2	2	2	3	3	3	3	1	1	1	1	20





Fitch/Wagner parsimony

affect obtained results

optimality criterion used has to be revealed & the basis why it has been used

Fitch/Wagner parsimony

part of the characters can be treated using Fitch, others using Wagner parsimony in the SAME analysis SIMULTANEOUSLY

TAXONOMIC CHARACTERS & their states

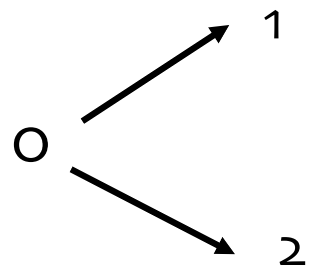
1. order

2. direction

0 --> 1 --> 2

2 --> 1 --> 0

0 --> 2 --> 1



NOT needed BEFORE analysis

the tree resulting from our analysis

will reveal direction of change

TAXONOMIC CHARACTERS & their states

1. order

2. direction

3. weight

are all characters equally important?

equally reliable signal about phylogeny?

CHARACTER WEIGHT

	1	2	3	4	5	6	7	8
OG	0	0	0	0	0	0	0	0
A	1	0	0	0	0	1	0	1
B	1	1	1	0	1	0	1	0
C	1	0	1	1	1	0	0	0
D	1	1	1	0	1	1	1	0
E	1	1	1	1	1	1	1	1

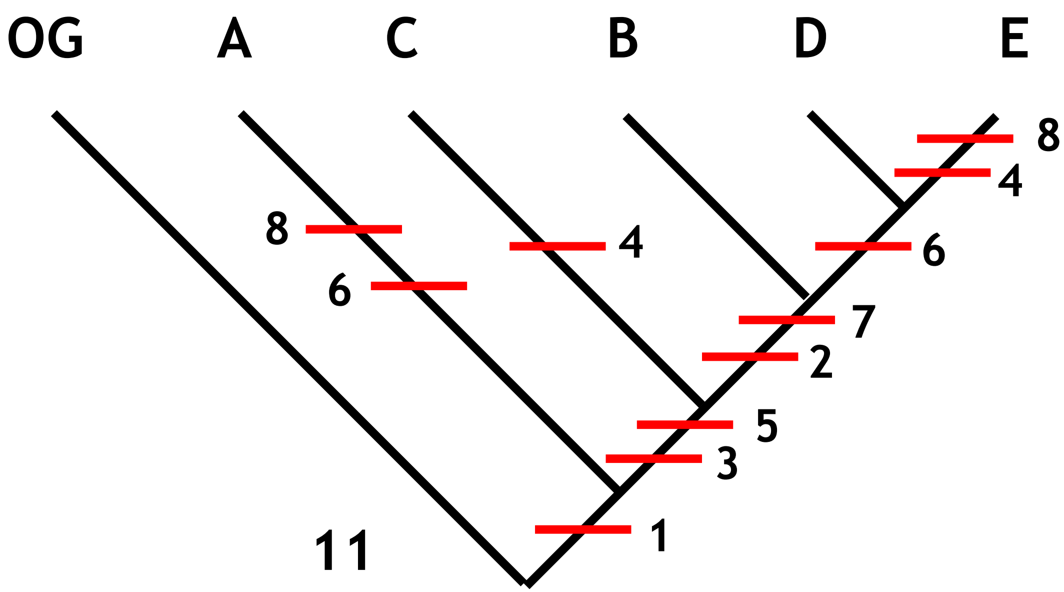
CHARACTER WEIGHT

	1	2	2a	2b	2c	2d	3	4	5	6	7	8
OG	0	0	0	0	0	0	0	0	0	0	0	0
A	1	0	0	0	0	0	0	0	0	1	0	1
B	1	1	1	1	1	1	1	0	1	0	1	0
C	1	0	0	0	0	0	1	1	1	0	0	0
D	1	1	1	1	1	1	1	0	1	1	1	0
E	1	1	1	1	1	1	1	1	1	1	1	1

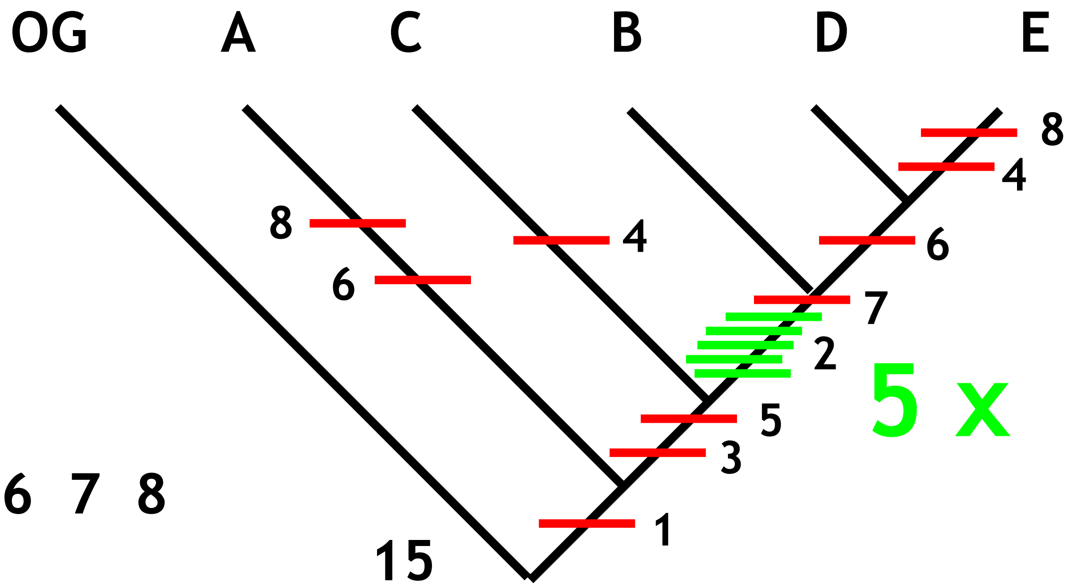
5 x

CHARACTER WEIGHT

	1	2	3	4	5	6	7	8
OG	0	0	0	0	0	0	0	0
A	1	0	0	0	0	1	0	1
B	1	1	1	0	1	0	1	0
C	1	0	1	1	1	0	0	0
D	1	1	1	0	1	1	1	0
E	1	1	1	1	1	1	1	1

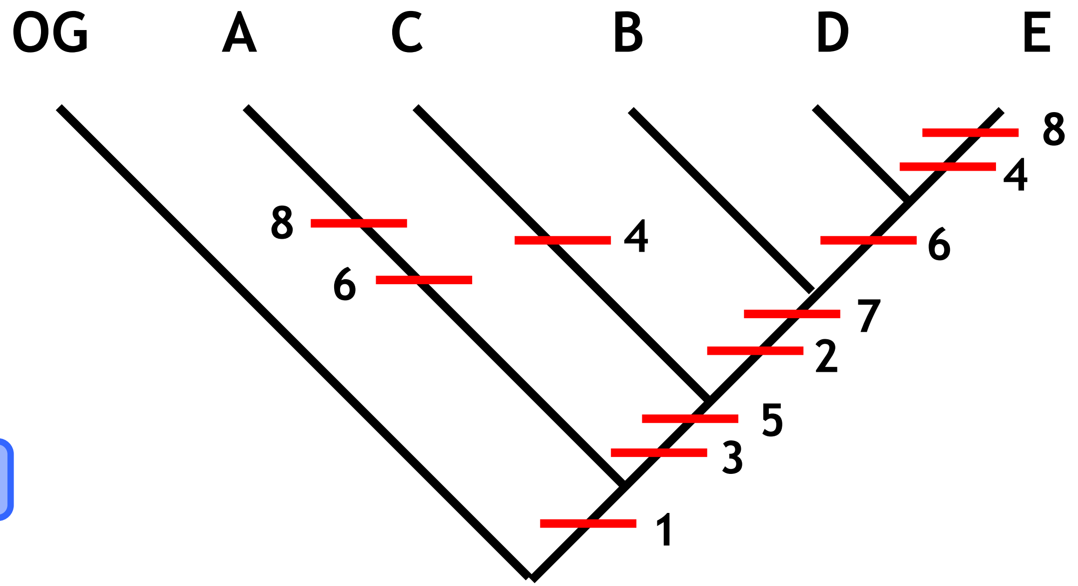


CHARACTER WEIGHT

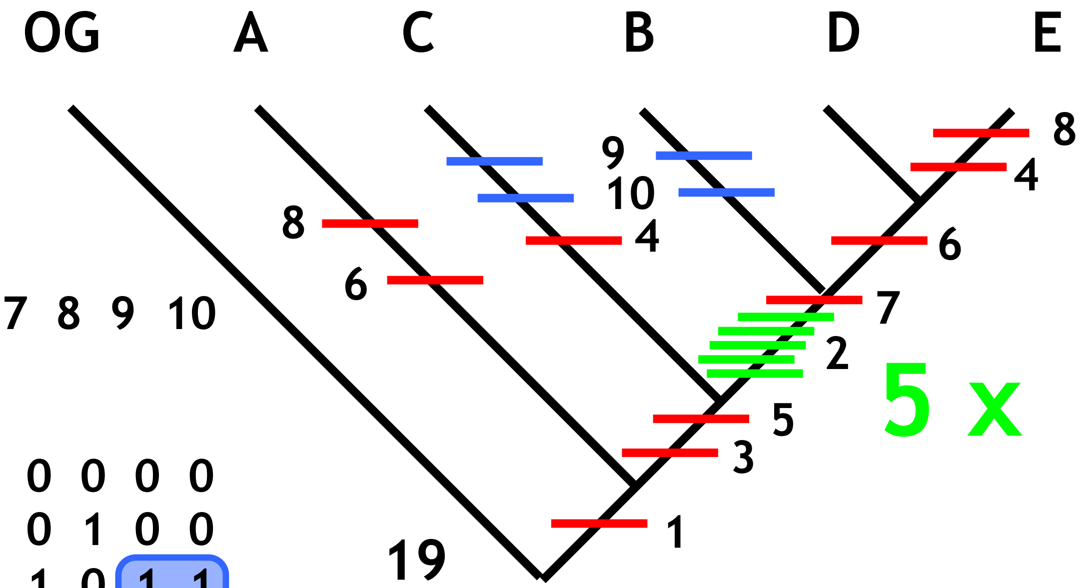


	1	2	2a	2b	2c	2d	3	4	5	6	7	8
OG	0	0	0	0	0	0	0	0	0	0	0	0
A	1	0	0	0	0	0	0	0	0	1	0	1
B	1	1	1	1	1	1	1	0	1	0	1	0
C	1	0	0	0	0	0	1	1	1	0	0	0
D	1	1	1	1	1	1	1	0	1	1	1	0
E	1	1	1	1	1	1	1	1	1	1	1	1

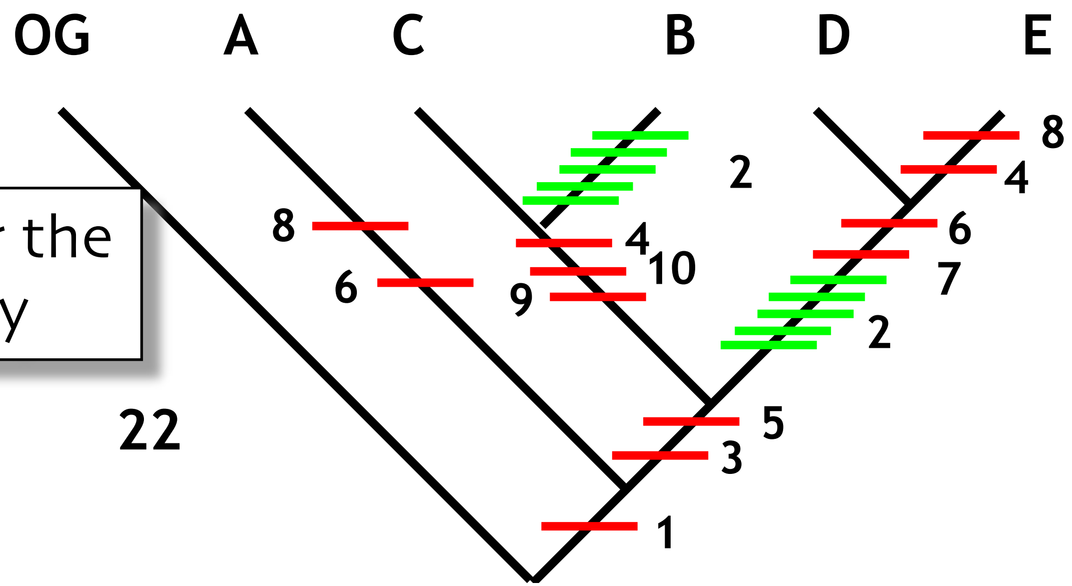
CHARACTER WEIGHT



	1	2	3	4	5	6	7	8	9	10
OG	0	0	0	0	0	0	0	0	0	0
A	1	0	0	0	0	1	0	1	0	0
B	1	1	1	0	1	0	1	0	1	1
C	1	0	1	1	1	0	0	0	1	1
D	1	1	1	0	1	1	1	0	0	0
E	1	1	1	1	1	1	1	1	0	0



	1	2	2a	2b	2c	2d	3	4	5	6	7	8	9	10
OG	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A	1	0	0	0	0	0	0	0	0	1	0	1	0	0
B	1	1	1	1	1	1	1	0	1	0	1	0	1	1
C	1	0	0	0	0	0	1	1	1	0	0	0	1	1
D	1	1	1	1	1	1	1	0	1	1	1	0	0	0
E	1	1	1	1	1	1	1	1	1	1	1	1	0	0



character weighting MAY alter the result, sometimes very radically

CHARACTER WEIGHT

1. order

2. direction

3. weight

should characters be weighted?

what is the basis for weighting?

CHARACTER WEIGHT

A PRIORI

PRESUMED that some of the characters are more "reliable"

a priori **assumptions** added to the analysis

are these ADDITIONAL assumptions warranted & realistic?

Neff, N.A. 1986. A rational basis for a priori character weighting. *Systematic Zoology* 35:110-123.

DESCENT WITH MODIFICATION

CHARACTER WEIGHT

A POSTERIORI

characters that show ***less homoplasy*** are given more weight

these characters show better FIT with all other characters

CHARACTER CONGRUENCE

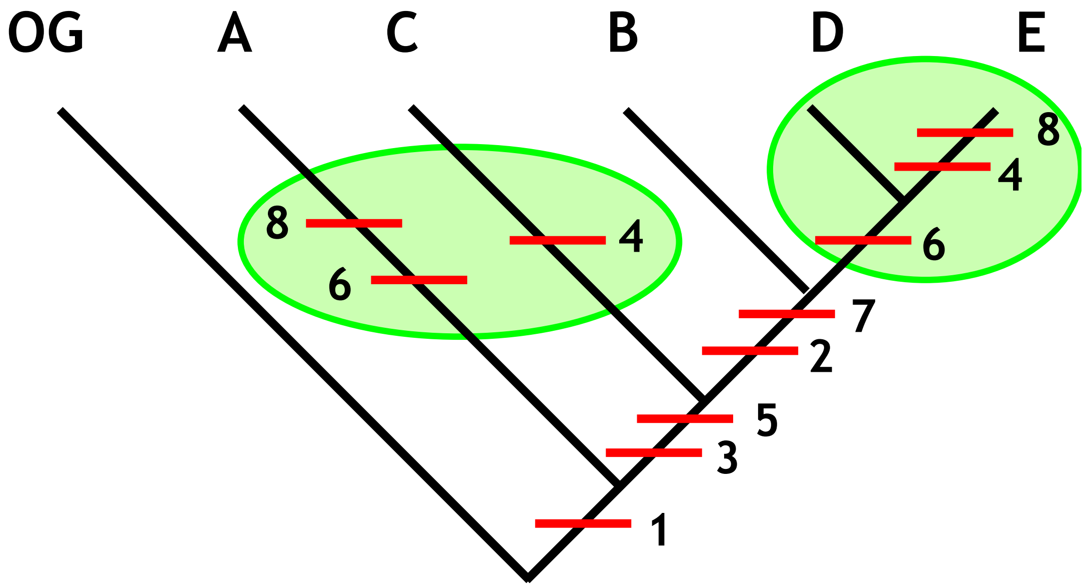
INDICES DESCRIBING CHARACTERS

consistency index, c

retention index, r

rescaled consistency index, rc

	1	2	3	4	5	6	7	8
OG	0	0	0	0	0	0	0	0
A	1	0	0	0	0	1	0	1
B	1	1	1	0	1	0	1	0
C	1	0	1	1	1	0	0	0
D	1	1	1	0	1	1	1	0
E	1	1	1	1	1	1	1	1
m	1	1	1	1	1	1	1	1
s	1	1	1	2	1	2	1	2



$$c = \frac{m}{s} = \frac{1}{2}$$

INDICES DESCRIBING CHARACTERS

consistency index , c

$c = m/s$

m = minimum number of character state changes

s = number of ch. state changes on the tree evaluated

ATTENTION! $m = n-1$ (n number of character states)

LOW value of c indicates POOR fit of character on a tree

ATTENTION! it might be HIGHLY informative to calculate index also LOCALLY, i.e. for certain clades

INDICES DESCRIBING CHARACTERS

retention index, r ri

$$r = (g-s)/(g-m)$$

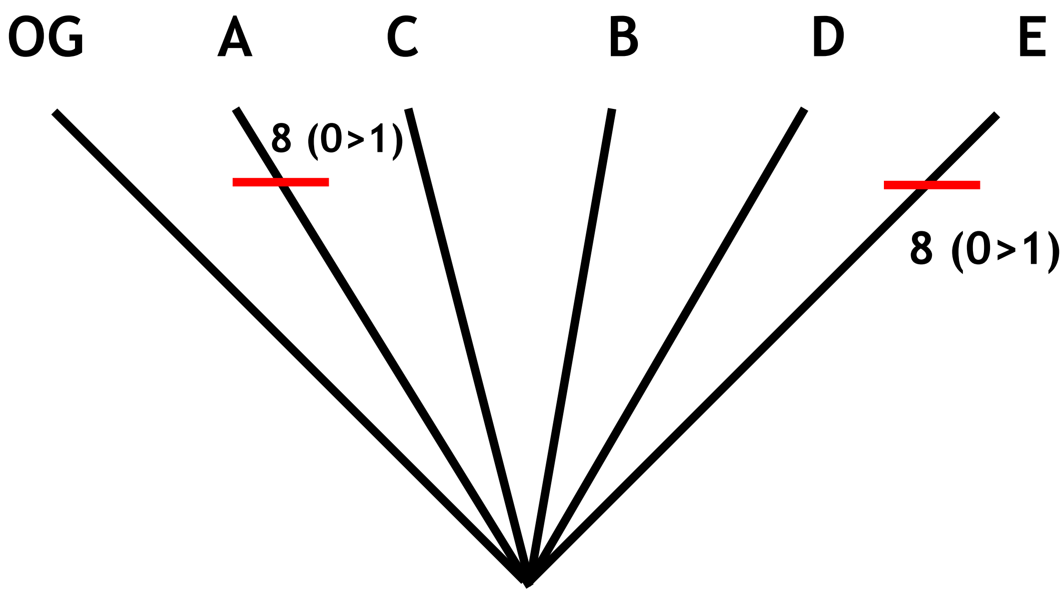
m = minimum number of character state changes

s = number of ch. state changes on the tree evaluated

g = minimum number of character state changes on UNRESOLVED TREE

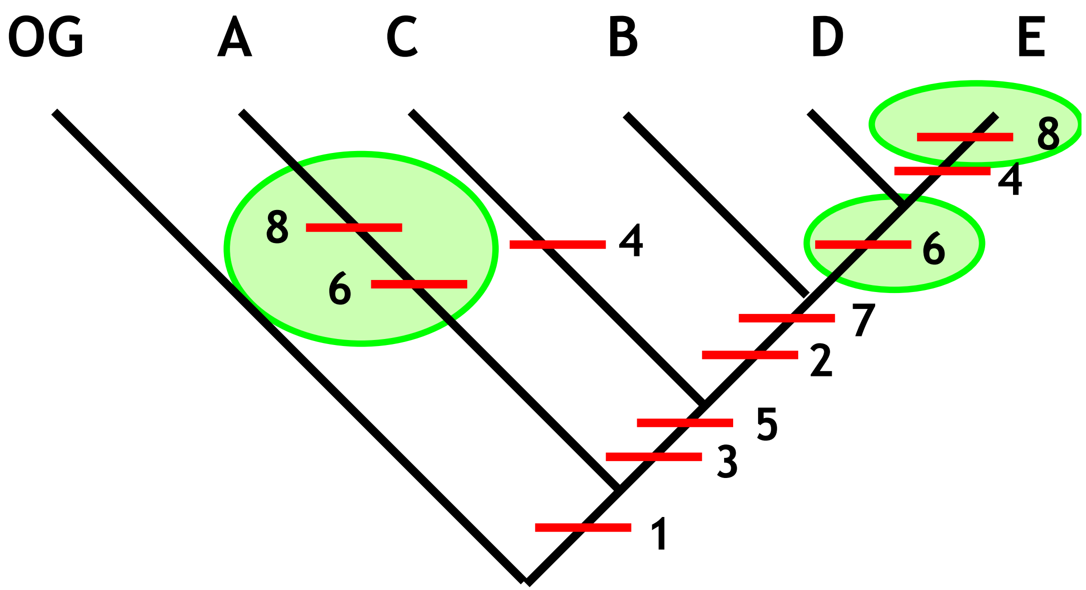
ATTENTION! g can be obtained directly from the matrix, for example for binary characters it is the number of those terminals with less common ch. state

	1	2	3	4	5	6	7	8
OG	0	0	0	0	0	0	0	0
A	1	0	0	0	0	1	0	1
B	1	1	1	0	1	0	1	0
C	1	0	1	1	1	0	0	0
D	1	1	1	0	1	1	1	0
E	1	1	1	1	1	1	1	1
g	1	3	2	2	2	3	3	2



state changes optimized on TOTALLY unresolved tree AS PARSIMONIOUSLY AS POSSIBLE

	1	2	3	4	5	6	7	8
OG	0	0	0	0	0	0	0	0
A	1	0	0	0	0	1	0	1
B	1	1	1	0	1	0	1	0
C	1	0	1	1	1	0	0	0
D	1	1	1	0	1	1	1	0
E	1	1	1	1	1	1	1	1
m	1	1	1	1	1	1	1	1
s	1	1	1	2	1	2	1	2
g	1	3	2	2	2	3	3	2



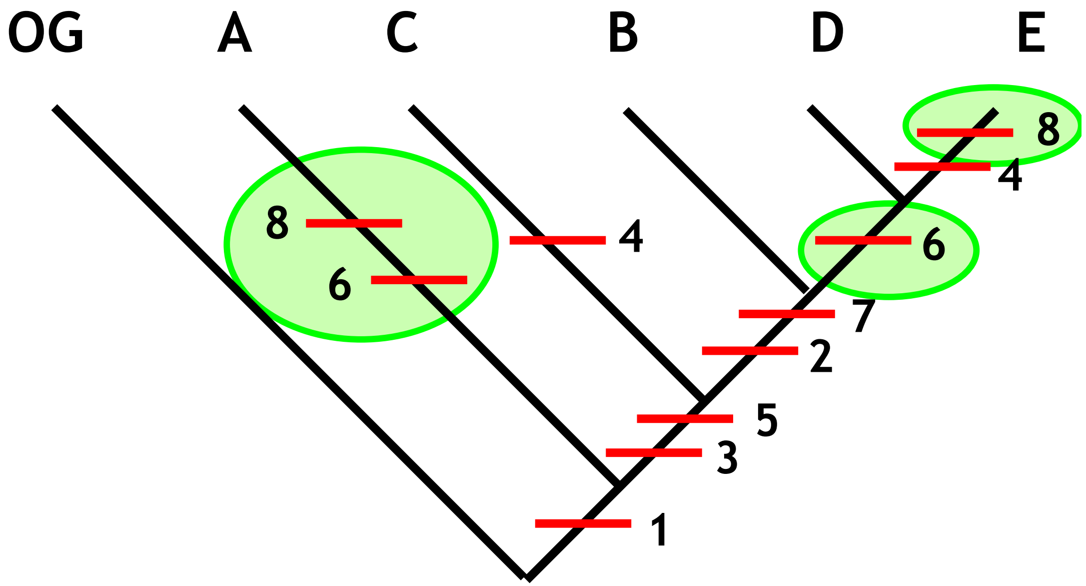
character 6

$$r = \frac{g - s}{g - m} = \frac{3 - 2}{3 - 1} = \frac{1}{2} = 0.5$$

character 8

$$r = \frac{g - s}{g - m} = \frac{2 - 2}{2 - 1} = \frac{0}{1} = 0$$

	1	2	3	4	5	6	7	8
OG	0	0	0	0	0	0	0	0
A	1	0	0	0	0	1	0	1
B	1	1	1	0	1	0	1	0
C	1	0	1	1	1	0	0	0
D	1	1	1	0	1	1	1	0
E	1	1	1	1	1	1	1	1
g	1	3	2	2	2	3	3	2



character 6

c = 0.5
r = 0.5
rc = 0.25

character 8

c = 0.5
r = 0
rc = 0

ch. 6 provides SOME information about phylogeny,

ch. 8 does NOT tell about it (at this level)

SUMMARY

for phylogenetic analyses basically ALL characters that show variation between terminals CAN/SHOULD be used

character states are distinguished within most characters

continuous characters & landmark data CAN also be used

when making analyses using *Wagner* parsimony for characters showing clear order of states it is advisable to make analysis ALSO so that even these are treated with *Fitch* parsimony

character congruence

a priori weighting is subjective and adds assumptions to analysis

consistency and retention indices tell how well each character is congruent with others